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RESEARCH ARTICLE

The *Brahea edulis* palm forest in Guadalupe Island: A North American fog oasis?

El palmar de *Brahea edulis* de Isla Guadalupe: ¿Un oasis de niebla en Norteamérica?

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ABSTRACT

Fog is a factor that affects deeply the structure of vegetation of coastal deserts. Guadalupe is an oceanic island located 260 km off the coast of Baja California, and is one of the few places of the Sonoran Desert coasts with scarped coastal topography and frequent fog. With the aim to identify the effect of fog on the community of the palm forest (palmar) of *Brahea edulis* located in the northern tip of the island: (1) we analyzed the richness and composition of vascular plants in the palmar compared to the remainder of the island, and (2) we analyzed the altitudinal variation of the abundance of palms, herbs and mosses to identify if there is altitudinal variation of the vegetation. Although species composition was not different between palmar and the rest of island, species richness and vascular plant cover were greater in the palmar. On the other hand, we found a clear altitudinal zonation of the vegetation in the palmar that is similar to that found in South American fog-driven plant communities such as the lomas. Thus, the palmar community of Guadalupe Island may be considered as a fog oasis, one of the very few that occur in North America.

Key words: altitudinal gradient, coastal desert, fog effect, Sonoran Desert, vegetation.

RESUMEN

La niebla es un factor que afecta profundamente la estructura de la vegetación de los desiertos costeros. Guadalupe es una isla oceánica a 260 km de la costa de Baja California y constituye uno de los pocos lugares de la costa del Desierto Sonorense donde se reúnen una topografía escarpada próxima a la costa y una alta frecuencia de nieblas. Con el objeto de identificar el efecto de la niebla sobre la comunidad del palmar de *Brahea edulis* presente en la ladera norte de la isla: (1) analizamos la diferencia de la riqueza y la composición de plantas vasculares del palmar respecto del resto de la isla, y (2) analizamos la variación altitudinal de la abundancia de palmas, plantas acompañantes y musgo para determinar si existe variación altitudinal de la vegetación. Encontramos que, aunque la composición de plantas del palmar no fue diferente del resto de la isla, la riqueza de especies y la cobertura fueron claramente superiores en el palmar. Finalmente, constatamos una clara zonación altitudinal de la vegetación en el palmar semejante a la encontrada en las comunidades dependientes de la niebla en Sudamérica, tales como las lomas. Por tanto, la comunidad del palmar de Isla Guadalupe puede considerarse como un oasis de niebla, uno de los pocos existentes en Norteamérica.

Palabras clave: desierto costero, Desierto Sonorense, efecto de niebla, gradiente altitudinal, vegetación.

INTRODUCTION

Water is the most relevant factor for arid ecosystems. Its spatio-temporal availability affects deeply the structure of communities (Ehleringer & Mooney 1983, Polis 1991). Between the latitudes 20° and 35° in the western coasts of most continents, a large proportion of the water available occurs in the form of fog because of cold ocean streams and the thermal inversion found inland (Rundel 1978, Schemenauer & Cereceda, 1991, Leipper 1994). Coastal deserts and Mediterranean scrubs occurring in those latitudes are subject to high water stress (Meigs 1966, Ezcurra et al. 2006).

In the extremely-dry coastal deserts of South America, it is possible to find genuine oases known as lomas in the sites where a topographic barrier intercepts the horizontal movement of the fog. Because this water source occurs in the form of an altitudinal belt, vegetation in the lomas shows a strong structure with a clear differentiation among plants with different growth forms and phenology occurring at separate elevational strata. In general, the portions of the elevational gradient that receive less water are dominated by cryptogams, while herbs, shrubs and even trees characterize belts with increasingly fog availability (Lydolph 1957, Rundel 1978, Rundel et al. 1991).

In North America, only the Baja California coastal desert is found in the latitudes (20-30º) where fog oases are found in other continents. Nevertheless, the effect of coastal fogs is diluted gradually as it is blown inland because of the absence of a steep topography that intercepts the humidity near the shore (Rundel & Mulroy 1972, Nash III et al. 1979, Martorell & Ezcurra 2002). However, there is one area where a high frequency of fogs occurs altogether with a scarped terrain: Guadalupe Island (Fig. 1). Steeply rising 1298 m from the sea in just 1.5 km, this island constitutes a barrier that intercepts thick and recurrent fogs coming from the northwest. In contrast, the annual rainfall is just 133 mm, making the climate at Guadalupe very similar to that of South American coastal deserts.

