



**UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS**

**INSTITUTO DE ECOLOGÍA
ECOLOGÍA**

**Interacciones planta-planta y su importancia en la dinámica de reemplazo en
la asociación *Larrea tridentata*-*Opuntia leptocaulis* en el Desierto**

Chihuahuense.

TESIS

**QUE PARA OPTAR POR EL GRADO DE:
DOCTOR EN CIENCIAS**

PRESENTA:

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**TUTOR PRINCIPAL: DR. CARLOS MONTAÑA CARUBELLI (Posgrado en
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MÉXICO, D.F.

DICIEMBRE 2013.

Dr. Isidro Ávila Martínez
Director General de Administración Escolar, UNAM
Presente

Me permito informar a usted, que el Subcomité de Biología Evolutiva y Sistemática, en su sesión ordinaria del día 13 de mayo de 2013, aprobó el jurado para la presentación de su examen para obtener el grado de DOCTOR EN CIENCIAS, del Posgrado en Ciencias Biológicas, del alumno FLORES TORRES JOSÉ ARNOLDO con número de cuenta 503007209 con la tesis titulada: titulada "INTERACCIONES PLANTA-PLANTA Y SU IMPORTANCIA EN LA DINÁMICA DE REEMPLAZO EN LA ASOCIACIÓN *Larrea tridentata*-*Opuntia leptocaulis* EN EL DESIERTO CHIHUAHUENSE." bajo la dirección del DR. CARLOS MONTAÑA CARUBELLI :

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Sin otro particular, me es grato enviarme un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARA EL ESPIRITU"
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DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA
COORDINADORA DEL PROGRAMA

c.c.p. Expediente del interesado

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Al Posgrado en Ciencias Biológicas, UNAM

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RESUMEN

Se ha sugerido que las interacciones entre dos especies de plantas vecinas de ambientes áridos cambian en función de la ontogenia de los interactuantes y de la disponibilidad de agua, que lo anterior incide en las dinámicas poblacionales y en el largo plazo estructura las comunidades vegetales perennes de ambientes áridos. Un ejemplo de esto se presenta en la relación arbusto-cacto, en la cual se ha propuesto que los arbustos facilitan el establecimiento de cactus y cuando estos últimos crecen, compiten (en intensidad proporcional a la falta de agua) y llegan a excluir a los primeros.

Esta tesis se centró en comprobar los efectos del agua y de las interacciones positivas y negativas entre distintas etapas ontogénicas de *Cylindropuntia leptocaulis* y su arbusto nodriza *Larrea tridentata* las cuales hipotéticamente presentan una dinámica cíclica de reemplazo en el Desierto Chihuahuense.

Como la relación entre ambas especies y su supuesta dinámica cíclica, se inicia con la facilitación de *L. tridentata* sobre *C. leptocaulis* la primera parte de la tesis se enfocó en entender el reclutamiento de *C. leptocaulis*. Registramos que el establecimiento clonal de *C. leptocaulis* es más frecuente que el sexual. Experimentalmente comprobamos que el establecimiento clonal depende del microambiente creado por el dosel de *L. tridentata*, mientras que el establecimiento sexual no, además en ambos tipos de reclutamiento los nuevos individuos crecen más rápido bajo el dosel de *L. tridentata* que en espacio abierto, lo anterior les permite escapar más rápido de las etapas más críticas del establecimiento. Estos resultados fueron corroborados por un estudio demográfico de 4 años de duración que demuestra que una población de *C. leptocaulis* asociados a *L. tridentata* tienen tasas de crecimiento mayores que una población de individuos solitarios debido a que presentan mayor reclutamiento clonal y supervivencia en etapas tempranas. Esto nos permite concluir que la mayor parte del reclutamiento de nuevos individuos del cacto se presenta

de manera clonal y bajo la sombra *L. tridentata* que es el arbusto nodriza más abundante en la zona de estudio.

Dado que se ha propuesto que la supuesta dinámica cíclica entre ambas especies termina con la exclusión competitiva de *L. tridentata* por *C. leptocaulis*, la segunda parte de la tesis se enfocó en entender los mecanismos y efectos de la competencia por agua entre ambas especies cuando son adultas, si dicha competencia conduce a una mortalidad diferencial entre plantas solas y asociadas y, en el largo plazo a patrones de distribución espacial interespecífica agrupada. Las consecuencias de crecer solo o asociado difieren según la especie y el estado hídrico. Arbustos adultos de *L. tridentata* son afectados por la competencia por agua que disminuye a medida que aumenta la oferta hídrica. Los adultos de *C. leptocaulis* no son afectados por la competencia por agua. Dicha competencia incrementa la cantidad de ramas muertas en arbustos asociados, pero como no registramos mayor mortalidad de arbustos asociados al cacto y como encontramos que todas las clases de tamaño de *C. leptocaulis* están asociadas espacialmente con arbustos adultos de *L. tridentata* no podemos concluir que dicha competencia conduce a la eliminación del arbusto de manera sistemática. Estos resultados fueron corroborados por el mismo estudio demográfico arriba citado, el cual demuestra que la tasa finita de crecimiento poblacional promedio de una población de arbustos solos y asociados no difiere, y es cercana a la unidad durante 4 años. Además, en dicho estudio demográfico no registramos mortalidad de arbustos adultos solos o asociados durante 4 años de muestreo.

Todos nuestros resultados observacionales, experimentales y demográficos nos permiten concluir que la dinámica cíclica de reemplazo entre *L. tridentata* y *C. leptocaulis* no es un evento frecuente en el sur del Desierto Chihuahuense y esto se ve reflejado en los patrones de distribución espacial agregado de ambas especies en la zona de estudio.

ABSTRACT

It has been suggested that interactions between two neighboring plant species in arid environments change as a function of the ontogeny of the interactants and of the availability of water, and that this affects the population dynamics and long-term structure of perennial plant communities in these arid environments. One example of this phenomenon is presented by the shrub-cactus relationship, in which it has been proposed that the shrubs facilitate the establishment of the cacti and that the latter, once grown, go on to compete (with an intensity that is inversely proportional to the availability of water), and ultimately exclude, the former.

This thesis compares the effects of water availability and of the positive and negative interactions between different ontogenic stages of *Cylindropuntia leptocaulis* and its facilitator shrub *Larrea tridentata*, species that hypothetically present a cyclic dynamic of replacement in the Chihuahuan Desert of northern Mexico.

Since the relationship between both species and their supposed cyclic dynamic begins with the facilitation of *C. leptocaulis* by *L. tridentata*, the first part of this thesis is focused on understanding the process of *C. leptocaulis* recruitment. We found that the establishment of *C. leptocaulis* is more frequently clonal than sexual. We demonstrated experimentally that such clonal establishment depends upon the microenvironment created beneath the canopy of *L. tridentata*, while sexual establishment does not. In both types of recruitment, however, new individuals grow more rapidly below the canopy of *L. tridentata* than in the open. Facilitation by *L. tridentata* permits the cactus to more rapidly transcend the most critical stages of establishment. These results were corroborated with a demographic study of four years in duration that showed that a population of

C. leptocaulis associated with *L. tridentata* presents greater growth rates than a population of solitary individuals, due to the fact that the plants grown under facilitation present higher clonal recruitment and survival in early stages. This allows us to conclude that the majority of the recruitment of new individuals of cactus occurs clonally and below the canopy *L. tridentata*, which is the most abundant nurse shrub in the study zone.

Given the proposal that the supposed cyclic dynamic between these species concludes with the competitive exclusion of *L. tridentata* by *C. leptocaulis*, the second part of the thesis examines the mechanisms and effects of competition for water between adults of both species, whether such competition causes differential mortality between solitary and associated plants and, in the long-term, produces patterns of clustered interspecific spatial distribution. Consequences of solitary or associated growth differ according to species and hydric status. Adult *L. tridentata* shrubs are affected by the competition for water that decreases with increasing water supply, while *C. leptocaulis* adults are unaffected by this competition. Competition for water increases the quantity of dead branches in associated shrubs, however, since we did not find higher mortality in shrubs associated with the cactus, and found that *C. leptocaulis* individuals of all size classes are spatially associated with *L. tridentata* adults, we cannot conclude that this competition causes the systematic elimination of the shrub. These results were also corroborated by the demographic study described above, which demonstrated that finite mean growth rate did not differ between populations of solitary and associated shrubs, and was close to unity over four years. Furthermore, we did not record mortality in solitary or associated adult shrubs in four years of sampling as part of the demographic study.

Our observational, experimental and demographic results allow us to conclude that the cyclic dynamic of replacement between *L. tridentata* y *C. leptocaulis* is not a frequent

occurrence in the south of the Chihuahuan Desert and this is reflected in the spatial distribution patterns of both species in the zone of stud

INTRODUCCIÓN

La estructura de las comunidades vegetales de ambientes áridos es afectada principalmente por las condiciones ambientales impredecibles, y ajustada a pequeña escala por interacciones ecológicas. Noy-Meir (1973) propone que el agua controla los procesos biológicos en los desiertos. Ejemplos de lo anterior son la observación de que el reclutamiento de nuevos individuos de especies perennes es infrecuente y se presenta únicamente durante los pulsos de agua (Goldenberg y Turner 1986; Wiegand *et al.* 2004, Bowers *et al.* 2004, Squeo *et al.* 2007), y el hecho de que la disponibilidad de recursos hídricos afecta a la intensidad de la competencia entre pares de adultos vecinos (Fonteyn y Mahall 1981; Briones *et al.* 1998; Flores-Martínez *et al.* 1998).

Además de la importancia del agua, las interacciones ecológicas planta-planta son determinantes en el mantenimiento de las comunidades vegetales de las zonas áridas. Luego de las primeras observaciones de que el reclutamiento de muchas especies en ambientes áridos es favorecido por un microambiente más sombreado localizado bajo el dosel de arbustos (Shreve 1931; Niering 1963), gran cantidad de estudios confirmaron dicha interacción en estos ambientes (Flores y Jurado 2003) y se ha evidenciado su importancia a distintas escalas ecológicas (para una síntesis de facilitación véase, Callaway 2007; Broker *et al.* 2007). La importancia de la competencia en la estructuración de la vegetación de ambientes áridos, generó una gran cantidad de trabajos que demostraron que en estos ambientes improductivos las plantas compiten de manera intensa por el recurso más limitante que es el agua, que las especies desarrollan mecanismos para coexistir evitando dicha competencia, o si esto no llega a suceder se presenta una mortalidad denso dependiente, lo cual causa que plantas con vecinos tengan mayor probabilidad de morir

que plantas sin vecinos (Fonteyn y Mahall 1981; Fowler 1986; Goldenberg y Barton 1992; Goldenber y Novoplansky 1997; Nobel 1997; Silvertown 2004)

No obstante las interacciones positivas y negativas no actúan separadas sino simultáneamente, el resultado final depende de la suma de los efectos positivos y negativos siendo éste dinámico y cambiante según la severidad del ambiente (Bertness y Callaway 1994; Holzapfel y Mahall 1999; Brooker y Callaghan 1998) y/o la ontogenia de las especies interactuantes, con interacciones positivas cuando la facilitada es juvenil y negativas cuando ésta se convierte en adulta. Algunos trabajos han sugerido que cambios importantes en la composición de las especies de los desiertos son originados mediante dinámicas cíclicas de reemplazo (estas involucran un cambio en el signo de la interacción originado por cambios en la ontogenia de las interactuantes) los cuales se dan a pequeña escala como lo es el área bajo el dosel de un arbusto (Vasek & Lund 1980; MacAuliffe 1988; Yeaton & Romero-Manzanares 1986; Cody 1993; Soriano *et al.* 1994; Armas y Pugnaire 2009).

Yeaton (1978), propone una dinámica cíclica de reemplazo entre el arbusto *Larrea tridentata* y el cacto *Cylindropuntia leptocaulis* en el norte del Desierto Chihuahuense. El autor sugiere que *L. tridentata* coloniza espacios abiertos y facilita el establecimiento de plántulas de *C. leptocaulis* bajo su copa; cuando *C. leptocaulis* se vuelve adulta mata a *L. tridentata* por efecto de exclusión competitiva y posteriormente muere por efecto de herbivoría y exposición de las raíces causadas por la actividad de roedores que cavan sus madriguera bajo el dosel de *C. leptocaulis*. En cuanto a los procesos de facilitación, el autor llega a estas conclusiones al observar que una mayor cantidad de individuos adultos de *C. leptocaulis* están asociados a individuos de *L. tridentata* adultos. Además el autor sugiere la exclusión competitiva de *L. tridentata* a partir de la observación de una mayor

cantidad de restos de *L. tridentata* muertos asociados a *C. leptocaulis* que restos del arbusto ubicados en el espacio abierto.

La presente tesis fue diseñada para evaluar a nivel individual y poblacional el papel de la disponibilidad de agua y de las interacciones ecológicas en la supuesta dinámica cíclica de reemplazo de *L. tridentata* y *C. leptocaulis*. Para lo anterior se utilizó una aproximación observacional y experimental y los resultados se muestran en tres capítulos, que representan distintas etapas en la ontogenia del cacto *C. leptocaulis*.

En el primer capítulo titulado “Recruiting Mechanisms of *Cylindropuntia leptocaulis* (Cactaceae) in the Southern Chihuahuan Desert”, el cual fue publicado en la revista *Journal of Arid Environments*, analizamos la frecuencia de establecimiento de nuevos individuos de origen sexual y clonal en 1 ha de la Reserva de la Biosfera de Mapimí. A la par realizamos experimentos de campo analizando el efecto del micromedio (bajo la copa de *L. tridentata* vs espacio abierto) y del tipo de suelo (suelos colectados bajo la copa del arbusto vs suelos colectados de espacio abierto) en el establecimiento sexual y clonal de *C. leptocaulis*.

En el segundo capítulo titulado “Mechanisms and consequences of a shift from a facilitative to a competitive interaction between *Larrea tridentata* and *Cylindropuntia leptocaulis* in the Southern Chihuahuan Desert” el cual fu enviado a la revista *Journal of Vegetation Science*, analizamos mediante experimentos de campo el efecto del vecindario (cuando ambas especies crecen solas o asociadas) y la disponibilidad de agua (plantas con y sin riego) en la fisiología, crecimiento, y reproducción del arbusto y el cacto cuando son adultos. Además se investigó si arbustos adultos solos eran más vigorosos (i.e. con más del 50% de ramas vivas) que arbustos asociados al cacto, si existía mayor mortalidad de arbustos adultos asociados que solos y si existían patrones de distribución espacial no agrupados que sugirieran la exclusión competitiva.

En el tercer capítulo titulado “Efectos de las interacciones en las dinámicas poblacionales de *L. tridentata* y *O. leptocaulis* en el Desierto Chihuahuense”, pusimos a prueba la hipótesis de que la tasa finita de crecimiento poblacional (λ) difiere en ambas especies en función de la condición de vecindario y la variabilidad ambiental. Para comprobarla, comparamos las dinámicas de poblaciones de *L. tridentata* y *C. leptocaulis* solas y asociadas en la Reserva de la Biósfera de Mapimí durante 4 años con precipitaciones contrastantes mediante matrices de proyección de Lefkovitch. También se realizaron análisis retrospectivos y prospectivos para estimar la contribución relativa de cada proceso demográfico (crecimiento, decrecimiento, estasis) y de cada clase de tamaño a la variabilidad de λ .

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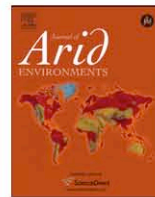
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Capitulo I

Recruiting Mechanism of *Cylindropuntia leptocaulis* (Cactaceae) in the Southern Chihuahuan Desert

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Recruiting mechanisms of *Cylindropuntia leptocaulis* (Cactaceae) in the Southern Chihuahuan Desert

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ABSTRACT

Sexual reproduction and vegetative propagation require the establishment of morphologically diverse reproductive structures (seedlings and stem segments). This study assesses both types of *Cylindropuntia leptocaulis* recruitment in two microenvironments protected from herbivory (in open space and under the canopy of *Larrea tridentata*) and with two soil types (collected below *L. tridentata* canopy and from open space).

An observational study revealed that sexual establishment was very limited (only 8 juveniles/ha were found), while clonal establishment was more frequent (59 juveniles/ha); both types of propagule were found only under shrub canopy.

Field experiments showed that, as in other *Cylindropuntia* species but contrasting with findings for *Opuntia* species, seeds germinated and seedlings survived under nurse plants as well as in open space, but they grew faster in the former environment. Faster growth under canopy shade provides better chances of successful recruitment to later life-cycle stages. Stem segments never established in open space, requiring the shade of nurse plants. This may be due to physiological constraints imposed by their small volume. In synthesis, the results indicate that clonal propagation is the most important recruitment mechanism in *C. leptocaulis* populations, and that it takes places under shrub canopy.

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1. Introduction

Recruitment in clonal plant populations occurs through two mechanisms: 1) sexual, when seeds are produced and seedlings establish, and 2) clonal, when vegetative shoots or clones are produced and establish. In the case of the genera *Opuntia* and *Cylindropuntia*, clonal propagation occurs when areoles from pads or stem segments, separated from the plant and propped up in soil, produce new roots and stems that constitute an individual that is independent from the mother plant (Gibson and Nobel, 1986). Plants produced by sexual reproduction are called genets (individuals that arise from a zygote), whereas those produced by clonal propagation are called ramets (individuals that arise from a vegetative meristem, Harper, 1977, 1985). It has been proposed that sexual reproduction permits both genetic recombination and the colonization of new environments through dispersal over long distances, while clonal establishment permits a rapid increase in the density of individuals when successful genotypes have already colonized suitable habitats (Cook, 1985; Eriksson, 1989, 1992; Harper, 1985).

The establishment of genets is a rare event in arid environments, as it relies on unpredictable water pulses (Bowers et al., 2004; Squeo et al., 2007; Wiegand et al., 2004) and, in some cases, also requires the presence of nurse plants (Flores and Jurado, 2003). The term 'nurse plant syndrome' was coined by Niering et al. (1963) to refer to the association between emergent seedlings and adult plants. After the original observation of Shreve, (1931) that the recruitment of many species in aridlands is favored under plant canopy shade, this biotic interaction has been confirmed for hundreds of species in several ecosystems (Flores and Jurado, 2003). The interaction is considered to be a type of facilitation (Bronstein, 2009) where plant propagules benefit from the shade of the nurse canopy which provides a buffered thermal microenvironment, reduced evaporatranspiration demand, increased water and soil nutrient availability, and protection against herbivory.

The dependence on nurse shrubs tends to vary depending on a particular species' growth pattern. Observational studies suggest that the genus *Opuntia* is dependent on nurse plants, while *Cylindropuntia* is a less dependent genus (López and Valdivia, 2007; Reyes-Olivas et al., 2002). Although experimental studies have been conducted to test the importance of nurse shrubs on genet establishment in some *Opuntia* species (Mandujano et al.,

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1998; Vargas-Mendoza and González-Espinosa, 1992), little is known about the role that nurse plants play in the establishment of genets of *Cylindropuntia* species. Only a handful of observational studies have been published, and with contradictory results: Yeaton (1978) and Cody (1993) report an association between nurse plants and juveniles produced by sexual reproduction, while Reyes-Olivas et al. (2002) observe no such association. Other observational studies on four species (Bobich and Nobel, 2001) and experimental studies on 10 species (Evans et al., 2004) of *Cylindropuntia* from the Sonoran Desert showed that all are able to propagate clonally, but no analysis was performed of the environmental conditions under which this type of plant recruitment takes place.

Ramet establishment is a frequent event in *Opuntia* and *Cylindropuntia*, but between species and between genera, variability has been reported (Allen et al., 1991; Bobich and Nobel, 2001; Ebert, 2006; Evans et al., 2004; Mandujano et al., 1998, 2007). Evans et al. (2004) analyzed the establishment of stem segments—also known as terminal joints, in the terminology of Bobich and Nobel (2001)—in ten *Cylindropuntia* species and in the pads of 15 *Opuntia* species in the southwestern United States; the terminal joints of the former were shown to have a lower rooting percentage than *Opuntia* pads (32 vs. 71%, respectively). Apparently, the greater volume of *Opuntia* cladodes permits a higher degree of water and carbohydrate storage, making survival during dry periods possible (Bobich and Nobel, 2001).

It has been proposed that ramet establishment is more efficient than genet establishment for the recruitment of new individuals of succulent species in arid environments (Arizaga and Ezcurra, 2002; Clark-Tapia et al., 2005; Liston et al., 2003). Furthermore, some authors (Allen et al., 1991; Mandujano et al., 1998, 2007) have observed that several *Opuntia* species in the Chihuahuan Desert undergo clonal propagation in highly stressful sites, such as intercanopy space, without the need for nurse plants. To date, however, no published study has assessed the association between ramets and nurse plants in *Cylindropuntia*.

The purpose of this research was to assess the importance of nurse plants in the two establishment modes (sexual reproduction and vegetative propagation) of a *Cylindropuntia* (*Cylindropuntia leptocaulis*) from the Southern Chihuahuan Desert. It was predicted that the processes of germination, survival, and growth of sexually derived seedlings would benefit from the more favorable microclimate found under the canopy of nurse plants, whereas rooted stem segments would not exhibit better survival and growth under the same circumstances due to their more advanced ontogenetic stage, with fully developed physiological and morphological functionality. In other words, it was expected that sexual reproduction would be favored under nurse plants while vegetative propagation would not.

As there was no knowledge about species seed germination and spatial distribution of sexually derived and clonally propagated individuals, the first phase involved an experimental study of seed germination in *C. leptocaulis* and an observational study of the spatial association between *C. leptocaulis* plants and shrub cover. On the basis of the results—which identified the optimal germination conditions and showed that ca. 75% of *C. leptocaulis* adults were associated with *Larrea tridentata* cover—experiments were undertaken to measure a possible differential influence of *L. tridentata* cover on genet and ramet establishment. Thus, the possible influence of a 'nurse plant syndrome' (Niering et al., 1963) benefiting *C. leptocaulis* under *L. tridentata* cover was experimentally studied by growing both genets and ramets in a factorial design aimed at separating the effect of the shade provided by the canopy from the effect of soil conditions.

2. Materials and methods

2.1. Study site and species

This research was carried out at the Mapimí Biosphere Reserve near the Desert Laboratory (Southern Chihuahuan Desert, N 103° 45' O 26° 41', 1100 m asl, 264 mm of annual rainfall and 20.8 °C mean annual temperature). Vegetation in the area is shrubland dominated by *L. tridentata*, *Jatropha dioica*, *Prosopis glandulosa* var *torreyana*, *Opuntia rastrera*, *Castela texana*, *Partenium incanum*, *Opuntia microdasys*, and *Fouquieria splendens* on gently sloping (2–5%) terrain where soils are gravelly sandy loam to clay loam (Montaña, 1990).

C. leptocaulis DC. (Cactaceae), which measures from 0.5 to 1.5 m in height, has a woody, well-defined trunk with cylindrical branches that form from the vertical juxtaposition of terminal joints (Bobich and Nobel, 2001) or stem segments (Evans et al., 2004). The terminal stem segments detach easily from the plant when touched, as the joints between them are extremely fragile. Incidentally, this easy detachment allows a zoochorous way of dispersal by which terminal segments attached by its spines to animal skin, feathers or fur can travel long distances. *Opuntia leptocaulis* has hermaphrodite flowers, and red, globous fruits. It is distributed throughout almost all North American deserts (Bravo-Hollis, 1978). The species produces many seeds each year (approximately 31,000 per ha in 2010, Flores-Torres and Montaña, data from an ongoing demographic study that began in 2008); it can establish through clonation, although in their experimental research, Evans et al. (2004) found that only 18% of its stem segments rooted, a lower rate than in other *Cylindropuntia* species (30–50%) and in the pads of *Opuntia* species (30–90%).

C. leptocaulis is commonly associated with shrubs, especially with *L. tridentata*. They form a common association throughout the Chihuahuan Desert, one that is also found from southern Texas to Querétaro, Mexico (Flores-Torres, personal observation). Moreover, based on observational data, Yeaton (1978) proposes a cyclical dynamic between the two species. The sequence begins with the establishment of *L. tridentata* in an open space and the subsequent establishment of *O. leptocaulis* under its canopy after the germination of seeds transported by birds and rodents. Some time later, *L. tridentata* dies due to water stress because soil water availability decreases in the deeper soil horizons as the shallow root system of *O. leptocaulis* develops. The cactus, in turn, dies after its shallow root systems are exposed due to the activity of burrowing rodents, wind, and water erosion. The cycle may restart with the establishment of a new *L. tridentata* in the now open space.

L. tridentata (Sesse & Moç. ex DC.) Coville (Zygophyllaceae) is a microphilic species, evergreen, and densely branched from its base; 0.6–3 m in height, it is the dominant shrub species in all North American warm deserts (MacMahon, 1979).

2.2. Germination experiments

In November of 2005, 2006, and 2007, *C. leptocaulis* fruits were randomly collected. Their seeds were extracted manually and washed to remove all remaining pulp; they were dried in the shade at environmental temperature. Once dry, they were stored in brown paper bags. From November 26, 2007, to January 8, 2008, an experiment was carried out in order to determine the scarification method that provides the highest germination rate and its statistical interaction with seed age. One hundred randomly selected seeds from each year were subjected to each of the following scarification treatments: 1) chemical: immersion in H₂SO₄ at 98% for 30 min, 2) mechanical: using fingernail clippers, a cut was made near the micropilar region, 3) hydration: seeds were immersed in

water for 24 h, and 4) control: no treatment. Seeds were placed on Petri dishes (20 seeds per dish) with bacteriological agar at 1%, and each of the treatments was repeated five times. The dishes were placed in a growth chamber at a constant temperature of 28 °C with a photoperiod of 12 h of white light/day (Potter et al., 1984). At intervals of four days, the number of germinated seeds on each Petri dish was recorded. A seed was considered germinated when the radicle was visible to the naked eye.

