

RECRUITMENT RESPONSE OF GUADALUPE CYPRESS (*CALLITROPSIS GUADALUPENSIS*) THREE YEARS AFTER GOAT ERADICATION ON GUADALUPE ISLAND

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Abstract—The only natural population of Guadalupe cypress (*Callitropsis guadalupensis*) occurs on Guadalupe Island, an oceanic island off the Baja California peninsula. This population has suffered an intense decline and a shift towards older individuals during the last 150 years, because feral goats have prevented recruitment of new individuals. After a goat eradication program began in 2004, intense seedling recruitment has been taking place in the Guadalupe cypress population. Our objective was to analyze how this new recruitment is occurring. We started in spring of 2004 with a demographic study of recruitment based on 515 new seedlings (< 1 year old) distributed inside forest patches and on patch borders. The new seedlings were labeled, and survival and growth were monitored each spring and autumn for three years. We also studied the spatial pattern of recruitment inside forest patches. We analyzed how gap size and percent canopy cover affected recruitment. Seed germination occurred both inside forest patches and along their borders, but mortality was higher in the forest interior than on the edge. Recruitment inside the forest was not clearly related to gap size or percent canopy cover. As a consequence, recruitment occurred mainly on the margins around the four patches, and more intensively in the west-southwestern borders.

INTRODUCTION

The Guadalupe cypress (*Callitropsis guadalupensis*, Cupresaceae) is, among the species of the genus *Callitropsis*, a paradigmatic case of geographical isolation and reduced population size. It is the only insular species of the genus, and its distribution is restricted to Guadalupe, a volcanic island located 260 km off the coast of Baja California, México (Fig. 1a).

Guadalupe is an oceanic island of about 250 km², characterized by a pronounced topography (highest point of 1295 m) and a climate controlled by frontal systems from the northwest, with an average annual precipitation about 133 mm (October to March) and monthly mean temperature varying from 16.2° C for April to 20.4° C for October (Moran 1996). However, there is a markedly climatic gradient from the higher northwestern part, with frequent fog and probably higher rainfall, to the more arid southern extreme of the island. Floristically, it is considered a

geographic outlier of the California Floristic Province (Moran 1996).

The Guadalupe cypress is a tall tree (15–20 m) that presents a well defined trunk (mostly 30–60 cm thick) and a dense to rather open crown (Moran 1996). At present, the extant population forms a mono-specific forest of 148 ha with mean density of 110.7 individuals/ha, distributed among four forest patches (9, 47, 4, and 88 ha) at altitudes of 800–1300 m in the northwestern part of the island (Fig. 1b).

The introduction of goats on the island during the nineteenth century resulted in a process of environmental and biological deterioration (Moran 1996; León de la Luz et al. 2003) that dramatically affected the population dynamics of the Guadalupe cypress. It is difficult to know the extent of the original range, but information reported by the first naturalists who explored the island (e.g., Greene 1885; Bryant 1887; Franceschi 1893; Howell and Cade 1954) allows us to suppose a significantly more extensive cypress forest (Moran 1996; Oberbauer 2005). Although natural mortality and

