



Effects of thinning on seed rain, regeneration and understory vegetation in a *Pinus canariensis* plantation (Tenerife, Canary Islands)

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ABSTRACT

Stand density management in even-aged coniferous plantations may increase biodiversity and enhance natural tree regeneration. Thinning of pine plantations has only recently been started on the Canary Islands, yet the ecological effects of this treatment are relatively unknown. Our objective was to investigate the impact of thinning on pine seed rain, natural pine regeneration and diversity of understory vegetation in *Pinus canariensis* plantations. Seven years after thinning, we sampled 60-year old plantations thinned by 60% of basal area, unthinned stands and adjacent semi-natural old-growth forests. Thinning significantly increased pine seed rain to levels similar to semi-natural stands. This is probably a result of fast crown development and enhanced cone production due to the immediate release of resources and reduction in competition. In contrast, plantations with the highest tree densities had very low seed production, limiting pine regeneration. Seed rain showed seasonal fluctuations with clear summer peaks of seed release. Thinning also significantly increased seedling, sapling and juvenile densities. However, thinned plantations still differed from old-growth forests in seedling and juvenile densities. Thinning promoted understory plant diversity, including typical endemic pine forest species, without triggering plant invasion, which is of great conservation interest. This study provides evidence that heavy thinning represents an important management tool to enhance naturalization and local biodiversity of Canary pine plantations, common in large areas of this Archipelago.

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1. Introduction

Thinning is a silvicultural technique that has traditionally been used to increase growth of residual trees (Smith et al., 1997). Remaining trees can use the released resources, such as light, water and nutrients, to expand their crowns and to grow faster in diameter (Mäkinen and Isomäki, 2004; González-Ochoa et al., 2004; Crecente-Campo et al., 2009; Pérez-de-Lis et al., 2011). Following silvicultural practices, thinning intensity is recommended to be kept low or moderate to restrict growth of understory shrubs or undesirable trees as well as to avoid the risk of wind damage soon after thinning (Smith et al., 1997). Furthermore, thinning strategies in even-aged coniferous forests have also been proposed to preserve biodiversity and to facilitate natural regeneration and the structural recovery of the forest (Bailey and Tappeiner, 1998; Montes et al., 2004; Zald et al., 2008; Ares et al., 2010). Even-aged plantations can be transformed into uneven-aged stands, as the opening of the canopy (available light) favors the establishment and survival of shade-intolerant trees and understory plant species (Zhu et al., 2003; Ares et al., 2010). When focusing on forest ecosystem restoration, thinning intensity should be high enough to

offer sufficient space between remaining trees to allow for the natural regeneration of target species, depending on their regeneration requirements, especially their shade tolerance. This type of stand density reduction has also been termed “shelterwood regeneration cutting” (Smith et al., 1997). With heavy thinning, intensity greater than 50% of density or basal area, an increase in the natural regeneration of light-demanding pioneer conifers has been observed (Smith et al., 1997). Not only do micro-environmental conditions for seed germination and seedling establishment change following heavy thinning (Hale, 2003; Ma et al., 2010), but also seed production of remaining trees might increase (Verkaik and Espelto, 2006; Peters and Sala, 2008), which could accelerate natural regeneration (Shepperd et al., 2006; Zald et al., 2008).

Recently, enhancing biodiversity has also become a focus in forest management (Keenan et al., 1997; Ares et al., 2010). In this context, thinning has been found to alter understory vegetation and, generally, increase abundance and richness of not only understory plant species (Parker et al., 2001; Chan et al., 2006; Metlen and Fiedler, 2006; Wolk and Rocca, 2009; Ares et al., 2010), but also birds (Luck and Korodaj, 2008; García-del-Rey et al., 2010), other vertebrate groups (Thompson et al., 2003) and insects (Taki et al., 2010). Occasionally, thinning has a negative or no effect on plant richness (Nagai and Yoshida, 2006; Lei et al., 2007; Taki et al.,

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2010). Stand density reduction can also trigger the colonization of non-native plants (Dodson and Fiedler, 2006; Miller and Seastedt, 2009). These findings are of special interest for forest managers on oceanic islands, since these are particularly prone to invasions by alien species, due to their unique ecological and biogeographical conditions (Denslow et al., 2009).

Canary pine forest, usually formed exclusively of *Pinus canariensis* Chr. Sm. Ex DC in Buch, was heavily disturbed and logged during the last five centuries following the European colonization of the Canary Islands (Parsons, 1981). Between 1945 and 1980, about 11,500 ha of pine forest have been reforested on Tenerife (Del Arco et al., 2006) in order to restore the original pine forest area. Today, pine stands of the Canary Islands are not managed anymore for timber production, but instead the Canarian authorities intend to naturalize these even-aged afforestations by heavy thinning in order to improve natural regeneration, structural complexity and biodiversity. However, the effects of this management practice on pine regeneration and understory vegetation have rarely been assessed. Arévalo and Fernández-Palacios (2005) evaluated, for the first time, the impact of an experimental thinning of Canary pine plantations performed in 1988 in northeastern Tenerife and reported that only heavy thinning (50% removal of density) increased tree size, dbh and density of certain sapling classes. Another study in the same region revealed that thinning intensities had different effects on each regeneration category (Arévalo and Fernández-Palacios, 2008), probably due to the small plot size (625 m²) used in the thinning trial. The fast closure of the canopy from the plot edge after thinning and the corresponding changes in light conditions did not probably allow functional pine regeneration. Finally, Perez-de-Lis et al. (2011) confirmed, applying dendroecological methods, that thinning intensity and aspect greatly influenced growth of Canary pine afforestations. The effect of thinning on seed rain and understory vegetation was never studied in this type of plantations.

In 2002, the Canarian authorities carried out thinning activities of dense pine plantations on Tenerife in a much larger area and with an even higher intensity of 60% of basal area, in order to facilitate functional pine regeneration and enhance biodiversity. This gave us the opportunity to investigate the effects of this management procedure on pine seed rain, natural pine regeneration and understory vegetation 7 years after thinning. We compared thinned stands with unthinned control plots and adjacent semi-natural old-growth forest. We hypothesized that pine seed production should increase after thinning due to canopy openness and the release of intra-specific competition, which should favor crown and cone development. Pine regeneration should also increase as a result of improved seed and light availability on the forest floor. We also expected that the composition and structure of the understory vegetation would change and species richness would increase after thinning. Finally, we still expected differences between thinned pine stands and semi-natural old-growth forest with respect to the analyzed parameters due to existing differences in stand structure.

