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## Seed bank analysis of tree species in two stands of the Tenerife laurel forest (Canary Islands)

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### Abstract

We analyzed the germination from the seed bank for two laurel forest stands (Moquinal versus Aguirre) of Tenerife collected at two different seasons (summer versus winter). We incubated and monitored germination in greenhouse conditions for 1 year. A high variability in germination was found between trays. Germination was much higher in summer than in winter, especially from Moquinal seed bank. Shade tolerant species (*Laurus azorica*, *Persea indica*, *Rhamnus glandulosa* and *Viburnum tinus*) have a shorter germination delay than shade-intolerant species (*Erica arborea*, *Erica scoparia* and *Myrica faya*), which dominate the seed bank. The species composition of germinating seeds after one year did not reveal any differences between sites nor between, despite the high differences in number between seasons.

We compared the species composition of germinating seeds to that of the canopy (expressed as basal area). The results indicate that the winter seed bank does not significantly differ from the canopy composition in the Aguirre stand. We interpret our results to imply that the Aguirre stand is of an earlier successional stage than the Moquinal stand, because of a higher species richness in the germinated tree seeds, and compositional similarities between the winter seed bank and the canopy (both characteristic of earlier successional stages). © 2000 Elsevier Science B.V. All rights reserved.

*Keywords:* Canary Islands; Buried seeds; Germination; Succession; Canopy

### 1. Introduction

A complete description of stand vegetation should include the analysis of buried seeds (Major and Pyott, 1966) as such information is indispensable in plant ecology (Grime, 1989). Although Farmer (1997) describes trees as “not very enthusiastic banking species”, a complete view of forest dynamics must include the seed bank.

The seed bank of mature forests generally differs from the canopy with respect to species composition (Thompson, 1992). Only in relatively few ecosystems, such as freshwater wetlands, is the soil seed bank composition similar to that of the canopy (Leck and Graveline, 1979). The seed bank is typically dominated by earlier successional species (Fenner, 1985; Thompson, 1992; Jankowska-Blaszczuk et al., 1998; Hanlon et al., 1998). Climax species can germinate from the seed bank, but their numbers are lower than those of shade intolerant species (Fenner, 1985). Seed bank dynamics are also highly dependent on distur-

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bance rates (Thompson, 1992; Vaughton, 1998). The analysis of the seed bank reveals the contribution of the seed bank to establishment after disturbance (Ash-ton et al., 1998). However, due to the difficulty of analyzing seed bank, very little is known about temporal and spatial variability of seed banks in ecosystems (Bazzaz, 1996).

Previous studies have reported the importance of shade-intolerant species in the seed bank of the Tenerife laurel forest (Arévalo, 1998; Fernández-Palacios and Arévalo, 1998). Unlike the previous studies, the current study has a larger sample size and germination was monitored for 1 year after being collected in summer (July 1996) and winter (December 1996). The aim of this work is to describe the implications of the seed bank for forest dynamics. This paper describes the seed bank in two study sites with different canopy composition, and relates the dynamics of the forest to the characteristics of the seed bank.

## 2. Methods

### 2.1. Study site

Tenerife's evergreen laurel forest has been extensively exploited since the arrival of Europeans in the 15th century (Parsons, 1981). Today, only 10% of the forest remains. The remaining laurel forest was formally protected beginning in 1988. These areas currently experience only minimal human disturbance. No data are available about the age of the forest (and dating the trees is impossible because the trees in the laurel forest do not possess annual rings), but based on indirect information (such as photographs from 40 years ago and checking governmental records of forest exploitation) we infer that it is at least three or four generations old. This assumption is supported by the lack of government exploitation (logging activity) reports from this area in the last two centuries (this information could be found in the records of logging activities of the Cabildo of Tenerife island). However, until 40 years ago some illegal use of the forest was occurring but on a small scale due to the public character of the forest and the protection of the same. Aerial photographs from 1952 show a forest similar to today's (in extent and physiognomy) without noticeable disturbance.

More than 95% of the regeneration of some tree species is asexual (primarily by basal sprouts) (Arévalo, 1998). This high rate of sprouting is not due to cutting because the available data do not show any history of logging and non-economic species also present high rates of asexual regeneration (e.g. *Prunus lusitanica*) while an economically valuable species does not (*Erica arborea*). The resulting dominance by a few species is characteristic of remnant communities (Eriksson, 1996) and a low disturbance level (Packham et al., 1992).

