

## From pine plantations to natural stands. Ecological restoration of a *Pinus canariensis* Sweet, ex Spreng forest

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### Abstract

We evaluated silvicultural thinning of pine plantations in order to determine the extent to which plantations treated in this way showed a greater structural similarity to natural stands. Specifically, we tested for differences in community structure (increase of DBH, increase of height and canopy height) and regeneration (seedlings and saplings <1, 1–2 and >2 years old) in response to thinning treatments (20% and 50% removal of density). We compared the variables of the thinned plots with those of the control plots (no thinning of living trees). Comparison of the structural variables between any treatments is of limited value due to the high intra- and inter-plot environmental variability (both slope and orientation affect tree growth to a significant degree). We therefore used ordination methods (Redundancy Analysis, RDA) to monitor covariation and to select non-redundant explanatory variables. We tested for differences between control and managed plots using Monte Carlo tests for the eigenvalues of the obtained axis of the RDA. Of the two treatments, only the 50% thinning treatment was significantly different from the control plots (in which only dead pines were thinned). In ten years, the basal area of pines showed a 10% increase in 50% thinned plots in comparison with the control plots. The number of saplings >2 years old was also significantly higher in 50% thinned plots. The control plots typically had an appreciably higher density of dead trees and a greater number of seedlings. Fifty percent thinning is having a positive effect on the naturalization of the stand but subsequent management will be needed to ensure establishment of advance regeneration.

### Introduction

Restoration is the process of reestablishing the structure and function of native ecosystems, and includes the development of management activities beneficial for humans (Moore et al. 1999). Plantations initially reflect high plant density and subsequently require thinning to reach the desired density (Smith et al. 1997). A restoration study needs to pinpoint an appropriate tree

density closely resembling the original structure of a given forest in order to allow natural regeneration. The use of silviculture to restore degraded stands ('naturalistic silviculture', Edminster and Olson 1996) has become very popular in the last decade.

The main objective of the plantations analyzed in this study is to restore the Canarian pine (*Pinus canariensis* Sweet, ex Spreng) forest, heavily disturbed as a result of intense logging

over the last 5 centuries, following the European colonization of the Canary Islands (Parsons 1981). In the last 60 years large areas of Tenerife have been reforested, but these initiatives have not been followed up with subsequent management or monitoring. In recent years, public authority forest managers have re-considered the usefulness of plantations, moving away from the idea of using them solely as a tool to control erosion towards management practices that will restore natural pine forest.

Unfortunately, little information is available on the pine forests' dynamics, and the few quantitative studies existing deal specifically with fire effects (Höllermann 2000; Arévalo et al. 2001).

We analyzed the changes that have occurred over the last 10 years in a 50 year-old plantation where thinning procedures, following the shelterwood method (McEvoy 2000), were applied to transform dense stands into natural-like pine forests. The method selected the best trees (in terms of DBH size and absence of infection) for retention. We also analyzed changes in regeneration density to determine whether thinning offered similar recruitment density and establishment to those found in natural stands. This variable can be measured accurately and precisely, so can be considered to be a very useful tool for the general purpose of this study (Block et al. 2001).

Although there are no remnants of natural forest in the studied area, we were able to study remnants of natural pine forest in other locations on the island with environmental characteristics similar to those we considered to be desirable for restored forest stands. We used that information to compare the effects of thinning procedures on the naturalization of the forest.

We aimed to test the following hypotheses: (1) Thinning has a positive effect on the 'quality' of vegetation structure, where 'quality' is a high resemblance between structure variables of the managed stand and the information that we have about a natural forest; (2) Sexual regeneration is enhanced by thinning, i.e. thinned stands have increased advance regeneration (< 2 year-old saplings) in comparison with densely planted stands. Thus, we also attempted to determine whether thinning favors self-maintenance of the stand or not.

## Materials and methods

### *Study site*

The study was conducted on the northeast slope of the Corona Forest Natural Park in Tenerife (28°19' N, 16°34' W), Canary Islands (Figure 1). The park extends over 46,636 ha, some 25% of which has been reforested with endemic *Pinus canariensis* (except for 2% of the reforested area, planted with *Pinus radiata*). These reforestations were carried out between 1930 and 1960 (del Arco et al. 1992). The sites selected for this study were planted between 1948 and 1952.

In the pine forest, situated mainly between altitudes of 1000 and 2000 m, *Pinus canariensis* is the dominant species, with a large area of potential distribution in Tenerife (del Arco et al. 1992). The dominant shrub species in the windward site are *Erica arborea*, *Adenocarpus viscosus* and *Chamaecytisus proliferus* while *A. viscosus* is dominant in the leeward site. A high number of annual and ruderal species are present at both sites, especially in the plots close to trails or those affected by other disturbances (Ceballos and Ortuño 1974). Nomenclature follows Hansen and Sunding (1985).