2. Material and methods

2.1. Study site

The study was conducted in the northeast part of the Corona Forestal Nature Park in Tenerife, Canary Islands (Fig. 1). The park has an extension of about 46,300 ha, of which 25% has been reforested with *P. canariensis* between 1945 and 1980 (Del Arco et al., 2006). The stands selected for this study were planted 60 years ago (1949–1953). On Tenerife, the potential area of the endemic monospecific *P. canariensis* forest ranges from 1000 to 2000 m

a.s.l. on the northern windward slope of the island and between 800 and 2300 m a.s.l. on the southern leeward slope. Study sites are all located between 1200 and 1600 m a.s.l. at the mountain crest called “Cumbre Dorsal” (Table 1), where mean annual precipitation reaches 900 mm and mean annual temperature is 13 °C. Climate is Mediterranean with most of the rain falling between October and March and with dry and hot summers. Fog drip, caused by the dominant northeastern trade winds, can improve water availability at exposed sites (Kämmer, 1974; Aboal et al., 2000). Therefore, the study area can be divided into a slightly more humid windward slope and a drier leeward slope, although differences might not be very pronounced since distances between sites do not exceed 2 km. Slope inclination of sites varies between 15° and 30°.

2.2. The species

P. canariensis Chr. Sm. ex DC. is an endemic monoecious pine species of the Canary Islands and is the only native pine on the archipelago. Old individuals can reach more than 50 m in height and an age of 800 years (Génova and Santana, 2006). Flowering occurs from late February to late March, dissemination takes usually place in the third summer after flowering. Seeds show long wings and are wind dispersed. The species has a great resistance to fire, producing epicormic shoots from the lower trunk (after fire), basal sprouts and serotinous cones (Méndez, 2010). It also has a high resistance to cold temperature (Köhler et al., 2006). Canary Island pine seedlings are susceptible to combined stress of shade and drought (Climent et al., 2006). Pine saplings need sufficient light to advance in growth and regeneration is very low in dense plantations (Arévalo and Fernández-Palacios, 2008). The heliophytic Canary pine is considered both a pioneer and a mature tree species, which is not substituted by other tree species during primary succession in its potential area of distribution.

Understory vegetation is usually dominated by shade-tolerant laurel forest trees, such as *Erica arborea*, *Ilex canariensis* and *Myrica faya*, in humid pine forests on the windward slope and by the more light-demanding leguminous shrubs, such as *Adenocarpus viscosus* and *Chamaecytisus proliferus*, in the typical rather open pine forests on the leeward slope. Annual herbs can be numerous depending on stand structure as well as light and soil availability. More information about the vegetation can be found in Ceballos-Ortuño (1974) and Blanco et al. (1989). Soils are usually poorly developed and classified in the order Entisol, suborder Orthens (Fernández-Caldas et al., 1985).

2.3. Sampling design and data collection

In the study area, 575 hectares of Canarian pine plantation were thinned in 2002 at an intensity of 60%, meaning the removal of 60% of basal area, by the local authorities “Consejería de Política Territorial”. Only intermediate and suppressed trees were removed. Understory cover was almost absent in these plantations and the few shrubs existing might have been damaged by thinning. Adjacent to the area of thinning, unthinned pine plantations can be found, growing in very similar ecological conditions (altitude, local climate, exposure, slope inclination, substrate type and age) and showing very similar tree densities compared to the pre-thinning situation (Table 1). Hence, we considered the pre-thinning forest situation a homogeneous stand, where the remaining dense plantations could serve as control plots, reflecting conditions before treatment. When focusing on structural parameters, such as tree diameter growth, the specific pre-thinning conditions should be known to obtain robust results of thinning experiments. When ecosystem response to disturbance is the main interest, the space-for-time-substitution approach in vegetation dynamic