The study was conducted in the Anaga Natural Park in the northeast corner of Tenerife, Canary Islands (28°19'N, 16°34'W). The park encompasses a 7–8 million-year-old basaltic massif (Ancochea et al., 1990) covering some 130 km<sup>2</sup>. The park represents 7% of Tenerife's total area. We selected two stations in the park as representing the best-conserved laurel forests of Anaga: 'El Moquinal' on the windward slope (700 m) and 'Aguirre' (900 m) on the leeward slope. We chose approximately 300 ha of the most intact forest in each station.

The annual precipitation of the park reaches 900 mm, but can be twice this amount if fog drip is considered (Kämmer, 1974). The mean annual temperature is close to 15°C with minimal annual and daily fluctuations. There are no frost events. Two seasons can be differentiated, winter and summer, but in most years, differences between the two most extreme months are not large (differences of the average of the extreme months: 8°C, 5% of relative humidity and 100 mm of rain) (Ceballos and Ortuño, 1974). The soils have been classified in the order Entisol, suborder Orthens. These soils are present in areas with a high slope. They maintain a high grade of humidity due to the hydrate aluminum silicates and they have a big horizon A (Fernández-Caldas et al., 1985). The content in organic matter is high (around 10%) and a pH around 5.5 (Fernández-Palacios and Arévalo, 1998).

The canopy of Anaga's laurel forest varies between 10 and 20 m high depending on slope. Maximal heights are found at the basin's floor decreasing progressively towards the basin's borders. The laurel forest of Tenerife contains a total of 19 tree species (Santos, 1990). Dominant species include *L. azorica* (Seub) Franco, *Erica scoparia* L., *E. arborea* L., *Ilex canariensis* Webb & Berth, *Prunus lusitanica* (Willd.)

Franco, *M. faya* Aiton and *Viburnum tinus* Vent. The dominance of one or other species will depend of the site, for example, *E. scoparia* in the mountain peaks, *L. azorica* in the mesic forest, *E. arborea* in more disturbed areas, etc. (Anon., 1973). At each plot we measured dbh (diameter at breast height) of the trees. We defined trees as stems of at least 4 cm dbh.

Further information about stand composition, structure and environment in the two sites can be found in Fernández-Palacios (1992), Arévalo and Fernández-Palacios (1998) and Arévalo (1998). For the denomination of the species included in our analysis we followed Hansen and Sunding (1985).

## 2.2. Data collection

We selected eight randomly located square plots of 625 m<sup>2</sup> in Moquinal (1–4) and Aguirre station (5–8). On a map we selected the UTM (Universal Transverse Mercator grid) of the plots with a random number table, and located the plots using GPS (Global Positioning System), maps and an altimeter. In each of the plots, we took three random samples of 4 kg of dry soil (0–5 cm) in June 1996 and three random samples in December 1996 (again we selected the random points with a table in a grid 1 × 1 m in the plot). We have a total of 48 samples plus nine control trays. The soil samples were placed in 4 cm deep, 40 × 55 cm plastic trays. The litter that originally covered the sampled soil was disposed. Samples were set to germinate under greenhouse conditions and were irrigated daily with purified water. Six additional trays filled with sterilized soil were used as controls in order to determine the seed rain, if any, existing in the greenhouse. Emerging seedlings were removed after they could be identified.

We monitored the seed bank for 1 year. Another study conducted in the same area for 2.5 years revealed that germination is infrequent after the first year (Arévalo, 1998).

## 2.3. Data analysis

There are many difficulties in the analysis of seed bank data. The requirement of a normal distribution for parametric tests is seldom met, and the low abundance of some species may invalidate the use of non-parametric tests (Warr et al., 1994). This suggested to

us that ordination methods would be a useful tool for the description, analysis and interpretation of seed bank data. Ordination techniques can help to explain community variation (Gauch, 1982). We used detrended correspondence analysis (DCA; Hill and Gauch, 1980) to analyze species composition in the annual germination of the trays. In the first analysis we summarized germination in three trays per plot, obtaining the total germination density for the plot. We did this for the eight plots in both the seasons, resulting in a total of 16 samples. We will use this statistical tool to evaluate differences in seed bank germination between different sites with different canopy composition.