2.3. Spatial association between *C. leptocaulis* and species specific plant cover

In January, 2011, a survey was done within a 31 km² area surrounding the Desert Laboratory on the Mapimí Biosphere Reserve. Twenty 50 m × 10 m plots were selected randomly, and the plant cover of each shrub was estimated as the area of an ellipse $A = \pi r_1 r_2$, where r_1 and r_2 are the major radius and the orthogonal radius to r_1 , respectively. *C. leptocaulis* adult individuals, juveniles (genets and ramets) were counted; a record was made of whether they were growing under the canopy of a nurse shrub or in an intercanopy area. In the field, it is easy to distinguish between juveniles (less than 20 cm height) of sexual and asexual origin because the latter remain attached to the stem segment from which they arose until it completely disintegrates several years later.

2.4. Sexual and clonal establishment

These experiments were launched in May of 2008 in the area around the Desert Laboratory. Using a split-plot design, the effects of shrub shade and soil type were evaluated in terms of *C. leptocaulis* seedling survival. Seven *L. tridentata* shrubs with a canopy of over 2 m wide were selected. Each shrub and the open space that surrounded it were considered a block. Above ground microenvironments (under *L. tridentata* canopy and in intercanopy space) constituted the main plots, and soil type (extracted from underneath *L. tridentata* canopy and in open space) constituted sub-plots. Soil samples were collected to a depth of 10 cm under the canopy of ten *L. tridentata* shrubs that had a canopy diameter of at least 2 m, as well as in the open spaces adjacent to them. Samples from each microenvironment were mixed and this mixture placed in 10 × 10 × 10 cm pots made from compressed peat.

Under each of the seven shrubs as well as in the adjacent intercanopy area (i.e. in each of the statistical blocks), we placed a pot filled with soil from the open spaces and another filled with soil collected under *L. tridentata* canopy. On May 15, 2008, 60 *C. leptocaulis* seeds scarified with H₂SO₄ for 30 min (the most successful treatment in promoting germination; see germination experiment results) were planted in each pot. To avoid the high seed and seedling predation typical of the study area (Mandujano et al., 1998; Montiel and Montaña, 2000), pots were protected with wire netting. In total, 1680 seeds were used (with two cover conditions × two soil conditions × 60 seeds per pot × seven blocks). Until July 15, around the time that the rain season begins, they were watered every four days with the equivalent of 10 mm of rain. Progress was reviewed weekly until the time of maximum seed germination (August 30, 2008). Germination percentages were used for statistical analysis, and the number of seedlings observable on that date was considered to be the initial number for evaluation of seedling survival. Periodically, the number of survivors was recorded; the last such reading was taken on October 8, 2010 (769 days after maximum germination had occurred). On that date, surviving individuals were harvested and dried (85 °C for 72 h), after which their dry weight was recorded.

This design was also used to examine the effect of the same factors on stem segment rooting in *C. leptocaulis*. Under each plant

used in the sexual establishment experiments and in the adjacent open space, we placed pots made of compressed peat, one filled with soil from the open spaces and another filled with that collected under *L. tridentata* canopies. On May 15, 2008, 20 terminal stem segments that had been detached from the mother plant during the previous growth period were planted. They were terminal stem segments less than 30 mm long. A total of 560 stem segments were used (two microenvironmental conditions × two soil conditions × 20 stem segments × seven blocks). From the day when they were planted, their survival was recorded along with that of seedlings from the sexual establishment experiment. The last record of rooted stem segment survival was taken on October 8, 2010 (876 days after planting). On that day, surviving stem segments were collected, dried, and weighed using the same methodology as for seedling survival in the sexual establishment experiments.

2.5. Microclimatic conditions and soil properties under canopies of *L. tridentata* and *C. leptocaulis* and in intercanopy areas

Photosynthetically active radiation (PAR) was measured under the canopy of the seven *L. tridentata* plants used in the sexual and clonal establishment experiments as well as in surrounding open areas. Measurements were taken with a radiometer (Li-250 Li-Cor) and quantum sensor (Li-210 Li-Cor) at three different times (0700–0800, 1300–1400, 1900–2000 h) on a clear summer day (June 22, 2010). Under the canopy of three of these plants (selected randomly) and in their surrounding intercanopy area, thermometers were placed in order to measure surface midday (1300 h) soil temperature. Paired PAR measurements under the canopy and in the surrounding intercanopy area were also done in seven randomly selected *C. leptocaulis* plants over 1 m in diameter, and midday (1300 h) soil temperature measurements were done in three of these seven plants and their surrounding intercanopy area.

Furthermore, under the canopy of three randomly selected plants of the two species studied (*L. tridentata* and *C. leptocaulis*) and in their corresponding intercanopy areas, 300 g of soil was collected at a maximum depth of 10 cm. Samples were transported to laboratory in black plastic bags. Total organic C (C) concentration was determined with an automatic CO₂ analyzer UIC model CM5012. Total N (N) soil concentration was measured after acid digestion with Kjeldahl's modified method (Technicon Industrial System, 1977) using a Braun-Luebbe auto analyzer 3 (Norderstedt, Germany). The cation exchange capacity (CEC) was determined with CH₃COONH₄ pH 7.1 N and quantified using atomic absorption spectrometry (Chapman, 1965).

2.6. Statistical analyses

The effects of seed age and scarification treatment on the percentage of *C. leptocaulis* seeds that germinated were analyzed using a Kruskal–Wallis two-way test with an approximation of χ^2 (Zar, 1999), as a large number of zeroes in the data set precluded the possibility of obtaining normality in the data distribution through data transformation.

The null hypothesis that the number of *C. leptocaulis* plants recorded under each shrub species is proportional to the area covered by each shrub species (i.e., that there is no association between species specific plant cover and *C. leptocaulis* plants) was tested using the χ^2 statistic along with calculation of standardized residuals (Everitt, 1977).

To test the effect of microenvironment (under *L. tridentata* canopy and in intercanopy space) and soil origin (collected below *L. tridentata* canopies and in intercanopy areas) on the germination and survival of seedlings and rooted stem segments, split-plot

ANOVAS were used (Montgomery, 2005). Blocks (i.e., the area consisting of the *L. tridentata* plant and its surrounding open space) were considered a random variable, while both the main plots (microenvironments) and sub-plots (soil type) were considered fixed effect variables. Through arcsin transformation, response variable percentages (germination and seedling survival) were normalized.

Because by the last sampling day, survival on some plots and sub-plots was nil and this prevented obtaining normality in data distribution, variability in dry weight data as a function of micro-environment and soil type was analyzed using the Kruskal–Wallis two-way test with an approximation of χ^2 (Zar, 1999).

Between microenvironment differences in PAR, midday soil temperature, pH, C, N, the C/N rate, and CEC were analyzed using one-way ANOVAs and Tukey test for post-hoc multiple comparisons. All statistical analyses were done with R (R Development Core Team, 2009) except split-plot ANOVAs, which were done with Statistica (Statsoft, 1993). Results are presented as mean values \pm 1 SE throughout the text.

3. Results

3.1. Germination experiments

In laboratory, *C. leptocaulis* seed germination began seven days after planting and ceased at 39 days in the most successful treatment. There was no interaction between scarification treatment and seed age ($\chi^2 = 2.87$, $df = 6$, $P = 0.8$). The treatment that produced the highest germination percentage was scarification with H_2SO_4 ($17.00 \pm 3.41\%$), followed by mechanical scarification ($3.00 \pm 1.27\%$); the hydration treatment ($1.00 \pm 0.72\%$) and the control ($1.00 \pm 0.53\%$) produced the lowest levels ($\chi^2 = 17.66$, $df = 3$, $P = 0.0005$). Germination decreased with age; younger seeds germinate better than older ones, although these differences are only marginally significant ($\chi^2 = 5.65$, $df = 2$, $P = 0.06$, Fig. 1). The highest germination rate ($31.00 \pm 3.92\%$) was obtained using chemical scarification in seeds from 2007, and this percentage dropped to $12.00 \pm 4.06\%$ and $8.00 \pm 4.64\%$ in 2006 and 2005, respectively.

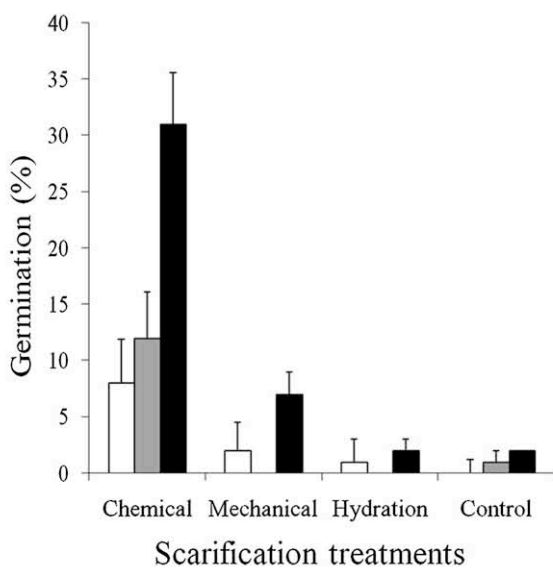


Fig. 1. Mean (\pm SE) of germination percentage of *C. leptocaulis* seeds collected in different years and subjected to different scarification treatments. Chemical = immersion in H_2SO_4 at 98% for 30 min. Mechanical = cut in the microcapilar region. Hydration = immersion in water for 24 h. Control = no treatment. $n = 5$ Petri dishes with 20 seeds for each treatment. Empty bars represent seeds collected in 2005, gray bars seeds collected in 2006, filled bars seeds collected in 2007.

3.2. Spatial association between *C. leptocaulis* and species specific plant cover

Intercanopy space made up 77.43% of the area, while 22.57% had some type of plant cover. *L. tridentata* was the most common species (17.73%), followed by *J. dioica* (1.74%); all other species constituted less than 1% of cover. A total of 484 *C. leptocaulis* adults were observed in association with some shrub species; in most cases (377), the association was with *L. tridentata* and only 59 were associated with no plant (Table 1).

For the eight juveniles of sexual origin that were recorded, distribution was not proportional to shrub cover ($\chi^2 = 51.87$, $df = 21$, $P < 0.0001$, Table 2). Standardized residuals indicated that they are positively associated with *L. tridentata* canopy. Fifty-nine juveniles of asexual origin were also recorded, with a distribution pattern that was not proportional to shrub cover ($\chi^2 = 262.24$, $df = 21$, $P < 0.0001$, Table 2). Forty-nine were found under lone shrubs, nine under shrubs associated with *C. leptocaulis* adults, and one in an open space. Standardized residuals indicate a positive association between juveniles of asexual origin and lone adults of *L. tridentata* and *P. glandulosa* var. *torreyana*, as well as with adults of *J. dioica* and *L. tridentata*, which have *C. leptocaulis* adults growing under their canopy (i.e., these *J. dioica* and *L. tridentata* plants had both adults and asexual *C. leptocaulis* juveniles under their canopies, Table 2).

3.3. Sexual establishment

Maximum germination in field experiments was observed at 107 days, and statistical analyses showed no differences (Table 3) between microenvironments or soil types (general mean $6.13 \pm 0.90\%$, $n = 28$). After 769 days, seedling survival did not differ (Table 3) between microenvironments or soil types (general mean $63.46 \pm 7.94\%$, $n = 28$).

Dry seedling biomass at the end of the experiment (769 days) differed between microenvironment and soil type (Fig. 2), and the interaction between these factors was significant according to a Kruskal–Wallis two-way test. Both in the shaded microenvironment (0.58 ± 0.06 g vs. 0.39 ± 0.06 g) and in the soil type obtained beneath *L. tridentata* (0.69 ± 0.09 g vs. 0.40 ± 0.04 g), total biomass was higher than that obtained in the microenvironment and soil of intercanopy space. The same phenomenon was observed when root and stem biomass were analyzed separately (these results are not shown, but the means can be construed from the data in Fig. 2).

Table 1

Plant cover and numbers of observed and expected (in parentheses) *Cylindropuntia leptocaulis* adults found under shrub canopies and in intercanopy areas on 20,500 m² plots in the Southern Chihuahuan Desert. The last column provides the standardized residuals (Everitt, 1977). Residuals in bold indicate that the number of *C. leptocaulis* plants observed differed from that expected at $P < 0.05$.

Cover type	Cover (m ²)	Number of <i>C. leptocaulis</i> plants	Standardized residuals
<i>Agave asperrima</i>	3.63	0 (0.18)	-0.42
<i>Castela texana</i>	38.17	4 (1.85)	1.58
<i>Euphorbia antisiphilitica</i>	66.62	4 (3.22)	0.43
<i>Fouquieria splendens</i>	62.06	3 (3.0)	0.00
<i>Jatropha dioica</i>	174.26	23 (8.43)	5.02
<i>Lippia berlandieri</i>	0.40	0 (0.02)	-0.14
<i>Larrea tridentata</i>	1773.40	377 (85.83)	31.43
<i>Opuntia microdasys</i>	7.60	0 (0.37)	-0.61
<i>Opuntia rastrera</i>	57.40	0 (2.78)	-167.00
<i>Opuntia macrocentra</i>	2.50	0 (0.12)	-0.35
<i>Prosopis glandulosa</i>	57.13	8 (2.77)	3.15
<i>Parthenium incanum</i>	11.40	6 (0.55)	7.33
<i>Yucca torreyi</i>	2.50	0 (0.12)	-0.35
Intercanopy areas	7742.90	59 (374.76)	-16.31
Total	10000	484	

Table 2

Plant cover and observed and expected (in parentheses) numbers of *Cylindropuntia leptocaulis* juveniles of sexual (SJ) and asexual (ASJ) origin found under canopy and in intercanopy areas on 20,500 m² plots in the Southern Chihuahuan Desert. The expression (+cl) accompanying the name of one species indicates that plants of this species have adult *C. leptocaulis* under their canopies. The last two columns show standardized residuals (SR, Everitt, 1977). Residuals in bold indicate that the number of *C. leptocaulis* plants observed differed from that expected by $P < 0.05$.

Cover type	Cover (m ²)	Number of <i>C. leptocaulis</i> SJ	Number of <i>C. leptocaulis</i> ASJ	SR IS	SR IAS
<i>Agave asperima</i>	3.63	0 (0)	0 (0.02)	-0.05	-0.15
<i>Castela texana</i>	28.56	0 (0)	0 (0.17)	-0.15	-0.41
<i>Euphorbia antisiphilitica</i>	56.97	0 (0)	0 (0.34)	-0.21	-0.58
<i>Fouquieria splendens</i>	56.27	0 (0)	0 (0.33)	-0.21	-0.58
<i>Jatropha dioica</i>	131.88	0 (0)	2 (0.78)	-0.32	1.39
<i>Lippia berlandieri</i>	0.38	0 (0)	0 (0.002)	-0.02	-0.05
<i>Larrea tridentata</i>	1336.15	8 (1)	44 (7.88)	6.70	12.86
<i>Cylindropuntia leptocaulis</i>	33.33	0 (0)	1 (0.20)	-0.16	1.81
<i>Opuntia microdasys</i>	7.60	0 (0)	0 (0.04)	-0.08	-0.21
<i>Opuntia rastrera</i>	57.38	0 (0)	0 (0.34)	-0.21	-0.58
<i>Opuntia macrocentra</i>	2.47	0 (0)	0 (0.01)	-0.04	-0.12
<i>Prosopis glandulosa</i>	43.60	0 (0)	2 (0.02)	-0.19	3.44
<i>Parthenium incanum</i>	7.43	0 (0)	0 (0.04)	-0.08	-0.21
<i>Yucca torreyi</i>	2.54	0 (0)	0 (0.02)	-0.05	-0.12
<i>Castela texana</i> (+cl)	9.61	0 (0)	0 (0.06)	-0.09	-0.24
<i>Euphorbia antisiphilitica</i> (+cl)	9.66	0 (0)	0 (0.06)	-0.09	-0.24
<i>Fouquieria splendens</i> (+cl)	5.79	0 (0)	0 (0.03)	-0.07	-0.18
<i>Jatropha dioica</i> (+cl)	42.38	0 (0)	3 (0.25)	-0.18	5.50
<i>Larrea tridentata</i> (+cl)	437.26	0 (0)	6 (2.58)	-0.59	2.13
<i>Prosopis glandulosa</i> (+cl)	13.53	0 (0)	0 (0.08)	-0.10	-0.28
<i>Parthenium incanum</i> (+cl)	3.97	0 (0)	0 (0.02)	-0.06	-0.15
Intercanopy areas	7709.61	0 (6)	1(45.49)	-2.48	-6.60
Total	10000	8	59		

Seedlings grown under the shade of *L. tridentata* produced 1.48 times the total biomass of those grown in full sunlight (these proportions were 1.54 for shoots and 1.24 for roots), whereas seedlings grown in soils developed under the canopy of *L. tridentata* produced 1.70 times the biomass of those grown in soils developed in open areas. These proportions were lower for shoots than for roots (1.65 vs 1.90).

3.4. Clonal propagation

After 876 days, none of the *C. leptocaulis* stem segments placed in the intercanopy space had managed to root. The survival of stem

Table 3

Split-plot ANOVAs of the germination and survival percentages of *Cylindropuntia leptocaulis* seeds and seedlings in a field experiment under the combination of two microenvironments (under *L. tridentata* canopy and in intercanopy areas) and two soil types (collected under *Larrea tridentata* canopy and in intercanopy areas). Seeds were planted under each treatment combination in May 2008. Final germination percentages were recorded after 107 days and seedling survival was recorded for the following 769 days.

Source	df	Germination			Survival		
		MS	F	P	MS	F	P
Block (B)	6	45.61			1096.11		
Microenvironment (M)	1	45.06	0.74	0.42	7306.26	2.73	0.14
Whole Plot Error (B × M)	6	60.42			2675.67		
Soil (S)	1	20.88	0.48	0.51	854.72	1.59	0.22
B × S	6	43.48			535.44		
M × S	1	1.69	0.05	0.82	269.70	0.58	0.49
Subplot Error (B × M × S)	6	31.66			458.73		

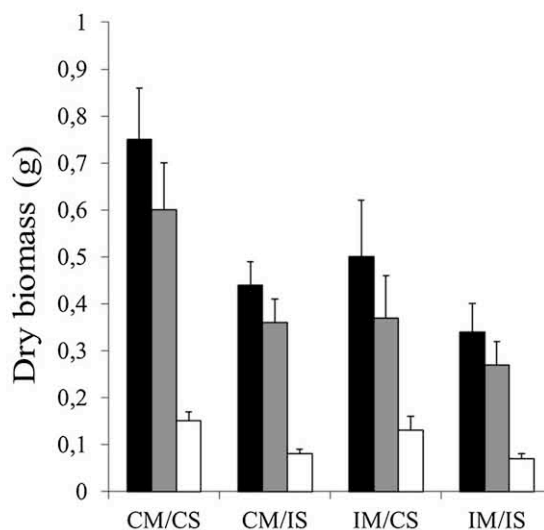


Fig. 2. Total (filled bars), aerial (gray bars), and root (empty bars) dry biomass (mean \pm SE) of *C. leptocaulis* seedlings after 769 days of growth under the combination of two microclimatic conditions (under *L. tridentata* canopy, CM, and in intercanopy areas, IM) and two soil types (collected under *Larrea tridentata* canopies (CS) and collected in intercanopy areas, IS). Kruskal–Wallis two-way ANOVA showed that the main effects (microenvironment and soil type) and the interaction between the two were significant ($P < 0.01$).

segments rooted under *L. tridentata* canopy ($10.35 \pm 3.43\%$) did not differ between soil types (t -test, $t = 0.14$, $df = 12$, $P = 0.9$).

The biomass production of stem segments that succeeded in rooting under *L. tridentata* did not differ between soil treatments (total biomass 0.47 ± 0.10 g, $\chi^2 = 0.02$, $df = 1$, $P = 0.9$, aerial biomass 0.33 ± 0.07 g, $\chi^2 = 0.07$, $df = 1$, $P = 0.9$, and root biomass 0.14 ± 0.03 g, $\chi^2 = 0.04$, $df = 1$, $P = 0.8$).

3.5. Microclimatic conditions and soil properties under *L. tridentata* and *C. leptocaulis* canopies and in intercanopy areas

The physical conditions of the three microenvironments were vastly different. PAR was four and two times lower, respectively, under *L. tridentata* and *C. leptocaulis* than in intercanopy areas ($F_{2,18} = 109.63$, $P = < 0.0001$). Midday soil temperature did not differ under the canopy of both species but was lower than in soil of intercanopy areas ($F_{2,6} = 34.51$, $P = 0.0005$, Table 4).

C concentration was higher under *L. tridentata* than under *C. leptocaulis* and in intercanopy areas, with no differences between the latter two ($F_{2,6} = 5.69$, $P = 0.04$, Table 4). N and C/N did not differ under the canopy of both species but were higher and lower, respectively, than in soil of intercanopy areas ($F_{2,6} = 53.75$, $P = 0.0001$, and ($F_{2,6} = 12.33$, $P = 0.007$, Table 4). pH and CEC did not differ between the soils of the three microenvironments ($F_{2,6} = 2.45$, $P = 0.2$, $F_{2,6} = 1.86$, $P = 0.2$, respectively, Table 4); general means: pH 8.44 ± 0.09 , CEC 1.01 ± 0.12 cmol/kg).

4. Discussion

4.1. Sexual establishment

Contrary to our predictions, neither seed germination nor seedling survival in the first two years increased under the shade of *L. tridentata* canopy. *C. leptocaulis* seeds germinate both in intercanopy areas and under *L. tridentata* canopy, and seedlings can survive in both settings. The fact that seed can germinate outside of the protective conditions of shrub canopy is a strong indicator that the species does not need nurse plants in order to establish

Table 4
Mean (\pm SE) of photosynthetically active radiation (PAR), integrated for the entire day, based on measurements taken between 0700 h and 2000 h; midday soil temperature measured at 1300 h (T); total organic C (C); total N (N) and C/N ratio, in three microenvironments from the Chihuahuan Desert. $n = 7$ for PAR and $n = 3$ for the other variables. Different letters in the same column indicate significant differences (Tukey multiple comparison test, $P < 0.05$) between the means of the three microenvironments.

	PAR $\mu\text{mol s}^{-1} \text{m}^{-2}$	T $^{\circ}\text{C}$	C mg C/g	N mg/g	C/N
Under <i>Larrea tridentata</i> canopy	216.13 ^a \pm 17.93	34.00 ^a \pm 2.11	6.8 ^a \pm 0.55	1.27 ^a \pm 0.07	5.38 ^{ab} \pm 0.36
Under <i>Cylindropuntia leptocaulis</i> canopy	465.91 ^b \pm 61.61	39.00 ^a \pm 2.89	3.7 ^b \pm 1.08	1.27 ^a \pm 0.10	2.83 ^{ab} \pm 0.61
Intercanopy areas	955.9 ^c \pm 13.58	58.66 ^b \pm 1.5	3.2 ^b \pm 0.75	0.37 ^b \pm 0.04	8.3 ^a \pm 1.15

(Fulbright et al., 1995; Kos and Poschod, 2007; Nolasco et al., 1997). This lack of reliance on the set conditions that a nurse plant provides is also evident during seedling establishment, as occurs in other *Cylindropuntia* species (Cody, 1993; López and Valvidia, 2007; Reyes-Olivas et al., 2002). Seedlings of certain *Opuntia* species (Mandujano et al., 1998; Vargas-Mendoza and González-Espinosa, 1992) survive only under nurse plants; in the case of *O. rastrera*, Mandujano et al. (1998) proved experimentally that, in this very same study area and vegetation type, seedlings can only survive if they are protected from the herbivory of heteromid rodents.

While seedlings can establish under *L. tridentata* canopy as well as in intercanopy areas, they grow better (accumulating more biomass) under shrub canopy, where the microclimate is more favorable and there is a greater concentration of soil organic matter. This contrasts with findings reported for other cacti such as *Carnegiea gigantea*, *Ferocactus acanthodes*, and *Pilosocereus leucocephalus* (Franco and Nobel, 1989; Munguía-Rosas and Sosa, 2008). Faster growth increases the chances of survival, as plants pass through the early stages of the life-cycle—when the mortality level is greatest—more quickly (Steenbergh and Lowe, 1977). For this reason, it is likely that in the long run, all sexual recruitment in *C. leptocaulis* takes place under shrub canopy, as suggested by our observational data on the spatial association of *C. leptocaulis* genets and ramets and shrub cover. This highlights the importance of shrub cover—especially that provided by *L. tridentata*, which creates a safe place where the most abundant recruitment of new *C. leptocaulis* individuals in the Chihuahuan Desert takes place (Casper, 1996; Zúñiga et al., 2005).