The annual precipitation in the studied area is 900 mm. The mean annual temperature is close to 12 °C with minimal annual and daily fluctuations. Frost events may occur but are uncommon (Peters 2001). Soils at the study site have been classified as order Entisol, suborder Orthens (Fernández-Caldas et al. 1985). Additional information on the sites can be found in Blanco et al. (1989).

### *Design of the experiment*

During the summer of 1988, park managers located the study site in the park. This site is representative of a larger area (around 1500 ha) of forest plantations with similar environmental conditions. The site can be divided into two parts, one facing south and the other north.

Three blocks comprising three 625 m<sup>2</sup> plots were established at each site (see Table 1 for abiotic parameters). Thinning started in all these blocks in 1988 following the shelterwood method. Thinning activities were carried out by a group of 5–10 men. No machinery was used in the plots,

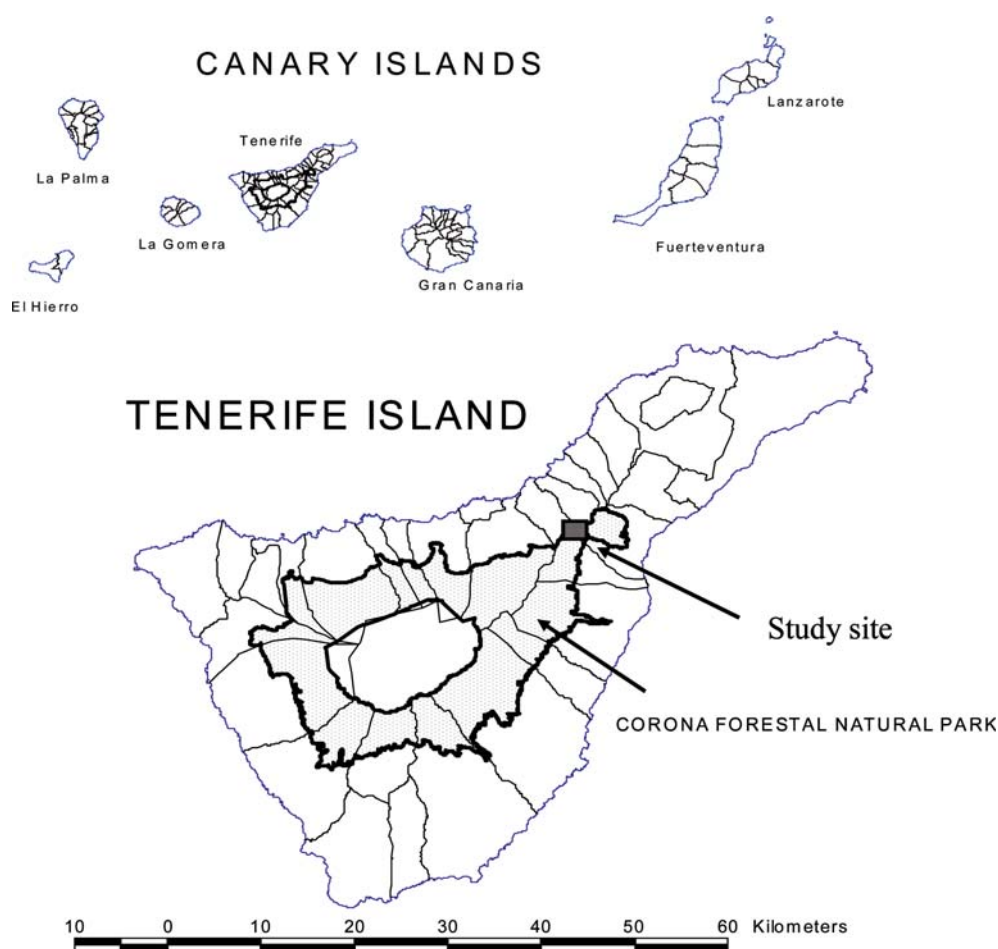


Figure 1. Map of the Canary Islands. On the map of Tenerife island the study area is indicated by a dark square (Corona Forestal Natural Park is also indicated).

and trees were extracted using poles from the road. Overtopped trees with smaller DBH size due to competition with other individuals for light or space or trees with some defect (such as infections or growth problems) were selected for cutting. All trees were even-aged.