In a second analysis, we test whether there are differences between canopy composition and seed bank germination (both normalized as percentages). For that purpose we used canonical correspondence analysis (CCA; ter Braak, 1986). We analyzed the basal area of the trees in the four Moquinal plots together with the seed bank data after 1 year for the summer samples (using the sum of the three trays of the plots). We then have eight samples, four from the basal area data and four from the germination composition data. In this analysis we used only one explanatory variable: a dummy variable that represents whether the sample belongs to the basal area or the germination data. Because there is only one variable, there is only one CCA axis. Samples or species scores along this axis represent the degree to which samples or species are more representative of the seed bank or the canopy composition. We used the same method to analyze basal area of Moquinal plots and winter germination composition in Moquinal, basal area of Aguirre plots and germination composition of Aguirre summer samples, and basal area of Aguirre plot and germination composition of Aguirre winter samples.

By testing the significance of the axis with a Monte Carlo test, we can test whether samples were distributed randomly among both categories of the explanatory variable. If the eigenvalue of the axis is higher than the eigenvalue of the randomized samples, we can conclude that the variable explains species composition (in this case, the variable basal area versus germination). We would interpret such a result to indicate a difference between canopy composition and germination composition.

Table 1

Basal area (m<sup>2</sup>/ha) in per species the plots and total basal area in the plots of Moquinal (plots 1, 2, 3 and 4) and Aguirre (5, 6, 7, and 8)

Species	Moquinal site				Aguirre site			
	1	2	3	4	5	6	7	8
<i>Apollonias barbujana</i>	–	–	–	–	–	–	–	0.02
<i>Erica arborea</i>	8.76	–	1.79	–	0.12	0.30	0.51	11.71
<i>Erica scoparia</i>	0.66	–	0.16	2.19	23.13	13.84	13.36	0.05
<i>Heberdenia excelsa</i>	–	–	–	–	–	0.03	–	0.45
<i>Ilex canariensis</i>	5.26	4.49	9.93	8.75	2.95	5.49	5.01	4.32
<i>Ilex perado</i>	3.72	–	1.26	4.02	–	–	–	–
<i>Laurus azorica</i>	3.67	9.98	4.46	4.96	6.61	8.53	8.04	12.78
<i>Myrica faya</i>	4.04	10.66	4.37	6.71	20.66	16.86	16.32	12.03
<i>Persea indica</i>	–	–	–	–	0.20	0.02	2.73	0.37
<i>Picconia excelsa</i>	–	–	–	0.16	–	–	–	–
<i>Prunus lusitanica</i>	8.19	17.98	14.68	14.70	–	0.01	–	0.06
<i>Rhamnus glandulosa</i>	–	–	–	–	0.26	0.78	0.15	1.03
<i>Teline canariensis</i>	–	–	–	–	0.21	–	–	–
<i>Viburnum tinus</i>	0.01	0.07	0.43	0.20	0.11	0.07	0.34	1.47
Total	34.31	43.18	37.08	41.69	54.25	45.93	46.46	44.29

We performed all multivariate analyses with the CANOCO package (ter Braak and Šmilauer, 1998) and tested the eigenvalue of the axis with a Monte Carlo test using 200 iterations.

### 3. Results

Nine species were found in the canopy of the Moquinal stand, with *L. azorica* and *P. lusitanica* being the dominant species. Twelve species were found in the Aguirre stand, with *E. scoparia* and *M. faya* being dominant (Tables 1, 2 and 3). There are appreciable differences between canopy composition and seed bank composition, with species richness

much higher in the canopy (14 species) than in the germinated seed bank (eight species).

Eight tree species germinated in the 48 seed bank trays analyzed: four shade tolerant species (*L. azorica*, *Persea indica*, *Rhamnus glandulosa* and *V. tinus*) and four shade intolerant species (*E. arborea*, *E. scoparia*, *M. faya* and *Teline canariensis*). Although there was high variability in the number of germinating seeds between both seasons and sites, the total germination of shade intolerant species accounted for more than 80% of germination in all trays (Tables 1 and 2). The winter seed bank germination was ca. 10 times lower than in the summer, and remarkably low germination occurred in the winter seed bank of the Moquinal site.