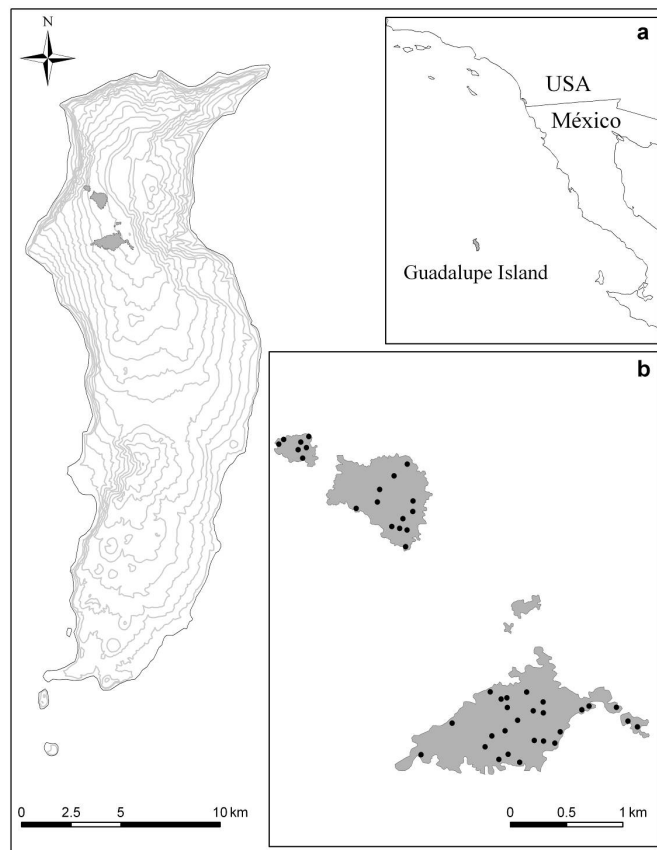


Figure 1. Guadalupe Island, showing (a) geographic location of Guadalupe Island; left panel: distribution of cypress patches (grey polygons) and contour lines at 100m intervals; and (b) locations of gaps analyzed inside the cypress patches.

occasional fires could have increased forest fragmentation (Moran 1996), the underlying cause of forest reduction has unquestionably been herbivory by goats, which prevents recruitment of new seedlings. The extinction risk caused by this situation compelled the Mexican government to declare this species as in “danger of extinction” (DOF 2001) and the IUCN to include it in its Red List under the category of “critical danger” (IUCN 2007).

After more than a century of island disturbance by goats, a multi-institutional program led by the Mexican governmental research agency Instituto Nacional de Ecología and the Mexican non-governmental conservation group Grupo de Ecología y Conservación de Islas started to eradicate the goats and restore the island in 2004. Two years later the goats were eradicated from Guadalupe Island.

As part of this program, a demographic study of the cypress population was started. The cypress patches on Guadalupe Island exhibit increased canopy gaps due to the high mortality of its aged population. Spatial canopy structure of the forest will affect seedling recruitment, because seedling establishment is a very sensitive stage in the life cycle of tree species (Harcome 1987), and it is well known that recruitment in other species of *Callitropsis* is a process positively affected by light availability (Vogl et al. 1977; Zedler 1981; Dunn 1987). Our hypothesis is that light availability also affects the recruitment process in *Callitropsis guadalupensis*. The objective of this work was to analyze how this heterogeneous scenario of light availability affected survival and spatial recruitment of cypress seedlings following goat eradication.

MATERIALS AND METHODS

Seedling Survival

We partitioned one of the large fragments (second northernmost patch in Fig. 1b) into three subjectively differentiated environments according to light availability on the ground. The first environment was “forest interior,” which was defined as area away from edges of gaps and patches, and characterized by dense canopy and low light availability. The second environment was “forest edge,” which was the area delimited by the vertical projection of the tree crowns located at the forest limit and characterized by medium light availability. The third environment was “forest exterior,” which was defined by an exterior band of approximately 10 m from the limit of the previously defined edge, and characterized by absence of canopy and higher light availability. The 10 m width of this band was defined by the distance of the most remote seedling found.

We searched all three environments for cypress seedlings in May and October 2004, and we measured and labeled all seedlings we found. We labeled a total of 515 cypress seedlings (Table 1). Of the 383 seedlings found in May, 90 were located in the interior, and 293 were on the edge. In October, 4 seedlings were found in the interior, 42 were found in the edge, and 86 were found in the exterior. Height and crown diameter of all individuals were measured, and seedlings were grouped into three size categories: small (S1; height ≤ 1 cm), medium (S2; 1–4 cm), and large (S3; height > 4 cm). Size classification was selected in order to have height categories useful in the three environments. These categories also reflected the population structure observed in the field. From May 2004 to October 2006, we recorded survival of the labeled individuals twice each year—once at the end of the rainy season (May) and again at the end of dry

season (October). In each survey period, we recorded the condition of the plant (dead or alive) and its height.