The following treatments had previously been carried out in all the plots: elimination of dead trees in 1975 to avoid disease and a moderate thinning (around 5–10% of the density of overtopped trees in the plots) in 1982 (Anon 1989). The dead trees had died because they were completely overtopped by surrounding trees. In each plot we noted aspect, altitude and slope and measured canopy cover using a convex spherical densiometer (Lemmon 1957). Trees in each plot were classified by relative height as dominant, codominant,

intermediate and overtopped. Diameter at breast height (DBH) and the height of 30 trees chosen at random (in those plots in which 50% thinning had left fewer than 30 trees standing all the remaining trees were measured) was measured. One of three treatments was randomly assigned to each plot: control plots (elimination of dead trees only); 20% thinning (thin20%); 50% thinning (thin50%). Only intermediate and overtopped trees were eliminated. Thinning over 50% can promote the production of heliophitic species, which we try to avoid (Smith et al. 1997). During the summer of 1999, both sites were resampled, and we measured DBH, tree height, canopy height (height of the canopy of each tree, measured from the first live branch) and the number of trees which had died since 1988 (Anon 1989).

Table 1. General abiotic characteristics of the plots.

Treatments*	Codes	Aspect	Slope (°)	Elevation (m)	Cover classes**			Canopy cover (%)
					Rock	Soil	Litter	
Control	a	N	15	1670	2	2	9	90
Control	a	N	15	1685	2	1	9	95
Control	a	N	14	1675	4	3	9	90
Control	a	S	12	1600	4	2	9	90
Control	a	S	15	1580	2	3	9	95
Control	a	S	4	1620	5	1	9	95
thin20%	b	N	13	1640	3	1	9	85
thin20%	b	N	18	1680	3	1	9	90
thin20%	b	N	24	1675	3	4	9	85
thin20%	b	S	4	1600	5	2	9	88
thin20%	b	S	25	1610	1	3	9	85
thin20%	b	S	8	1620	5	1	9	90
thin50%	c	N	3	1640	4	1	9	80
thin50%	c	N	14	1680	2	1	9	85
thin50%	c	N	37	1680	3	3	9	80
thin50%	c	S	4	1590	5	1	9	85
thin50%	c	S	31	1600	2	4	9	75
thin50%	c	S	17	1600	4	2	9	85

\*Control: Control plots; thin20%: Plots with 20% treatment; thin50%: Plots with 50% thinning.

\*\*Cover classes: 1: traces, 2: 0–1%, 3: 1–2%, 4: 2–5%, 5: 5–10%, 6: 10–25%, 7: 25–50%, 8: 50–75%, 9: > 75%.

In July 2000, we recorded the number of seedlings (S) as individuals with cotyledons, and saplings aged <1 year old (S1) with no presence of cotyledons, 1–2 years old (S2) and >2 years old (S3). Our personal observation in the studied area over the last 15 years indicated a low level of disturbance (such as litter collection, excessive human trampling or just recreational use) commonly found in other areas.

### Statistical analysis

We evaluated the increase in DBH (calculated as the mean of the growth percentage of DBH for all the trees per plot), increase in height (calculated in the same way), canopy height (height of the first branch of the stem >2.5 cm in diameter), dead trees, S, S1, S2 and S3 density with respect to the treatments, using an ANOVA and *post-hoc* Tukey's tests to detect differences between groups. We used the Shapiro–Wilks test to test the normality of the data. We used increase in DBH and increase in height instead of values of DBH or height because the latter ones are directly related to the treatment.

Ordination techniques can help to explain community variation and distribution of species

with respect to environmental gradients (Gauch 1982) and can be used for purposes other than species ordination, as is the case with Principal Components Analysis, originally developed in fields other than ecology or Correspondence Analysis (de Miguel et al. 1997). We performed three Redundancy analyses (RDA, Rao 1964) with plots control and thin20% plots, plots control and thin50% and thin20% and thin50% plots. Canonical Analyses such as RDA are useful when one wishes to relate a table of variables (commonly a species matrix) to another matrix (environmental matrix or explanatory variables matrix) (Legendre and Legendre 1998). In this case we used the variable matrix rather than a species matrix. RDA is the canonical form of PCA (Jongman et al. 1987) and it allows us to constrain all the variation in the analysis to the explanatory variable matrix. The scores are restricted by these variables. Using RDA rather than CCA (more popular in vegetation studies) ensured an automatic standardization of the variables because we used the correlation matrix to carry out the analysis. RDA was also deemed suitable given the linear distribution of the variables in relation to the explanatory variable.

The variables used in the matrix were: the mean percentage of increase in basal area, the

mean percentage of increase in height, the mean percentage of trees with canopy, the number of S, the number of S1, the number of S2, the number of S3 and the number of dead trees.

One explanatory variable, a dummy variable, indicated whether the plot was control vs. thin20% or control vs. thin50% (or thin20% vs. thin50%, when two treated plots were compared). Because there is only one variable, there is only one RDA axis, and the variables' scores along this axis represent the degree to which the variable represents control or managed treatments. The axis is also a convenient index for measuring which of the variables are responding more intensively to the treatment. We incorporated a covariable matrix, thereby ensuring the elimination of any variation produced by the covariables and restricting the analysis to residual variability (ter Braak 1988). The covariables were site (north or south) and slope, since these variables could interfere with the results of the analysis, given the degree to which they affect growth rate. Areas with higher slopes present a less organic soil horizon. Moreover, north-facing plots show some differences in rainfall and temperature in comparison with south-facing plots (Ceballos and Ortuño 1974).