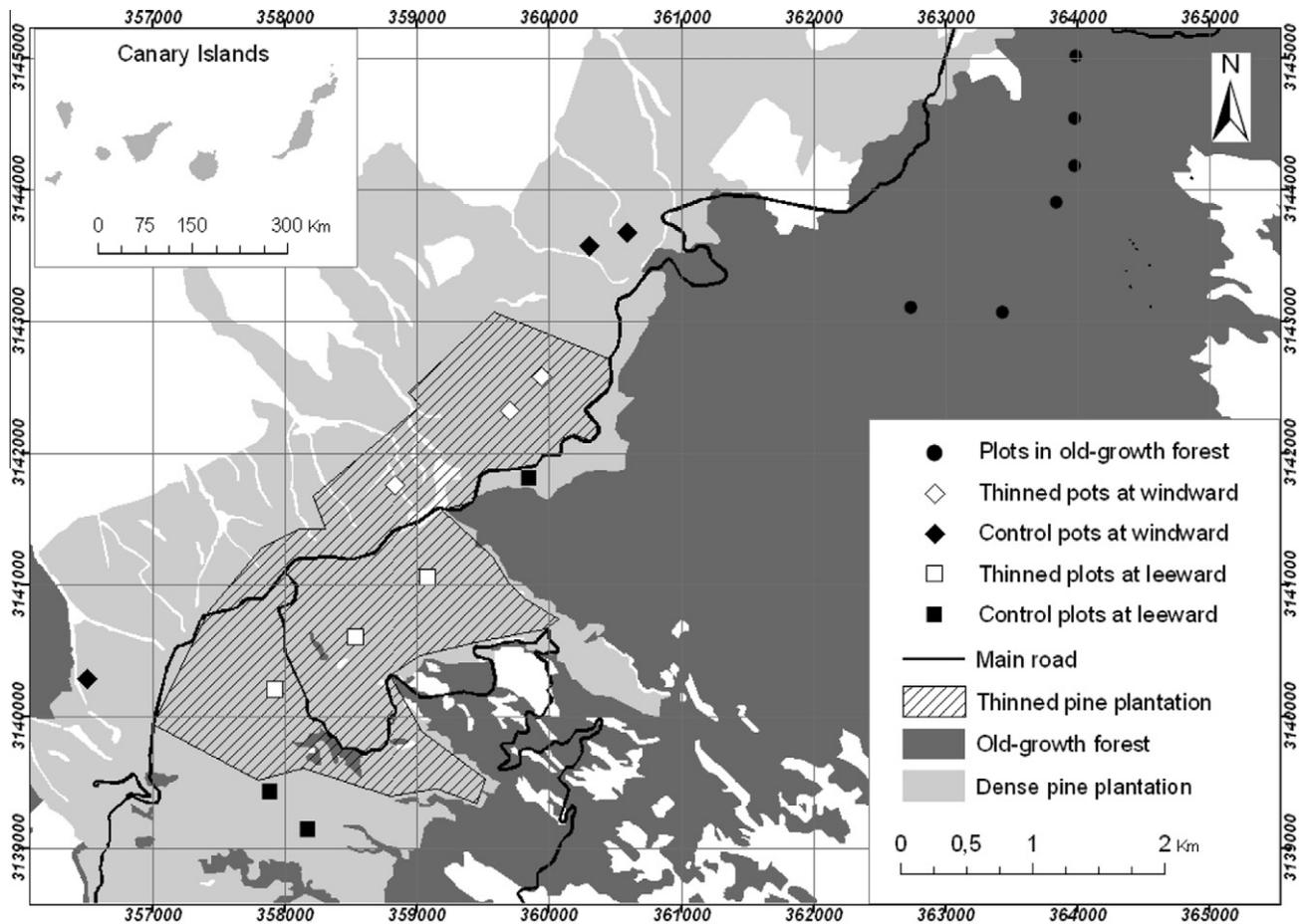


Fig. 1. Location of study area and sampled plots in *Pinus canariensis* forest of Tenerife.

Table 1

Characteristics of unthinned pine plantations (control plots) and plantations thinned by 60% of basal area at two different stands (windward/leeward), compared to semi-natural old-growth forests.

Stand and site characteristic	Stand				
	Old-growth	Windward		Leeward	
		Control	Thinned	Control	Thinned
Altitude (m)	1168.2 (33.2)	1527.7 (40.8)	1528.7 (40.2)	1619.3 (58.0)	1608.3 (17.7)
Slope inclination (°)	15.3 (2.0)	28.3 (1.7)	31.7 (3.3)	13.3 (1.7)	16.7 (1.7)
Density before thinning (stems/ha)	–	1083 (72.6)	942 (58.3)	1558 (44.1)	1450 (104.8)
Density (stems/ha)	641.7 (84.3)	1083 (72.6)	225 (14.4)	1558 (44.1)	575 (28.9)
Canopy cover (%)	77.3 (4.1)	85.5 (1.4)	54.6 (2.4)	82.4 (4.5)	66.7 (1.7)
Mean dbh (cm)	26.5 (3.2)	27.1 (1.0)	32.0 (1.8)	24.5 (1.3)	29.7 (0.3)
Basal area (m ²)	56.2 (5.3)	67.4 (7.8)	19.4 (3.7)	78.1 (5.9)	40.8 (2.9)
Understory cover (%)	41.3 (8.1)	13.0 (3.6)	61.7 (11.8)	<1	48.0 (17.9)
Pine needle cover (%)	72.5 (3.7)	92.9 (1.8)	90.0 (1.4)	87.9 (4.2)	67.1 (10.9)
Pine needle depth (cm)	4.9 (0.2)	7.4 (0.9)	5.2 (0.3)	4.9 (0.4)	4.1 (0.6)

studies has been widely applied, especially concerning ecological succession (Pickett, 1989; Foster and Tilman, 2000), including silvicultural treatments (Bailey and Tappeiner, 1998).

We first stratified the study area with respect to thinned and unthinned plantations and between a windward and leeward stand. Then, we randomly selected a total of 12 square plots, each 400 m² in area, with three plots in each stratum (thinned-windward, thinned-leeward, unthinned-windward and unthinned-leeward). To avoid road edge effects, we established plots always maintaining a minimum distance of 50 m to the next forest road. In order to compare the effect of thinning with natural populations of *P. canariensis* and to better understand the processes of natural

regeneration, we additionally installed six plots of the same size in semi-natural old-growth Canarian pine forests in the same region with windward exposure.

In spring 2009, we recorded altitude and slope inclination and measured diameter at breast height (dbh) of all pine trees in each plot (excluding trees with dbh < 5 cm), which allowed us to calculate basal area and tree densities. We measured canopy closure using a convex spherical densitometer (Lemmon, 1957) at the four corners of the plot, where we also established subplots of 1 m² to record pine needle cover (visual estimation in %, 4 per plot) and needle depth (four measurements per subplot, 16 per plot) and averaged.

In May 2009, 7 years after thinning, we recorded the natural regeneration of *P. canariensis* at all the 18 sites within the whole 400-m² plot by dividing the plot in 100 subplots of 4 m² and counting the following categories: the number of seedlings (hereafter se, whole plant photosynthetic, up to one year old); sapling category 1 (hereafter sa_1, greater than one but only a few years old, with main stem clearly differentiated into a green photosynthetic part and a wooden part with bark, height ≤ 20 cm) and sapling category 2 (hereafter sa_2, several years old with a well-developed stem, height > 20 cm); juvenile category 1 (hereafter juv_1, with a bunch of large adult needles at the top of the stem and height usually >40 cm but less than one meter) and juvenile category 2 (hereafter juv_2, height > 1 m). The last category can be considered a young tree and is used to indicate functional regeneration.

Seed rain of *P. canariensis* was captured by five litter traps per plot located near the corners and in the center of the plot. The trap consists of a metal structure with a ring at 45 cm above the ground, 70 cm in diameter and 0.385 m² in area, which supports a nylon net of 40 cm depth and 1 mm mesh width. A small stone in the center of the net avoids litter loss by wind. The trap is not protected by a grid on the top, since long pine needles would accumulate and cover it. This method has been used successfully in the pine forest in La Palma (Méndez, 2010).