Survival functions are a common statistical tool for characterizing and summarizing the risk of dying in a population. If such an analysis is to be performed, there are two main aspects that must be taken into account. The first is related to the fact that survivorship can change through time (Deevey 1947). It is therefore important to include the temporal variation of the risk of dying in the modeling of survival process. The second involves the type of data used to fit the survival model. Due to biological and methodological restrictions, sometimes it is not possible to quantify the complete span of life of an individual. That is, there are individuals in the population that have no date of death (they outlive the observation period, or migrate, or simply disappear). Such subjects may yield information about surviving, but not for dying (Crawley 1993). A function widely used for modeling survival processes is the Weibull function (Weibull 1951). One of its main advantages is that it can model several shapes of curves (Ebert 1999), allowing the data to determine whether the risk of dying is constant or not. Also, it is possible to include in the analysis those individuals we know that die and those about whom we have no certainty.

Survivorship—the probability that seedlings survive to time t —is described by the Weibull survival function: $S(t) = e^{-(\alpha \cdot t^{\gamma \cdot \mu})}$ where $S(t)$ represents the proportion of seedlings that survive to time t , and α , γ , and μ are scale, shape, and treatment parameters, respectively. The value of α indicates how the hazard of death changes with time. If $\alpha = 1$, the hazard is constant; if $\alpha > 1$, then the hazard increases with age; and finally, if $\alpha < 1$, it decreases with age (Crawley 1993). To estimate the parameters α , γ , and μ , we fit the Weibull model to survivorship and time data using the statistical software “R” (R Development Core Team 2007). Some data were considered as “right censored” (some individuals survived the experiment and were used to estimate the survival function, but not the function of mortality) and some were considered as “interval” type (some individuals were added to the experiment after it started). The survival package of R was used to take into account these aspects (Therneau and Lumley 2007).

Table 1. Abundance and size structure of the labeled cypress seedlings among the three environments. Plant size categories: S1 ≤ 1 cm, S2 = 1–4 cm, and S3 > 4 cm. Forest environments: interior, edge, and exterior of forest patch.

	S1	S2	S3
Interior	63	31	0
Edge	32	220	83
Exterior	0	30	56

The independent variables used in this regression model include one continuous (time to death) and two categorical (seedling size and environment) with three levels each. Therefore, we obtained the average effect of treatment, standard errors and the significance level for all the regression parameters in each analysis. Since the three size categories of seedlings are not present in all the environments (Table 1), we performed independent analyses for each environment. Survival of small (S1) plants was compared between the “forest interior” and the “forest edge”; survival of medium (S2) plants was compared in all the environments; and survival of large (S3) plants was compared between the “forest edge” and the “forest exterior.”

Seedling Recruitment

In November of 2006, we randomly selected 44 canopy gaps in the forest patches (Fig. 1b), and for each one we measured gap size, percent canopy, and number of seedlings. We measured the distance from the center of each gap to the trunk of the nearest tree. We used this distance as the radius of the gap circle and then calculated the gap size as the area of this circle. In ArcGIS, we added a concentric buffer of 15 m (approximate average individual crown diameter) around each gap circle to create the buffered gap circle (gap radius + 15 m). We used ArcGIS to calculate the canopy area found inside the buffered gap circle. We defined the percent canopy as the proportion of canopy area with respect to the area of the buffered gap circle. Association between seedling number and two gap locations (near the edge vs. interior of forest) was tested with a χ^2 test. To examine the relationship between seedling recruitment and gap characteristics, we employed the linear regression models $D = \beta_1 A - \beta_2$ and $D = \beta_3 C - \beta_4$ to determine how density of seedlings (D) is influenced by gap size (A) and percent canopy (C), respectively.