By testing the significance of the axis using a Monte Carlo test, we can determine whether samples are distributed randomly for the explanatory variable. If the eigenvalue of the axis is higher than the eigenvalue of the randomized samples composition, we can conclude that the axis is useful for separating samples, and that the explanatory variable has a significant effect on the group of variables analyzed.

This approach is useful to test for significant effects of explanatory variables on species composition (Arévalo and Fernández-Palacios 1998, 2000). The difference here is that we tested the effect of treatments (explanatory variable) on different variables rather than on different species.

We performed all the 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 of the samples. Basic statistical methods followed Zar (1984) and were applied using the SPSS statistical package (SPSS 1986).

## Results

There was a high degree of variability in basal area before treatments, from 43 to 73 m<sup>2</sup>/ha. Even in treatment A, some trees were removed because they were dead. This degree of variability is directly related to the different environmental conditions of each plot (Table 2). Pine height was not significantly different in the various treatments. Sprouts were present only in C-plots (except for two plots, with resprouts of cut trees). Sprouting is an important characteristic of *Pinus canariensis*, but it was not very high in the analyzed plots. Density after treatment was obviously related to the treatment applied, with a decrease of between approximately 1% (control plots) and 55% (50% thinned plots).

We used the information about regeneration and density in some plots of natural stands of pine forest in Tenerife for comparisons with the control plots and managed plots of our study (Table 3). Unfortunately, the size of the plots is different and also information such as basal area is not provided for the natural stands. However as we mentioned above, the information available on natural stands can be useful to evaluate the results of the treatments.

The increase in DBH (mean increase per plot as a percentage) was significantly different between control and both treatments and between treatment plots ( $p < 0.001$ ). Mean increase in DBH was ca. 25% in treatment thin50% (Figure 2a). The percentage of increase in height between treatments was not significantly different (Figure 2b). Dead trees (after the first sampling in 1988) were significantly more abundant in control ( $> 100$ /ha) and 20% thinning treatment ( $> 10$ /ha) than in 50% thinning treatment (no dead trees) ( $p < 0.001$ ; Figure 2c). The increase in the percentage of canopy height did not reveal any difference between treatments (for a  $p < 0.05$ , Figure 2d).

There were no significant differences in regeneration between treatments in any of the categories established. S1 saplings were roughly equally abundant in the three treatments. There were also a high number of S3 saplings in treatment c, but the high degree of variability did not allow us to differentiate between treatments (Figure 2e).

The axes resulting from the different RDAs are shown in Figure 3. The only explanatory variable

Table 2. Biotic characteristics of the canopy in each plot.

Treatments	Codes	Density (Ind/ha)		Basal area (m <sup>2</sup> /ha)			Mean height (m)				Sprouts (ha)	Tree canopy height (m)	
		1988	1999	1988	1988	1999	1988		1999		1999	1999	
		<u>Bt*</u>		<u>Bt*</u>	At**		Mean	Std.***	Mean	Std.		Mean	Std
Control	a	1088	992	62.56	60.46	71.21	16.77	4.60	19.84	3.94	0	10.40	2.34
Control	a	1392	1056	69.03	62.04	70.94	16.91	5.39	21.37	2.66	0	12.92	2.52
Control	a	992	992	56.54	56.54	67.64	17.89	6.51	20.43	4.19	0	10.22	2.47
Control	a	1456	1424	59.76	59.26	75.24	15.49	6.15	18.06	2.08	0	10.48	2.64
Control	a	1664	1520	65.65	62.50	73.76	15.52	2.07	19.43	2.25	0	11.89	2.37
Control	a	2448	1920	73.24	66.98	81.88	15.95	5.20	18.76	2.07	0	12.65	1.76
thin20%	b	752	656	53.35	49.21	65.30	16.77	7.10	24.15	2.15	0	13.17	1.62
thin20%	b	1312	896	69.90	58.07	70.58	16.47	6.43	21.97	2.85	0	11.32	2.32
thin20%	b	752	656	50.52	47.30	61.08	14.28	8.02	22.64	3.17	0	9.71	2.16
thin20%	b	1504	1216	58.15	50.23	63.87	15.88	4.29	18.71	2.00	224	11.11	2.07
thin20%	b	1600	1264	52.62	44.97	51.97	14.25	1.70	16.47	2.59	624	10.35	1.95
thin20%	b	2000	1360	68.32	55.89	64.59	15.99	3.51	20.16	3.12	0	14.12	2.91
thin50%	c	800	352	52.06	24.94	36.44	16.63	5.28	23.25	1.97	176	12.43	2.41
thin50%	c	704	368	45.89	27.37	39.82	17.79	3.65	22.33	1.66	176	9.72	1.69
thin50%	c	928	352	49.62	26.50	36.76	17.27	2.91	20.50	2.31	48	7.24	1.21
thin50%	c	1312	528	54.93	29.89	41.15	17.39	5.92	19.59	1.42	1792	9.63	1.74
thin50%	c	1600	800	43.81	27.09	34.90	16.18	1.58	20.16	2.22	256	10.47	2.38
thin50%	c	1488	544	60.76	29.81	40.32	17.27	5.39	20.58	2.34	992	10.97	1.99

\*Bt: Before thinning.