Table 2

Total germination in the plots of Moquinal (plots 1, 2, 3 and 4) and Aguirre (5, 6, 7, and 8). The number is the total germination per plot considering the tree trays of each plot. This is the total germination after one year of incubation. This table present the results of the seed-bank collected in summer from June 1996 to May 1997

Species	Moquinal site					Aguirre site				
	1	2	3	4	Total	5	6	7	8	Total
<i>Erica arborea</i>	259	75	162	367	863	17	1	21	34	73
<i>Erica scoparia</i>	276	7	10	1	294	293	13	22	1	329
<i>Myrica faya</i>	16	–	1	35	52	–	8	2	2	12
<i>Rhamnus glandulosa</i>	–	–	–	1	1	–	2	–	–	2
<i>Teline canariensis</i>	–	–	–	–	–	4	2	–	–	6
<i>Viburnum tinus</i>	–	–	–	–	–	2	–	–	–	2
Total	551	82	173	404	1,210	316	26	45	37	424

Table 3

The table present the results of the seed-bank collected in winter from December 1996 to November 1997

Species	Moquinal site					Aguirre site				
	1	2	3	4	Total	5	6	7	8	Total
<i>Erica arborea</i>	1	–	–	1	2	4	36	1	2	43
<i>Erica scoparia</i>	–	–	–	3	3	13	97	–	2	112
<i>Myrica faya</i>	–	–	–	2	2	1	–	1	1	3
<i>Laurus azorica</i>	–	–	–	–	–	–	–	2	–	–
<i>Persea indica</i>	–	–	–	–	–	–	–	2	–	–
<i>Rhamnus glandulosa</i>	–	–	–	1	1	–	–	–	–	–
<i>Teline canariensis</i>	–	–	–	–	–	–	1	–	–	1
<i>Viburnum tinus</i>	–	–	–	–	–	–	–	–	2	2
Total	1	–	–	7	8	18	134	6	7	161

The germination of the majority of the species stabilized after 9 months, with the highest germination occurring in the 4th through 7th month for both Moquinal and Aguirre (Fig. 1). Shade tolerant species did not germinate after the 7th month, while shade intolerant species showed germination in some plots after the 10th month.

No woody plants germinated in the control trays, indicating no seed rain of woody species from the laurel forest in the greenhouse.

The ordination (Fig. 2) of the germination plot data for the year revealed that germination was dominated by *E. scoparia*, *E. arborea* and *M. faya*. Only one of the plots showed some minor differences with respect to the remaining plots. The winter seed bank of Aguirre plot 7 had occasional germination of shade tolerant species as *L. azorica* and *P. indica*. Some differences were evident between sites: *E. arborea* is more representative of Moquinal and *E. scoparia* is more representative of Aguirre.

The CCA axis using the explanatory variable ‘basal area versus germination’ explained a significant pro-

portion of the variability between basal area and seed bank germination in all analyses except for the analysis of Aguirre basal area and the winter germination composition (Table 4).

#### 4. Discussion

We showed that shade-tolerant species germinated during the first seven months, while shade-intolerant species germinated, in some cases, up to the 10th month. A higher persistence in the seed bank is a recognized character of shade intolerant species compared to shade tolerant species. Seed bank composition depends on the input of seeds of local plants and input from outside plant dispersal (Harper, 1977). Since the presence of shade intolerant species at Moquinal (*E. scoparia*, *E. arborea* and *M. faya*) is very low, so we infer that seeds of these species have great ability for long-distances dispersal, as another characteristic of this ecological group. The small size of the seeds with respect the other species allow a

Table 4

General results of the 4 CCA ordinations using the percentage of the basal area of the plots for the different sites and the percent germination for both the seasons

Explanatory variables	Eigenvalue	% variance species data	Montecarlo test <sup>a</sup>
Moquinal			
Basal area versus summer seed bank	0.820	46.7	$p < 0.05$
Basal area versus winter seed bank	0.655	57.9	$p < 0.05$
Aguirre			
Basal area versus summer seed bank	0.420	28.0	$p < 0.05$
Basal area versus winter seed bank	0.271	14.6	Not significant

<sup>a</sup> The null hypotheses is rejected when  $p < 0.05$ .