Litter traps were installed in late June 2009 to capture the peak of seed release that occurs in July or August and is triggered by high air temperature and low air humidity (García-del-Rey et al., 2011). Seed rain was monitored three times: at the end of October 2009, at the end of June 2010 and at the end of October 2010. At each monitoring, total litter was collected and transported to the laboratory, where it was dried in an oven at 60 °C till constant weight. Afterwards, pine seeds were separated from the rest of litter and counted. We did not check for viability of seeds. Seed counts were averaged (five measurements per plot) and seed density per square meter was calculated.

In May 2009, vegetation was sampled by identifying all the vascular plants at the species level and by visually estimating the percent cover for each species growing within the whole plot of 400 m². The value of 0.1% cover was assigned to rare species, 0.5% cover to species with numerous individuals but not reaching 1% total cover in the plot. One percent steps from 1% to 5% cover, 5%-steps from 5% to 30% and 10%-steps from 30% to 100% were used. In general, spring can be considered the peak of phenological development of species in the pine forest at the study site, although this also depends on meteorological conditions during the year. Taxonomical classification followed the most recent check-list of Canary flora (Arechavaleta et al., 2010). Furthermore, all species were classified according to their status as species endemic to the Canary Islands, non-endemic native species and alien species. Recent checklists for the archipelago were used for this classification (von Gaisberg, 2005; Stierstorfer and von Gaisberg, 2005; Arechavaleta et al., 2010).

Characteristics of the three selected forest stands including altitude, slope inclination, stem density, canopy cover, mean dbh, basal area, understory cover and pine needle accumulation are shown in Table 1. Stem density is the only structural data that was recorded by the Canary authorities before thinning was carried out.

2.4. Data analysis

We investigated the effects of thinning on pine seed rain, regeneration and species richness of understory vegetation applying generalized linear mixed-effects models (GLMMs, using the R package lme4; Bates and Sarkar, 2007). GLMMs are extensions of generalized linear models (GLMs, McCullagh and Nelder, 1989), including random effects to deal with correlated data structures, in particular, with clustered and/or longitudinal data (Hedeker,

2005; Bolker et al., 2009). In GLMMs, the probability distributions of the dependent variable also include distributions of the exponential family such as the Poisson or binomial distribution. Since response variables did not show normal distribution in our case, we selected a Poisson error distribution, using a log-link function, as recommended for count data in ecological analysis (Zuur et al., 2007). The link function provides the relationship between the linear predictor that incorporates the information of the independent variables and the mean of the distribution function. Predictor variables may be either quantitative or categorical. In this study, treatment (dummy variable = thinned/control or old-growth/thinned) was entered as a fixed factor in the model, while the categorical variable “stand” was included as random factor. The windward stand differs from the leeward stand in aspect and related climatic conditions, as well as in slope inclination and pre-thinning stem density. Since we cannot disentangle the influences of these factors on the dependent variables, we decided to treat “stand” as a random factor, rather than a fixed factor. We also tested the effect of thinning on pine needle cover, needle depth and understory shrub cover, since these structural characteristics could potentially influence regeneration and species composition. GLMMs were constructed separately for each seed rain monitoring, for each regeneration class and for each species group. We investigated the differences between the thinned pine plantations and the old-growth stands, again constructing GLMMs, using the same response variables and forest type as fixed factors.

We compared the GLMM model including the random factor with the GLM model including the same explanatory variable but without random factor and then checked the AIC values of the two models. Additionally, we performed Likelihood Ratio Tests (LRT) to test the significance of the random term as suggested by Zuur et al. (2009). In all cases, GLMMs showed always much lower AIC values than GLMs and the random factor resulted to be always significant. All models and model comparison were performed in R (R Development Core Team, 2008).

We tested for differences in understory species composition between control plots and thinned plantations by means of multi-response permutation procedures (MRPP). This is a non-parametric multivariate test similar to a multivariate ANOVA, which might be used to compare floristic differences in groups (McCune and Grace, 2002). We used Sørensen (Bray-Curtis) distance measure and PC-ORD default group weightings for all MRPP analyses (McCune and Grace, 2002). MRPP generates a *T*-statistic with its associated significance values that indicates the floristic dissimilarity between groups and a chance corrected measure of within-group agreement (*A*-statistic), which describes the floristic homogeneity within groups. The more negative *T* is, the stronger the separation is between groups. *A* values range from −1 to 1, with 1 indicating that all objects are identical within groups, a value of 0 suggests that group membership tends towards randomness (Chávez and Macdonald, 2005). *A*-statistic values of less than 0.1 occur frequently using community data, although separation of groups might be significant (McCune and Grace, 2002).

Indicator species analysis (ISA) was performed to identify which species were most associated with each treatment (thinned plantation, control plot, old-growth stand). Indicator species analysis provides a method of combining the relative abundance and relative frequency of each species into an indicator value (Dufrene and Legendre, 1997). A good indicator species has a high frequency within a group and is most abundant in that group. Indicator values were tested for statistical significance using a randomization technique (Monte Carlo test) with 4999 iterations. The randomizations were used to test the statistical significance of each species. In order to visualize floristic similarities between plots and forest treatments, we constructed an ordination diagram by means of Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980).

Ordination techniques are very useful in explaining variation in the species composition of communities (Gauch, 1982). For floristic composition analyses, we applied the software PC-Ord Version 6.0 (McCune and Mefford, 2011).

3. Results

3.1. Seed rain

Thinning had a strong and positive effect on seed rain (Table 2, Fig. 2), considering the period of the whole year (July 2009–June 2010), each summer peaks (July–October 2009, July–October 2010), as well as for the period between winter and spring (November 2009–June 2010), although this effect was less pronounced in the latter case. 70% of pine seeds had fallen during summer and autumn (range 66–75%) in all three forest types. Plots

on the windward slope received, in general, more seeds than plots on the leeward slope (Fig. 2). There was almost no seed production in control plots on the leeward slope. We detected no significant difference in seed rain comparing thinned pine plantations with semi-natural old-growth forests for all the selected periods (Table 2). Summer seed release differed between years: in thinned plantations on the windward slope, maximum values of seed rain was recorded in summer 2010, while for old-growth forests it was in summer 2009. However, the monitoring period was too short to detect general trends in inter-annual fluctuations.