\*\*At: After thinning.

\*\*\*Std.: Standard deviation.

Table 3. Biotic characteristics of several plots in natural stands of Tenerife (Blanco et al. 1989).

Stand	Plot size (m <sup>2</sup> )	Density (ind./ha)	Regeneration (ind/ha)	Comments
Vilaflor	225	180	< 10	Natural stand
Pinar	225	490	< 10	Natural stand
Chio	225	220	< 10	Natural stand
Chafa	225	130	< 10	Natural stand

used in the analyses was control-treatment (thin20% for 20% thinning or thin50% for 50% thinning, indicated on the right of the graph), with the exception of axis number I (Figure 3), which used thin20% vs. thin50% plots. This is a dummy variable, indicating 1 for the control plot and zero for the managed plots. This axis is interpreted as a response to management: the stronger the response, the more positive the score of the variable, except where the treatment gives rise to a decrease in the value of the variable, in which case the scores will drop as the value of the variable decreases.

We tested the eigenvalue of each axis with the Monte Carlo test. The only significant eigenvalue

observed was for the RDA axis III using control plot and treatment c ( $p < 0.01$ ), suggesting that for the studied variables, only treatment C shows significant differences. These differences can be specified with the variables' scores. In this analysis basal area (ba) showed an important increase in comparison with control plots. Dead trees were present in control plots and almost absent in the managed plots. There was an appreciable increase of S2 and S3 saplings in the managed plots. S were significant in the control plots, probably due to the higher density of these plots and canopy height showed also higher values in these plots.

Because the RDA axes I and II did not show significant differences with respect to a random model, differences can not be related to the treatment, although it is worth noting that variables along the RDA showed the same pattern as in the control-treatment C analysis.

## Discussion

Although there is no information about natural stands in this area, it is possible to compare the