However, our results show that the effect of soil developed under *L. tridentata* on seedling biomass production was greater than that of microclimate, created by plant shade: 1.70 times more biomass was produced from the soil effect than from shade, at 1.48. Upon independent analyses of stem and root biomass, the effect of soil was shown to be much greater for roots (1.90) than for stems (1.24). In terms of shade, there was a less dramatic difference in proportions, with 1.65 for roots and 1.54 for stems. This means that the benefits of attenuating sunlight are inferior to those of providing soil favored by the biological activity possible in rich organic matter, as verified under canopy due to the “fertility island” effect (García-Moya and Mckell, 1970; Tiedemann and Klemmedson, 1973) along with more water due to hydraulic lift (Caldwell and Richards, 1989; Richards and Caldwell, 1987; Yoder and Nowak, 1999).

The superior accumulation of biomass in seedlings that grew under *L. tridentata* canopy and the close spatial association between juveniles derived from sexual reproduction and *L. tridentata* cover suggest a better long-term performance by seedlings under *L. tridentata* canopy. This highlights the importance of analyzing the different stages that lead to establishment separately, as both the microclimatic and edaphic conditions generated by canopy shade affect different physiological processes differently. Thus, the absence of a nurse effect during first-year germination and survival stages seems to revert in the long run, quite possibly due to better conditions for biomass accumulation in the under canopy microenvironment.

4.2. Clonal propagation

Contrary to our expectations, results show that *C. leptocaulis* terminal stem segments cannot root in intercanopy areas but can under *L. tridentata* canopy (10.35% establishment under *L. tridentata* vs. 0% in intercanopy areas). This seems to indicate the importance of certain microenvironmental conditions under *L. tridentata* canopy (in all likelihood, protection against high temperature, less evapotranspiration demand, and less sunlight) in facilitating terminal stem segment establishment. The limited ability to colonize high-stress environments could be linked to the low volume of terminal stem segments (which are cylindrical and have a diameter of under 1 cm) in *C. leptocaulis* ($0.26 \pm 0.01 \text{ cm}^3$, $n = 45$). The low volume of *C. leptocaulis* terminal stem segments makes it extremely difficult for them to store the amount of water and carbohydrates that they need in order to survive until reaching the independent plant stage (Bobich and Nobel, 2001). Furthermore, the threshold at which temperatures begin to affect the capacity of photosynthetic tissue decreases along with stem segment volume (Smith et al., 1984). This inability to establish in intercanopy areas contrasts with the results of studies done in the Chihuahuan Desert (Allen et al., 1991; Mandujano et al., 1998, 2007) that showed that pad rooting allows clonal propagation in *O. rastrera*, *Opuntia macrocentra*, and *Cylindropuntia imbricata* under the stressful environmental conditions found in intercanopy areas. Nevertheless, it is noteworthy that the pad volumes of these *Opuntia* species ($272.98 \pm 22.9 \text{ cm}^3$, $65.26 \pm 4.2 \text{ cm}^3$ y $28.69 \pm 1.4 \text{ cm}^3$ respectively, $n = 45$ in all cases, Flores-Torres and Montaña, unpublished data) are far higher than that reported above for *C. leptocaulis*.

Observational data on the spatial association between *C. leptocaulis* genets and ramets and shrub cover show that most *C. leptocaulis* terminal stem segments root under adult *L. tridentata* plants, unlike some *Opuntia* species whose vegetative propagules favor establishment under the plant from which they originated (Allen et al., 1991; Palleiro et al., 2006). Intercanopy space represents the worst site for rooting due to its extreme climatic conditions and the lack of protection from herbivores. In the short run, rooting under a *C. leptocaulis* adult means insufficient protection from sunlight and extreme temperatures, because the architecture of its canopy only shields out 52% of photosynthetically active radiation as compared to *L. tridentata*, which shields out 77.4%. In the near term, the new individual may face strong intraspecific competition with the adult plant or with other individuals that have established under it (Ebert, 2006). In the long run, the abundance and clumped spatial distribution of flowering genets can cause pollinator visits to promote inbreeding between genetically similar individuals (along with geitonogamy) and a resulting loss in genetic variability (Charpentier, 2002).

Terminal stem segments have the ability to establish under shrub canopies after being transported by animals; this is a common occurrence, as their spines easily attach to animals' skin, feathers, or fur, and stem segments detach easily from the plant due to quick joint breakage. They are also carried along by runoff after falling to the ground. This dispersal capacity, added to the limited sunlight protection provided by adults of the species, could explain

the absence of juveniles of asexual origin under the canopy of sole *C. leptocaulis* plants. In most cases, such juveniles were found under *L. tridentata* canopy. The only instance in which juveniles of asexual origin were observed in association with adult *C. leptocaulis* plants was when such plants were growing under the canopy of other shrub species that provided shade, both to adult and juvenile *C. leptocaulis* plants. *Opuntia* pads (e.g., *O. rastrera* and *O. microdasys*) can root without the need for shade—although as PAR decreases, their rooting percentage increases (Mandujano et al., 1998; Palleiro et al., 2006). But both our observational and experimental results demonstrate that in *C. leptocaulis*, clonal propagation depends on the shade protection that shrubs offer, and that *L. tridentata* provides the most abundant such areas.

4.3. The importance of the two types of recruitment

Although sexual reproduction has a limited impact on the population growth rate of clonal cacti (Clark-Tapia et al., 2005; Mandujano et al., 2001, 2007), it plays a vital role in genetic recombination and dispersal over long distances (Cook, 1985). The importance of sexual establishment is reflected in the great reproductive effort (ca. 31,000 seeds/ha in 2010, data from an ongoing demographic study, Flores-Torres and Montaña, unpublished) that *C. leptocaulis* exhibits annually; it can be concluded that there is no limitation in seed availability, and that the species' sexual establishment limitations depend on the attenuation of solar radiation, higher organic C concentrations under *L. tridentata* canopy due to leaf and shoot shedding, higher N concentrations under *L. tridentata* and *C. leptocaulis* canopies due to root and microbial activity, protection against frequent depredation (Montiel and Montaña, 2000), heavy-rainfall years, which are rare in the area, and increased soil water availability due to hydraulic lift. The reliance on heavy rainfall has two components. On the one hand, blooming and flowering require water (Flores-Torres and Montaña, unpublished); on the other, so does germination arising from a very short-lived seed bank, making at least two consecutive years of ample rainfall necessary for substantial germination to take place. In effect, in laboratory, the highest level of *C. leptocaulis* germination occurs in one-year-old seeds and decreases as they age. This suggests that there is no dormancy period related to an immature embryo, as has been reported for *Opuntia* species (see review in Orozco-Segovia et al., 2007). This lack of a post-maturation period, along with a decrease in germination efficiency over time, may lead to the absence of a long-lived seed bank in *C. leptocaulis*, in contrast to species such as *O. rastrera* (Mandujano et al., 1998, 2005; Montiel and Montaña, 2003). Furthermore, endozoochory seems vital for seed dispersal as suggested by an increase in the germination levels of *C. leptocaulis* seeds following sulphuric acid scarification, as has also occurred in *Opuntia* species (Potter et al., 1984; Olvera-Carrillo et al., 2003).

In an observational study of January, 2011, on the spatial association of *C. leptocaulis* genets and ramets and shrub cover, it was found that only two seedlings had established in the summer of 2010, this after a remarkable succession of rainy months (with the exception of March) that had begun the previous Autumn and that culminated in an astounding rainfall of 158.7 mm in July of 2010. Keeping in mind that in other clonal species such as *O. rastrera* (Mandujano et al., 2001), clonal propagation has been reported to contribute much more than sexual reproduction to the recruitment of new individuals, this is probably also the case for *C. leptocaulis*.

The clonal propagation of *C. leptocaulis* requires shrub-provided shade and is favored by rainfall. In January, 2011, the observational study on the spatial association of *C. leptocaulis* genets and ramets and shrub cover revealed that on a 1-ha area, 814 terminal stem segments had rooted under various shrub species. Furthermore, in

the previously mentioned demographic study, the annual census recorded 60, 24, and 0 rooted stem segments in May–June of 2011, 2010, and 2009 respectively. The corresponding levels of total annual rainfall (measured from June to May to match *C. leptocaulis* annual growth cycle) were 308, 290, and 151 mm, respectively. Recording of sexually derived seedlings in the same study only registered one seedling in May–June 2011.

Seedlings derived from *C. leptocaulis* terminal stem segments are more resistant to environmental inclemency than sexually derived seedlings due to their different physiological and morphological characteristics. Their metabolic pathway (CAM, Holthe and Szarek, 1985) is more efficient in terms of water use than that of sexually derived seedlings (C3, Altesor et al., 1992, but see also Hernández-González and Briones, 2007). Furthermore, terminal stem segments have spines and secondary metabolites that protect them from herbivore predation (Arizaga and Ezcurra, 2002; Holthe and Szarek, 1985; Mandujano et al., 1998).

Thus, the relatively small size of *C. leptocaulis* terminal stem segments makes rooting more difficult yet permits them greater dispersal, making it possible for them to establish under shrubs and to propagate successful genotypes in sites that have already been colonized. The common clonal establishment that this species features could favor positive population growth rates that ensure its permanence and eventual expansion during periods of climatic bonanza, as has been previously reported for other *Opuntia* species in the study zone (Mandujano et al., 2001, 2007).

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Capítulo II.

Mechanisms and consequences of a shift from a facilitative to a competitive interaction between *Larrea tridentata* and *Cylindropuntia leptocaulis* in the Southern Chihuahuan Desert

Mechanisms and consequences of a shift from a facilitative to a competitive interaction between *Larrea tridentata* and *Cylindropuntia leptocaulis* in the Southern Chihuahuan Desert

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Abstract

Question. Can the cactus eliminate the shrub through a cyclic succession mechanism, alternating between facilitation and competition during the ontogeny of the cactus?

Location. Mapimí Biosphere Reserve (Southern Chihuahuan Desert, 103° 45' N, 26° 41' W; 1100 m a.s.l, annual precipitation of 264 mm and mean annual temperature of 20.8 °C). The vegetation is scrub dominated by *Larrea tridentata*, on slightly sloping (2-5%) terrain featuring gravelly sandy loam to clay loam soils.

Methods. Interspecific spatial association between adult *L. tridentata* and different sized *Cylindropuntia leptocaulis* plants was analyzed using Ripley's *K* function, exploring the hypothesis that facilitation causes differential recruitment of cactus below the shrub and a consequent interspecific association the intensity of which declines with cactus size due to competitive elimination of the shrub.

Competition for water among adult plants was investigated by irrigating solitary and associated plants of both species. The proportion of vigorous (measured by percentage of dead branches) and dead *L. tridentata* plants associated with adult cacti was compared to that of solitary *L. tridentata* individuals, testing the hypothesis that competition between associated adults reduces the vigor and increases the proportion of dead shrubs, relative to that of solitary individuals.

Results. In every cactus size category, *C. leptocaulis* was observed to clump around the *L. tridentata* adults. *L. tridentata* suffered the effects of interspecific competition for water, but these diminished with increased water provision. In contrast, *C. leptocaulis* was unaffected by interspecific competition for water. The proportion of vigorous shrubs was higher in solitary than in associated individuals; however, the proportion of dead shrubs was ten times higher in the solitary individuals.

Conclusion The irrigation experiment and the proportion of dead branches suggest the existence of interspecific competition. However, the interspecific spatial association of the shrubs with each of the cactus size classes, and the proportion of dead shrubs associated with the cacti both suggest that replacement of the shrub by the cactus is an infrequent event. Cyclic succession therefore appears to be the exception rather than the rule. This study discusses the possible scenarios under which cyclic succession may occur.

Key Words: Biotic interaction, cyclic succession, interspecific spatial association, photosynthetic system efficiency, resource availability, xylem water potential.

Running head: Shift from facilitative to competitive interaction

Introduction

The importance of plant-plant ecological interaction in vegetation dynamics and structure in arid environments has been widely discussed (Fowler 1986; Brooker et al 2008). Facilitation is common in these systems (Flores and Jurado 2002) and favors the establishment of cactus in particular (Niering et al 1963; Mandujano et al 1998; Zúñiga et al 2005). Cactus seedlings have problems colonizing open spaces in arid environments due to the extreme conditions found in these habitats (Shreve 1931; Holthe and Szarek, 1985; Nobel 2002).

What is less understood is how the cacti interact with their nurse shrubs on reaching adulthood. It has been proposed that the plant that is a beneficiary during its establishment competes with and even excludes its nurse plant as an adult (Yeaton 1978; MacAuliffe 1988) due to ontogenetic changes in the interacting species (Soriano et al 1994; Armas and Pugnaire 2009). However, few studies have used experimentation to demonstrate these negative effects (Flores-Martínez et al 1994) or the variability of the competitive intensity between pairs of adult plants that can occur as a function of water availability (Briones et al 1998; Flores-Martínez et al 1998), a factor that can strongly influence experimental results.

While the effect of interaction between cacti and shrubs has been evaluated, quantifying variables that express the accumulation of biomass and reproduction (MacAuliffe 1984; Flores-Martínez et al 1998), and it has been inferred that competition between these taxa promotes regular distribution patterns within their communities (Phillips and MacMahon 1981; Yeaton and Romero-Manzanares 1986; Briones et al. 1996), quantification of physiological variables in order to detect this competition has been less common, especially under variable conditions of water availability (but see Briones et al 1998).

Larrea tridentata facilitates the sexual establishment and clonal propagation of *Cylindropuntia leptocaulis* in the Chihuahuan desert (Flores-Torres and Montaña 2012). In this desert, Yeaton (1978) proposed that when *C. leptocaulis* reaches adulthood, it competes with its nurse plant *L. tridentata* causing the death of the shrub. This author reached these conclusions after observing that the number of dead branches on *L. tridentata* individuals associated with *C. leptocaulis* increased with the size of the accompanying *C. leptocaulis* plant, and that the proportion of dead *L. tridentata* plants is greater in those associated with *C. leptocaulis* than in solitary individuals.

In this paper, the replacement hypothesis proposed by Yeaton (1978) was evaluated through the study of interspecific spatial association, monitoring of physiological, growth and reproduction effort variables in solitary and associated plants of both species under different experimentally-controlled levels of water availability and an observational study that evaluated the same variables used by Yeaton (1978).

If the establishment of *C. leptocaulis* benefits from facilitation provided by *L. tridentata*, an interspecific spatial association could be expected between adults of both species. This prediction was investigated with an analysis of spatial distribution using Ripley's K function (Hase et al 1996). If the adults of both species are in competition, this would be expected to be expressed in differences in physiological, growth and reproduction variables measured in associated and non-associated plants. This prediction was tested in a field experiment where the conditions of association and water availability were manipulated. Expression of such competition would also be expected in terms of the vigor (percentage of dead branches) and proportion of live and dead plants under associated and non-associated conditions. This final prediction was tested in an observational study, analyzing the percentage of dead branches in individuals of *L. tridentata* that were associated or non-associated with *C. leptocaulis*, as well as the

proportion of dead individuals in solitary *L. tridentata* plants and in those associated with *C. leptocaulis*.

Materials and methods

Study site and species

The studies were conducted in the area surrounding the Desert Laboratory of the Mapimí Biosphere Reserve (Southern Chihuahuan Desert, 103° 45'N, 26° 41'W, at 1100 m a.s.l., with annual precipitation of 264 mm and mean annual temperature of 20.8 °C; Montaña 1990). The vegetation is scrub, dominated by *Larrea tridentata*, *Jatropha dioica*, *Prosopis glandulosa* var *torreyana*, *Opuntia rastrera*, *O. microdasys*, *Castela texana*, *Parthenium incanum*, and *Fouquieria splendens* on slightly sloping (2-5%) terrain where the soil texture ranges from gravelly sandy loam to clay loam (Montaña 1990). A more detailed description of the study species and plant community can be found in Flores-Torres and Montaña (2012).

Variability of water potentials, branch growth and reproductive effort as a function of irrigation and association

An experiment was designed in which the variability of the response variables was evaluated for each species as a function of two main factors: association (solitary or associated) and irrigation (addition or non-addition of water). Twenty plants of each species were used (i.e., 5 for each combination of levels of the 2 main factors). In March 2008, 20 adult *L. tridentata* shrubs (of between 0.45 and 0.60 m³ in volume) were selected: 10 of these were solitary (i.e., with no adult neighbor of any species within a 4 m radius) and 10 were associated (i.e. with one individual adult of *C. leptocaulis*, of between 0.35 m³ and 0.45 m³ in volume, rooted below its canopy). Five solitary and five associated shrubs

were randomly selected for the application of irrigation, while the remaining 10 shrubs (5 solitary and 5 associated) were not irrigated. Irrigation implied the provision of a quantity of water equivalent to a rainfall event of 40 mm and was carried out by adding 500 liters of water to a circular area of 12.56 m² (the area of horizontal spread of *L. tridentata* roots according to Briones et al. 1996) in one irrigation event. Another 10 adult individuals of *C. leptocaulis* were randomly chosen (of between 0.35 m³ and 0.45 m³ in volume), with no adult plant within a 4 m radius. Five of these 10 individuals were irrigated while the other five were not. The 10 associated individuals of *C. leptocaulis* were those chosen simultaneously with the associated *L. tridentata* plants assigned to the irrigation (5 individuals) and non-irrigation (5 individuals) treatments.

Physiological response variables.

From the second day following irrigation and for 30 days thereafter, the predawn xylem water potential (XWP) of each of the 10 *L. tridentata* plants used in the experiment was measured with a pressure pump of gauge 0-10 MPa (PMS Instrument, Corvallis, Ore) on two small terminal branches of each of the 10 *L. tridentata* plants used in the experiment. Measurements were taken every fourth night in the irrigated plants (8 measurements per month) while, due to low temporal XWP variation, the predawn XWP of the non-irrigated plants was measured every 15 days (3 measurements per month). In addition, the predawn sap osmotic potential (SOP) was measured in two terminal joints of the 10 *C. leptocaulis* used in the experiment. This was carried out with a sampling chamber (Wescor, C-52) connected to a microvoltmeter (Wescor, HR-33T). Predawn SOP measurement in *C. leptocaulis* was conducted with the same frequency as the measurement of predawn XWP in *L. tridentata*.

During the first 18 days after irrigation, prior to the measurement of water potential, the same small branches and joints were used to measure the maximum efficiency of the

photosystem II (F_v/F_m , Maxwell and Johnson 2000). For that purpose, they were covered with paper bags at dusk and uncovered at dawn. These measurements were taken with a portable fluorometer (MINI-PAM Walz, Effeltrich, Germany), with a light pulse of PPFD $2000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. These measurements were taken every fourth night in the irrigated plants (5 measurements in 18 days) but only on days 2 and 18 in the non-irrigated plants (2 measurements), due to the low temporal variation in photosynthetic efficiency in these plants.

All physiological response variables were analyzed with a repeated measures analysis of variance (ANOVAR), using the statistical program SPSS 19 (SPSS Inc 2007). The mean of the two measurements per plant on each date was used as a response variable. “Date” (3 levels) was considered a within-subjects factor, and Irrigation (2 levels) and Association (2 levels) as between-subjects factors. The equality of variance in the differences between levels of the repeated measures factor (i.e. the sphericity hypothesis) was analyzed with the Mauchly (1940) test. In the case of rejection of the sphericity hypothesis, the degrees of freedom were modified using the Greenhouse-Geisser (1959) epsilon for a correct interpretation of the significance of the F test. Where statistically significant differences were found in the interactions, means were compared using a multiple comparisons test with Bonferroni correction.

Morphometric response variables.

Immediately prior to irrigation, and 31 days thereafter, the length of 20 previously marked small terminal branches in each of the selected *L. tridentata* plants was measured. Growth of these small terminal branches was estimated as the difference between the lengths recorded on the two dates. To estimate the production of leaflets on these small branches, on the same dates, the number of leaflets was counted on the terminal 5 cm of the previously marked small branches, which had been wrapped with tulle mesh to prevent

herbivory. To measure reproductive effort, the number of flowers and fruits produced on 3 small terminal branches (of between 20 and 25 cm in length) per plant was counted. The number of fruits and flowers was counted at 30 and 45 days after irrigation (no plant flowered prior to irrigation). All measurements and counts were conducted on all the *L. tridentata* plants used under each condition of association and irrigation treatment.

In *C. leptocaulis*, 20 terminal branches of less than 30 cm in length were randomly chosen and marked in each of the plants utilized under each condition of association and irrigation treatment. The number of stem segments was counted on these branches prior to and 146 days after irrigation. The difference between the lengths recorded before and after irrigation was not used as a measure of branch growth since preliminary observations showed that, in some cases, the apical tip of the terminal joint dies and new primordia are produced in areoles below the dead apex. The portion of the terminal joint located between the dead apex and the first areole that produced a primordium dries and eventually falls off, thus reducing the length of the original branch. This observation led us to the conclusion that the best measurement of growth in the terminal branches would be the number of stem segments they produce. The incorporation of new joints (or stem segments) is estimated as the difference between the quantities of joints recorded on the first and second observations. The number of flowers and fruits was quantified 40 and 86 days after irrigation (no plant flowered prior to irrigation).

All the morphometric response variables were analyzed using two-way factorial ANOVA (with association and irrigation as the principal factors), using the statistical program SPSS 19 (SPSS Inc 2007).

Interspecific spatial association and proportion of dead individuals or branches in associated and solitary plants

All field surveys were conducted in an area of 31 km² surrounding the Desert Laboratory of the Mapimí Biosphere Reserve. To measure the spatial association between adults of both species, in June 2008, all of the *C. leptocaulis* and *L. tridentata* plants found in four 50 x 50 m plots (each included within larger plots of different sizes that together comprise a total of 2.6 hectares utilized in a separate ongoing demographic study) were mapped on a Cartesian plane. Individual *C. leptocaulis* plants were classified as small (<0.01 m³), medium (0.01-0.09 m³) and large (>0.1 m³) according to volume, assuming that the shape of the plants is that of an inverted conical ellipsoid, using the formula: Volume = $(\pi \varnothing M \varnothing m / 4) h / 3$ (where $\varnothing M$ is the largest diameter, $\varnothing m$ is the smallest diameter and h is the height). For each size category of *C. leptocaulis* and for the total number of individuals of all categories, it was determined whether there was a spatial association between the two species (specifically, whether the *C. leptocaulis* plants were grouped around *L. tridentata* adults larger than 0.03 m³ (the size at which they begin to reproduce) using Ripley's *K* function (Hasse et al 1996). This method assumes that if the plants (points in the Cartesian plane) have a Poisson random distribution, the accumulated number of plants $K(t)$ in circles of radius t around each plant is πt^2 , i.e., that $\sqrt{K(t)}$ is a linear function of t . The statistic $\sqrt{[K(t) / \pi] - t}$ is usually shown because the expected value of this expression is zero for all values of t when plants have a Poisson random distribution (Skarpe 1991). In other words, positive values of $\sqrt{[K(t) / \pi] - t}$ will indicate clumped distribution of plants, whereas negative values will indicate regular distribution of plants.

The sample statistic calculated from the data is contrasted with the null hypothesis of random spatial distribution, by randomly repositioning all the points in the Cartesian plane and then analyzing the new data with the same method. Confidence intervals are obtained by conducting 100 or more resamples of the original data. The positive and

negative values outside the confidence interval indicate aggregated and uniform distributions of the plants, respectively (Diggle 1983). In the case of a spatial association between two species, a version that has been modified for analysis of bivariate distribution patterns is used (Diggle 1983; Upton & Fingleton 1985; Andersen 1992) and, in the same manner as in the univariate case, the results are presented graphing the values of $\sqrt{([K(t) / \pi] - t)}$ and their confidence intervals as a function of t . These analyses were conducted with the program (Spatial Point Pattern Analysis, SPPA, Hasse 1995).

To estimate the frequency of dead *L. tridentata* adults, whether solitary or associated with *C. leptocaulis*, the numbers of live and dead solitary and associated adult individuals (larger than 0.03 m³) of each species were recorded in June 2012 in the four 50 x 50 m plots used in the interspecific-spatial association study mentioned above. For easy comparison all density results are expressed in number of plants ha⁻¹. Dead individuals of these species are easily identifiable, since *L. tridentata* presents a woody stump composed of multiple branches that persists for a long period of time following the death of the shrub. *C. leptocaulis* presents a single stemmed stump in which it is easy to recognize the typical woody structure of the cylindropuntias (Gibson and Nobel 1986). Variability of the number of individuals in each species was analyzed with a two-way ANOVA: condition (live and dead) and association (associated and solitary). The response variable was transformed beforehand to achieve normality of the data.

To estimate the vigor of the *L. tridentata* plants, live and dead basal branches (i.e., primary branches that grow from the crown and not from other branches) were counted in all the adult *L. tridentata* plants (of more than 0.03 m³ in volume), whether solitary or associated with adult cactus (of more than 0.03 m³ in volume), in January 2007 within an area of 2500 m² (five 50 m x 10 m plots located in different sites of the reserve). The volume of each plant was calculated with the same formula described in the previous

section. An individual was considered vigorous if the percentage of live basal branches was greater than 50% and non-vigorous if this parameter was below 50%. Variability of the number of individuals in each species was analyzed using a two-way ANOVA: vigor (vigorous and non-vigorous) and association (associated and solitary). The response variable was transformed beforehand to achieve normality of the data. Throughout this article, the measure of dispersion reported for the mean is the standard error (SE).