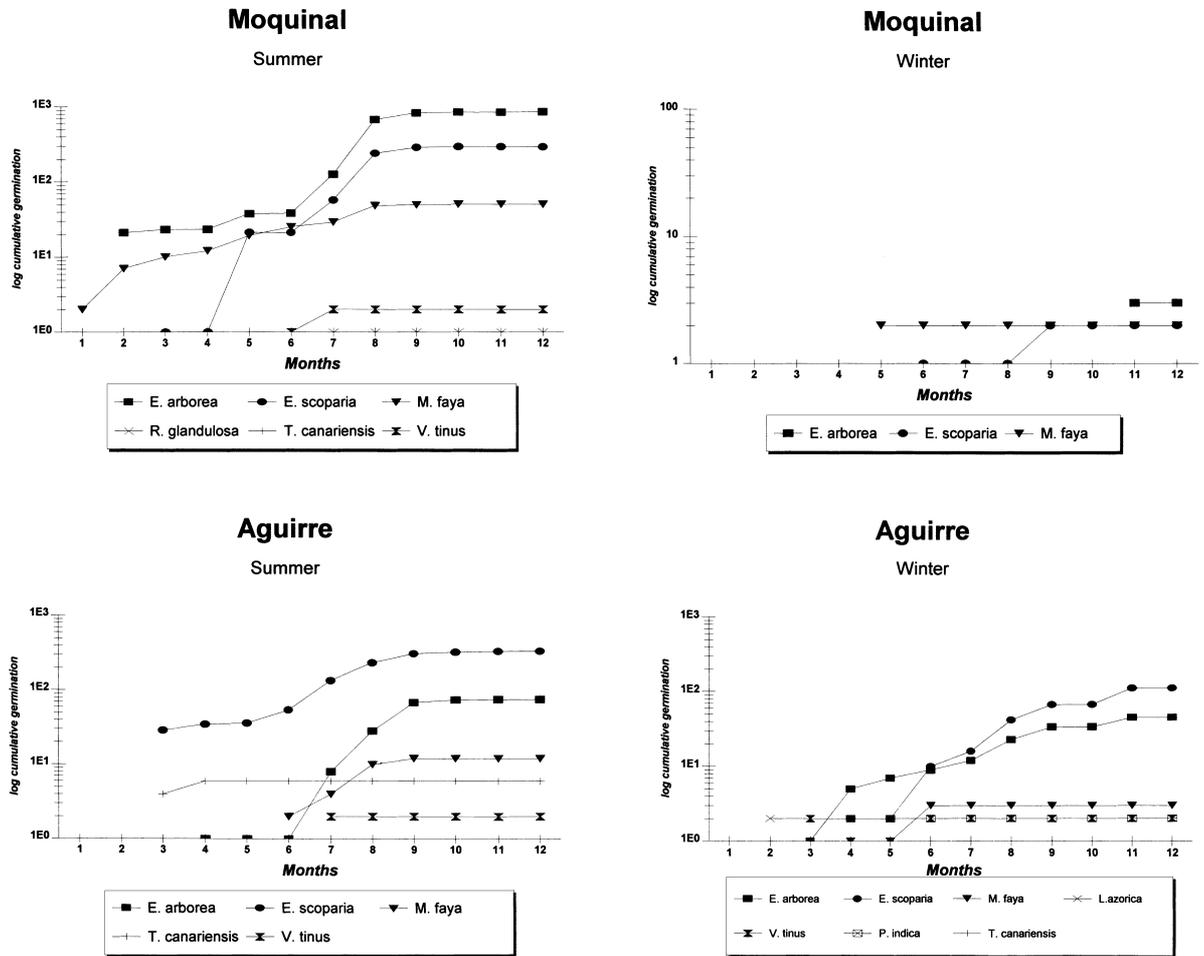


Fig. 1. Logarithm of the accumulative germination of the species in the seed bank collected in both seasons (winter and summer) for the sites (Moquinal and Aguirre).

greater long-distance dispersal. Although longevity could be another reason for the high number of shade-intolerant species germinating in the seed bank, previous seed banks monitored for 2.5 years (Fernández-Palacios and Arévalo, 1998) did not support this idea, since after the first 10 months, the germination of these species was infrequent. Shade tolerant species are species with larger seeds and much shorter latent periods. They have been called species with ‘Oskar’s syndrome’; they have sapling banks instead of seed banks (Silvertown, 1982).

The results of the seed banks in the present study, and the results of previous (Fernández-Palacios and Arévalo, 1998), both indicated high dominance of shade-intolerant species in the germinating seed-bank.

Although differences between the germination density of different trays were evident, we did not find differences in species composition of germinated seeds between plots (Moquinal versus Monte de Aguirre) nor seasons (winter versus summer) (Fig. 2). The three shade intolerant species (*E. scoparia*, *E. arborea* and *M. faya*) were generally dominant.