Ever since the first naturalist, Edward Palmer, visited Guadalupe in 1875, the presence of fogs and their effect on the vegetation in the northern tip of the island have been repeatedly reported, (e.g., Watson 1876, Bryant 1887, Franceschi 1893, Sutliffe 1933, Weber 1993, Moran 1996, Oberbauer 2005). Furthermore, by looking at the potential vegetation map by León de la Luz et al. (2003) it is possible to notice an intriguing paralelism between the altitudinal

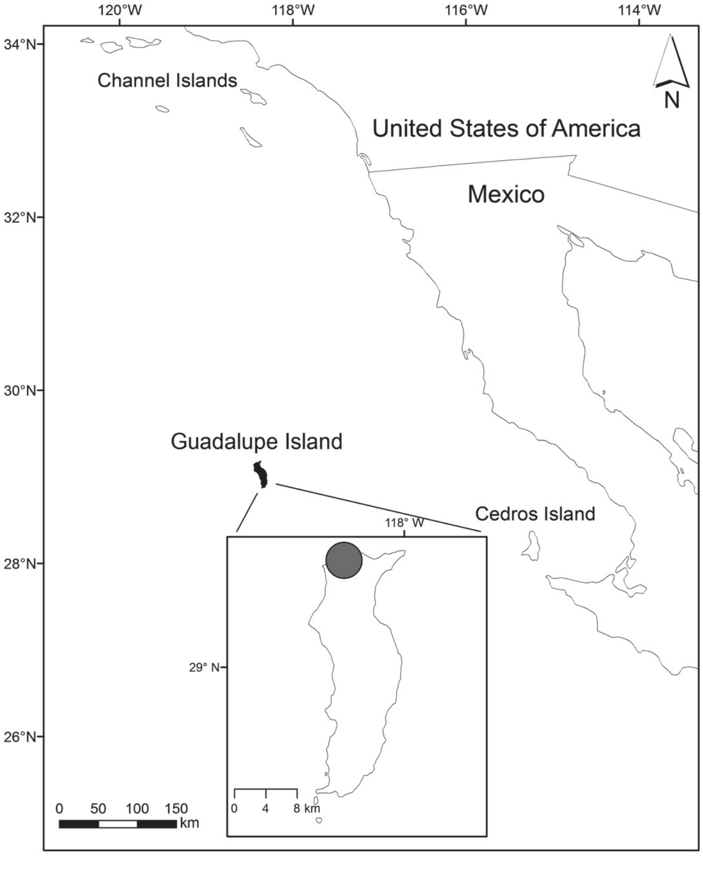

Fig. 1: Location of Guadalupe Island in the Pacific island corridor of the California Floristic Province. The inset shows location of palmar of *Brahea edulis* (gray circle) in the island.

Ubicación de la Isla Guadalupe en el corredor de islas del Pacífico de la Provincia Florística de California. El recuadro muestra la localización del palmar (círculo gris) en la isla.

zonation of Peruvian lomas (Rundel 1978, Rundel et al. 1991) and the south-north vegetation gradient of the island: In its southern third, which has a very low fog input, the landscape is dominated by succulent plants and rupicolous lichens; herbs and small shrubs characterise the island's center, and forests dominated by either *Pinus radiata* D. Don, *Callitropsis forbesii* (S. Watson) D. P. Little, and *Brahea edulis* (H. Wendl) are present at the foggy northern third of Guadalupe. Moreover, these fog-dependent forests are also similar to the relictual fog-dependent rainforest patches found at similar latitude (30° S) in northern Chile (del Val et al. 2006). They are also relict populations of tree species located several hundreds of km away from their current range distribution or of their closest relative species, and persist in a matrix of arid land thanks to the fog.

The palmar, a community dominated by an open monospecific grove of the palm *Brahea edulis*, occurs in some 20 ha in the northernmost slope of the island. Because of their rosette morphology, long caudices and narrow leaves, these palms may intercept and funnel towards their shoots large amounts of fog (Martorell & Ezcurra 2002, 2007). Rosette plants are also a common element in South American lomas (Rundel et al. 1991, Rundel & Dillon 1998).

In this work, we analyze the palmar community to assess (a) whether its species richness and composition differ from those found in the remainder of the island where fogs are unusual, and (b) if the community is altitudinally structured in terms of the abundance of palms, herbs and mossess as it occurs in other fog oases (Rundel et al. 1991, Rundel & Dillon 1998, Martorell & Ezcurra 2002). Mosses were included in the analyses because they have been considered to be indicators of fog availability (Frahm & Gradstein 1991, Bruijnzeel 2001).