Results

Variability of water potential, growth of branches and reproductive effort as a function of irrigation and association condition

Hydric relationships and efficiency of photosystem II

From the sixth day after irrigation, the predawn xylem water potential (XWP) of *L. tridentata* increased considerably relative to the pre-irrigation values and remained at this increased level throughout the 30 days of measurements. ($F = 137.02$, $P < 0.05$, Appendix S1, Figure 1a). The interaction between irrigation and condition of association was significant ($F = 7.77$, $P < 0.05$) indicating that the difference in XWP observed in non-irrigated individuals (lower XWP in associated individuals) disappears with irrigation (Figure 1a).

The predawn sap osmotic potential (SOP) of *C. leptocaulis* showed a rapid response to the irrigation and by the second day after irrigation showed significantly higher values in the irrigated compared to the non-irrigated plants (Figure 1b, $F = 237.54$, $P < 0.05$, Appendix S2); this difference remained constant during the 30 days of measurement. There were no differences in the SOP of solitary *C. leptocaulis* and those associated with *L. tridentata* during the 30 days of measurement; this was true for irrigated as well as for

non-irrigated plants (Figure 1b, Appendix S2). The interaction between irrigation and association condition was non-significant ($F = 0.31$, $P = 0.36$), reflecting the fact that the difference between irrigated and non-irrigated plants was similar (Figure 1b).

The maximum efficiency of the photosystem II (F_v/F_m PSII) in *L. tridentata* behaved similarly to the XWP: it was greater in irrigated than in non-irrigated plants (Figure 1c, $F = 9.39$, $P < 0.05$, Appendix S3) and the interaction between irrigation and condition of association was significant ($F = 8.96$, $P < 0.05$, Appendix S3), indicating that the difference in the efficiency of the photosystem II (lower in associated individuals) disappears with irrigation (Figure 1c).

The maximum efficiency of the photosystem II (F_v/F_m PSII) in *C. leptocaulis* behaved in a similar manner to the SOP: irrigated plants had higher F_v/F_m PSII values than non-irrigated plants (Figure 1d, $F = 49.07$, $P < 0.05$, Appendix S4), there were no differences between conditions of association and the interaction between irrigation and association was non-significant.

Both species attained values close to the optimum ecological state (800 F_v/F_m PSII, according to Maxwell and Johnson 2000) by the sixth day after irrigation, and maintained these values throughout the remaining days of measurement.

Morphometric response variables.

Seventy one of the 200 marked small terminal branches in irrigated *L. tridentata* were lost (40 of the 100 marked in solitary shrubs and 31 of the 100 marked in shrubs associated with *C. leptocaulis*) through herbivory, while none of the non-irrigated plants were consumed.

Growth in length of the small terminal branches in *L. tridentata* was affected by irrigation, condition of association and the interaction between both of these factors (Appendix Table 5). In both irrigated and non-irrigated shrubs, the small terminal branches

presented more growth in solitary than in associated shrubs (Table 1) but the interaction indicates that this difference diminished with irrigation (Table 1, Appendix Table 5). The production of leaflets per branch was affected by the irrigation and the interaction between irrigation and condition of association (Appendix S5). The branches of irrigated shrubs produced a greater quantity of leaflets than the non-irrigated shrubs (24.58 ± 1.03 vs. 16.02 ± 0.79 leaflets, Table 1). Multiple comparisons did not accurately indicate the direction of these differences (Table 1).

The *L. tridentata* shrubs did not produce flowers in the non-irrigated treatment. Maximum flowering was produced after 20 days in the irrigated shrubs, but there were no differences in the production of flowers (general mean 22.20 ± 2.09 , $t = 1.02$, $gl = 28$, $P = 0.32$) or fruits (general mean 15.77 ± 1.84 , $t = 0.88$, $gl = 28$, $P = 0.38$) as a result of the condition of association.

After 146 days, 21 of the 200 marked branches in the irrigated *C. leptocaulis* (5 of 100 marked in solitary cactus plants and 16 of 100 marked in cactus plants associated with *L. tridentata*) and 45 of the 200 non-irrigated plants (21 of 100 in solitary cactus plants and 24 of 100 in cactus plants associated with *L. tridentata*) were lost by detachment in *C. leptocaulis*. There were no differences between irrigation treatments and conditions of association in terms of the production of new joints (general mean 4.99 ± 0.32 , $n = 334$, Appendix S6).

Non-irrigated *C. leptocaulis* plants did not produce flowers. Maximum production of flowers and fruit in the irrigated cactus was presented after 28 and 54 days, respectively, but there were no differences in the production of flowers (general mean 31.70 ± 11.37 , $t = 0.27$, $gl = 8$, $P = 0.79$) and fruits (general mean 17.10 ± 7.89 , $t = 1.00$, $gl = 8$, $P = 0.79$) between conditions of association.

Interspecific spatial association and proportion of dead individuals or branches in associated and solitary plants

Three hundred and five *L. tridentata* individuals ha^{-1} ($\pm 55.56\text{SE}$, $n = 4$) were recorded, with a mean volume of $0.45 \pm 0.17 \text{ m}^3$. Densities of *C. leptocaulis* were: 150.0 ± 39.48 small individuals ha^{-1} , 164.0 ± 27.16 medium sized individuals ha^{-1} , and 43.0 ± 13.68 large individuals ha^{-1} ($n = 4$ for all sizes), with mean volumes of $0.003 \pm 0.0002 \text{ m}^3$, $0.038 \pm 0.004 \text{ m}^3$ and $0.19 \pm 0.03 \text{ m}^3$, respectively.

The distribution of *C. leptocaulis* plants in the four plots was clumped around the *L. tridentata* adults. Three of the plots presented maximum intensity at a scale of 1 m radius, i.e., for a radius that is nearly equivalent to the average diameter of an adult shrub ($1.24 \pm 0.32 \text{ m}$, $n = 305$, Figure 2 a, i and m). In the fourth plot, the distribution of *C. leptocaulis* is clumped around the *L. tridentata* adults, but only at a radius greater than 2.5 m (Figure 2 e), representing double the average diameter of the adult shrubs. Analysis of the small and medium categories of *C. leptocaulis* showed the same patterns (Figure 2 b, f, i, n). The large *C. leptocaulis* plants present a distribution that is clumped around the *L. tridentata* at 1 m^2 in all the plots (Figure 2 d, h, l, p).

Ten times the number of dead solitary *L. tridentata* individuals ($126.0 \pm 37.4 \text{ ha}^{-1}$, $n = 4$) were found, compared to those associated with *C. leptocaulis* (13.0 ± 5.0 $16.25 \pm 6.25 \text{ ha}^{-1}$, $n = 4$), a difference that was statistically significant ($F = 18.69$, $P < 0.05$, Appendix Table 7). There were no differences between the number of dead individuals in solitary *C. leptocaulis* and in those associated with *L. tridentata* (Fig. 3 A, Appendix S7)

In solitary plants, the number of vigorous *L. tridentata* individuals was more than three times greater than non-vigorous individuals (756 ± 196.6 vs. 236 ± 48.8 individuals ha^{-1} , respectively). This difference was not so marked in plants associated with *C.*

leptocaulis (280 ± 58.4 vs. 168 ± 38.2 individuals ha^{-1} , respectively, $n = 5$, Fig. 3 B, Appendix S8).

Discussion

Competition between adults. Effect of condition of association and water availability on water status, growth and reproduction.

The consequences of solitary growth or in association differ depending on species and water status. In the case of *L. tridentata*, the growth of terminal branches depends on the level of irrigation and on association with *C. leptocaulis*; however, in the case of *C. leptocaulis*, the production of new stem segments depends on neither irrigation nor the presence of *L. tridentata*. Reproduction in both species depends on the level of irrigation but not on association with the other species.

Different authors have reported that *L. tridentata* produces more biomass as soil water content increases, but that it can also show some growth even in conditions of extreme drought (see Oachel 1972; Cunningham et al 1979; Reynolds et al 1999). It has also been reported that *L. tridentata* is quite susceptible to competition for water during periods of drought when it is associated with other shrubs and grasses (Fonteyn and Mahall 1981; Castellanos et al 2008). Since the ratio F_v/F_m PSII is particularly sensitive to drought (Hamerlynck et al 2000; Hamerlynck and Huxman 2009), reduced water status caused by competition for water can be reflected in the photosynthetic efficiency (Armas and Pugnaire 2009).

One of the most controversial aspects of the role of competition in plant community structure in arid environments is whether the intensity of competition varies with water availability (Fonteyn and Mahall 1981; Fowler 1986; Chesson 2000). Specifically in the

interaction between shrub and cactus, results have differed depending on life form. McAuliffe (1984) reports that the competitive relationship between the columnar cactus *Carnegiea gigantea* and the small leguminous tree *Cercidium praecox* changes throughout the ontogeny of the plants. Flores-Martínez et al (1998) found that competition between the columnar cactus *Neobuxbaumia tetetzo* and the small leguminous tree *Mimosa luisana* increased with increased size of the cactus but diminished with increased water availability. Briones et al. (1998) found that the negative effects of competition increased in *L. tridentata* with irrigation when this species coexisted simultaneously with the tussock grass *Hilaria mutica* and the platyopuntia *Opuntia rastrera* in the Mapimí Biosphere Reserve.

The results of this study suggest that irrigation acts to buffer the negative effects of the cactus on the shrub. This trend of decreasing competition for water between a perennial shrub and a cactus during periods of abundant water resource supports the proposal that different life forms present different strategies to address scarcity of resources (Ogle and Reynolds 2004). In the case of the non-irrigated shrubs, the relatively reduced growth found in the associated shrubs may be due to direct competition for water, as demonstrated by the poorer water status found in the measurements of XWP and F_v/F_m PSII in these plants compared to those of solitary shrubs. In the irrigated shrubs, however, there were no differences between the water status of solitary and associated plants (*i.e.* the XWP and the F_v/F_m PSII did not differ). For this reason, it is possible that the relatively lower growth of the irrigated associated shrubs is the result of competition for other resources triggered by the availability of water. Ettershank *et al* (1978) demonstrated that during periods of abundant water, nitrogen becomes the most limiting factor in desert plant productivity and *L. tridentata* is particularly sensitive to the water-nitrogen interaction (Sharifi et al 1988; Lajtha and Withford 1989).

The possible mechanisms by which *C. leptocaulis* competes with *L. tridentata* for water could be: 1) the interception of water infiltrating the soil by the broad superficial root system of *C. leptocaulis* (an adult of 1.02 m² in canopy coverage presents 5.54 m² of root horizontal spread, distributed throughout the first 32 cm in depth of the soil, Flores-Torres and Montaña unpublished data). In comparison, the roots of adult *L. tridentata* plants in the study area are distributed from the soil surface to a depth of more than 75 cm, with a peak in root density at a depth of 22.5 cm (Briones et al 1996). 2) *L. tridentata* has the capacity to perform “hydraulic lift” (Yoder and Nowak, 1999), which consists of the transport of water via the roots from the deep moist layers of the soil during the day for subsequent release into the shallow dry soil layers during the night. During the early hours of the morning, solitary shrubs can utilize all of this water; however, those that are associated with *C. leptocaulis* must share this water with the cactus since there is no complete spatial separation between the roots of the two species. Ludwig et al (2004) showed that *Acacia tortillis* and grasses associated with its canopy compete during the day for the water that the shrub distributes in the shallow layers of the soil during the night.

The reduced competition for water with irrigation found between the species of this study can be explained by the different times taken to utilize the soil water and by the different capacities for conducting photosynthesis in the absence of water. In effect, despite the fact that water was still available in the rooting zone at least 30 days after irrigation (Briones et al, 1998), the different life forms took different times to utilize the resource: *C. leptocaulis* began to use the soil water immediately after irrigation so that, by 48 h after irrigation, the tissues of this species had reached their optimum osmotic potential (from -2.73 ± 0.25 MPa before irrigation to -1.21 ± 0.06 MPa 48 h after irrigation). Such rapid absorption of water is possibly related to the production of “rain roots” in the Cactaceae, as reported by Gibson and Nobel (1986). *L. tridentata*, in contrast, takes much

longer to reach its optimum water status; its XWP increased from an initial value of -8.43 ± 0.24 MPa before irrigation to -2.68 ± 0.07 MPa at 14 days after irrigation.

Despite the differences in times required to improve water status, both species require a similar time in order to attain maximum efficiency of the photosynthetic apparatus. In *C. leptocaulis*, measurement of F_v/F_m PSII prior to irrigation showed low efficiency in the photosynthetic apparatus (461 ± 51) but the species presented values close to the optimum physiological status (799 ± 12 , see Maxwell and Johnson 2000) six days after irrigation. In contrast, the F_v/F_m PSII in non-irrigated *L. tridentata* plants showed a relatively higher efficiency of photosynthetic apparatus (649 ± 22 and 719 ± 18 , in solitary and associated plants, respectively), although they also reached their optimum values (799 ± 12) six days after irrigation. These results indicate that, compared with *C. leptocaulis*, the photosynthetic efficiency of *L. tridentata* is less dependent on water status. According to Reynolds et al. (1999) and Hamerlynk and Huxman (2009), *L. tridentata* can withstand high stress and water loss while still exhibiting photosynthetic activity and growth. In contrast, Nobel (1977) and Bronson et al. (2011) report that succulents such as *C. leptocaulis* base their water economy on the storage of water and reduce both photosynthetic activity and growth during drought.

Production of new stem segments in *C. leptocaulis* did not depend on irrigation, condition of association or on the interaction between these two factors. This differs from that found by other authors in platyopuntias, where drought (Luo and Nobel 1993) and competition (Burger and Louda 1995) negatively affect the production of biomass. There were no significant differences in the production of flowers or fruits as a result of association, but reproductive effort in *C. leptocaulis* did depend on water availability. Unlike other sympatric species of the genus *Opuntia*, such as *O. rastrera* and *O. microdasys*, which are capable of producing flowers and fruits during the spring before the

wet season (Mandujano et al 1998; Palleiro et al 2006), *C. leptocaulis* is unable to do this in the absence of water. This difference could be due to the low volume of stem segments in this species (Flores-Torres and Montaña 2012), which confers a low capacity for water and carbohydrate storage with which to begin flowering before the wet season.

Spatial distribution and mortality.

Some studies have proposed cyclic dynamics of replacement in different arid zones of the world (Vasek and Lund 1980; MacAuliffe 1988; Yeaton and Esler 1998; Armas and Pugnaire 2009), where the nurse species is replaced by the protégé through competitive exclusion. Specifically for our study species, Yeaton (1978) suggests that *C. leptocaulis* replaces *L. tridentata* in the north of the Chihuahuan Desert. This conclusion was reached after finding more solitary vigorous shrubs (> 51% of basal branches alive) than those associated with the cactus (35 vs. 18, respectively) and because he found a higher quantity of dead *L. tridentata* plants that were associated with the canopy of the cactus than were solitary (82 vs. 18%, respectively). Our analyses show that the solitary shrubs are more vigorous than the associated shrubs and, although this supports the competition found in the experiments manipulating irrigation and association, finding that the number of dead shrubs did not differ between solitary plants and those associated with *C. leptocaulis* means that this competition does not end inevitably in the death of the *L. tridentata* plant.

Furthermore, the study of spatial association showed that all the size classes of *C. leptocaulis* are associated with adult *L. tridentata* shrubs. This suggests that there is no elimination by competition, since in that case we would have detected a trend in which the small size classes of *C. leptocaulis* would have been associated with *L. tridentata* while the plants in the large size classes would be solitary. The presence of the remains of dead *L. tridentata* plants associated with *C. leptocaulis* can be explained by two possible scenarios:

1) The establishment of the cactus below a shrub that, due to its age may have a higher probability of natural death, coupled with an intense competition for water during a sequence of dry years. In this sense, Flores-Martínez et al (1998) demonstrated that the negative effects of *N. tetetzo* on the growth of branches in *M. luisana* are stronger in large than in small plants and Flores-Martínez et al (1994) showed through an analysis of the demography of modules that the nurse shrub can be replaced by the cactus in the event of recurrent droughts. 2) Greater longevity of ramets of the cactus due to clonal establishment. Flores-Torres and Montaña (2012) showed that *C. leptocaulis* could propagate clonally through the rooting of terminal segments when associated with *L. tridentata*. In an on-going demographic study, where the clonal propagation of the cactus has been evaluated for five years (Flores-Torres and Montaña, unpublished data) it was found that this process can repeat itself over time below the canopy of the same shrub so that a sequence of propagules of the same clone may accompany the shrub until its death, which may be the result of many factors, but not necessarily due to competition with the cactus.

In summary, experimental evidence of competition between the species was found and *L. tridentata* presented a greater number of dead basal branches when associated with *C. leptocaulis* than when solitary. Despite this, for two reasons we did not find evidence that the competition led to the systematic elimination of *L. tridentata*: the frequency of dead *L. tridentata* adults associated with *C. leptocaulis* was no higher than in solitary *L. tridentata*, and a spatial association was maintained between adults of *L. tridentata* and plants of all the size classes of *C. leptocaulis*.

The capacity of *L. tridentata* to remain physiologically active and to photosynthesize during drought could mean that the reduced water availability suffered as a result of association with the cactus is insufficient to cause death in this species.

Furthermore, both species present different strategies for utilizing water following an irrigation or rainfall event, and this may contribute to a reduction in the intensity of competition and allow the shrub to better endure the competitive effects caused by the cactus during periods of drought and of greater competitive intensity.

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Table 1. Growth of small branches and quantity of leaflets (31 days after an irrigation event of 40 mm) of *Larrea tridentata* as a function of two factors: irrigation (with or without) and association (solitary or associated with *Cylindropuntia leptocaulis*). Values represent the mean (\pm 1 standard error, $n = 5$ plants), different letters denote statistically different means according to a Tukey-Kramer post-hoc test.

Irrigation	Association	Growth of small branches (mm)	Number of leaflets
Irrigated	Solitary	11.88 (\pm 1.07) ^a	26.96 (\pm 1.52) ^A
	Associated	8.46 (\pm 0.85) ^b	22.22 (\pm 1.23) ^A
Non-irrigated	Solitary	0.49 (\pm 0.28) ^c	15.08 (\pm 1.11) ^B
	Associated	0.06 (\pm 0.32) ^d	16.96 (\pm 1.23) ^B

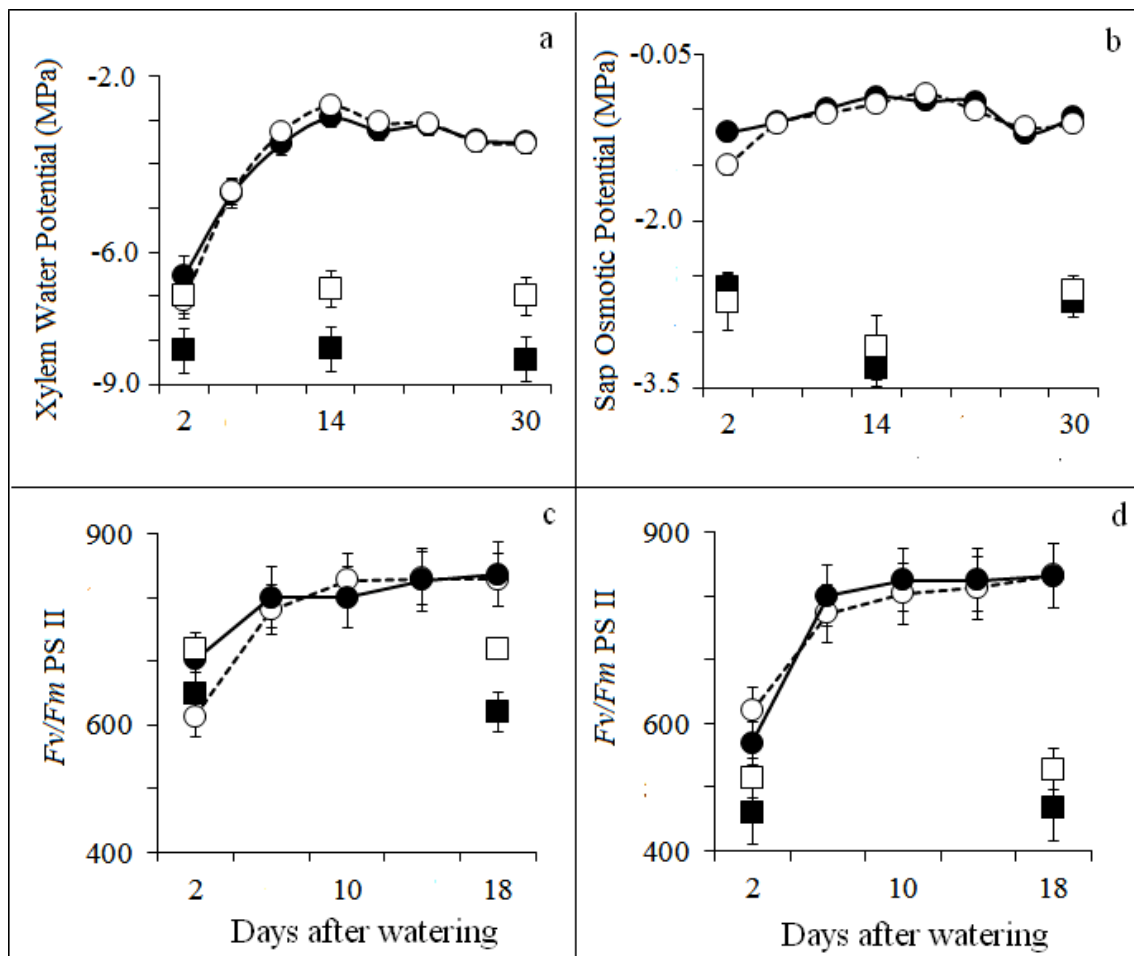


Figure 1. Predawn xylem water potential (XWP) of *Larrea tridentata* (a) and predawn sap osmotic potential (SOP) of *Cyindropuntia leptocaulis* (b) over a period of 30 days following an irrigation event. Maximum photochemical efficiency of the photosystem II in *Larrea tridentata* (c) and *Cyindropuntia leptocaulis* (d), at 18 days after irrigation. Each point represents the mean (± 1 standard error) of 5 plants with (circles) and without irrigation (squares), growing in association (solid symbols) and solitary (open symbols).

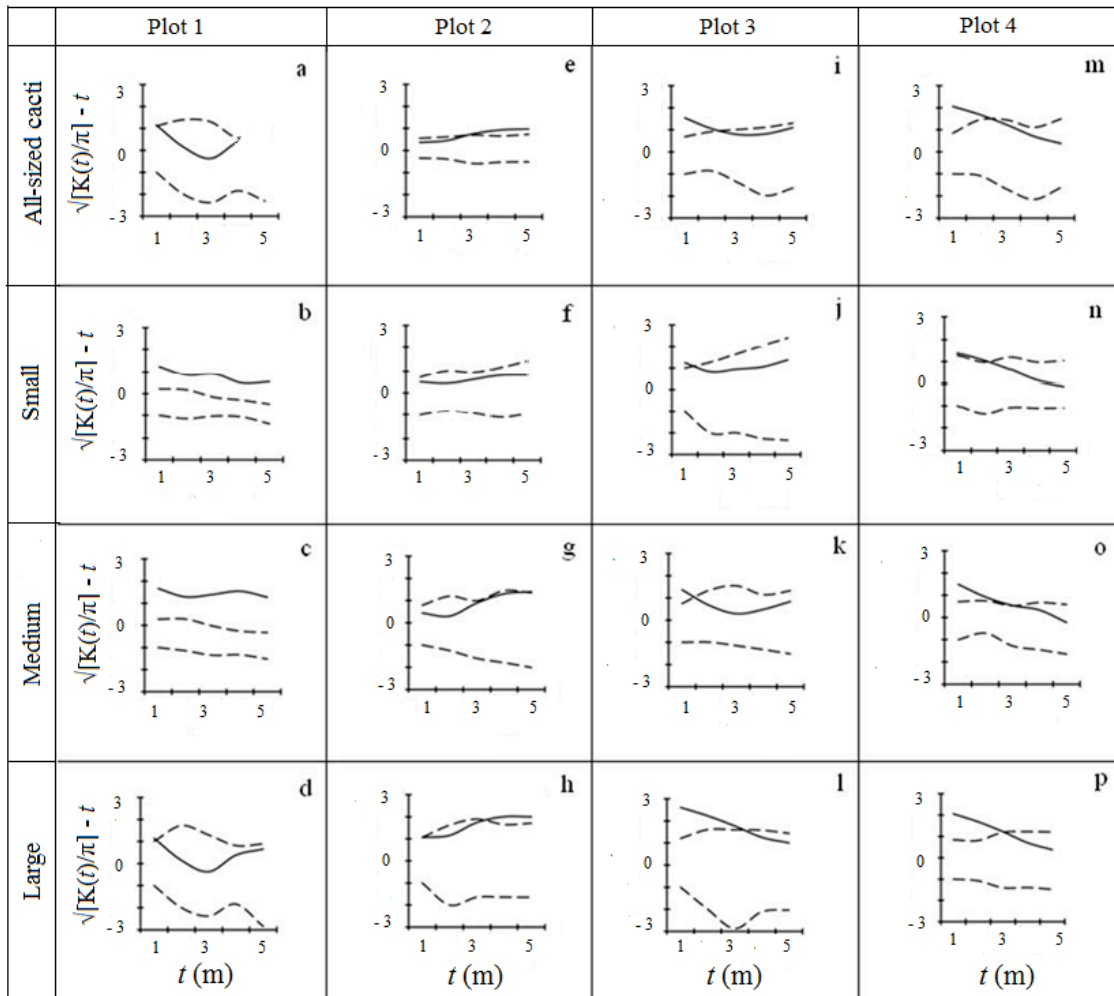


Figure 2. Second-order spatial analysis of the patterns of distribution of *Cylindropuntia leptocaulis* plants of all size classes (a, e, i, m), small plants ($<0.01 \text{ m}^3$, b, f, j, n), medium plants ($0.01\text{-}0.09 \text{ m}^3$, c, g, k, o) and large plants ($>0.1 \text{ m}^3$ d, h, l, p) in circles of different radii (t) centered on large ($> 0.03 \text{ m}^3$) *Larrea tridentata* shrubs in four sites within the Mapimí Biosphere Reserve. Each graph represents the statistic derived from the Ripley's K function ($\sqrt{[K(t)/\pi]-t}$) against the radius in meters of a circle centered on an adult *Larrea tridentata* plant. Positive values of the continuous line indicate clumped patterns while negative values indicate regular patterns. Dotted lines represent the confidence intervals (95%) for a completely randomized distribution.