RESULTS

Seedling Survival

We found a significant effect of light environment on survival of different size cypress seedlings. Survival of small plants was significantly higher at the edge than inside the forest ($P <$

0.0001). All the small seedlings (S1) in the interior of forest were dead at the end of census, whereas at the edge 20% of small seedlings survived (Fig. 2a). Medium seedlings (S2) showed similar behavior, with significantly higher mortality in the interior of the forest than at the edge ($P = 0.01$) or at the exterior of the patch ($P < 0.0001$) (Fig. 2b, Table 2). Finally, survival rate of large seedlings (S3), which was the highest rate of the three sizes and greater than 90%, was not significantly different between the edge and the exterior of the forest (Fig. 2c, Table 2).

The shapes of the survival curves are different for each environment (Fig. 2). In the interior of the forest the curves show high mortality in the initial stages. However, in the environments with more light, mortality is higher in the final stages. In

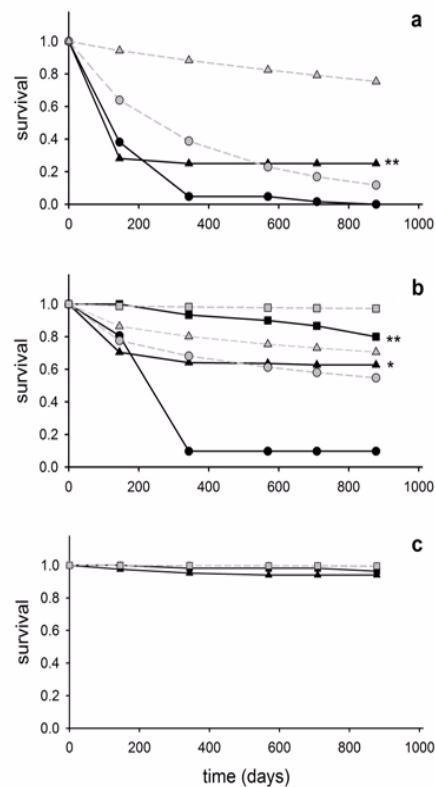


Figure 2. Survival curves of cypress seedlings according to environment and height category. (a) small plants (height = 1 cm); (b) medium plants (h = 1–4 cm); and (c) large plants (h > 4 cm). Solid black lines indicate observed survival, and dashed gray lines indicate estimated survival. Forest interior is denoted by circles, edge by triangles, and exterior by squares. Asterisks refers to survival curves significantly higher than the interior survival curve (* $P = 0.01$; ** $P < 0.0001$).

Table 2. Coefficients of Weibull survival curves and their significance levels, compared against the first level of the factor. Plant size categories: S1 < 1cm, S2 = 1–4 cm, and S3 > 4 cm. Forest environments: interior, edge, and exterior of forest patch.

	γ	α	μ	s.e.	z	P
S1						
Interior	0.869	1.000	0	0.145	0	
Edge	0.869	0.131	2.33	0.313	7.43	< 0.0001
S2						
Interior	0.480	0.395	1.93	0.399	4.84	
Edge	0.480	0.228	3.07	0.472	2.42	0.0157
Exterior	0.480	0.018	8.32	0.973	6.56	< 0.0001
S3						
Edge	0.793	0.003	7.11	0.843	8.442	
Exterior	0.793	0.002	7.80	0.776	0.884	0.3770

general, the values in the regressions are < 1, which suggests that the risk of dying diminishes with age (Table 2). The only exception was the curve of the S1 plants in the interior of the forest, where γ value was equal to one, indicating that the risk of dying is constant over time.

Seedling Recruitment

The gaps ranged in size from 127 m² to 2827 m² (average value of 1175 m²), and we found values of seedling density from 0 to 0.091 seedlings/m², with an average density of 0.013 seedlings/m². The linear regression indicated a higher density of seedlings in gaps with a larger gap area ($\beta_1 = 0.018$, $\beta_2 = 3.43$, $R^2 = 0.1631$, $P = 0.0038$) and at sites with a higher percent canopy ($\beta_3 = 0.023$, $\beta_4 = 38.62$, $R^2 = 0.1668$, $P = 0.0034$). Results of the χ^2 test also indicated that there was higher seedling density in gaps within 50 m of the forest edge than in interior gaps. All 18 gaps close to the edge had seedlings, whereas only 10 of the 26 gaps in the interior of the forest were occupied ($\chi^2 = 19.18$, $df = 1$, $P < 0.0001$). Seedling density in the border gaps (0.028 ± 0.026 s.d. seedlings/m²) was four times higher than in the interior gaps (0.006 ± 0.006 s.d. seedlings/m²) ($t = 3.38$, $df = 20$, $P = 0.003$).