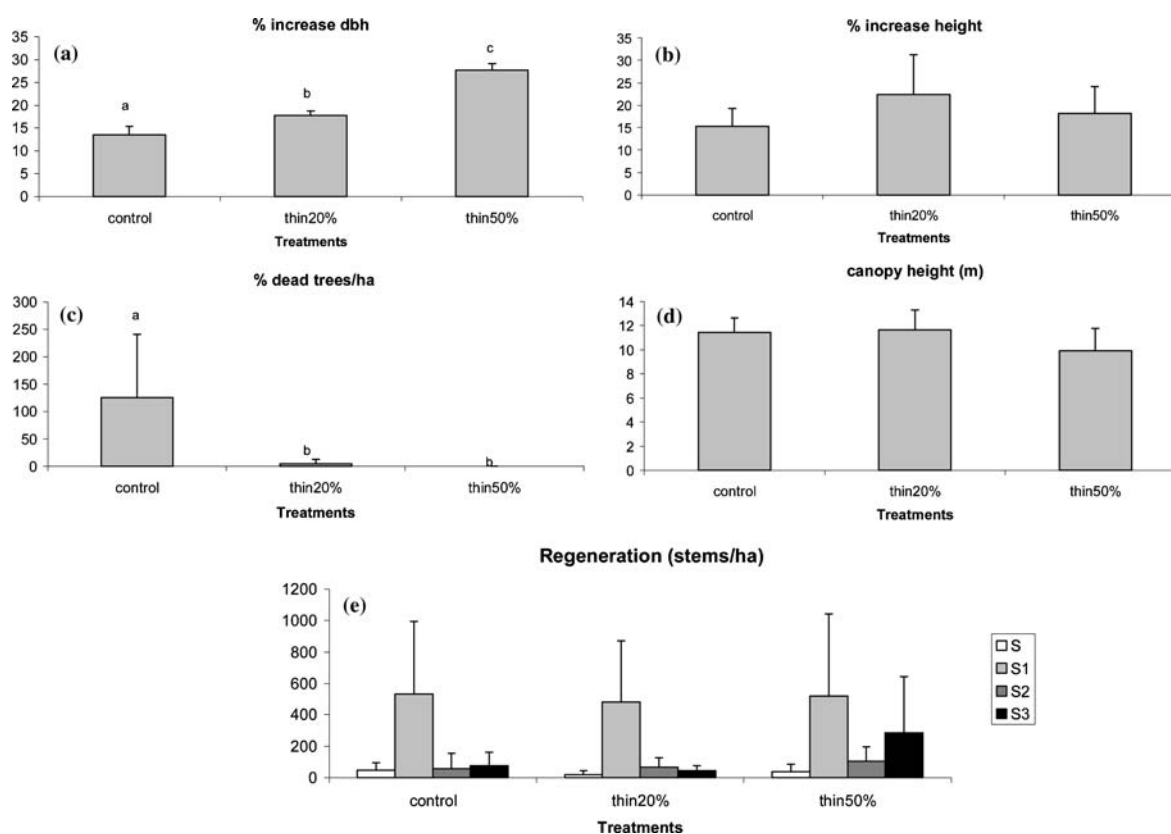


Figure 2. For each different treatment (a: control, b: 25% thinning, c: 50% thinning): (a) Mean increase in DBH for each treatment, (b) Mean percent increase in height, (c) density of dead trees/ha, (d) Mean depth of the canopy and (e) density for seedlings 'S', saplings less than 1 year old 'S1', saplings between 1 and 2 years old 'S2' and saplings older than 2 years 'S3'. Each graph includes the three different treatments. Bars reflect standard deviation. Identical letters above the bars indicate non-significant differences (control: control plots; thin20%: 20% thinning treatment of the plots; thin50%: 50% thinning treatment of the plots).

results with some small remnants of natural stands of pine forest. Although these natural stands have not been monitored in recent years, some of their characteristics can be compared with the plots analyzed in this study to evaluate the effect of the restoration activity. Alternative approaches, such as the use of areas considered natural in different parts of the islands, are needed to evaluate the success of restoration (Block et al. 2001). Density and regeneration are much lower in natural stands than in plantations, as is regeneration density. These parameters can be considered indicators of naturalness of the stand (Blanco et al. 1989 del Arco et al. 1992).

The different thinning intensities used in this study showed that a 50% removal of basal promotes natural stand replacement, with a lower incidence of dead trees and increased establishment of saplings > 2 years old. Other variables

used in the analysis, such as canopy height (the height of the stem at which branches > 2.5 cm of diameter are present) and seedling density, indicated that control plot pines develop more branches along the stem, while trees in managed plots, have larger canopy diameters as a result of the extra space, and therefore a larger surface area of leaves receiving direct solar radiation. Seedlings are also more abundant in control plots (in relation to the overall high density of trees). Moreover, the 50% thinning treatment results in a tree density closer to natural stands (Table 3).

One direct effect of thinning is a reduction in density. Should there be a wild fire, it is more likely to be a surface fire than a catastrophic one, which may be difficult to control if it threatens properties or infrastructures. The Canarian pine forest has a low rate of fires, but when fires occur, they are catastrophic because of the high density of trees

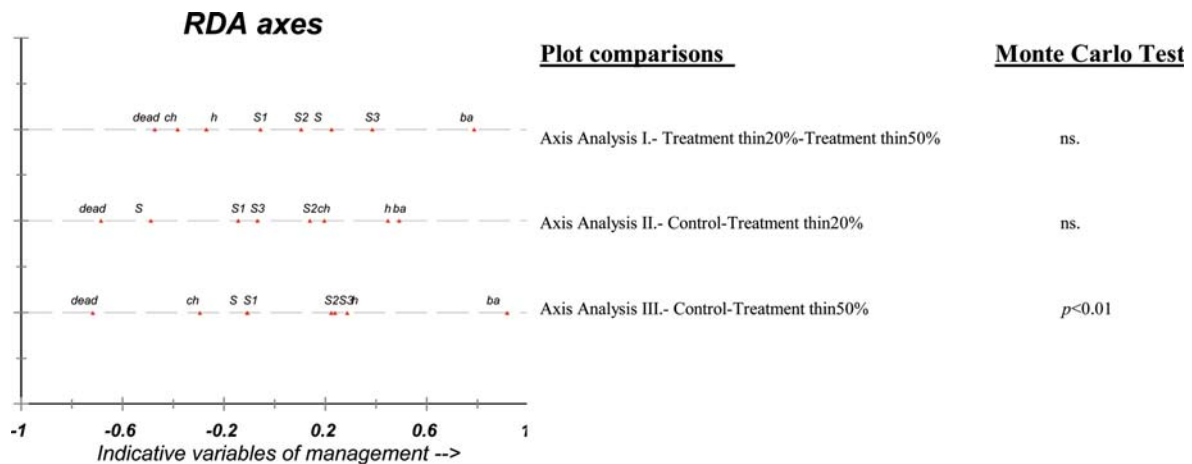


Figure 3. Variable scores of RDA-axis I. Each horizontal line is the axis of a different analysis, each using control plot vs. treatment as the explanatory variable. To the right of the graph we have specified the plots used in the analyses (control, treatment thin20% or treatment thin50%). The eigenvalues and the percentages of explained variance for these axes were: Axis I: 0.159 and 24.1%, Axis II: 0.122 and 17.5% and Axis III: 0.207 and 30.1%. The Monte Carlo test indicated that the only significant axis was Axis III (for  $p < 0.01$ ; for the others we indicated ns: non significant for a  $p < 0.05$ ). (ba: mean percentage increase in the basal area; h: mean percentage increase in height; ch: mean depth of the canopy; dead: density of dead trees; S: density of seedlings; S1: density of saplings less than one year old; S2: density of saplings between 1 and 2 years old; S3: density of saplings older than two years).