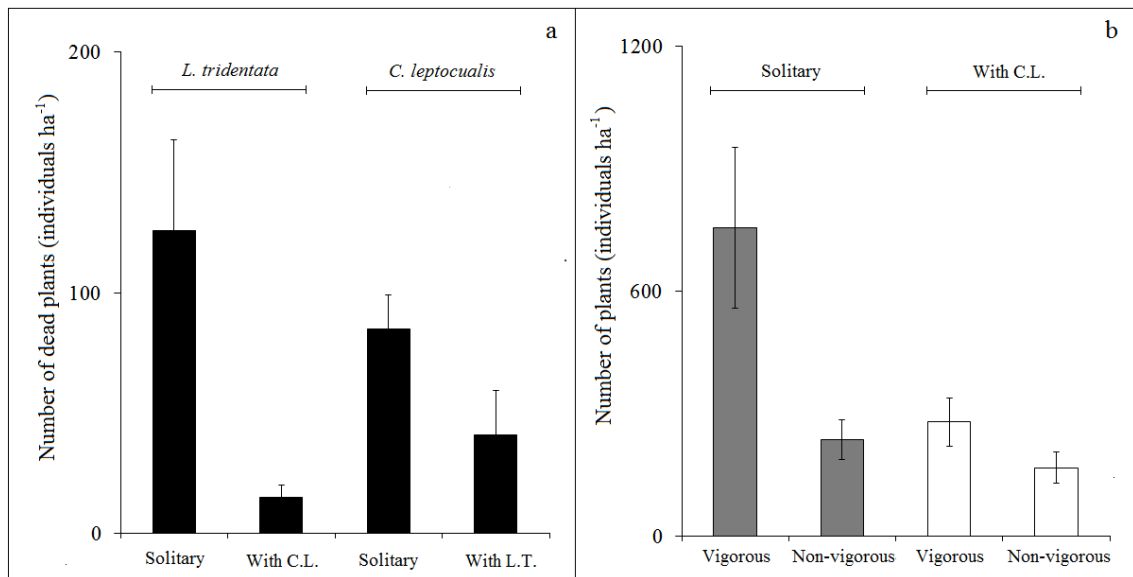


Figure 3. A) Mean \pm SE of the number of dead individuals of *Larrea tridentata* and of *Cylindropuntia leptocaulis*, both solitary and associated with individuals of the other species (*Cylindropuntia leptocaulis* = C.L. and *Larrea tridentata* = L.T.) in plots of 2500 m², $n = 4$. B) Mean \pm SE) of vigorous (> 50 % of basal branches live) and non-vigorous (< 50 % of basal branches live) *L. tridentata* individuals, either solitary (grey bars) or associated with *C. leptocaulis* (white bars) in plots of 500 m², $n = 5$.

Electronic Appendices

Appendix S1. Repeated measures ANOVA of the pre-dawn xylem water potential (XWP) in small terminal branches of *Larrea tridentata* as a function of two two-level between-subjects factors: irrigation (with and without) and association (solitary or associated with *Cylindropuntia leptocaulis*), and a within-subjects factor: time. The df of the analysis of the within subject variability were modified using a Greenhouse-Geisser (1959) test since a Mauchly (1940) test allowed rejection of the sphericity hypothesis.

Source of Variation	SS	df	MS	F	P
Within subjects					
Time	5303.41	1.23	4298.16	64.85	< 0.05
Time * Irrigation	5354.78	1.23	4339.79	65.48	< 0.05
Time * Association	62.51	1.23	50.66	0.76	0.42
Time * Irrigation * Association	66.18	1.23	53.63	0.81	0.40
Error (T)	1308.47	19.74	66.28		
Between subjects					
Intersection	207740.50	1	207740.50	1580.58	< 0.05
Irrigation	18009.34	1	18009.34	137.02	< 0.05
Association	408.20	1	408.20	3.11	0.10
Irrigation * Association	1020.94	1	1020.94	7.77	< 0.05
Error	2102.93	16	131.43		

Appendix S2. Repeated measures ANOVA of the pre-dawn sap osmotic potential (SOP) in terminal joints of *Cylindropuntia leptocaulis* as a function of two two-level between-subjects factors: irrigation (with or without) and association (solitary or associated with *Larrea tridentata*), and a within-subjects factor: time.

Source of Variation	SS	df	MS	F	P
Within subjects					
Time	45.57	2	22.79	3.11	0.06
Time * Irrigation	276.82	2	138.41	18.87	< 0.05
Time * Association	24.43	2	12.21	1.67	0.21
Time * Irrigation * Association	1.93	2	0.96	0.13	0.88
Error (T)	234.72	32	7.34		
Between subjects					
Intersection	23475.70	1	23475.70	1217.07	< 0.05
Irrigation	4581.86	1	4581.86	237.54	< 0.05
Association	6.00	1	6.00	0.31	0.58
Irrigation * Association	17.41	1	17.41	0.90	0.36
Error	308.62	16	19.29		

Appendix S3. Repeated measures ANOVA of the maximum efficiency of photosystem II (F_v/F_m PII) in leaflets of *Larrea tridentata* as a function of two two-level between-subjects factors: irrigation (with or without) and association (solitary or associated with *Cylindropuntia leptocaulis*), and a within-subjects factor: time.

Source of Variation	SS	Df	MS	<i>F</i>	P
Within subjects					
Time	64160.10	1	64160.10	17.08	< 0.05
Time * Irrigation	88548.10	1	88548.10	23.57	< 0.05
Time * Association	7672.90	1	7672.90	2.04	0.17
Time * Irrigation * Association	1822.50	1	1822.50	0.49	0.50
Error (T)	60113.40	16	3757.09		
Between subjects					
Intersection	20217996.10	1	20217996.10	4071.05	< 0.05
Irrigation	46648.90	1	46648.90	9.39	< 0.05
Association	3062.50	1	3062.50	0.62	0.44
Irrigation * Association	44488.90	1	44488.90	8.96	< 0.05
Error	79460.60	16	4966.29		

Appendix S4. Repeated measures ANOVA analyzing the maximum efficiency of photosystem II (F_v/F_m PII) in terminal joints of *Cylindropuntia leptocaulis* as a function of two two-level between-subjects factors: irrigation (with or without) and association (solitary or associated with *Larrea tridentata*), and a within-subjects factor: time.

Source of Variation	SS	df	MS	<i>F</i>	P
Within subjects					
Time	128482.23	1	128482.23	68.11	< 0.05
Time * Irrigation	107640.63	1	107640.63	57.07	< 0.05
Time * Association	0.22	1	0.22	0.00	0.99
Time * Irrigation * Association	189.23	1	189.23	0.10	0.76
Error (T)	30180.20	16	1886.26		
Between subjects					
Intersection	14778049.23	1	14778049.23	1370.31	< 0.05
Irrigation	529230.03	1	529230.03	49.07	< 0.05
Association	9828.23	1	9828.23	0.91	0.35
Irrigation * Association	6786.03	1	6786.03	0.63	0.44
Error	172551.00	16	10784.44		

Appendix S5. Two-way ANOVA for the growth of terminal branches and number of leaflets in shrubs of *Larrea tridentata* as a function of two two-level factors: irrigation treatment (with or without irrigation) and association (solitary or associated with *Cylindropuntia leptocaulis*).

	Source of Variation	SS	df	MS	F	P
Branch growth	Irrigation	6837.2	1	6837.2	193.4807	< 0.05
	Association	303.2	1	303.2	8.5788	< 0.05
	Irrigation*Association	284.6	1	284.6	8.0533	< 0.05
	Residuals	11484.8	325	35.3		
Leaflets	Irrigation	1831.8	1	1831.8	457.512	< 0.05
	Association	51.8	1	51.8	12.947	0.26
	Irrigation*Association	275.6	1	275.6	68.823	0.01
	Residuals	3843.8	96	40.0		

Appendix S6. Two-way ANOVA of the change in the number of joints of *Cylindropuntia leptocaulis* terminal branches as a function of two two-level factors: association (solitary or associated) and irrigation treatment (with and without irrigation).

	Source of Variation	df	SS	MS	<i>F</i>	P
New Joints	Irrigation	1	25.1	25.2	14.218	0.2340
	Association	1	2.8	2.9	0.1601	0.6893
	Association*Irrigation	1	0.01134	0.01135	0.0006	0.9798
	Residuals	330	5829.3	17.7		

Appendix S7. Two-way ANOVA of the number of *L. tridentata* and of *C. leptocaulis* individuals per ha as a function of two two-level factors: condition (live or dead) and association (solitary or associated).

Species	Source of variation	SS	df	MS	<i>F</i>	P
<i>C. leptocaulis</i>	Condition	0.25	1	0.25	0.28	0.60
	Association	0.61	1	0.61	0.69	0.42
	Association * Condition	1.75	1	1.75	1.98	0.18
	Error	10.61	12	0.88		
	Total	13.23	15			
<i>L. tridentata</i>	Condition	10.79	1	10.79	25.55	< 0.05
	Association	7.89	1	7.89	18.69	< 0.05
	Association * Condition	2.51	1	2.51	5.94	< 0.05
	Error	5.06	12	0.42		
	Total	26.26	15			

Appendix S8. Two-way ANOVA of the number of *L. tridentata* individuals per ha as a function of two-two level factors: association (solitary or associated with *C. leptocaulis*) and vigor (vigorous or non-vigorous).

Source of variation	SS	df	MS	<i>F</i>	P
Association	1.76	1	1.76	4.67	< 0.05
Vigor	3.15	1	3.15	8.35	<0.05
Association * Vigor	0.36	1	0.36	0.95	0.034
Error	6.04	16	0.37		
Total	11.33	19			

Capítulo III.

Efectos de las interacciones en las dinámicas poblacionales de *Larrea tridentata* y *Cylindropuntia leptocaulis* en el Desierto Chihuahuense

Efectos de las interacciones en las dinámicas poblacionales de *Larrea tridentata* y *Cylindropuntia leptocaulis* en el Desierto Chihuahuense

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Resumen

Es bien conocido que en ambientes áridos, dos de los factores mas importantes que determinan el resultado de las interacciones interespecíficas en plantas vecinas son: a) la ontogenia de las interactuantes y b) la poca e impredecible precipitación característica de estas zonas. Sin embargo la influencia de estos factores en la dinámica poblacional de plantas vecinas no ha sido estudiada desde una perspectiva bidireccional arbusto nodriza-cactus facilitado.

En este estudio comparamos la demografía de 1) una población de *Larrea tridentata* dividida en dos sub-poblaciones definidas por la presencia o ausencia de un individuo de *C. leptocaulis* que crece bajo su copa (solas = LTS y asociadas = LTA) y 2) una población de *Cylindropuntia leptocaulis* dividida en dos sub-poblaciones definidas por la presencia o ausencia de un individuo de *L. tridentata* creciendo asociado a su copa (solas = CLS y asociadas = CLA). El trabajo fue realizado en la Reserva de la Biosfera de Mapimí, durante 4 años con precipitaciones contrastantes, poniendo a prueba la hipótesis de que la tasa finita de crecimiento poblacional (λ) difiere en ambas especies en función de la condición de vecindario y la variabilidad ambiental.

En *L. tridentata* las λ 's son cercanas a la unidad (LTS λ promedio 2008-2012 = 0.993 y LTA λ promedio 2008-2012 = 0.990, IC = 0.0001) y los intervalos de confianza muestran diferencias apenas perceptibles en las λ 's de ambas sub-poblaciones. Los análisis prospectivos de elasticidad muestran que el mayor impacto a λ en ambas poblaciones la proporciona la estasis pero de diferentes clases de tamaño (individuos pequeños en la sub-

población LTS y grandes en la sub-población LTA). En *C. leptocaulis* las λ 's promedio 2008-2012 fueron significativamente menores para CLS que para CLA (0.9143 y 1.0071 respectivamente. IC = 0.1440). Esta diferencia es mayor en años secos donde CLS presentó una reducción en λ del 43%, mientras CLA únicamente se redujo 14%. Los análisis de elasticidad muestran que la mayor contribución relativa a λ la proporciona la estasis, de todos los tamaños en CLS, mientras en CLA se incrementa la importancia de los juveniles en la contribución. Los análisis retrospectivos (LTRE) en ambas especies de estudio muestran que la fecundidad no contribuye significativamente a λ , que el crecimiento contribuye positivamente en años lluviosos, y negativamente en años secos (presentando el decrecimiento un comportamiento contrario) y que estas contribuciones son mayores en las sub-poblaciones asociadas que en las solas.

Estos resultados sugieren que *L. tridentata* puede permanecer como población sola o coexistiendo con el cacto independientemente del nivel de precipitación, mientras que la población de *C. leptocaulis* es susceptible a desaparecer cuando no se encuentra asociada al arbusto y luego de una secuencia de años con poca precipitación. Lo anterior respalda los resultados de capítulos anteriores de esta tesis, ya que *L. tridentata* facilita el establecimiento sexual y clonal de *C. leptocaulis*, cuando el cacto se convierte en adulto compite con *L. tridentata*, pero dicha competencia no resulta en la exclusión del arbusto.

Palabras clave: Competencia, *Cylindropuntia leptocaulis*, demografía, Desierto Chihuahuense, elasticidad, facilitación, *Larrea tridentata*, matrices periódicas, LTRE, México.

Introducción

La mayoría de los estudios sobre interacciones interespecíficas de plantas vecinas en ambientes áridos se han enfocado a descubrir los mecanismos por los cuales se establecen esas interacciones y demostrar los efectos de la competencia y de la facilitación en la adecuación de plantas vecinas (Shreve 1931; Fowler *et al.* 1986). Se ha demostrado que la competencia por agua, así como por otros recursos asociados movilizados por esta, reducen las capacidades fisiológicas, crecimiento y reproducción entre plantas vecinas. (Briones *et al.* 1998, Flores-Martínez *et al.* 1994; 1998, Sharifi *et al.* 1988). También se ha demostrado que arbustos nodriza (Niering *et al.* 1963) facilitan el establecimiento de plántulas porque promueven un microambiente con menor radiación, más agua y más nutrientes bajo su dosel (Shreve 1931; García Moya y Mckell 1970 Valiente-Banuet *et al.* 1991; Mandujano *et al.* 1998) y en algunas ocasiones estos efectos positivos se conservan entre vecinos adultos (Pugnaire *et al.* 1996; Tirado y Pugnaire 2003)

Se ha propuesto que las interacciones interespecíficas entre plantas vecinas estructuran las comunidades vegetales de ambientes áridos y promueven distintos tipos de distribución espacial. Además se ha sugerido que la competencia entre plantas tiende a excluir al vecino y puede promover patrones espaciales de distribución uniforme (Yeaton y Cody 1976; Phillips y MacMahon 1981) mientras que otros sugieren que los efectos facilitativos entre vecinos promueven patrones de distribución agrupados (Hasse *et al.* 1996; Tirado y Pugnaire 2003).

También se ha sugerido que las interacciones positivas y negativas no actúan separadas sino simultáneamente, y que la primacía de alguna interacción depende de los estadios del ciclo de vida de las plantas involucradas y de la disponibilidad de los recursos que afectan la intensidad e importancia de la interacciones (Aguilar *et al.* 1992; Brooker y Callaghan 1998; Holzapfel y Mahall 1999; Armas y Pugnaire 2005).

Como enlistamos anteriormente, los efectos de las interacciones se han estudiado analizando variables fisiológicas, morfológicas, de crecimiento, de reproducción, o de distribución espacial (Briones *et al.* 1996, 1998, Holzapfel and Mahall, 1999) pero rara vez se han estudiado los efectos de las interacciones a nivel demográfico, para conocer su importancia en el mantenimiento de la población de especies vegetales de ambientes áridos.

Aunque Goldenberg y Barton (1992) han puntualizado la necesidad de incorporar mediciones de respuesta a la competencia a nivel poblacional, en ambientes áridos son pocos los ejemplos de este tipo de estudios. Miriti *et al.* (2001) analizan el efecto que tienen la presencia de arbustos vecinos (principalmente *Larrea tridentata*) y la heterogeneidad ambiental en la tasa finita de decrecimiento poblacional (λ) del arbusto nodriza *Ambrosia dumosa* en el Desierto Sonorense. Los autores encuentran que, tanto en años lluviosos como en secos el crecimiento poblacional *en Ambrosia dumosa* es mayor cuando está sola que cuando está asociada. Griffith (2010) reporta que la tasa de crecimiento del pasto invasor *Bromus tectorum* en el microhabitat bajo arbustos (*Artemisa tridentata* y *Purshia tridentata*) se incrementa durante periodos lluviosos, y que no existen diferencias en el crecimiento poblacional de solas y asociadas en periodos secos. Estos dos estudios proveen evidencia de que la competencia y facilitación tienen efectos a nivel poblacional en una especie que se ha seleccionado como objetivo, pero no analizan los efectos que dicha especie objetivo tiene en la otra especie interactuante, esto es particularmente importante por que, como hemos mencionado, los efectos de la interacción facilitada-facilitadora pueden cambiar por ontogenia o por nivel de recursos, pudiendo afectar los mecanismos de coexistencia conduciendo a una exclusión competitiva de una de las interactuantes y de esta manera afectar la tasa de crecimiento poblacional.

En los dos capítulos anteriores de esta tesis hemos demostrado los efectos de las interacciones de manera bidireccional entre el arbusto nodriza *Larrea tridentata* y el cacto *Cylindropuntia leptocaulis*. *L. tridentata* facilita el establecimiento sexual y clonal de *C. leptocaulis* y cuando este último se convierte en adulto compete con el primero de manera intensa durante periodos secos, disminuyendo la intensidad de la competencia cuando existe agua en el suelo. Contrario a lo sugerido por Yeaton (1978) nuestros análisis de distribución espacial de plantas muertas y de vigor sugieren que, a pesar de esta competencia no existe la exclusión del arbusto por el cacto. Con el objetivo de comprobar cuál es el efecto conjunto de las interacciones positivas y negativas en las dinámicas poblacionales del arbusto y el cacto, en este capítulo comparamos la demografía de una población de *Larrea tridentata* dividida en dos sub-poblaciones definidas por la presencia o ausencia de un individuo de *C. leptocaulis* creciendo bajo su copa (en adelante referido como, solas = LTS y asociadas = LTA) y de una población de *Cylindropuntia leptocaulis* dividida en dos sub-poblaciones definidas por la presencia o ausencia de un individuo de *L. tridentata* creciendo asociado a su copa (en adelante referido como, solas = CLS y asociadas = CLA). Utilizando matrices de proyección de Lefkovitch (1965), pusimos a prueba la hipótesis de que la λ del arbusto y del cacto se ve afectada por la presencia de la otra especie debido a las interacciones de competencia y facilitación. Si la hipótesis anterior es correcta esperamos que: 1) LTS tenga un mayor λ que LTA. 2) CLS tenga un menor λ que CLA.

Material y métodos

Sitio y especies de estudio

Todo el trabajo se llevó acabo en la Reserva de la Biosfera de Mapimí. Para una descripción detallada de las especies de estudio, las comunidades vegetales y las características edáficas del sitio de estudio ver Flores-Torres y Montaña (2012). La precipitación media anual es de 264 mm. Durante el periodo de estudio la precipitación anual del 2008 fue de 255 mm (84.43% en la temporada de lluvias julio-septiembre), 2009 fue 292.90 mm (54.28%), 2010 fue 283.6 (61.67%) 2011 fue 106 mm (100%)

Colecta de datos

En junio del 2008 se etiquetaron y midieron 618 arbustos de *L. tridentata* (asociados = 314, solos = 304) y 628 cactus de *C. leptocaulis* (asociados = 314, solos = 314) dentro de cuatro parcelas de diferentes tamaños que suman un área de 2.6 hectáreas. Debido a que la forma de ambas asemeja a un elipsoide cónico invertido, el tamaño de cada arbusto se calculó con la fórmula $Volumen = 1/3 \pi \varnothing M \varnothing m / 4 h$ (donde $\varnothing M$ = a diámetro mayor, $\varnothing m$ = diámetro menor y h = altura). De acuerdo al volumen las plantas fueron clasificadas en cinco categorías de tamaño por especie (Tabla 1). Este mismo método ha sido empleado con éxito para estudios demográficos en otros arbustos de zonas áridas (Golubov *et al.* 1999; Miriti *et al.* 2001; Verhulst *et al.* 2008). Todas las plantas marcadas se volvieron a medir en junio luego de 1, 2, 3 y 4 años para estimar el crecimiento y la supervivencia.

Fecundidad de las especies de estudio

Anualmente se revisaron cuidadosamente las parcelas en busca de nuevos individuos producto de reproducción sexual o de propagación vegetativa. La única especie que mostró propagación vegetativa fue *C. leptocaulis*: a través de segmentos terminales enraizados, con longitud menor a 30 mm y con pedúnculo de crecimiento vertical no mayor a 30 mm que fueron encontrados en espacios abiertos, bajo el dosel de arbustos

solitarios o bajo el dosel de la asociación arbusto-cacto. En todos los casos fueron marcados y medidos, y el individuo de *C. leptocaulis* más cercano (solo o asociado a *L. tridentata*) fue considerado como la planta madre.

Flores-Torres y Montaña (2013) demuestran que la condición de vecindario no afecta la producción de frutos en *L. tridentata* y *C. leptocaulis*, por lo que en octubre de cada año se contaron los frutos presentes en 10 individuos solitarios de cada clase de tamaño reproductiva (3 y 4 categorías de adultos en *C. leptocaulis* y *L. tridentata* respectivamente) elegidos aleatoriamente. Con estos datos se predijo el número de frutos producidos por individuo de cada categoría de tamaño reproductivo, en cada sub-población, mediante una regresión lineal considerando el volumen como variable independiente y el número de frutos como variable dependiente. La producción de frutos, por periodo de muestreo, en cada clase de tamaño, de cada sub-población (sola o asociada), de cada especie, fue estimada sumando los frutos producido por todos los individuos presentes en cada clase de tamaño

En cada sub-población de *L. tridentata*, la fecundidad fue calculada con el método de la reproducción anónima *sensu* Caswell (2001) por medio del cual las plántulas reclutadas en un área en el tiempo $t + 1$ se asignan a cada adulto existente en cada categoría en el tiempo t sobre la base de su esfuerzo reproductivo individual en el tiempo t . Con este método el número de plántulas producidas por el individuo i de la categoría j en el tiempo $t + 1$ se puede obtener multiplicando el número de plántulas encontradas en el tiempo $t + 1$ por el cociente del número de frutos producido por el individuo i de la categoría j en el tiempo t entre el número de frutos producidos por todos los individuos de la población en el tiempo t . La fecundidad *per capita* de los individuos de una clase de tamaño (que es la que se incorpora en la primera fila de la matriz de transición) se obtiene sumando las fecundidades de todos los individuos de esa clase y dividiéndola por el número de

individuos de esa clase. Como únicamente registramos el reclutamiento de una plántula del arbusto en todo el periodo de muestreo (2008-2012). Para evitar posibles problemas en la convergencia de las matrices en LTS y LTA, el calculo de la fecundidad *per capita* por clase de tamaño se realizó con el procedimiento antes descrito considerando el establecimiento de una plántula por año.