3.2. Pine regeneration

Thinning had a strong and positive effect on pine regeneration (Table 2, Fig. 3), since significant increases of individuals in all the regeneration categories were observed. In control plots, only

Table 2

Results of generalized linear mixed-effects models (GLMMs) for pairwise comparison between thinned and control plots, as well as between thinned and semi-natural old-growth forests. Seed rain, regeneration and understory vegetation characteristics were selected as dependent variables. Treatment was introduced as fixed factor and stand as random factor. In both cases, Poisson error distribution with log-link function were selected in GLMMs (se, seedling up to one year; sa_1, saplings >1 year, but only few years old, height <20 cm; sa_2, saplings several years old, height >20 cm; juv_1, juveniles <1 m, with adult needles; Total regeneration includes all categories).

Dependent variable	Treatment					
	Thinned/control			Old-growth/thinned		
	Estimate	Z value	Pr(> z)	Estimate	Z value	Pr(> z)
<i>Seed rain</i>						
Seeds (1 year 09–10)	–1.293	–6.058	<0.001	–0.212	–0.373	0.710
Seeds (summer 09)	–1.275	–4.912	<0.001	–0.266	–0.517	0.605
Seeds (winter/spring 09–10)	–1.386	–3.503	<0.001	–0.085	–0.129	0.898
Seeds (summer 10)	–1.716	–6.318	<0.001	0.350	0.644	0.520
<i>Regeneration</i>						
Se	–3.066	–20.33	<0.001	–2.038	–2.365	<0.05
Sa_1	–3.306	–14.15	<0.001	–0.142	–2.360	<0.05
Sa_2	–	–	–	0.441	3.637	<0.001
Sa total	–3.595	–15.46	<0.001	–0.024	–0.450	0.650
Juv_1	–	–	–	–1.044	–10.820	<0.001
Total regeneration	–3.334	–26.42	<0.001	–1.381	–3.182	<0.01
<i>Understory vegetation</i>						
Total species richness	–0.864	–4.28	<0.001	–0.041	–0.196	0.845
Endemic species richness	–1.065	–2.903	<0.01	0.423	1.433	0.152
Alien species richness	–1.253	–2.210	<0.05	–0.406	–1.175	0.240
Annual species richness	–0.619	–1.320	0.187	0.486	1.080	0.280
Shrub species richness	–1.056	–2.573	<0.05	–0.008	–0.120	0.923
Understory shrub cover	–2.058	–12.56	<0.001	0.282	2.548	<0.05
Pine needle cover	0.1380	2.190	<0.05	0.076	0.559	0.576
Pine needle depth	0.3054	1.225	0.220	0.001	0.001	0.999

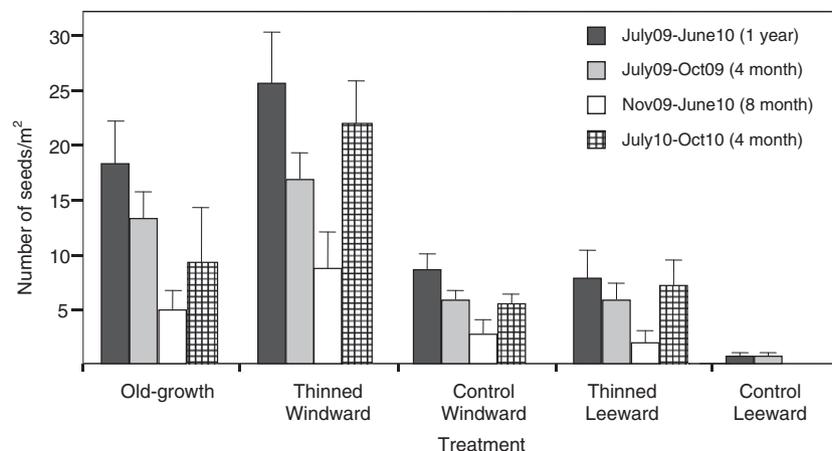


Fig. 2. Seed rain of *Pinus canariensis* captured in semi-natural old-growth forests, thinned pine plantations seven years after thinning and control plots between July 2009 and October 2010.

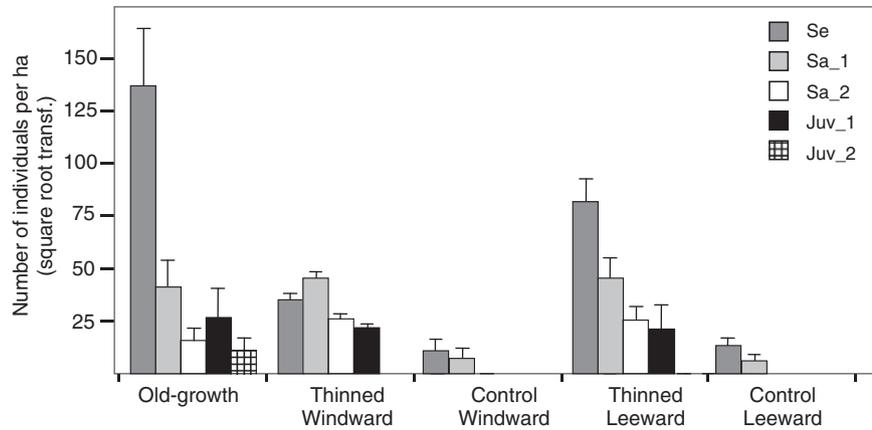


Fig. 3. Natural regeneration of *Pinus canariensis* in semi-natural old-growth forests, thinned pine plantations seven years after thinning and control plots (densities are square root transformed).

200 se/ha and between 60 and 100 sa_1/ha were counted, whereas in thinned stands up to 30 times more se/ha and 38 times more sa_1 had grown. Regeneration categories sa_2 and juv_1 could only be detected in thinned plantations with densities between 500 and 700 individuals/ha. In thinned leeward plots, seedling density was higher than in thinned windward plots, values of the other regeneration categories were very similar. Semi-natural old-growth forests showed significantly higher densities for se, sa_1, juv_1 and total regeneration and lower densities for sa_2 compared to thinned plantations, but no differences could be observed for sa total (Table 2). Category juv_2 was only present in semi-natural old-growth forests.

3.3. Understory vegetation

Thinning significantly increased understory species richness for all species groups, except for annual species (Table 2, Fig. 4). Diversity of vascular plant species in control plots is generally very low, both for total species richness (5–7 species in 20 × 20 m plots) and for endemic species (1–2), while 10–18 species, out of which 5 were endemic ones, grew in the thinned stands. Alien species richness showed the same trend. There was no difference between thinned plantations and semi-natural old-growth forests for any species group (Table 2).