DISCUSSION

Cypress vital rates seem to be significantly related to the type of environment and size class.

The interior of the forest appears to be the most restrictive environment. We did not find large seedlings (S3) inside the forest, and survival rates of the two other size classes found (S1 and S2) were almost zero after the first year. In contrast, survival at the edge and exterior of the forest were significantly higher. It is very likely that the main abiotic factor involved is light availability. This strong light requirement is reported in other studies of cypress species (Vogl et al. 1977; de Gouvenain and Ansary 2006). However, seedling recruitment inside the forest showed a strong relationship with edge proximity, in addition to gap size or percent canopy cover around the gap. Due to the fact that some factors can be correlated in a gap (e.g., light, temperature, and humidity), it is possible that other environmental factors besides light may be affecting seedling recruitment, such as water availability caused by fog influence (Garcillán, personal observation). Biological processes may also be important, like higher seed production at the edge, or higher concentration of seeds in the soil downslope of the western borders, due to water transport after rain. All these factors deserve to be experimentally tested in order to gain understanding of the seedling recruitment. In this context, it is possible that this remnant population, even with its high disturbance level, can exhibit “classical” gap dynamics like that of tropical and temperate forests (Pickett and White 1985; Barnes et al. 1998).

Seedling survival increases with size. Small plants suffered elevated mortality in any light environment, whereas medium size seedlings showed higher survival, even in the interior. Survival of plants taller than 4 cm is almost 100% in the edge and the exterior of forest. These findings coincide with previous studies of other species (e.g., Turner 1990; Masaki and Nakashizuka 2002). This study suggests that the seedling height of 4 cm may be considered as a survival threshold; above which mortality is very low. The existence of such a threshold, although of higher value, is reported for other tree species (Harcombe 1987). This pattern is perhaps evidence that these species face similar pressures at the initial growth stages. They must reach a size that allows them to tolerate shadowing, dryness, competition, pathogens, and other selection pressures. Nevertheless, more studies are needed in order to confirm this finding. In a similar way, values show that survival also increases with age (Streng et al. 1989; Sacchi and Price 1992). However, some caution must be taken with this conclusion, because age is not always a fine indicator of seedling strength. Finally, there may be some other processes influencing seedling survival that cause an overestimation of the predicted survivorship curves. In order to have a better fit, other factors like soil properties may be added to improve the model.

This study provides information for the development of a management and recovery program for this species. The ongoing natural recruitment process can be accelerated through collecting seeds and sowing them in strategic zones, like gaps near the edge of the forest. Also, natural recruitment can be supplemented with the introduction of new individuals grown in greenhouses. Trees have several ecological roles (Jones et al. 1997), so it is very likely that some key ecosystemic processes of the island (like water infiltration to the ground) will be increased if the forest cover grows up.

Fortunately, the extinction risk of the Guadalupe cypress has diminished considerably, owing to the first recruitment of seedlings after perhaps more than a century. Nevertheless, the demographic viability of this species depends on the development of a robust population structure that will allow it to face the evolutionary processes (inbreeding or genetic drive) and hazards (e.g.,

pathogens, fires) that may extinguish a small isolated population. Although many years are needed before such a population structure can be achieved, the observation of new individuals, less than 3 years old, which are already producing reproductive cones, suggests a very promising future for this species. These good signs reflect the efforts of many persons, institutions, and organizations to stop ecosystem degradation and recover the biological richness of Guadalupe Island.

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