No se encontraron plántulas de *C. leptocaulis* dentro de los cuadros de muestreo en todo el periodo de muestreo (2008-2012), pero de manera consistente registramos individuos producidos por propagación clonal en cada año de muestreo. Dado que un análisis incluyendo la fecundidad sexual (realizado con la misma metodología descrita para *L. tridentata*) no demostró cambios importantes en la estimación de los parámetros poblacionales, solo se incorporó a las matrices de transición la fecundidad calculada con los datos de propagación clonal (llamada en adelante fecundidad clonal). En cada sub-población de *C. leptocaulis*, la fecundidad clonal *per capita* por clase de tamaño para cada año se determinó como el cociente del número de clones producidos por clase de tamaño entre el total anual de clones producidos, dividido entre la cantidad de individuos por clase de tamaño. La propagación clonal fue considerada como “fecundidad pura” (i.e sin contribución a la retrogresión) dado que esta se realiza mediante artículos terminales de no más de 3 cm de largo, los cuales al desprenderse de la planta no tienen efectos detectables en el decrecimiento (se estimó una disminución de 10 cm en cada una de las medidas tomadas para determinar su volumen, para que un cacto regrese a una categoría de tamaño anterior)

Dinámicas poblacionales

Definimos las sub-poblaciones como *Larrea tridentata* sola (LTS), *L. tridentata* asociada al cacto (LTA), *Cylindropuntia leptocaulis* sola (CLS), y *Cylindropuntia leptocaulis* asociada al arbusto(LTA). Para cada una de ellas se prepararon matrices de

transición anual de Lefkovitch (1965) donde se calculó la tasa finita de crecimiento poblacional (λ) y demás parámetros demográficos mediante 4 matrices de transición anual de cada especie en cada sub-población (sola o asociada, 2008-2009, 2009-2010, 2010-2011 y 2011-2012). Todos los valores de la matriz de transición (excepto las fecundidades) se calcularon con los datos de presencia de los individuos en las categorías de tamaño recabados en los censos anuales. El modelo utilizado fue:

$$\mathbf{n}_{(t+1)} = \mathbf{A}\mathbf{n}_{(t)}$$

En el cual $\mathbf{n}_{(t+1)}$ representa el vector del número de individuos en cada categoría al tiempo $t + 1$ y $\mathbf{n}_{(t)}$ representa el vector poblacional al tiempo t . \mathbf{A} es una matriz en la cual la entrada a_{ij} representa la probabilidad de número de un individuo de una determinada clase de tamaño en el tiempo t , a una determinada clase de tamaño al tiempo $t + 1$. Los valores del primer renglón de la matriz correspondientes a las clases de tamaño reproductivas representan la contribución de cada clase de tamaño a la fecundidad. Los valores dentro de la diagonal principal representan la probabilidad de quedar en la misma clase de tamaño (estasis) en un intervalo de tiempo. Los valores dentro de la diagonal inferior representan los valores de pasar a la siguiente clase de tamaño (crecimiento), mientras que los valores dentro de la diagonal superior representan la probabilidad de regresar a una categoría anterior (decrecimiento, Caswell 1989).

Para determinar la sensibilidad de λ de cada proceso demográfico (fecundidad, crecimiento, estasis y decrecimiento) y de cada clase de tamaño, se realizaron análisis prospectivos mediante el cálculo de la elasticidad (de Kroon *et al.* 1986). Estos parámetros demográficos que se reportan se calcularon con el paquete STAGECOACH 2.3.

Para estimar el efecto del año (variabilidad en la precipitación anual) y sub-población (sola vs asociada) y la interacción de ambos factores en la contribución a λ , usamos experimentos de respuesta a tabla de vida (por sus siglas en inglés LTRE). Los

LTRE's tienen n tratamientos, que producen matrices poblacionales de proyección $\mathbf{A}^{(m)}$ y tasas de incremento $\lambda^{(m)}$ para $m=1, \dots, n$. Los efectos principales de cada factor y la interacción de ambos pueden ser descompuestos como sigue. $\mathbf{A}^{(m)} = \mathbf{A}^{(ij)}$ es una matriz de transición que resulta del i ésimo nivel del tiempo (año, con cuatro niveles, 2008-2009, 2009-2010, 2011-2012, 2012-2013.) y el j ésimo nivel de sub-población (sola o asociada) y $\lambda^{(ij)}$ es su autovalor. $\mathbf{A}^{(r)}$ es la matriz de proyección poblacional de referencia (matriz promedio) con su tasa de incremento correspondiente $\lambda^{(r)}$. El efecto de un tratamiento m en λ puede ser descompuesto en las contribuciones de cada una de las entradas de la matriz (Caswell 1996).

$$\lambda^{(m)} - \lambda^{(r)} \approx \sum \left(a_{ij}^{(m)} - a_{ij}^{(r)} \right) \frac{\partial \lambda}{\partial a_{ij}} \Big|_{\mathbf{A}^\dagger}$$

donde $\mathbf{A}^\dagger = (\mathbf{A}^{(m)} + \mathbf{A}^{(r)})/2$. Cada termino de la suma de esta ecuación define el efecto del tratamiento m en λ . Las contribuciones dependen de los efectos del tratamiento en la matriz de entrada y de la sensibilidad de λ a tal efecto. Siguiendo a Caswell (1989; 2001) el modelo empleado fue:

$$\lambda^{(ij)} = \lambda^{(\cdot)} + \alpha^{(i)} + \beta^{(j)} + \alpha\beta^{(ij)}$$

donde $\lambda^{(\cdot)}$ es la media general de la tasa finita de incremento poblacional, $\alpha^{(i)}$ y $\beta^{(j)}$ son los efectos principales y $\alpha\beta^{(ij)}$ el efecto de la interacción entre tratamientos. Estimar el efecto de los tratamientos se da por:

$$\begin{aligned} \bar{\alpha}^{(i)} &= \lambda^{(i\cdot)} + \lambda^{(\cdot)}, \\ \bar{\beta}^{(j)} &= \lambda^{(\cdot j)} + \lambda^{(\cdot)}, \\ \bar{\alpha}\bar{\beta}^{(ij)} &= \lambda^{(ij)} - \bar{\alpha}^{(i)} - \bar{\beta}^{(j)} - \lambda^{(\cdot)} \end{aligned}$$

Estos efectos pueden descomponerse de la siguiente manera:

$$\bar{\alpha}^{(i)} = \sum_{k,l} (a_{kl}^{(i)} - a_{kl}^{(\cdot)}) \frac{\partial \lambda}{\partial a_{kl}} \bigg|_{\frac{(\mathbf{A}^{(i)} + \mathbf{A}^{(\cdot)})}{2}},$$

$$\bar{\beta}^{(j)} = \sum_{k,l} (a_{kl}^{(j)} - a_{kl}^{(\cdot)}) \frac{\partial \lambda}{\partial a_{kl}} \bigg|_{\frac{(\mathbf{A}^{(j)} + \mathbf{A}^{(\cdot)})}{2}},$$

$$\bar{\alpha}\bar{\beta}^{(ij)} = \sum_{k,l} (a_{kl}^{(ij)} - a_{kl}^{(\cdot)}) \frac{\partial \lambda}{\partial a_{kl}} \bigg|_{\frac{(\mathbf{A}^{(ij)} + \mathbf{A}^{(\cdot)})}{2}} - \bar{\alpha}^{(i)} - \bar{\beta}^{(j)}.$$

cada una de estas ecuaciones representa un cambio observado en λ originado por cambios en la entrada de la matriz. La sensibilidad en la ecuación $\lambda^{(m)} - \lambda^{(r)} \approx \sum (a_{ij}^{(m)} - a_{ij}^{(r)}) \frac{\partial \lambda}{\partial a_{ij}} \big|_{\mathbf{A}^\dagger}$ fue evaluada de una matriz media \mathbf{A}^\dagger entre las dos matrices $\mathbf{A}^{(m)}$ y $\mathbf{A}^{(r)}$ (Caswell, 2001).

Análisis estadísticos

En ambas especies, la variabilidad en la cantidad de frutos producidos en función de los factores: sub-población (solos o asociados) periodo de muestreo (2008-2009, 2009-2010, 2010-2011 y 2011-2012) y tamaño (3 y 4 categorías de adultos para la producción de frutos en *L. tridentata* y *C. leptocaulis* respectivamente), fue analizada con un análisis de devianza y usando modelos lineares generalizados (GLM) con un error tipo Poisson y función liga tipo log (Crawley 2007). Con el mismo procedimiento (pero incluyendo en el factor tamaño todas las categorías) se analizó la variabilidad en la cantidad de individuos muertos en ambas especies y la cantidad de clones (artículos terminales enraizados) producidos por *C. leptocaulis*

Variabilidad de las tasas de crecimiento en función de la condición del vecindario

Las diferencias entre las tasas de crecimiento promedio ($\lambda = 2008-2012$) de las sub-poblaciones sola o asociada en ambas especies se analizaron mediante pruebas de aleatorización (Caswell 2001, pp. 335-345). Las diferencias reales observadas se compararon con la distribución de frecuencias de 5000 diferencias obtenidas por

aleatorización de las matrices consolidadas (es decir matrices donde se incluyeron los datos de los 5 años de observación). El valor de lambda de la matriz consolidada es igual a la de la matriz promedio cuando el número de individuos no varía entre años. Estos análisis se realizaron con el paquete estadístico R-proyect versión 2.9.2

Resultados

Fecundidad sexual.

La producción de frutos en *L. tridentata* se ve influida por el factor sub-población, el periodo de muestreo y el tamaño del arbusto (Figura 1 A y B, Tabla 2). La sub-población LTA produjo aproximadamente 2.5 veces más frutos que la sub-población LTS en todos los años. La mayor producción de frutos fue en el periodo 2008-2009 (82693 en LTS vs 209201 en LTA), seguido por 2010-2011 (35559 en LTS vs. 84635 en LTA), 2009-2010 (26119 en LTS vs 64325 en LTA) y 2011-2012 (13862 en LTS vs. 33787 en LTA) (Figura 1 A y B) En ambas sub-poblaciones la categoría de adultos 4 produjo mayor cantidad de frutos, seguida de adultos 3, adultos 2 y adultos 1 (Figura 1 A y B, Tabla 2). Únicamente se registró una plántula de *L. tridentata* en junio del 2010 en las parcelas de estudio.

En *C. leptocaulis* la producción de frutos también se ve influida por el factor sub-población, el periodo de muestreo y el tamaño del cacto (Figura 1 C y D, Tabla 3). En promedio, durante 3 periodos de transición, la sub-población CLA produjo 1.86 veces más frutos que la población CLS. La población de *C. leptocaulis* no produjo frutos cuando fue revisada en el periodo 2011-2012, la máxima producción de frutos se dio en 2010-2011 (4637 CLS vs. 6382 CLA), seguidas por 2009-2010 (2116 en CLS vs 4383 CLA) y 2008-2009 (1408 CLS vs. 3000 CLA). En ambas sub-poblaciones la categoría de adultos 3

produjo mayor cantidad de frutos, seguida de adultos 2, y adultos 1. (Figura 1 C y D, Tabla 3). En ningún año registramos plántulas de *C. leptocaulis* dentro de las parcelas.

Fecundidad clonal

La producción de nuevos individuos de *C. leptocaulis* mediante el enraizamiento de artículos terminales (clones) se ve influida por el factor sub-población, el periodo de muestreo y el tamaño del cacto (Figura 2 A y B, Tabla 4). Registramos mayor cantidad de clones producidos por la sub-población CLA que por la CLS (4.75 veces más en 2011-2012, 8.28 veces más en 2010-2011 y 7.66 veces más en 2009-2010) no se registraron clones en el periodo 2008-2009. Registramos mayor cantidad de clones en 2011-2012 lo cual coincide con en el periodo con menor precipitación. En periodos no tan secos (2010-2011 y 2009-2010) registramos menor cantidad de clones. Durante los años de mayor producción, registramos clones en todas las categorías de tamaño de la sub-población CLA (Figura 2 A), mientras que en la sub-población CLS solamente en las categorías menores (J1, J2 y A1, Figura 2B). También se registraron clones en arbustos solitarios de *L. tridentata* en los periodos 2010-2011 y 2011-2012 (3 y 17 respectivamente) y en espacio abierto en los mismos periodos (2 y 2 respectivamente)

Mortalidad

El porcentaje de mortalidad de arbustos de *L. tridentata* no se vio influido por el factor sub-población (2.63% en LTS vs 0.95% en LTA) o periodo de muestreo, pero si por la categoría tamaño (Tabla 5). Durante los cuatro años de muestreo 2008-2012 murieron únicamente juveniles, 8 de la sub-población LTS vs. únicamente 3 de LTA. La única plántula registrada en junio del 2010, se registró muerta en junio del 2012.

La mortalidad de cactos de *C. leptocaulis* se vio influida por el factor sub-población, periodo de muestreo y el tamaño del cacto (Tabla 6). La sub-población CLS presentó mayor mortalidad de individuos que CLA (50.63 vs 26.11%, respectivamente).

En los cuatro años de muestreo 2008-2012 murieron 159 cactus de la sub-población CLS vs 82 de la población CLA. En todos los años, la mayor mortalidad de cactus, en ambas poblaciones se presentó en las categorías de juvenil 1 y 2, siendo el periodo 2011-2012 el año en que más muertos registramos (110 en cactus en CLS vs 67 en CLA), seguido de 2010-2011 (18 vs 8), 2008-2009 (19 vs 2) y 2009-2010 (12 vs 5).

Durante los cuatro años de muestreo 2008-2012, la mayor mortalidad de clones registrados se presentó en la sub-población CLS (82.25%) contra en CLA (57.18%). En este mismo periodo, los clones registrados en arbustos solitarios presentan una mortalidad de 65%, mientras que todos los clones registrados en espacio abierto murieron.

Dinámicas poblacionales

Las tasas finitas de crecimiento poblacional (λ) tuvieron menor variabilidad interanual en *L. tridentata* ($\lambda = 0.9869 \pm 0.0079EE$ para las asociadas y $\lambda = 0.9891 \pm 0.0026EE$ para las solitarias) que en *C. leptocaulis* ($\lambda = 1.0199 \pm 0.0581EE$ para las asociadas y $\lambda = 0.8639 \pm 0.0977EE$ para las solitarias). Las pruebas de aleatorización de las matrices consolidadas (esto es, donde se incluyen los datos de los 5 años) mostraron que los valores de lambda difieren entre las condiciones de vecindario (calculadas siempre como lambda de asociadas menos lambda de solitarias) en ambas especies. En *C. leptocaulis* los lambdas son considerablemente más grandes en las asociadas (diferencia 0.1440, IC 95% de las diferencias -0.1445 - 0.1069) mientras que en *L. tridentata* las lambdas son apenas perceptiblemente mayores en las solitarias (diferencia -0.0001, IC 95% de las diferencias -0.0013 - 0.0012, Figura 3)

Análisis prospectivos de la elasticidad muestran que el mayor impacto a la λ promedio 2008-2012 por proceso demográfico en las sub-poblaciones LTS ($\lambda = 0.993$) y LTA ($\lambda = 0.990$) lo tiene la estasis (0.81 vs 0.82), seguida por crecimiento (0.10 vs 0.09), decrecimiento (0.07 vs 0.08) y fecundidad (0.02 vs 0.01, respectivamente. Figura 4). Por

categoría el mayor impacto a la λ promedio 2008-2012 en la sub-población LTS fue de la categoría A2 (0.31), seguido de A1 (0.27), A3 (0.22), A4 (0.13) y J (0.07). En la sub-población LTS el mayor impacto a la λ promedio 2008-2012 por clase de tamaño fue de A4 (0.35), seguido de A3 (0.25), A2 (0.24), A1(0.14) y J (0.02, Figura 5)

Los análisis prospectivos de elasticidad muestran que el proceso demográfico que más impacta a la λ promedio 2008-2012 de la sub- población CLS ($\lambda = 0.914$) y CLA ($\lambda = 1.007$) es la estasis (0.76 vs 0.71), seguido por crecimiento (0.14 vs 0.18), decrecimiento (0.08 vs 0.05) y fecundidad (0.02 vs 0.06, respectivamente. Figura 4). Por categoría de tamaño el mayor impacto a la λ promedio 2008-2012 de la sub-población CLS fue de la categoría A2 (0.31) seguido de A3 (0.26), A4 (0.23), A1 (0.13) y J (0.06). En la sub-población CLA el mayor impacto a la λ promedio 2008-2012 por categoría de tamaño fue de A2 (0.36), seguido de A1 (0.24), J (0.22), A3(0.13) y A4 (0.06, Figura 5)

Los análisis retrospectivos de experimentos de respuesta a tablas de vida (LTRE) muestran que para ambas especies la fecundidad (sexual en el caso de *L. tridentata* y propagación clonal en el caso de *C. leptocaulis*) no contribuyen de manera importante a λ , y que el factor vecindario (solo y asociado) y año (variabilidad en la precipitación anual) y su interacción no tienen efectos en la contribución de la fecundidad (figura 6 y 7)

En *L. tridentata* las contribuciones del crecimiento, estasis y decrecimiento varían en función de la condición de vecindario, año y su interacción. En el año más lluvioso (2009-2010, 292.90 mm) el crecimiento y estasis contribuyen positivamente, mientras que el decrecimiento contribuye negativamente a la λ con valores ligeramente mayores en la sub-población LTA que en LTS (Figura 6 i y j). En el año más seco (2011-2012, 106.70 mm) el crecimiento contribuye negativamente y el decrecimiento lo hace positivamente a la λ en la sub-población LTS, con un ligero aporte negativo de la estasis. El crecimiento y

decrecimiento de la sub-población LTA presenta un patrón similar, con contribuciones ligeramente superiores y una contribución positiva de la estasis. (Figura 6 m y n)

En *C. leptocaulis* las contribuciones del crecimiento, estasis y decrecimiento varían en función de la condición de vecindario, año y su interacción. En el año más lluvioso (2009-2010, 292.90 mm) el crecimiento y estasis contribuye positivamente, mientras que el decrecimiento lo hace negativamente a la λ de ambas sub-poblaciones, con valores superiores de contribución del crecimiento y decrecimiento en la sub-población CLA (Figura 7 I y J). En el año más seco (2011-2012, 106.70 mm) el crecimiento y estasis contribuye negativamente y el decrecimiento lo hace positivamente a la λ de ambas sub-poblaciones, mayores contribuciones del decrecimiento y crecimiento son observados en la sub-población CLA y de la estasis en la sub-población CLS (Figura 7 M y N)

Discusión

Reclutamiento sexual

Igual que otras especies de arbustos desérticos (Jiménez-Lobato y Valverde 2006) y cactáceas (Steenbergh y Lowe 1977; Mandujano *et al.* 2001; Contreras y Valverde 2002) la producción de frutos en las especies de este estudio se incrementa con el tamaño, y de manera consistente se estimó una mayor producción de frutos en las sub-poblaciones asociadas en las solas. Sin embargo, como las sub-poblaciones LTA y LTS no difieren entre sí en la producción de frutos *per cápita* por clase de tamaño ($F = 0.05$, *g.l.* = 3 $P = 0.98$), la mayor producción de frutos estimada en la sub-población LTA puede ser originado por que posee mayor cantidad de individuos de las categorías más grandes. Como se estimó mayor cantidad de frutos *per cápita* en todas las categorías de tamaño de la sub-población CLA que en la CLS (1.40 veces más en la categoría A1, 2.14 en la A2 y 3.16 en la A3. $F = 6.77$, *g.l.* = 2, $P = < 0.05$), la mayor diferencia de frutos producidos por la sub-población asociada pueden originarse en efectos facilitativos que el arbusto tiene en

la fecundidad del cacto y no en la diferencia de estructura poblacional. Tirado y Pugnaire, (2003) demuestran que los efectos positivos de una planta nodriza pueden continuar sobre la facilitada aun cuando estas son adultas incrementando su fecundidad.

La máxima producción de frutos en la población de arbustos solos y asociados se dio durante el periodo 2008-2009, seguido del 2010-2011, 2009-2010 y 2011-2012, lo que corresponde cercanamente con la precipitación total de la temporada de lluvias (julio, agosto y septiembre para cada periodo fue de 215.90 mm, 174.90 mm, 148.30 mm y 102.1 mm respectivamente). Otros autores han reportado que *L. tridentata* tiene la facultad de producir frutos en periodos muy secos, pero su máxima producción se da en periodos de altas precipitaciones (Oachel 1972; Cunningham *et al.* 1979).

Algunos estudios realizados en cactos columnares muestran que la producción de frutos es muy variable (con años de mucha producción y años sin producción) y no responde de manera directa al patrón de precipitaciones del año en curso (Esparza-Olguín *et al.* 2006, Nassar y Emalde 2008). Del mismo modo, la máxima producción anual de frutos en la población de CLS y CLA no se presentó en el periodo que más precipitación tuvo en su temporada de lluvias (2008-2009) sino luego de tres años con temporadas de lluvia relativamente abundantes (2010-2011). En contraste ambas poblaciones de *C. leptocaulis* no producen en años con poca lluvia (2011-2012 = 102.1 mm, 2012-2013 = 146.5 mm. Dat sin Pub.). Estos datos corroboran lo encontrado por Flores- Torres y Montaña (2013), quienes sugieren que la reproducción de *C. leptocaulis* es extremadamente dependiente de la lluvia por que sus pequeños cladodios no le permiten almacenar suficiente agua y carbohidratos con los cuales florecer antes del periodo de lluvias.

A pesar de la gran producción de frutos en *L. tridentata*, en los cuatro periodos anuales únicamente registramos un juvenil en junio del 2010 en 2.6 ha (esto es

aproximadamente 0.38 ind/ha); lo cual corresponde con una rara alta precipitación de los primeros cinco meses del 2010. Esto difiere con lo reportado por Goldberg y Turner (1986) en el norte del Desierto Sonorense quienes reportan alto reclutamiento del arbusto un año donde las lluvias de invierno fueron abundantes (49 juveniles en 1 ha)

No encontramos ninguna planta juvenil de origen sexual de *C. leptocaulis* dentro de las parcelas, pero en un estudio previo (Flores-Torres y Montaña 2012) en enero de 2011, encontramos 2 juveniles bajo un arbusto de *L. tridentata* los cuales se habían establecido en verano el 2010, además del ya mencionado principio de año lluvioso, junio del 2010 registró una inusual precipitación de 158.7 mm. Lo anterior sugiere la importancia de la precipitación, seguido por el efecto nodriza en el establecimiento de individuos de origen sexual en los cactus (Godínez-Álvarez *et al.* 2003).

Fecundidad clonal

Las sub-poblaciones CLS y CLA, presentaron un evento masivo de reclutamiento clonal en junio del 2011 luego de un periodo de 12 meses secos (174.9 mm en total y 8 meses sin precipitaciones) precedidos por dos periodos anuales de mayor precipitación (ambos con menor reclutamiento clonal). Esto permite suponer que durante periodos de precipitaciones regulares el cacto retiene sus artículos terminales y crece, pero en periodos muy secos estos se desprenden como un mecanismo para hacer frente a la sequía. Similares resultados son reportados en *Opuntia macrocentra* (Mandujano *et al.* 2007a). Pimienta-Barrios *et al.* (2002; 2005) han encontrado que los cladodios jóvenes de *O. robusta* y *O. ficus-indica* demandan grandes cantidades de agua y carbohidratos de la planta madre durante la sequía y reportan que dichas especies regulan la producción y el tamaño de estos cladodios como un mecanismo que permite hacerle frente a años muy secos.

La mayor cantidad de estos clones fueron producidos por la sub-población CLA (esto es, se registraron bajo la copa de cactus asociados a arbustos), y en menor cantidad

por la sub-población de CLS. También registramos clones que colonizaron arbustos de *L. tridentata* solos y espacios abiertos. Esto sugiere que aunque la mayoría de los artículos enraízan bajo la planta madre, tienen la capacidad de colonizar otros ambientes. Flores-Torres y Montaña (2012) reportan individuos juveniles de *C. leptocaulis* (de hasta 20 cm alto) de origen clonal bajo las mismas condiciones microambientales anteriores en la zona de estudio y comprueban de manera experimental la dependencia estricta de un arbusto nodriza para el establecimiento de éstos, en contraste con otras especies de opuntias (Mandujano *et al.* 2001; 2007a; Bobich y Nobel 2001; Evans *et al.* 2004). Al parecer la desventaja de tener clones pequeños incapaces de colonizar ambientes estresantes, es suplida por la ventaja de ser transportados más fácilmente por animales o por escurrimiento superficial a sitios seguros donde establecerse. Los artículos terminales de *C. leptocaulis* presenta menor volumen (0.26 ± 0.01 SE cm³, $n = 45$) que los de otras especies clonales de la zona de estudio. *Opuntia rastrera* (272.98 ± 22.9 SE cm³, $n = 45$), *Opuntia macrocentra* (65.26 ± 4.2 SE cm³ $n = 45$) y *C. imbricada* (28.69 ± 1.4 SE cm³ $n = 45$)

Mortalidad

La población de *L. tridentata* presenta una baja mortalidad (comparada con *C. leptocaulis*) y cuando ésta se presentó siempre fue en juveniles, además de la única plántula registrada en junio del 2010. Goldberg y Turner (1986) sugieren que la probabilidades de morir de las plántulas del arbusto disminuyen a partir de los 2 años luego de la germinación. Además reportan que la mortalidad de *L. tridentata* en el norte del Desierto Sonorense es baja, pues 74% de los arbustos de su zona de estudio han sobrevivido más de 50 años (aunque probablemente sean más longevos que 72 años).

Luego de registrar más arbustos muertos solos que asociados al cacto, Flores-Torres y Montaña (2013) sugieren que la mortalidad de individuos adultos de *L. tridentata* no esta influida por la presencia de individuos de *C. leptocaulis*. Al no encontrar

diferencias en la mortalidad entre las sub-poblaciones LTS y LTA, nuestros resultados respaldan dicha propuesta y fortalecen la hipótesis de que el reemplazo del arbusto por el cacto no es un evento frecuente como sugiere Yeaton (1978).

Durante los cuatro periodos de estudio, los individuos pequeños de *C. leptocaulis* (juveniles 1 y 2) murieron más que los grandes, y esta mortalidad es el doble en la sub-población CLS que en la CLA. Flores Torres y Montaña (2012) demuestran que juveniles de *C. leptocaulis* crecen más en el microambiente creado por *L. tridentata* que en espacio abierto lo cual les permite abandonar rápidamente las etapas ontogénicas tempranas que son más susceptibles a la mortalidad. La mortalidad en cactus adultos es igual entre ambas sub-poblaciones, lo cual sugiere que *L. tridentata* no tiene efectos positivos o negativos sobre estos individuos. Por tanto, la mortalidad registrada en estas clases de tamaño en ambas sub-poblaciones puede ser originada por senectud de los mismos. Flores-Torres y Montaña (2013) no registran diferencias en la frecuencia de individuos muertos de *C. leptocaulis* adultos solos o asociados a *L. tridentata* en 1 ha en la misma zona de estudio. Se ha sugerido que las cactáceas poseen periodos de vida largos (Godínez-Álvarez *et al.* 2003; Reyes-Agüero *et al.* 2006, pero véase Keeler y Tenhumberg 2011), pero Goldberg y Turner (1986) han reportan que ningún *C. leptocaulis* puede vivir más de 50 años en el norte del Desierto Sonorense.