and the suppression of fire over the last 50 years (Arévalo et al. 2001).

The results from the 20% thinning plots offered similar patterns to the 50% thinning plots as compared to the control plots. However, the lack of significance in the ordination for the 20% thinned plots (Figure 3) indicates that the changes are not large enough in this case to detect differences between control and treatment plots.

Based on the structure of the canopy and on the dynamics of regeneration demonstrated by Blanco et al. (1989) in different natural pine forest of the archipelago, we suggest that the managed plots are closer to a natural stand and that they will be easier to manage. Regeneration suggested by the data (saplings and sprouts) and growth of the trees revealed a healthy situation with low mortality. While waiting for a larger data set we suggest that 50% thinning intensity is a valuable tool for stand restoration, although natural regeneration can not be assured without subsequent management.

Thinning has been extensively used as a stand restoration tool over the last decade (Cochran and Barret 1993; Edminster and Olson 1996; Feeney et al. 1998; Moore et al. 1999; Stone et al. 1999) as opposed to the traditional use of this technique as a way of making stands more commercially productive (Sucoff and Hong 1974; Clark et al. 1994;

Baldwin et al. 2000). The first direct result is that thinning can be applied to obtain natural tree density. The results obtained indicated that the treatments did not transform plantations into natural stands, but increased the similarities between the two, with a reduction in stand density and in regeneration rate, which was very high in the plantation control plots.

Restoration proposals aim to be suitable for widespread application. The design of experiments should therefore be stricter (Block et al. 2001) and should include, for example, monitoring for pseudoreplication and obligatory statistical testing of hypotheses. High levels of variability, together with the fact that many different variables may be used in the analysis, constitute important problems. We want to discriminate which variables offer the most valuable information about the management practice in question. Due to the special characteristics of the dataset of managed plots under thinning practices, multivariate analysis can be a useful tool for understanding the effect of thinning on plot variables and on stand restoration.

Analyzing variables individually, we detected many variables that did not show significant difference between treatments (regeneration, percentage increase of height or canopy height). This can be interpreted as a null effect of the treatment



on the variable (Figure 2). Using multivariate analysis we can extract more information from the group of variables, and ordinate the variables in relation to how they are affected by the management.

With respect to the hypothesis about the similarities between thinned stands and natural stands, we can state that the decrease in density of the stems, together with the decrease in regeneration densities, approximates the thinned stands to natural stands (Table 3). Moreover, other characteristics, such as a higher growth rate of DBH and height and a lower canopy height, are related to characteristics of natural stands. We can conclude that 50% thinning is having a positive effect on the naturalization of the stands but subsequent management will be needed to assure the establishment of advance regeneration. However, other variables, such as wildlife composition or other structural stand variables, should be included to complete the information about the restoration practice.