METHODS

Guadalupe Island (29° N, 118° W) is a seven million years old volcanic island (Batiza 1977) located 260 km west off the peninsular coast. Its total area is 250 km^2 (33 km × 8 km, Fig. 1). Climatically, it is driven by a regime of frontal systems from the northwest and a Mediterranean-type seasonality with frequent fogs. Mean annual temperature is 17.9 °C, and mean rainfall 133 mm (Moran 1996). Floristically it has been considered an outlier of the Floristic Province of California (Moran 1996). It contains a remarkable small-scaled replicate of the mainland transition between Mediterranean and desert scrubs (González-Abraham et al. 2010). The palmar is located in a northwestern-facing, very steep (45 %) hillside found in the northern tip of the island. The substrate is largely covered by large rocks. The vegetation is composed mostly of herbs and palms, but some scattered pines (*Pinus radiata* var. *binnata*) occur near the hilltop. The large number of fallen trunks and rotting stumps suggest that a pine forest once developed in the higher portions of the area until it was cleared by two centuries of extreme overgrazing by goats. Nomenclature follows Moran (1996), and Little (2006) for *C. forbesii*.

In May 2004, we set 23 transects 30 × 2 m each along the northern slope of the island. Transects were located following intervals of 30 m in altitude, encompassing an elevational range from 430 to 1090 masl. Below 430 m there was a vertical cliff reaching down to the ocean. In every transect, we recorded the vascular plant species present, and estimated visually the vegetation cover. Botanical vouchers were deposited at the BCMEX (Universidad Autónoma de Baja California, Ensenada, B.C., Mexico) herbarium and identified with the help of Steve Junak and José Delgadillo. In the center of each transect, in a 2 × 2 m quadrat, we estimated visually the cover of mosses occurring over the stones. We used this cover as a proxy for atmospheric humidity because it would not be greatly affected by run-off or sub-surface water flow from the upper basin, evapotranspiration by neighboring vegetation, soil texture, etc. Thus, we assumed that mosses on rocks reflect more or less accurately the spatial availability of atmospheric water along the slope while avoiding the effects of water available in the soil. To compare the palmar with the vegetation at areas with lower fog input in the island, we used data from Garcillán et al. (2008). In that work, the authors systematically placed 110 transects (50 m long ′ 2 m wide each) throughout the entire Guadalupe island, and recorded the presence of all vascular plant species within each transect. To avoid any potential confounding effect, we only used for our comparison those transects inside the same altitude range as the palmar transects, but outside the palmar area. In total, data on species composition and vascular-plant cover were available for 71 transects 50 × 2 m each, sampled between 425 and 1100 m in altitude. Data were not rarefied to account for the difference in the area sampled in the palmar and the remainder of the island.

We recorded the position of every *B. edulis* individual on a QuickBird image taken in April, 2004. Using a topographic chart with 100 m contour lines (INEGI 1998), we measured the areas comprised between contour lines using ArcMap 9.3 (Environmental Systems Research Institute, Redlands, California) and counted the number of individuals that occurred within each 100 m altitudinal interval. As inclination was similar along the hillside, we estimated the surface encompassed within two contour lines from the vertical projection of the contour lines without correcting for the slope angle. Finally, we calculated palm density for each 100 m altitudinal interval as the number of palms growing inside it divided by its area.

We analyzed the changes in vascular plant and moss cover, and palm density over the elevational gradient using generalized additive models (GAMs) using the package mgcv (Wood 2006) for R (R Development Core Team 2009) assuming a normal error distribution. The mgcv package is based on thin-plate regression splines, an efficient procedure that avoids model overparameterization by means of generalized cross-validation (Wood 2003). We compared the changes in species richness over altitude in the palmar and the remainder of the island by means of a GAM assuming a Poisson error. The correct distributions for estimating significance are F for the models in which a normal distribution was assumed, and χ^2 for Poisson errors (Crawley 2007).

RESULTS

In the Palmar, we found 33 vascular plant species. All of them were annual species, except *Brahea edulis* and *Ambrosia camphorata*. At the palmar we found two taxa endemic to Guadalupe (*Githopsis diffusa* var. *guadalupensis* and *Brahea edulis*), three more taxa that are only found in Guadalupe and the Channel Islands of California (*Phacelia floribunda*, *Lepidium oblongum* var. *insulare* and *Linanthus pygmaeus* subsp. *pygmaeus*), and a new record for Guadalupe Island: *Yabea microcarpa* (Apiaceae) (See Appendix). Except for the latter, all the species are also present outside the palmar.