Aunque los años muy secos incrementan la cantidad de artículos terminales que caen y enraízan, la supervivencia de estos clones depende de: 1) un año inmediato posterior con altas precipitaciones, como siguieron las altas mortalidades de clones registrados vivos en 2011 y muertos en 2012 2) establecerse bajo la asociación *L. tridentata-C. leptocaulis*, ningún clon registrado en *C. leptocaulis* solo o en espacio abierto logró sobrevivir 3 años, mientras que 17 (73 %) de clones en *C. leptocaulis* asociados al

arbusto si lo hicieron, lo cual corrobora la dependencia de un arbusto nodriza para el establecimiento clonal (Flores-Torres y Montaña 2012)

Dinámicas poblacionales

Otras especies de arbustos desérticos presentan en promedio tasas de crecimiento positivas) con cambios importantes en λ originados por años lluviosos o secos. (Golubov *et al.* 1999; Jiménez-Lobato y Valverde 2006; Verhulst *et al.* 2008). Contrario a esto, nuestros resultados muestran que las sub-poblaciones de LTS y LTA se encuentran estables (como sugiere la λ promedio 2008-2012 en ambas sub-poblaciones), con una λ mayor (0.3%) apenas perceptible en la sub-población sola que en la asociada. Una comparación entre años sugiere que los efectos negativos de *C. leptocaulis* en la λ de *L. tridentata* se incrementan en años más secos (2011-2012 = 106.7 mm, reducción del 3% en las asociadas en comparación con las solas), mientras que prácticamente el cacto no tiene efecto en el arbusto en años más lluviosos (2009-2010 = 292.9, reducción del 0.4% en las asociadas en comparación con las solas). Miriti *et al.* (2001) reporta que *L. tridentata* tiene efectos competitivos más intensos en la λ de su arbusto nodriza *Ambrosia dumosa* durante periodos de años muy secos en el Desierto Sonorense.

Usando métodos retrospectivos (LTRE) mostramos que en años muy secos, el crecimiento contribuye negativamente en λ en ambas sub-poblaciones pero con valores menores en LTA, mientras que en años lluviosos contribuye positivamente en ambas sub-poblaciones con valores mayores apenas perceptibles en LTS. Este patrón respalda lo encontrado por Flores-Torres y Montaña (2013) a nivel de individuo, quienes reportan que una mayor intensidad de la competencia por agua en plantas no regadas provoca un menor crecimiento de arbustos asociados a *C. leptocaulis* que en arbustos solos, y que la intensidad de la competencia y sus efectos disminuyen en plantas regadas.

Las altas contribuciones anuales del crecimiento y decrecimiento a las λ 's anuales calculadas con los LTRE, se diluyen cuando usamos métodos prospectivos (análisis de elasticidad) donde demostramos que las λ 's promedio 2008-2012 son más sensibles a la estasis, al igual que otros arbustos de ambientes áridos (Silvertown *et al.* 1996; Golubov *et al.* 1999; Miriti *et al.* 2001; Jiménez-Lobato y Valverde 2005; Verhulst *et al.* 2008).

Hasta donde sabemos, nuestro estudio es el primero en analizar las dinámicas poblacionales de una *Cylindropuntia* complementando el conocimiento demográfico de las distintas formas de vida de la familia cactaceae. Trabajos de este tipo se han realizado en cactus columnares (Esparza-Olguín *et al.* 2005; Méndez *et al.* 2004; Rae y Ebert 2002; Ortega-Baez 2001) globosas (Ferrer-Cervantes *et al.* 2012; Flores-Martínez *et al.* 2010; Jiménez-Sierra *et al.* 2007; Mandujano *et al.* 2007 b; Valverde and Zavala-Hurtado 2006; Valverde *et al.* 2004; Contreras y Valverde 2002; Schmalzel *et al.* 1995) y platyopuntias (Keeler y Tenhumberg 2011; Mandujano *et al.* 2001; Mandujano *et al.* 2007 a). Nuestros datos muestran que, durante los cuatro años de muestreo, la población CLS se reduce en promedio 9% mientras que la población CLA permanece estable. Generalmente la λ de cactus no difiere de la unidad (Godínez-Álvarez *et al.* 2003 y trabajos arriba citados). En *C. leptocaulis*, el decremento en λ en la sub-población CLS se origina en la ausencia de efectos facilitativos de *L. tridentata* en individuos de la categoría J1 y J2. Esto origina una mayor mortandad de individuos de estas categorías, sobre todo en años secos (2011-2012) donde la λ decreció 3.5 veces más en plantas solas que en asociadas (λ CLS = 0.573 vs λ CLA = 0.866).

Los análisis retrospectivos (LTRE) muestran que durante años lluviosos el crecimiento aporta positivamente a las λ 's de ambas sub-poblaciones pero con valores mayores en CLA que en CLS. Por el contrario, en años secos el crecimiento aporta negativamente con valores menores en CLA que en CLS. Estos datos contrastan con

Flores-Torres y Montaña (2013) quienes reportan que *L. tridentata* tiene efectos neutros en el crecimiento de *C. leptocaulis* a nivel de individuo independientemente de la disponibilidad de agua y sugieren un cambio en el signo de la interacción originado por la disponibilidad de agua (Broker y Callaghan 1998; Holzapfel y Mahall 1999).

El análisis de elasticidad demuestra que en ambas sub-poblaciones del cacto la estasis contribuye más a λ promedio, seguido por el crecimiento, decrecimiento y fecundidad. Similares resultados son encontrados en otras especies de *Opuntia* (Mandujano *et al.* 2001; Mandujano *et al.* 2007 a; Keeler y Tenhumberg 2011). Rosas y Mandujano (2002) sugieren que las platyopuntias se comportan como una hierba perenne del bosque, las cuales se reproducen tempranamente, con eventos de reproducción masiva esporádicos y clonación. Estas características están presentes en *C. leptocaulis*. El análisis de elasticidad por clase de tamaño muestra que en la sub-población CLS las categorías donde mayor mortalidad se presentó (juveniles 1, 2 y adultos 1) aportan más a λ , lo cual sugiere la importancia de la facilitación del arbusto sobre dichas etapas. Por el contrario, en la sub-población de CLA todas las categorías de tamaño contribuyen en proporción casi similar evidenciando lo importante de cada categoría para su permanencia.

En síntesis, *L. tridentata* puede permanecer como población sola o coexistiendo con el cacto independientemente del nivel de precipitación, mientras que la población de *C. leptocaulis* es susceptible a desaparecer cuando no se encuentra asociada al arbusto y luego de una secuencia de años con poca precipitación. Estos resultados sumados con los dos capítulos anteriores de esta tesis donde, 1) se muestra que el cacto depende del arbusto para su reclutamiento y 2) se demuestran que la mortalidad del arbusto no se ve influida por la competencia por agua con el cacto, nos permiten sugerir que la dinámica cíclica dirigida por interacciones planta-planta (Yeaton 1978) no se presenta en la zona sur del desierto Chihuahuense. Esto demuestra como el uso de herramientas demográficas

permite llegar a conclusiones más completas sobre el efecto de las interacciones en la dinámica de dos especies que coexisten.

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Tabla 1. Categorías de clases de tamaño de cada especie utilizadas en las matrices de Lefkovitch. Entre paréntesis se muestra la *n* de plantas asociadas (A) y solas (S) en cada categoría. P = plántulas, J1 y J2 = juveniles, A1, A2, A3 y A4 = adultos.

Clase tamaño	<i>Larrea tridentata</i> Volumen en m ³	Clase tamaño	<i>Cylindropuntia leptocaulis</i> Volumen en m ³
J1	0.0001 - 0.029 (A = 19, S =120)	J1	0.0001- 0.007 (A = 35, S= 57)
A1	0.03 - 0.19 (A = 100, S =93)	J2	0.008 - 0.032 (A = 66, S = 113)
A2	0.20 - 0.49 (A = 107 S = 53)	A1	0.033- 0.089 (A = 154, S =121)
A3	0.50-1.00 (A =51, S = 25)	A2	0.90 - 0.199 (A = 41, S = 18)
A4	> 1.00 (A =41, S = 13)	A3	> 0.20 (A = 18, S = 5)

Tabla 2. Análisis de devianza para la producción de frutos en arbustos de *L. tridentata* en función de tres factores: Sub-población (LTS y LTA), Año (4 periodos de transición 2008-2009, 2009-2010, 2010-2011, 2011-2012) y Categoría de tamaño (Adultos 1, 2, 3 y 4).

Factor	GL	Devianza	P(<Chi)
Sub-población	117	629834	<0.05
Año	115	492666	<0.05
Categoría de Tamaño	115	492439	<0.05
Total	118	725246	

Tabla 3. Análisis de devianza para la producción de frutos en cactus de *C. leptocaulis* en función de tres factores: Sub-población (CLS y CLA), Año (4 periodos de transición 2008-2009, 2009-2010, 2010-2011, 2011-2012) y Categoría de tamaño (Adultos 1, 2, 3).

Factor	GL	Devianza	P(<Chi)
Sub-población	64	12987.5	<0.05
Año	63	12381.2	<0.05
Categoría de Tamaño	63	13527.2	<0.05
Total	65	14497.3	

Tabla 4. Análisis de devianza para la frecuencia de enraizamiento de artículos terminales de *C. leptocaulis* en función de tres factores: Sub-población (CLS y CLA), Año (4 periodos de transición 2008-2009, 2009-2010, 2010-2011, 2011-2012) y Categoría de tamaño (Juveniles 1, 2 y Adultos 1, 2, 3).

Factor	GL	Devianza	P(<Chi)
Sub-población	157	1152.60	<0.05
Año	155	780.71	<0.05
Categoría de Tamaño	154	1232.05	<0.05
Total	158	1293.63	

Tabla 5. Análisis de devianza para la frecuencia de arbustos muertos de *L. tridentata* en función de tres factores: Sub-población (LTS y LTA), Año (4 periodos de transición 2008-2009, 2009-2010, 2010-2011, 2011-2012) y Categoría de tamaño (Juveniles 1, 2 y Adultos 1, 2, 3).

Factor	GL	Devianza	P(<Chi)
Sub-población	158	65.90	0.125
Año	156	65.57	0.440
Categoría de Tamaño	155	32.86	<0.05
Total	159	68.264	

Tabla 6. Análisis de devianza para la frecuencia de cactos muertos de *C. leptocaulis* en función de tres factores: Sub-población (CLS y CLA), Año (4 periodos de transición 2008-2009, 2009-2010, 2010-2011, 2011-2012) y Categoría de tamaño (Juveniles 1, 2 y Adultos 1, 2, 3).

Factor	GL	Devianza	P(<Chi)
Sub-población	158	665.65	<0.05
Año	156	437.93	<0.05
Categoría de Tamaño	155	504.46	<0.05
Total	159	690.14	

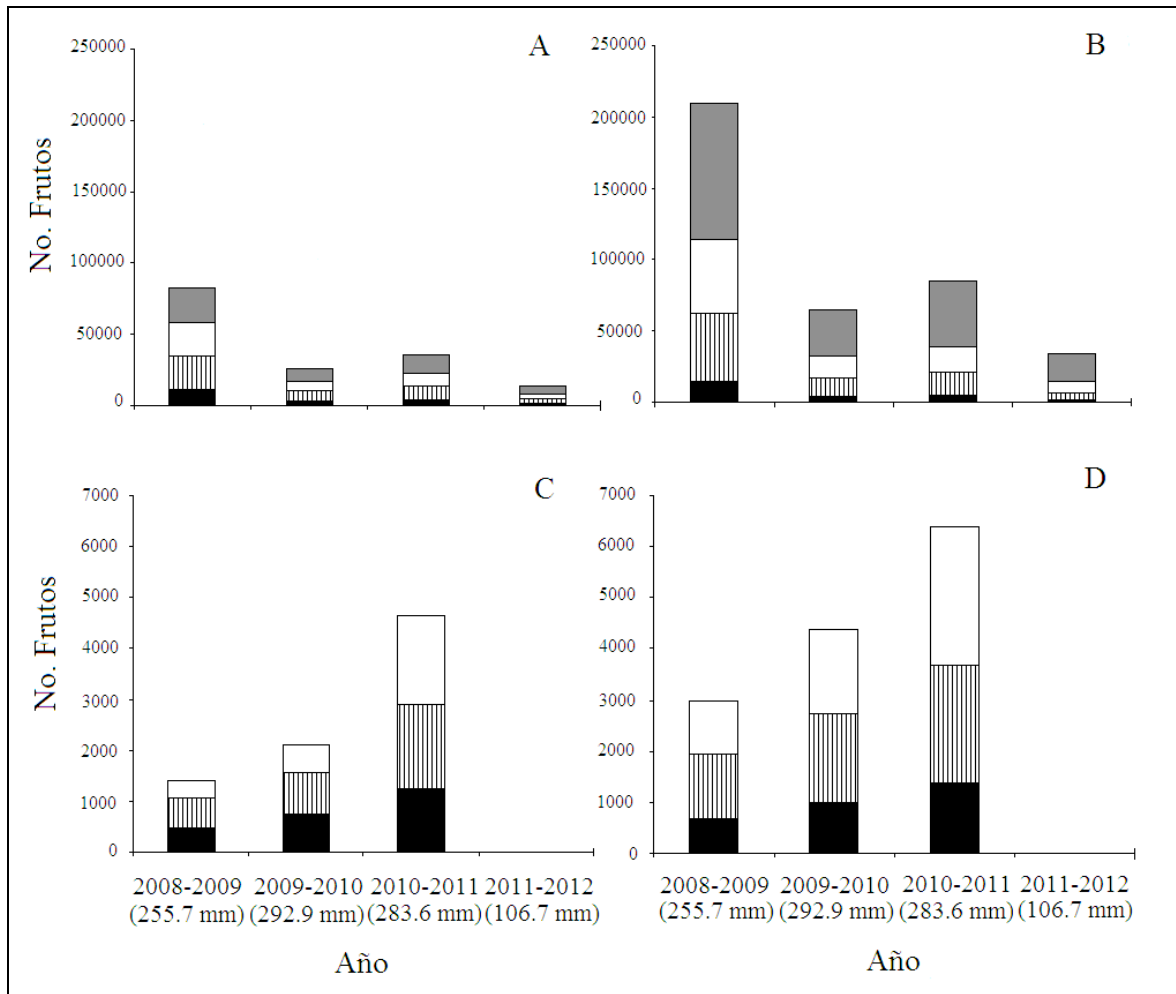


Figura 1. Producción de frutos por sub-población de LTS (A), LTA (B), CLS (C) y CLA (D) por periodo de muestreo. En cada barra, la sección en negro corresponde a adultos 1, con líneas verticales a adultos 2, en blanco a adultos 3 y en gris a adultos 4. La precipitación total anual de cada periodo se muestra en paréntesis.

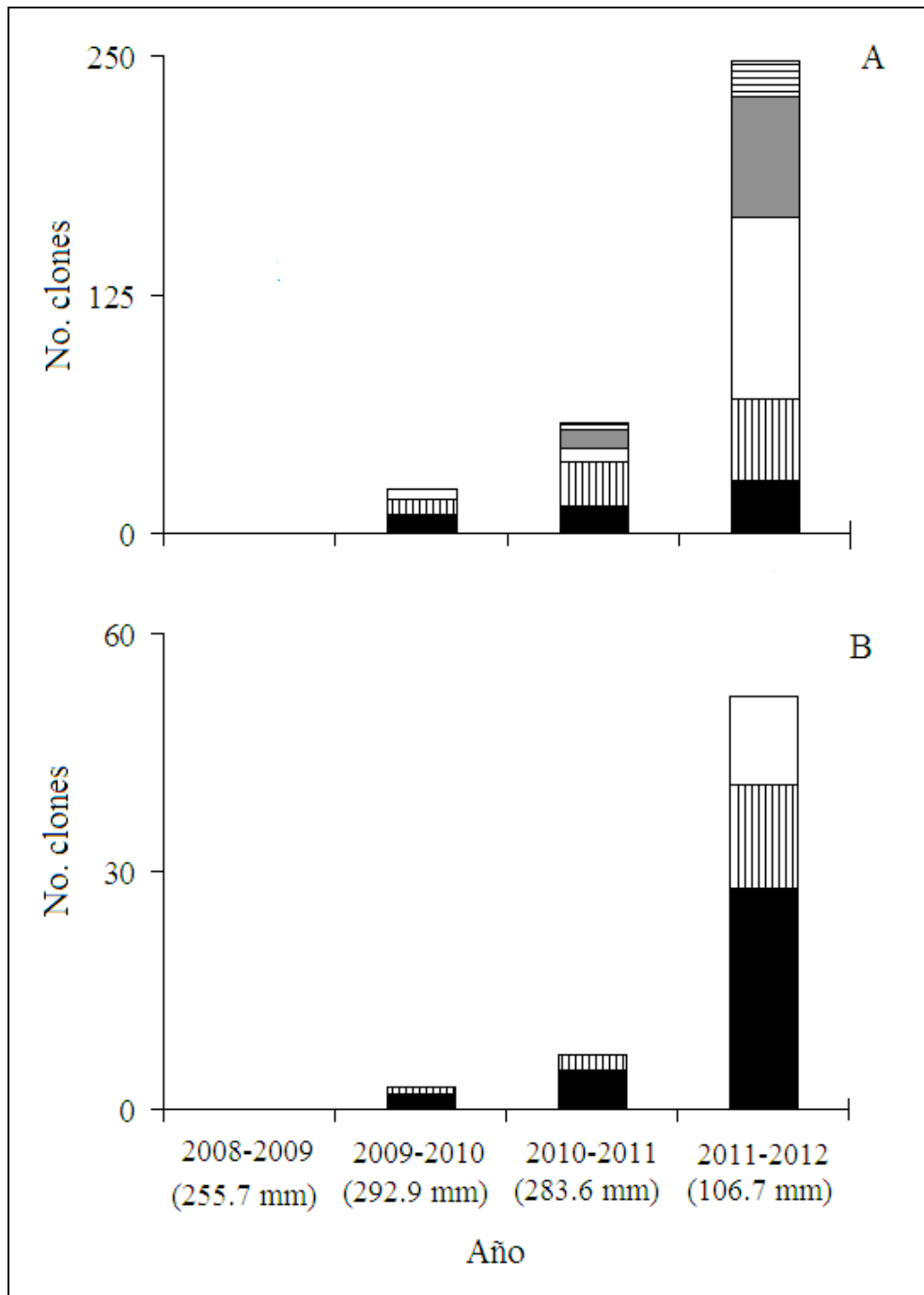


Figura 2. Artículos terminales enraizados (clones) de *C. leptocaulis* en la sub-población CLA (A) y CLS (B) en cada periodo de muestreo. En cada barra, la sección en negro corresponde a los clones producidos por la categoría juveniles 1 (J1) con líneas verticales a juveniles 2 (J2) en blanco a adulto 1 (A1) en gris a adultos (A2) y con líneas horizontales adultos 3 (A3) La precipitación total anual de cada periodo se muestra en paréntesis.

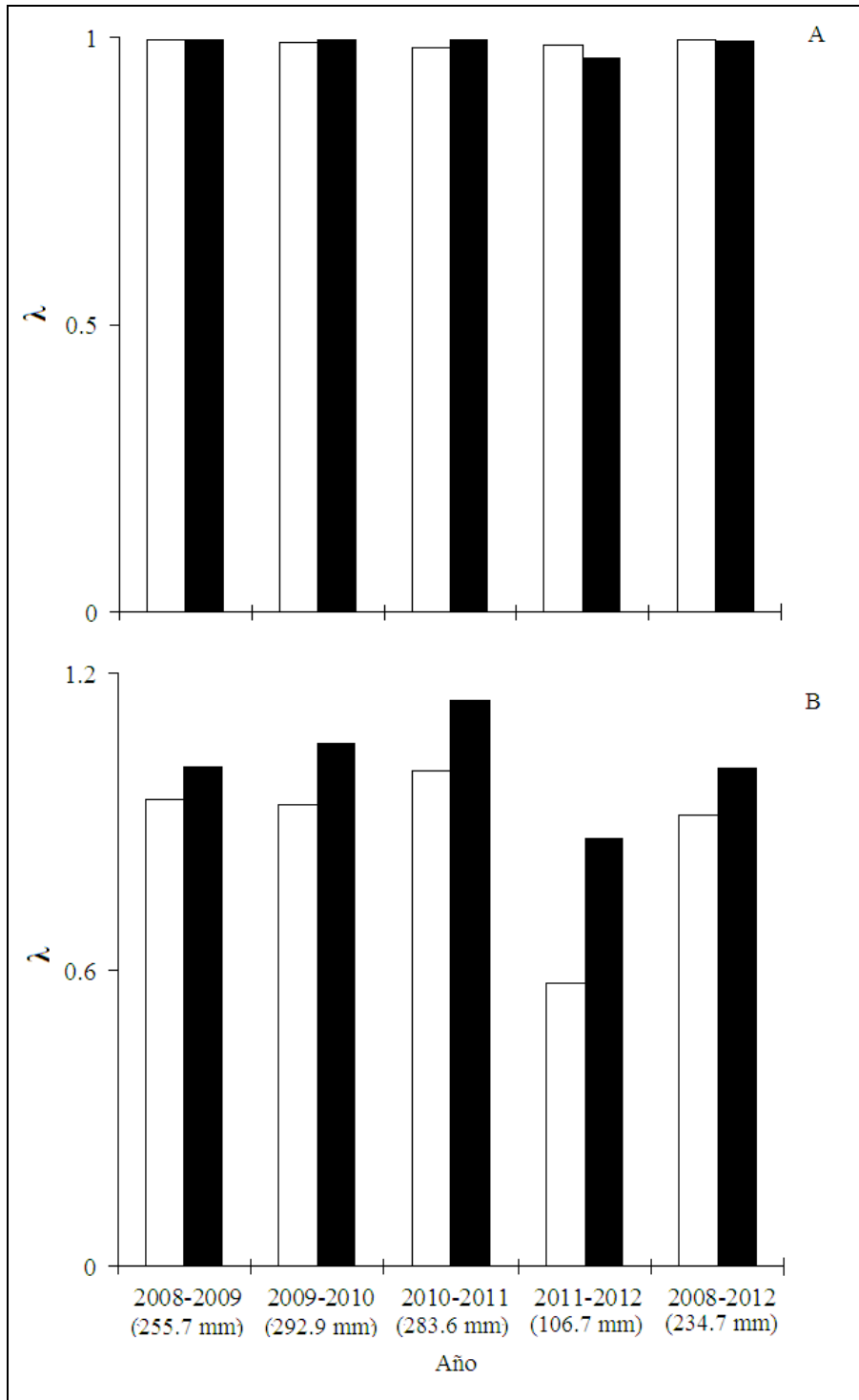


Figura 3. Tasa finita de crecimiento poblacional (λ) promedio (2008-2012) y en cada periodo de muestreo de las poblaciones de A) *L. tridentata* B) *C. leptocaulis*. Las barras blancas representan poblaciones solas y barras negras poblaciones asociadas. La precipitación total anual de cada periodo se muestra en paréntesis.