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### References

- Anon 1989. Estudio de la selvicultura de las masas artificiales de *Pinus canariensis* Sweet, ex Spreng. Dirección General de Medio Ambiente, Gobierno de Canarias. S/C de Tenerife y Madrid.
- Arévalo J.R. and Fernández-Palacios J.M. 1998. Treefall gap characteristics and its influence on regeneration in the laurel forest of Tenerife. *J. Vege. Sci.* 9: 297–306.
- Arévalo J.R. and Fernández-Palacios J.M. 2000. Seed bank analysis of tree species in two stands of the Tenerife laurel forest (Canary Islands). *For. Ecol. Manage.* 130: 177–185.
- Arévalo J.R., Fernández-Palacios J.M., Jiménez M.J. and Gil P. 2001. The effect of fire in the understory of two reforested stands of *Pinus canariensis*. Tenerife. Canary Islands. *For. Ecol. Manage.* 148: 21–29.
- Baldwin V.C.Jr., Peterson K.D., Clark A.III, Ferguson R.B., Strub M.R. and Bower D.R. 2000. The effects of spacing and thinning on stand and tree characteristics of 38-year-old Loblolly Pine. *For. Ecol. Manage.* 137: 91–192.
- Blanco A., Castroviejo M., Fraile J.L., Gandullo J.M., Muñoz L.A. and Sánchez O. 1989. Estudio ecológico del pino canario. Serie Técnica No. 6. Ministerio de Agricultura, Pesca y Alimentación. Madrid.
- Block W.M., Franklin A.B., Ward J.P.Jr., Ganey J.L. and White G.C. 2001. Design and implementation of monitoring studies to evaluate the success of ecological restoration on Wildlife. *Restor. Ecol.* 9: 293–303.
- Ceballos L. and Ortuño F. 1974. Vegetación y flora forestal de las Canarias Occidentales. 2nd. Cabildo Insular de Tenerife, S/C de Tenerife.
- Clark A.III, Saucier J.R., Baldwin V.C.Jr. and Bower D.R. 1994. Effect of initial spacing and thinning on lumber grade yield and strength of loblolly pine. *For. Prod. J.* 44: 14–20.
- Cochran P.H. and Barret J.W. 1993. Long-term response of planted ponderosa pine to thinning in Oregon's Blue Mountains. *West J. Appl. For.* 8: 126–132.
- del Arco M.J., de Paz P.L., Salas M. and Wildpret W. 1992. Atlas cartográfico de los pinares canarios. II Tenerife. Viceconsejería de Medio Ambiente, Santa Cruz de Tenerife.
- de Miguel J.M., Rodríguez M.A. and Gómez-Sal A. 1997. Determination of animal behavior-environment relationships by Correspondence Analysis. *J. Range Manage.* 50: 85–93.
- Edminster C.B. and Olson W.K. 1996. Thinning as a tool in restoring and maintaining diverse structure in stands of southwestern ponderosa pine. In: Covington W.W. and Wagner P.K. (eds), *Convergence on Adaptive Ecosystem Restoration and Management*, Flagstaff, Ariz. USDA, For. Serv. Gen. Tech. Rep. No. RM-GTR-278 pp. 62–68.
- Feeney S.R., Kolb T.E., Covington W.W. and Wagner M.R. 1998. Influence of thinning and burning restoration on pre-settlement ponderosa pines at the Gus Pearson Natural Area. *Can. J. For. Res.* 28: 1295–1306.
- Fernández-Caldas E., Tejedor M. and Quantin P. 1985. Los suelos volcánicos de Canarias. Servicio de Publicaciones de La Universidad de La Laguna, La Laguna.
- Gauch H.G.Jr. 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge.
- Hansen A. and Sunding P. 1985. Flora of Macaronesia. Checklist of vascular plants. 3rd. rev. ed. *Sommerfeltia* 1: 1–167.
- Höllermann P. 2000. The impact of fire in canarian ecosystems 1983–1998. *Erkunde* 54: 70–75.
- Jongman R.H.G., ter Braak C.J.F. and van Tongeren O.F.R. 1987. *Data Analysis in Community Landscape Ecology*. Pudoc, Wageningen.
- Legendre P. and Legendre L. 1998. *Numerical ecology*. 2nd ed. *Developments in Environmental Modelling* 20. Elsevier, Amsterdam.
- Lemmon P. E. 1957. A new instrument for measuring forest overstory density. *J. For.* 55: 667–668.

- McEvoy T.J. 2000. Introduction to Forest Ecology and Silviculture. Natural Resources, Agriculture and Engineering Service, Ithaca.
- Moore M.M., Covington W.W. and Fulé P.Z. 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. *Ecol. Appl.* 9: 1266–1277.
- Parsons J.J. 1981. Human influence in the pine and laurel forest of the Canary Islands. *Geogr. Rev.* 71: 253–271.
- Peters J. 2001. Ecofisiología del pino canario. PhD Thesis dissertation, Universidad de La Laguna, La Laguna.
- Rao C.R. 1964. The use and interpretation of principal component analysis in applied research. *Sankhya A* 26: 329–358.
- Smith D.M., Larson B.C., Kelty M.J. and Ashton P.M. 1997. The Practice of Silviculture. Applied Forest Ecology. 9th ed. John Wiley and Sons, Inc, New York.
- Stone J.E., Kolb T.E. and Covington W.W. 1999. Effects of restoration thinning on presettlement *Pinus ponderosa* in northern Arizona. *Restor. Ecol.* 7: 172–182.
- SPSS. 1986. SPSS/PC+ V.6.0. Base Manual. SPSS Inc, Chicago, IL.
- Sucoff E. and Hong S.G. 1974. Effects of thinning on needle water potential in red pine. *For. Sci.* 20: 25–29.
- ter Braak C.J.F. 1988. Partial canonical correspondence analysis. In: Bock H.H. (ed.), *Classification and Related Methods of Data Analysis*. North-Holland, Amsterdam, pp. 551–558.
- ter Braak C.J.F. and Šmilauer P. 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). Microcomputer Power, Ithaca, NY.
- Zar J.H. 1984. *Biostatistical Analysis*. 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.