The understory plant composition differed between the three forest types (MRPP test, $T = -6.368$, $A = 0.173$, $p < 0.001$). Pairwise comparison showed significant differences between control and thinned stands ($T = -5.787$, $A = 0.215$, $p < 0.001$) as well as between thinned plantations and semi-natural old-growth forests ($T = -5.478$, $A = 0.183$, $p < 0.001$). Results of the indicator species analysis revealed that twelve species were significantly associated (indicator value > 50 and $p < 0.1$) with one of the three forest types (Table 3). Semi-natural old-growth forest, exhibiting the highest number of annual species, had three annuals as indicator species: two alien *Trifolium* species and *Tuberaria guttata*, a typical native therophyte in Canary pine forests. The native shrub *Daphne gnidium* and the endemic small shrub *Lotus campylocladus* were also exclusive to this type. Thinned stands were characterized by three endemic, shade-intolerant shrubs (*Sideritis oroteneriffae*, *Pterocophalus lasiospermus* and *Carlina xeranthemoides*), two native species (*Oreganum vulgare*, *Cerastium glomeratum*) and one alien annual herb (*Sonchus tenerrimus*). Additionally, the endemic shrub *A. viscosus* showed high cover values in thinned stands, but was not exclusive to this management type. The endemic shade tolerant small shrub *Tolpis lagopoda* was the only one exclusive to the control plots. Species recorded in the three forest types showing mean values of estimated cover are listed in Table A1. The ordination diagram of the first two DCA axes, which explained 34% of the total

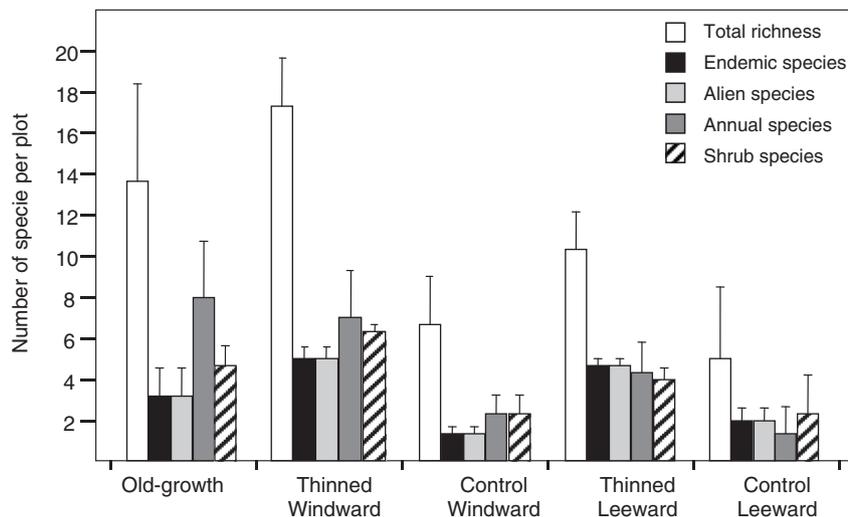


Fig. 4. Richness per plot for different species groups in semi-natural old-growth forests, thinned pine plantations seven years after thinning and control plots.

Table 3

Results of the indicator species analysis for the three forest types (semi-natural old-growth forests, thinned pine plantations, control plots), identified by means of a Multi-Response Permutation Procedure (MPPP). IV: indicator value, *p*: *p* value, LF: species life form, NPh = nanophanerophyte, Ch = chamaephyte, Th = therophyte, Origin: End = Canary endemic, Nat = native non-endemic).

Treatment	Species	IV	<i>p</i>	LF	Origin
Old-growth	<i>Daphne gnidium</i>	50	0067	NPh	Nat
	<i>Lotus campylocladus</i>	50	0067	Ch	End
	<i>Trifolium campestre</i>	66.7	0014	Th	Alien
	<i>Trifolium ligusticum</i>	83.3	0002	Th	Alien
	<i>Tuberaria guttata</i>	100	0001	Th	Nat
Thinned	<i>Carlina xeranthemoides</i>	50	0073	NPh	End
	<i>Cerastium glomeratum</i>	50	0073	Th	Nat
	<i>Oreganum vulgare</i>	64.6	0071	Ch	Nat
	<i>Pterocarpus lasiospermus</i>	50	0073	NPh	End
	<i>Sideritis oroteneriffae</i>	100	0001	NPh	End
	<i>Sonchus tenerrimus</i>	50	0098	Th	Alien
	<i>Tolpis lagopoda</i>	54.5	0071	Ch	End

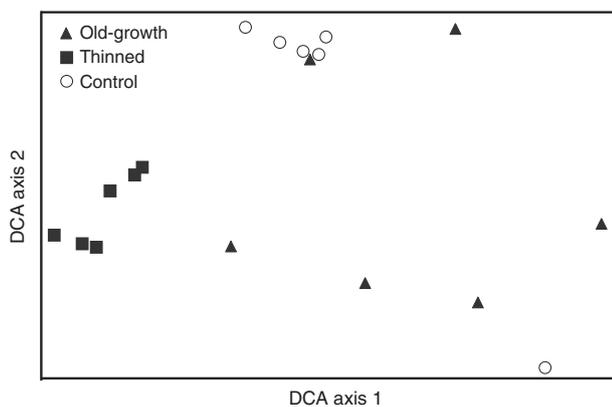


Fig. 5. DCA ordination diagram of the first two axes displaying samples of semi-natural old-growth forests, thinned pine plantations seven years after thinning and control plots. The eigenvalues of the axes were 0.616 and 0.167, the cumulative percentage variance of species data of the first two axes reached 34%. Gradient length of the first axis reached 3.48 SD and the second axis 2.15 SD. Square root transformation of species cover values and down weighting of rare species were selected as options of analysis.

variation in species composition (Fig. 5), displays all thinned plots separate from the corresponding control plots and is placed on the left side of the diagram. This indicates that thinning was negatively related to the first DCA axis and that floristic change had a particular direction, i.e. thinned plots shared many species, although stands (windward/leeward) could still be differentiated (clusters).