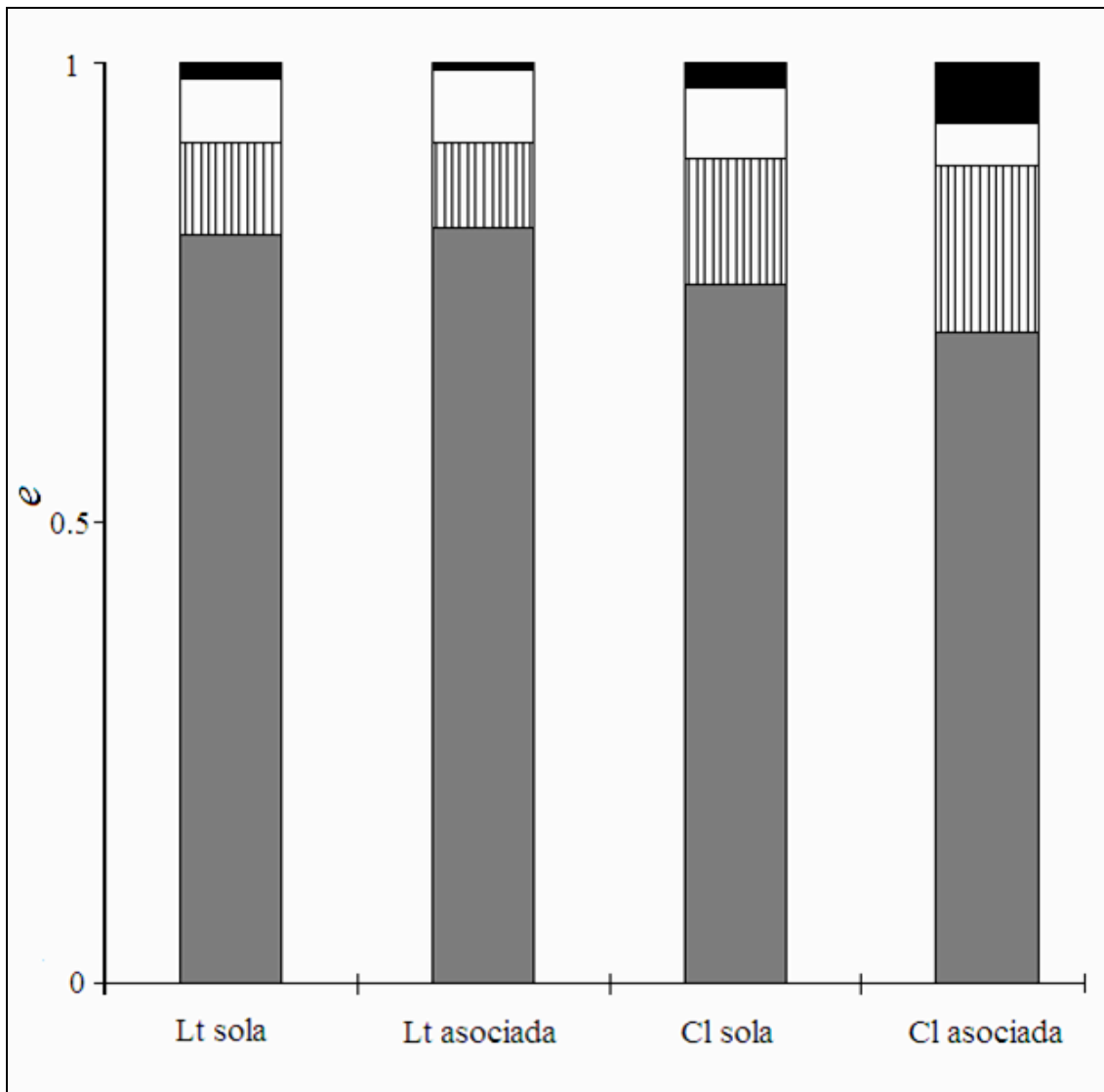


Figura 4. Elasticidad (e) por proceso demográfico a λ promedio 2008-2012 en las poblaciones de *L. tridentata* y *C. leptocaulis* solos y asociados. La sección gris de la barra representa la estasis, con líneas verticales crecimiento, en blanco decrecimiento y en negro la fecundidad (clonal en el caso de *C. leptocaulis*).

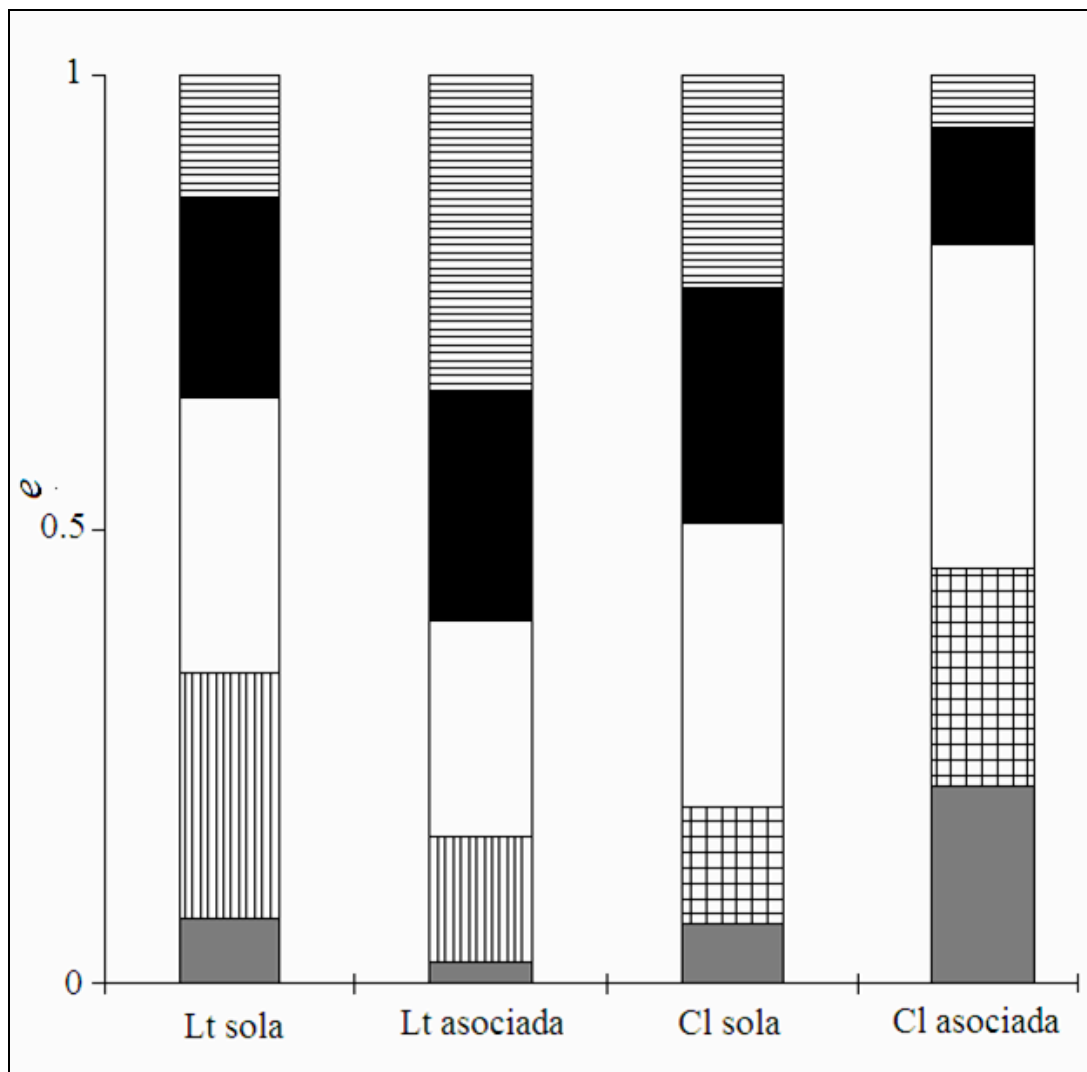


Figura 5. Elasticidad (e) por clase de tamaño a λ promedio 2008-2012 en las poblaciones de *L. tridentata* y *C. leptocaulis* solos y asociados. En *L. tridentata* la sección gris representa a juveniles, las líneas verticales a adultos 1 (A1) en blanco adultos 2 (A2) negro adultos 3 (A3) y líneas horizontales adultos 4 (A4) En *C. leptocaulis* la sección gris de la barra representa a juveniles 1 (J1) la sección cuadriculada a juveniles 2 (J2) en blanco adultos 1 (A1) en negro adultos 2 (A2) y con líneas horizontales adultos (A3).

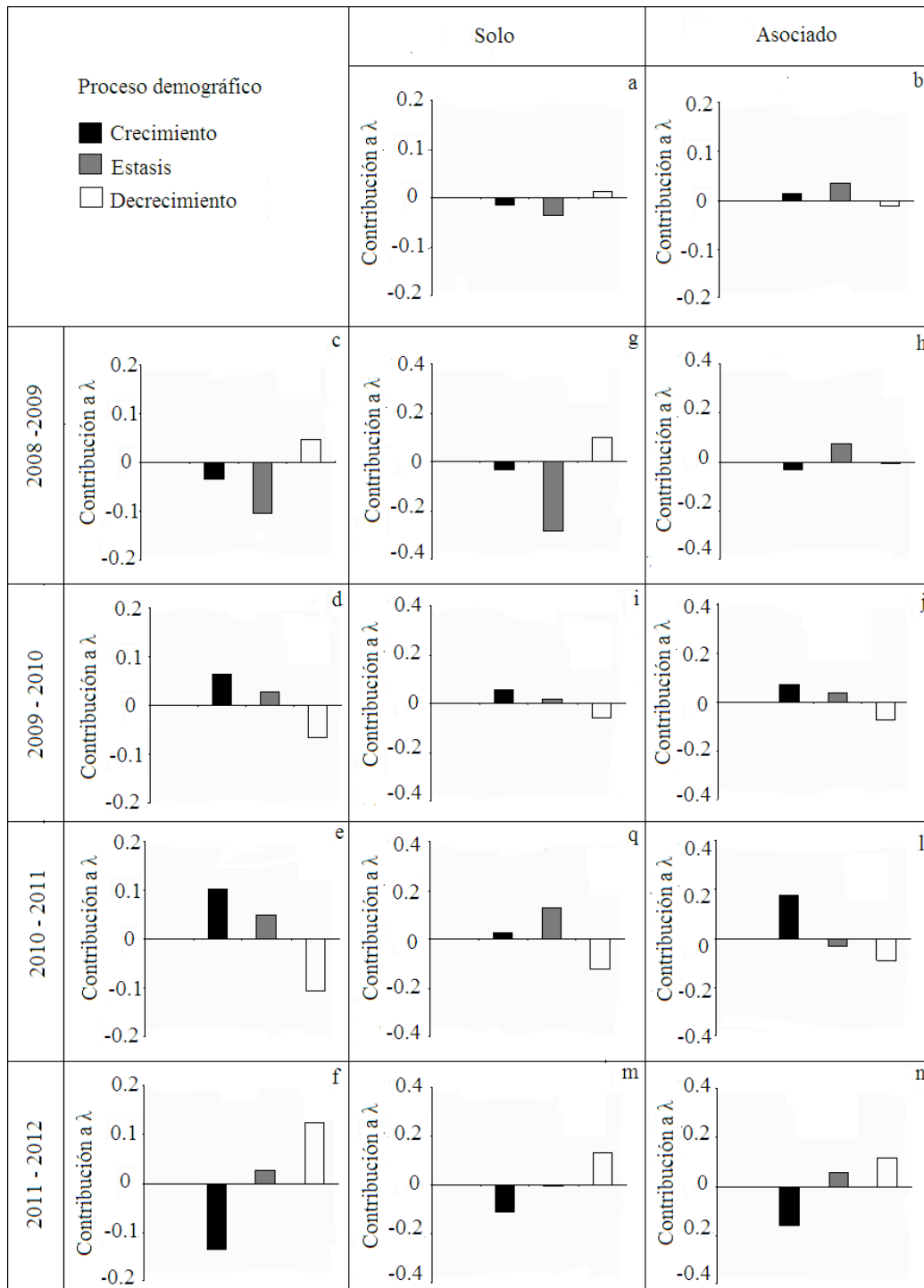


Figura 6. Contribucion de cada proceso demografico a λ de *L. tridentata* por: tratamiento (A, B), y año (C, D, E, F) como factores principales y la interaccion de ambos (G, H, I, J, K, L, M, N)

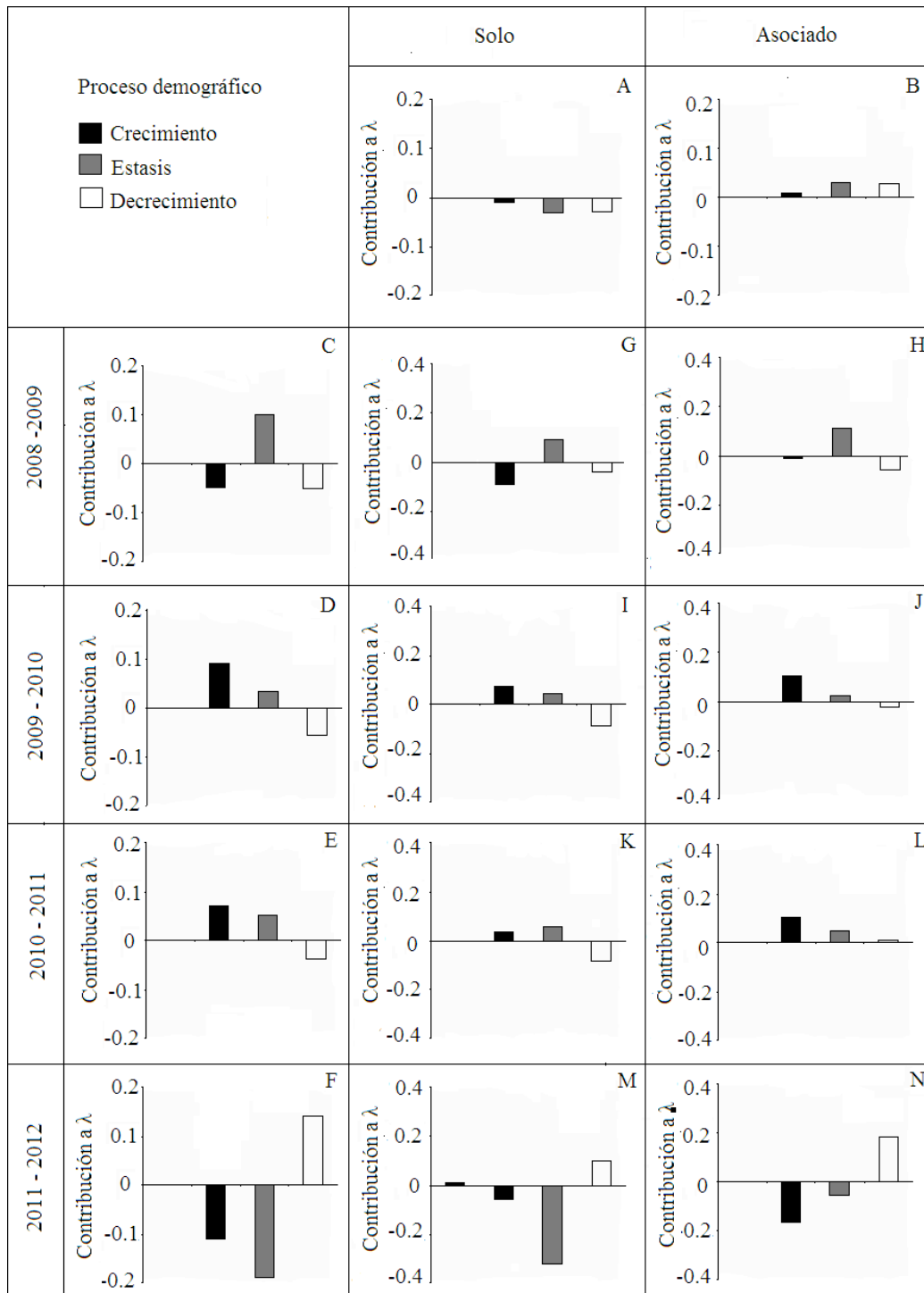


Figura 7. Contribucion de cada proceso demografico a λ de *C. leptocaulis* por: tratamiento (A, B), y año (C, D, E, F) como factores principales y la interaccion de ambos (G, H, I, J, K, L, M, N)

CONCLUSIONES GENERALES

Desde mediados del siglo pasado (Watt 1947) se ha sugerido que importantes cambios en la composición y estructuración de las comunidades vegetales de especies perennes se dan a pequeña escala en sitios puntuales (como puede ser el área bajo el dosel de una planta) y que estos cambios son dirigidos por interacciones ecológicas planta-planta como facilitación y competencia. Lo anterior, es conocido como dinámicas cíclicas de reemplazo y se ha reportado para distintas zonas áridas del mundo (Vasek & Lund 1980; Cody 1993; Yeaton 1978; Yeaton & Romero-Manzanares 1986; MacAuliffe 1988; Soriano *et al.* 1994; Yeaton 1989; Yeaton & Esler 1990; Armas y Pugnaire 2009). A excepción de Soriano *et al.* (1994) quien discute datos de trabajos anteriores (Soriano y Sala 1986; Aguiar *et al.* 1992) donde se utilizan métodos experimentales y ecofisiológicos para evaluar los efectos de facilitación y la competencia, todos los trabajos arriba citados proponen dichas dinámicas mediante métodos observacionales. Una aportación considerable al entendimiento de los mecanismos por los cuales las interacciones conducen a este tipo de dinámicas cíclicas fue realizado por Armas y Pugnaire (2009), quienes reportan que la intensidad de la competencia por agua entre arbustos adultos de la nodriza y la facilitada es mayor durante los meses secos y disminuye en los meses lluviosos. Esto es importante por que uno de los puntos más controversiales sobre el papel de la competencia en la estructuración de comunidades vegetales de ambientes áridos es si su intensidad varía con la disponibilidad de agua (Fonteyn y Mahall 1981; Fowler 1986; Chesson 2000). Específicamente en la interacción arbusto-cactus, se han encontrado resultados contradictorios (Flores-Martínez *et al.* 1998; Briones *et al.* 1998).

Nuestro trabajo demuestra mediante métodos experimentales los efectos de las interacciones y del agua en distintas etapas ontogénicas de la asociación *Cylindropuntia leptocaulis* y su arbusto nodriza *Larrea tridentata*. También, evalúa mediante un estudio

demográfico si los factores arriba descritos afectan la permanencia de el arbusto y el cacto a nivel poblacional.

En el primer capítulo registramos mediante un estudio observacional que, de manera natural, el establecimiento sexual del cacto es reducido (únicamente 8 juveniles de origen sexual en 1 ha) mientras que la propagación clonal es frecuente (59 juveniles de origen asexual en 1 ha), y ambos tipos de reclutamiento son más frecuentes bajo la copa de *L. tridentata* que bajo cualquier otra especie de arbusto, o en espacios desnudos. Nuestro trabajo representa el primer registro experimental que comprueba que plantas de *Cylindropuntia* no dependen de arbustos nodriza para la germinación y supervivencia de plántulas, como ya se había propuesto mediante observaciones por algunos autores (Cody 1993, López y Valvidia 2007; Reyes-Olivas 2002). En especies de *Platyopuntia* se ha comprobado que la supervivencia de plántulas se presenta obligatoriamente a la sombra de arbustos nodriza (Mandujano *et al.* 1998; Vargas-Mendoza y González- Espinosa 1992). Contrario a otras opuntias simpátricas (Allen *et al.* 1991; Mandujano *et al.* 1998; 2007) la propagación clonal mediante el enraizamiento de artículos terminales, solo puede realizarse bajo un arbusto nodriza y esto quizá se debe al pequeño volumen de los artículos de *C. leptocaulis* que les confiere poca capacidad para almacenar agua y carbohidratos para sobrevivir hasta ser una planta independiente (Bobich y Nobel 2001). Esto último lleva a que, de manera natural, el establecimiento de artículos terminales solo puede realizarse en años lluviosos (ver discusión en capítulo 3). Este pequeño tamaño de los artículos terminales también puede ser considerado una ventaja pues son fácilmente transportados por animales o agua para colonizar otros sitios (Flores-Torres y Montaña 2012). En ambos tipos de reclutamiento un mayor crecimiento bajo la copa del arbusto (originado principalmente por mejores condiciones edáficas, y por la disminución de la radiación) permite a los propágulos crecer con mayor velocidad que en áreas desnudas y

escapar más rápidamente de las etapas tempranas que son más susceptibles a la mortalidad. Todos estos datos sugieren que virtualmente todo el establecimiento de *C. leptocaulis* es llevado a cabo mediante propagación clonal pero a la sombra de *L. tridentata* que es la nodriza más disponible en el Desierto Chihuahuense.

En el segundo capítulo encontramos que en plantas adultas, las consecuencias de crecer solo o asociado difieren según la especie y el estado hídrico. Cuando hay baja disponibilidad de agua el estado fisiológico y el crecimiento de *L. tridentata* adultos son afectados por la competencia por agua pero esa competencia disminuye a medida que aumenta la oferta hídrica. *C. leptocaulis* no es afectada por la competencia por agua. Otros estudios han comprobado que los arbustos nodriza de los desiertos se establecen en sitios estresantes como los espacios abiertos y facilitan el establecimiento de otras especies, sufren los efectos competitivos de las facilitadas (Soriano *et al.* 1994; Flores-Martínez *et al.* 1994; 1998 Armas y Pugnaire 2009) por lo que se puede inferir que su estrategia es colonizadora antes que competitiva (Tilman 1994; Silvertown 2004). En nuestro caso *L. tridentata* pueden hacer frente a la competencia de *C. leptocaulis* debido a que: 1) la economía hídrica del arbusto le permite ser tolerante a la pérdida de agua por sequía o competencia y pese a esto realizar fotosíntesis y crecer (Reynolds *et al.* 1999; Ogle y Reynolds 2004; Hamerlynk y Huxman 2009; Flores-Torres y Montaña 2013) 2) y por que en tiempo de lluvias, *C. leptocaulis* responde más rápido a la precipitación tomando toda el agua que requieren en los primeros dos días luego de una lluvia abundante, dejando disponible el recurso en el suelo el resto del tiempo. Lo anterior le permite al arbusto soportar el menor crecimiento y la reducción del vigor que conlleva el vivir asociado al cacto, sin que se presente mayor mortalidad en arbustos asociados que solos. *L. tridentata* adultos tiene efectos neutros en *C. leptocaulis* adultos independientemente de si existe o no agua disponible en el suelo. La capacidad de soportar la competencia por parte de *L.*

tridentata adultos y de no sufrir afecto alguno en *C. leptocaulis* adultos cuando ambas especies viven asociadas les permite coexistir durante el tiempo que dure su periodo de vida, promoviendo así patrones de distribución espacial agrupados en las dos especies en la zona de estudio

Dado que las especies perennes de ambientes áridos son de vida larga lo cual hace imposible seguir todo su ciclo de vida (Vasek 1980; Goldenberg y Turner 1986) el punto más difícil de comprobar en las dinámicas cíclicas, ha sido el reemplazo de la especie facilitadora por la facilitada, aunque algunos autores han usado modelos matemáticos para calcular la probabilidad de que esto ocurra. (McAuliffe 1988; Flores- Martínez *et al.* 1994). En el tercer capítulo usamos matrices de proyección de Lefkovitch (1965) con el fin de predecir el efecto de la variabilidad ambiental (años lluviosos vs. años de sequía) y del vecindario (cuando ambas especies crecen solas o asociadas) en la tasa finita de crecimiento poblacional (λ) de ambas especies y utilizamos dicha medida para conocer si las poblaciones de *L. tridentata* y *C. leptocaulis* tiende a decrecer cuando están asociadas, lo cual sugeriría la exclusión competitiva. Si bien otros estudios han evaluado el papel de la facilitación (Griffith 2010) o la competencia (Miriti *et al.* 2001) en la tasa finita de crecimiento poblacional (λ), nuestro trabajo representa el primer esfuerzo en evaluar el papel de ambas interacciones de manera bi direccional entre la facilitada y la facilitadora.

En *L. tridentata* las λ 's son cercanas a la unidad (LTS λ promedio 2008-2012 = 0.990 y LTA λ promedio 2008-2012 = 0.993) y los intervalos de confianza muestran diferencias apenas perceptibles en las λ 's de ambas poblaciones durante cuatro años de muestreo. En *C. leptocaulis* las λ 's promedio 2008-2012 difieren entre CLS (0.914) y CLA (1.007) y los intervalos de confianza muestran que estas diferencias son considerablemente mayores al compararse con las del arbusto. Además, una revisión por periodo de muestreo comprueba que esta diferencia es mayor en años secos, ya que durante el año más seco la

población del cacto sola presenta una reducción del 43%, mientras que la asociada al arbusto únicamente reduce 14%. Este estudio provee evidencia demográfica que respalda los resultados de capítulos anteriores de esta tesis. *L. tridentata* facilita el establecimiento de *C. leptocaulis*, y es más importante la propagación clonal que la sexual. Lo anterior pudo ser comprobado al no encontrar juveniles de origen sexual del cacto durante 5 años de revisión dentro de las parcelas de demografía, y por que durante los 4 periodos de muestreo, mayor cantidad de artículos terminales del cacto enraizaron y sobrevivieron a la sombra del arbusto (328 bajo arbustos asociados vs. 20 bajo arbustos solos en un área de 2.6 ha) que en espacio abierto (4) o bajo el mismo cacto (68). Cuando *C. leptocaulis* se convierte en adulto compite con *L. tridentata*, y aunque dicha competencia puede afectar el vigor esto no resultó en una mayor mortalidad del arbusto durante los cuatro periodos de muestreo.

En resumen, la impredecibilidad en la precipitación en la zona de estudio es la principal fuerza estructuradora de nuestra comunidad vegetal compuesta por dos especies. Ésta es afinada a pequeña escala por las interacciones positivas y negativas que cambian a lo largo de la ontogenia y de la disponibilidad de recurso hídrico. *L. tridentata* coloniza espacios abiertos y cuando se vuelve adulta, facilita el establecimiento de *C. leptocaulis* el cual se da principalmente por propagación clonal y en años lluviosos. Cuando *C. leptocaulis* se convierte en adulto compite con *L. tridentata* y dicha competencia se reduce cuando hay disponibilidad de agua. A pesar de que esta competencia está presente durante la mayor parte del tiempo y afecta el vigor del arbusto no conduce a la mortalidad del mismo y su permanencia como población no se ve afectada por la presencia del cacto. Por su parte *L. tridentata* tiene efectos neutros en el crecimiento y la fisiología de *C. leptocaulis* adultos, pero la persistencia del cacto a nivel poblacional depende de la presencia del arbusto. Lo anterior conduce a patrones de distribución espacial agrupados

que son típicos en la zona de estudio. Por todo lo anterior podemos concluir que en el sur del Desierto Chihuahuense no se presenta la dinámica cíclica de reemplazo que Yeaton (1978) propuso para las mismas especies en el norte del mismo desierto.

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