Despite the smaller size of transects in the palmar compared to transects for the remainder of the island, they contained on average a greater species richness ($\chi^2_1 = 18.09$; $P < 0.0001$). The shape of the functions relating richness to altitude differed between the palmar and the rest of the island ($\chi^2_3 = 14.45$; $P = 0.0023$): While at the former richness increased steadily from 430 to 800 masl and then stabilized, there were no significant changes in richness in the remainder of the island ($\chi^2_6 = 7.73$; $P = 0.2593$; Fig. 2A).

Vascular plant cover was near 100 % between 490 and 910 m, and dropped at both ends of the gradient ($F_{3,19} = 10.27$; $P = 0.0003$; Fig. 2B). On average, cover was greater in the palmar than in the remainder of the island ($F_{1,91} = 7.461$; $P = 0.0072$). Moss cover was largest between 600 and 950 m ($F_{3,19} = 11.13$; $P = 0.0002$; Fig. 2C).

We recorded a total of 3870 palms. Some of them were recorded in inaccessible areas below our lowest transect. Palm density increased rapidly from about 150 to 500 m, and dropped back to zero at 850 m ($F_{4,4} = 18.45$; $P = 0.0076$; Fig. 2D). A very similar pattern was observed if only palms occurring less than 200 m away from our set of transects are considered, with the only difference that no individuals occur below 430 m where the cliff starts (data not shown).

DISCUSSION

Our results confirm that species richness and vascular plant cover in the palmar were greater than those observed in the remainder of the

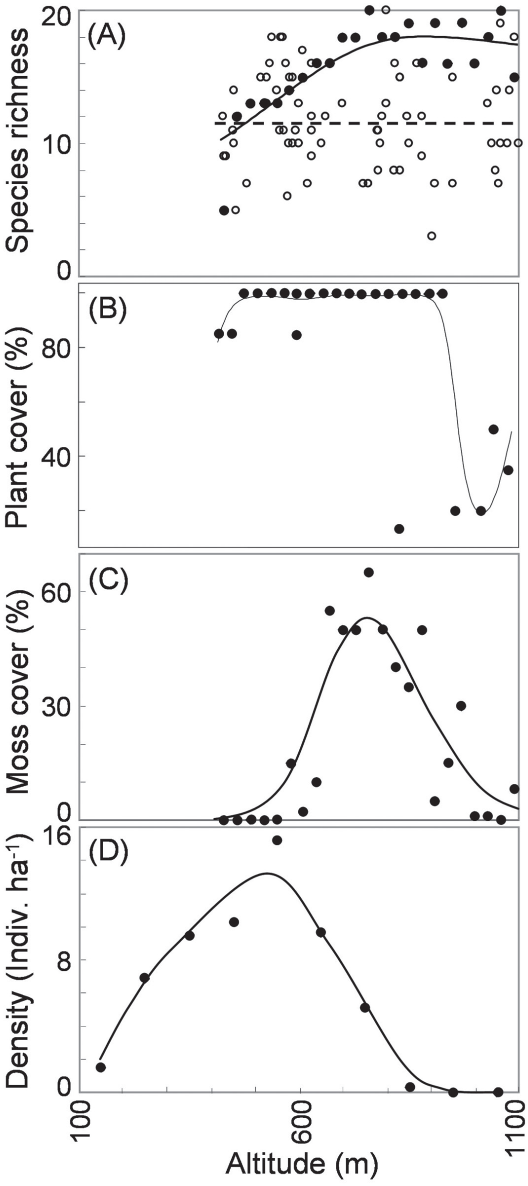

Fig. 2: Altitudinal variation of vegetation attributes in the palmar (—○—) and the remainder of the island (—●—): (A) vascular-plant species richness; (B) vascular plant cover; (C) moss cover; and (D) density of palms.

Variación altitudinal en los atributos de la vegetación en el palmar (—○—) y en el resto de la isla (—●—): (A) riqueza de especies de plantas vasculares; (B) cobertura de plantas vasculares; (C) cobertura de musgos; y (D) densidad de palmas.

island, and that there was a clear altitudinal zonation of the vegetation in the palmar like that found at the South American lomas. This is consistent with a significant, sparse and altitudinal structured source of water in the northern slope of Guadalupe Island, i.e., with fog.