Pine needle cover was significantly lower in thinned than in control stands, but similar to old-growth forests, whereas pine needle depth did not differ (Table 2). We observed a strong increase in understory shrub cover after thinning, which could be assigned to the rapid expansion of the endemic, shade-intolerant shrub *A. viscosus*.

4. Discussion

4.1. Seed rain

Our results confirm the fast response of seed production of *P. canariensis* to heavy thinning of dense plantations seven years after thinning. This is probably a result of the fast, mainly horizontal growth of the crowns and the enhanced cone production due to the immediate release of resources, such as light, and the reduction of the strong intra-specific competition. Similar results showing an increase in cone production after thinning were reported for *Pinus halepensis* and *Pinus ponderosa* (González-Ochoa et al., 2004;

Verkaik and Espelta, 2006; Peters and Sala, 2008). Although we did not directly record cone production, the increase of seed rain is likely to be a result of both an increase in the number of reproductive pines and an increase in the number of new cones per tree as observed in *P. halepensis* (Verkaik and Espelta, 2006). Greene et al. (2002) highlighted the importance of light availability for cone production in conifer plantations, whereas González-Ochoa et al. (2004) related the female cone production in thinned stands of *P. halepensis* to the increased availability of nitrogen for residual trees.

Very dense pine plantations (>1500 stems/ha) showed almost no seed production and, as a consequence, very scarce natural pine regeneration. It has been reported by other studies that high intra-specific competition in dense plantations, due to overstocking, may have negative effects on seed production (Greene and Johnson, 1994; Thanos and Daskalaku, 2000; Borchert et al., 2003). This has been explained by both preferential allocation of the available resources to vegetative growth and by the interference among tree crowns (Verkaik and Espelta, 2006).

By contrast, in natural pine forests on the island of La Palma with much lower stand densities, a positive correlation between density of adult pines with pine seed production was observed (Méndez, 2010), highlighting the importance of big adult pines as major seed producers. The positive relationship between tree size and cone production in pines has been documented earlier (Cramer, 1992). Interestingly, control plots on the windward slope received the same amount of seeds as thinned plots on the leeward slope, despite differences in tree density (883 stems/ha vs. 575 stems/ha). This might be the response to differences in site conditions or simply be related to structural differences, i.e. size of seed pines.

Seed production and seed rain of the Canary pine are not only characterized by a high spatial variability, but also by marked seasonal and inter-annual fluctuations (García-del-Rey et al., 2010; Méndez, 2010). We also detected a clear seasonal trend of seed rain in all three forest types in both years of observation, with a peak during the three summer months (July, August, September), which was explained by the massive liberation of seeds during periods of hot and dry air (García-del-Rey et al., 2010; Méndez, 2010). On the other hand, we could not confirm a common tendency of inter-annual fluctuations in seed rain due to the short period of monitoring. Inter-annual differences might be related to stand age and structure as well as to masting years. Although never monitored scientifically, the Canary pine is expected to show masting every 3–4 years (Tapias et al., 2004).

We can also confirm low levels of pine seed release during the winter and spring (Méndez, 2010), which indicates the existence of a reduced soil seed bank, while most of the seeds are stored in

cones in the canopy (normal and serotinous cones). This soil seed bank is considered to be transient, since seed viability of *P. canariensis* decreases rapidly after seed liberation, a common characteristic of Mediterranean pine species (Escudero et al., 1999). A reduced soil seed bank has also been found for *Pinus nigra*, a pine species adapted to low fire intensity and low fire frequency (Kerr et al., 2008) as well as for *P. halepensis* (Nathan et al., 1999).

4.2. Pine regeneration

Thinning had an overall positive effect on natural pine regeneration. In control plots, although differing in tree density between windward and leeward stands, only few seedlings germinated and very few saplings survived, usually for not more than a few years. By contrast, in thinned stands, seedlings and saplings were very numerous and lived longer. Additionally, juveniles up to 1 m in height with long adult needles were found. This impact was related to both the increase in seed production and the changed micro-environmental conditions, especially light availability at the forest floor due to canopy opening. It has been shown for other conifer species that heavy thinning of up to 60% of stand volume clearly favored natural tree regeneration (Bailey and Tappeiner, 1998; Zald et al., 2008; Ares et al., 2010). Additionally, Bailey and Tappeiner (1998) confirmed a positive relation between thinning intensity and density of established tree seedlings. Zald et al. (2008) reported different responses of tree species to thinning, depending on their shade tolerance. Earlier studies confirmed that heavy thinning of dense Canary pine plantations facilitated natural regeneration, whereas lower thinning intensities did not show satisfying results (Arévalo and Fernández-Palacios, 2005, 2008). However, thinning was carried out in very small plots (625 m²) in this thinning trial, which probably reduced survival of older saplings due to fast closure of the canopy from the plot edge (Arévalo and Fernández-Palacios, 2008). This could explain the 10-fold higher densities of seedlings and saplings in thinned stands found in our study.

Negative effects of this treatment, such as an increased risk of wind damage, have not been observed on Tenerife. The subtropical archipelago of the Canary Islands rarely suffers from tropical storms. On the contrary, heavy thinning of Canary pine plantations favored not only the growth of remaining trees, but also changed tree sensitivity to limiting climatic conditions, which could lead to increased tree vigor and resistance to drought (Pérez-de-Lis et al., 2011) and probably also to wind damage. This can be important for the development of good seed trees, crucial in stand regeneration (Smith et al., 1997).

It has been suggested that thinning can substantially enhance regeneration of trees species, especially of light-demanding pioneer species, by reducing litter accumulation (Seiwa et al., 2009). In our study, thinning significantly reduced litter cover, which might also have positively influenced pine regeneration due to more favorable micro-site conditions. On the other hand, needle litter cover has been reported to have a positive effect on pine seedling density in early post-fire conditions when burned soil surface is often uncovered by vegetation, probably due to micro-climatic amelioration on the forest floor (Pausas et al., 2003; Otto et al., 2010). The overall effect of needle cover and depth on seed germination and seedling establishment of *P. canariensis* has yet to be investigated.