We expected significant differences between species composition in the seed banks and species composition in the canopy because they are typically similar only in areas of high disturbance (Pickett and McDonnell, 1989) or in particular ecosystems such as freshwater wetlands (Leck and Graveline, 1979). We found differences between standing vegetation and seed banks, except in one case: the winter

**Seed bank plots (winter and summer) and species scores**

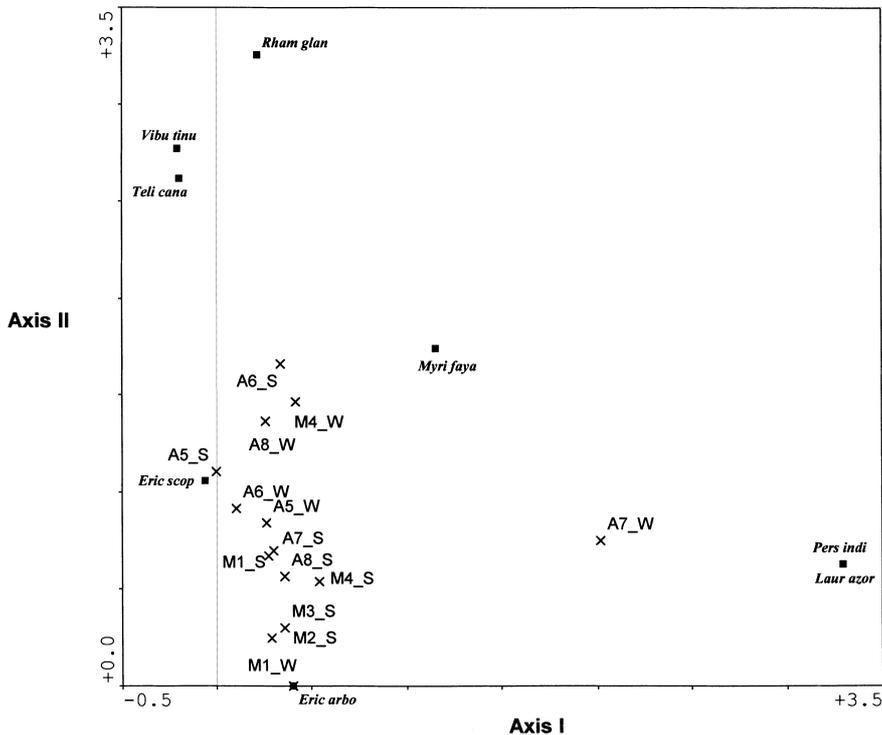


Fig. 2. Species and plot scores of the seed banks germination in both seasons. The site acronym follow the following nomenclature: sites (A for Aguirre and M for Moquinal), number of the plot and season in which the seed bank was collected (S for summer and W for winter). Species names are indicated with the four first letters of genus and species. We represent axis I and II of the DCA (Eigenvalues were 0.501 and 0.168 and the cumulative percentage of variance of both axis was 61.5%). Winter seed bank of plots 2 and 3 did not have occurrences.

seed bank composition of Aguirre showed no significant difference in canopy composition (with respect to the basal area parameter). This suggests high spatial and temporal variability of the seed bank, although a low statistical power due to the characteristics of the data (as low sample size) could be also suggest.

The canopy composition in Aguirre presents also a higher dominance of shade intolerant species that made similarities greater among seed bank and canopy composition. In the case of Moquinal, the seed germination is also decreased, but the dominance of shade tolerant species in the canopy does not allow similarities to exist between seed bank and canopy composition.

As in other studies (Warr et al., 1994), our study revealed high temporal and spatial variability of the seed bank. Nevertheless some generalities can be extracted from the results. The dominance of shade

intolerant species in the seed bank is common in later successional forests (Thompson, 1992). Shade tolerant species can not be detected easily in this kind of analysis. Furthermore, both *P. lusitanica* and *I. canariensis*, the dominant species of Moquinal, have been considered remnant species (Fernández-Palacios and Arévalo, 1998) that can be characterized by their tendency to produce banks of basal sprouts asexually.

We suggest that differences in composition among both stands are due to the different environmental conditions that do not allow to have a similar succession, leaving Aguirre site in a more earlier successional stage. It has been recognized that communities in a more advanced successional stage show higher differences between the species composition of the seed bank and canopy (Thompson, 1992). Also, a decrease in species richness of the seed banks during

succession has been indicated (Pickett and McDonnell, 1989). Due to the special characteristics of the seed bank data, multivariate analysis can be a useful tool for understanding the role of the seed banks in the forest dynamics.

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