Despite we used smaller transects than those reported by Garcillán et al. (2008), the mean richness in the palmar transects was greater than that observed at similar altitudes in the remainder of the island. If both sets of transects had had the same area, this difference would have been even larger. This, altogether with the greater plant cover at the palmar, suggests that water availability there is larger than in the rest of the island.

Based on palms distribution, the source of water does not seem to be spatially localized around delimited zones such as canyon bottoms, springs, fracture-associated percolations, and areas where runoff accumulates, as it occurs in other palmares of the Sonoran Desert (Schwenkmeyer 1986). In contrast to the mainland oases, where palms are densely clumped around the water sources (Vogl & McHargue 1960, Franco-Vizcaíno et al. 2007), palms in Guadalupe are scattered throughout the slope, with only a weak trend to occur in the vicinity of ravines.

Instead, water availability seems to change with elevation. The narrow altitudinal belt with considerable moss cover confirms the existence of an altitudinal belt with a high atmospheric humidity in the 600-950 m interval, which is probably the altitude where fogs are more frequent. This is in rough agreement with Dorman’s (1994) delimitation of the thermal inversion at Guadalupe Island, which oscillates between 544 and 1120 m, with an average at 862 m. The last figure coincides with the altitude where moss cover is greatest. The elevational trends in vascular plant richness support this interpretation: Richness attains its maximum values in the 600-1100 m interval. The lower boundary of this interval coincides with the lowest elevation at which fog seems to be significant. Further conformation of altitudinal patterns in the distribution of life forms, such as that found in other arid foggy mountains (Rundel et al. 1991, Martorell & Ezcurra 2007), was not observed. This probably results from the limited diversity of life forms in the palmar, where all the species (except *B. edulis* and *Ambrosia camphorata*) are annuals. However, the long period of goat herbivory may have contributed to the structural and spatial simplification of the palmar community.

It must be noted that palms are distributed mostly between 300-750 m, and thus occur below the putative fog belt. In Peruvian lomas, other rosette species are also dominant in the lower margins of the fog zone (Rundel & Mahu 1976). Rosette species, especially those with palm-like morphological attributes, are highly efficient at harvesting fog (Martorell & Ezcurra 2007), and thus may profit more than other species from light and infrequent fogs occurring in the margins of fog belts. By reaching high into the atmosphere, palms may have greater access to fog than mosses and herbs (Martorell & Ezcurra 2002). Thus, there may be fog available in the area where *B. edulis* occurs that may go undetected if mosses or herbs are used as a phytometer.

The high density of palms and cover of vascular plants below the moss belt may also be related to the fact that water availability in the soil may be greater below the fog interception zone than inside it. Ingraham and Matthews (1988, 1995) found that, if enough fog is collected, it may seep into the soil. In turn, this may allow for subsurface flow if slope is steep enough, replenishing the deep horizons of the soil at lower altitudes. Ellenberg (1959, in Rundel 1978) found that vascular plant development in fog-dependant ecosystems was related to the depth of edaphic water. Moreover, presence of fog on mountaintops during spring and summer not only increases water input, but also seems to reduce evapotranspiration of the vegetation below (Huntley et al. 1997, Ewing et al. 2009, Fisher et al. 2009). Thus, combination of direct fog interception, surface and subsurface runoff from heavy interception in the upper basin (around 600-950 m, as indicated by mosses) and evapotranspiration reduction may support the palms and the dense vegetation occurring downslope.

On the other hand, the expected decrease in temperature with altitude may set a limit to the distribution of cold-sensitive palms (Tomlinson 2006) in the upper parts of the gradient, or else a competitive effect of the pines may have excluded palms from higher areas. Nowadays, no pines are found there as a result of overgrazing, but it is likely that they occurred immediately above the palmar (León de la Luz et al. 2003, Oberbauer 2005). The complete absence of recruitment over the last 150 years because of overgrazing has most likely precluded palms from colonizing this now competition-free environment. Due to the steepness of the palmar slope and the low density of palms, a "fog shadow" (i.e., windward to leeward reduction in fog interception; Del-Val et al. 2006) due to heavy interception and depletion of water seems unlikely. Consequently, no edge effects in terms of water and nutrients deposition (Weathers et al. 2000, Ewing et al. 2009) are apparent. Therefore, we would expect these effects to affect spatial distribution of recruitment as has been observed in other fog-dependent forests (Del-Val et al. 2006, Gutiérrez et al. 2008).

Overall, our results suggest that the presence and structure of the palmar at Guadalupe Island is largely determined by fog. Thus, this community may be considered as a fog oasis, one of the very few that occur in North America. This ecosystem may have formed a now vanished continuum with the pine, oak and cypress forests that probably were also dependent on fog (Moran 1996, Oberbauer 2005, Rogers et al. 2005). The only four tree-species (pine, oak, cypress and palms) of these communities are threatened, and the two last are endemic to this island (Moran 1996, León de la Luz et al. 2003, Rogers et al. 2005).

The destruction of the palms and trees in Isla Guadalupe has probably had a number of direct and indirect negative effects on the whole community, many of which may be difficult to reverse. Although eradication of vertebrate herbivores on small islands uses to be followed by rapidly appreciable recovery of vegetation, a cryptic and complex ecological legacy of herbivore disturbance remains for long time (Cauapé-Castells et al. 2010). For example, the community of dispersers on islands, especially birds that strongly depend on trees, affect deeply forest succession after ungulates eradication (Luna et al. 2005, Bellingham et al. 2010). More directly, trees in fog oases are ecosystem engineers that are responsible for most of the interception and redistribution of water (Dawson 1998, Barbosa et al. 2010). Therefore, many other plant and animal species are dependent on them (Moran 1996, Rogers et al. 2005, Oberbauer 2005). Forest size, fragmentation or tree removal in fog-dependent ecosystems also affects ecosystem processes because moisture declining affects nutrient inputs, decomposition and mineral cycling in soil (Huntley et al. 1997, Weathers & Likens 1997, Barbosa et al. 2010). Gutiérrez et al. (2008) suggested that in fog-influenced forests in arid Chile recruitment is reduced in small patches due to their drier environment. The consequences of the removal of the formerly fog-harvesting forest are already apparent in the collapse of some water springs in the island (Jacobs et al. 1985, Moran 1996, Dawson 1998, Fisher et al. 2009), and may have already had large impacts on the insular biota that we are unaware of. It could be expected that under these new, drier conditions tree and palm saplings would be unable to recolonize areas that were formerly covered by forests, and that the community would thus have undergone an irreversible, catastrophic shift (Scheffer et al. 2001). However, after more than a century of destruction, the eradication of goats in 2004-2006 has given new hope to this unique community, as the renewed recruitment of palms, pines and cypresses reveals (Junak et al. 2005, Garcillán et al. 2009).

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APPENDIX

List of the 33 vascular plant species found in the palmar of Guadalupe Island. Non-native species are marked with an asterisk (*).

Listado de las 33 especies de plantas vasculares encontradas en el palmar de Isla Guadalupe. Las especies que no son nativas están señaladas con un asterísco(*).

- APIACEAE
  - _Yabea microcarpa_
- ARECACEAE
  - _Brahea edulis_
- ASTERACEAE
  - _Ambrosia camphorata_
  - _*Centaurea melitensis_
  - _*Hypochaeris glabra_
  - _Logfia filaginoides_
  - _*Sonchus oleraceus_
- BORAGINACEAE
  - _Pectocarya linearis_ ssp. _ferocula_
- BRASICACEAE
  - _Lepidium oblongum_
- CAMPANULACEAE
  - _Githopsis diffusa_
  - _Triodanis biflora_
- CARYOPHYLLACEAE
  - _*Cerastium glomeratum_
  - _*Herniaria hirsuta_
  - _*Silene gallica_ ssp. _capitatum_
- CRASSULACEAE
  - _Crassula connata_
- FABACEAE
  - _Trifolium gracilentum_
  - _Trifolium microcephalum_
- GERANIACEAE
  - _*Erodium brachycarpum_
  - _*Erodium cicutarium_
  - _*Erodium moschatum_
- HYDROPHYLLACEAE
  - _Phacelia floribunda_
- OROBANCHACEAE
  - _Castilleja attenuata_
- POACEAE
  - _*Bromus madritensis_ ssp. _rubens_
  - _*Hordeum murinum_
  - _*Polypogon monspelienses_
  - _*Vulpia muro_
- POLEMONIACEAE
  - _Leptosiphon pygmaeus_
- POLYGONACEAE
  - _Pterostegia drymarioides_
- PORTULACACEAE
  - _Calandrinia ciliata_
  - _Claytonia perfoliata_ ssp. _mexicana_
- ROSACEAE
  - _Aphanes occidentalis_
- RUBIACEAE
  - _*Galium aparine_
- URTICACEAE
  - _Parietaria hespera_