Of interest was the finding that thinned plantations on the leeward slope showed 40-fold seedling density and 65-fold sapling establishment compared to unthinned plantations on the windward slope, despite receiving almost the same amount of pine seeds. This highlights the importance of light availability for seedling establishment of the heliophytic Canary pine and the role of general micro-site conditions, i.e. litter accumulation, water supply

and soil condition. Overall, we propose a hierarchical scheme of factors explaining regeneration in these pine plantations, which depends on (1) overall seed availability, (2) light availability, mainly conditioned by stand density, and (3) favorable micro-site conditions as well as biotic interaction, such as competition with understory shrubs.

Although similar in overall sapling densities, thinned plantations showed even lower densities of seedlings and a lack of well-developed pine juveniles, compared to semi-natural old-growth forests. Time after thinning was probably just too short to develop taller juveniles. We also attribute differences in regeneration to important structural differences between the two forest types, max. dbh in old-growth forests reached 100 cm, compared to 50 cm in thinned stands. Hence, we cannot yet confirm complete functional regeneration of thinned plantations and monitoring of regeneration should be continued.

4.3. Understory species richness and composition

Many studies have shown that thinning altered understory vegetation and increased plant species richness (Parker et al., 2001; Thysell and Carey, 2001; Chan et al., 2006; Metlen and Fiedler, 2006; Dodson et al., 2008; Ares et al., 2010). Few investigations reported a negative or no effect of thinning on plant richness (Nagai and Yoshida, 2006; Lei et al., 2007; Taki et al., 2010). This second group of studies commonly focused on short time response to stand density reductions. Therefore, Thomas et al. (1999) concluded that the effect of thinning on understory vegetation could vary with time after thinning, environmental conditions and target species. Wolk and Rocca (2009) suggested that this effect might also depend on spatial scale.

Our results revealed a significant increase in species richness of vascular plants seven years after heavy thinning of pine plantations. This pattern was consistent for all species groups, except for annuals. Annual richness might have peaked earlier during the colonization process after thinning as suggested for other coniferous forests (Thysell and Carey, 2001). Plant diversity of dense plantations of *P. canariensis* is usually very poor, and understory vegetation is composed of a few generalist annual species with a wide ecological niche and very few shade-tolerant endemic pine forest species, such as *T. lagopoda*. Thinned stands were colonized, at the same time, by native or endemic shrub and herb species typical of this forest type and by alien therophytes due to changed micro-environmental and biotic conditions. The first species group is very important in recovering and maintaining local biodiversity in Canary pine forests. The second group might represent a threat to this ecosystem. However, all of the alien species were annuals that did not reach cover values >1%. Our findings are, therefore, consistent with other studies that reported an increase in non-native species richness after thinning, although their relative abundance remained low (Dodson et al., 2008; Ares et al., 2010).

Up to now, non-native invasive shrub species have not been reported for the Canary pine forest, with the exception of the introduced *Eschscholzia californica*, which is mostly restricted to heavily disturbed areas, such as roadsides. This species was not present in our plots, indicating no threat of invasion. However, heavy disturbances in forest ecosystems on islands, such as gap dynamics or forest management procedures like thinning, can potentially trigger plant invasion and threaten native understory vegetation (Baret et al., 2008; Rasingam and Parthasarathy, 2009).

Floristic composition of thinned pine plantations still differed considerably from semi-natural old-growth forest, which showed the highest floristic variation within the same forest type. These differences can be partly explained by structural differences between both forest types, but probably also by different environmental

conditions. Semi-natural old-growth forests are located at lower elevations and are slightly more humid compared to the pine plantations. Furthermore, identified indicator species of thinned stands are typical upper pine forest species (between 1500 and 2000 m a.s.l.), indicating that thinned stands might exhibit drier micro-sites at the forest floor, favoring the establishment of species typical of higher and drier zones. Thinned pine plantations on Tenerife have been reported to receive lower amounts of horizontal fog drip formed by the humid trade winds compared to dense plantations (Aboal et al., 2000), which supports our hypothesis. Studies on the effect of thinning on micro-climate in conifer forests confirmed the increase in soil temperature in thinned areas (Weng et al., 2007; Ma et al., 2010).

The observed change in floristic composition after thinning was accompanied by a structural change, since at both slope orientations the understory shrub cover increased to 40–70% in thinned stands, mainly due to the increase in abundance of the endemic shrub *A. viscosus*, although other species, such as *E. arborea*, *M. faya* or *C. proliferus*, also participated. The fact that thinning can trigger the fast recovery of an understory shrub layer has been confirmed for other conifer forests (Bailey and Tappeiner, 1998). Although the colonization of gaps by understory shrub species might facilitate natural regeneration of tree and herb species in an initial phase, by creating higher micro-site diversity, high understory shrub cover could negatively influence plant diversity and natural tree regeneration as a response to increasing competition (Bailey and

Table A1

List of species recorded in the three forest types (old-growth forests, thinned pine plantations, control plots) showing mean values of estimated cover.

Species	Treatment				
	Old-growth	Thinned windward	Control windward	Thinned leeward	Control leeward
<i>Adenocarpus foliolosus</i>	5.0				
<i>Adenocarpus viscosus</i>		30.0	0.2	43.3	0.2
<i>Aira caryophyllea</i>	0.3	0.5	0.2	0.3	0.2
<i>Anagallis arvensis</i>					
<i>Andryala pinnatifida</i>	0.2				
<i>Asplenium onopteris</i>	0.2	0.3	0.2		0.2
<i>Asteracea</i> sp.	0.2	0.2			
<i>Asterolinon linum-stellatum</i>	0.3	0.3			
<i>Brachypodium sylvaticum</i>	0.2	0.3	0.2		0.2
<i>Briza maxima</i>	0.7				
<i>Bromus rigidus</i>	0.2				
<i>Bystropogon canariensis</i>	0.8				
<i>Cardamine hirsuta</i>		0.2			
<i>Carlina salicifolia</i>	0.2				
<i>Carlina xeranthemoides</i>				0.3	
<i>Cerastium glomeratum</i>		0.2		0.3	
<i>Chamaecytisus proliferus</i>	9.5			4.7	0.3
<i>Cistus monspeliensis</i>	4.2				
<i>Conyza canadensis</i>		0.2		0.2	
<i>Cynosurus echinatus</i>	0.2			0.2	
<i>Daphne gnidium</i>	0.8				
<i>Drimia maritima</i>	1.0				
<i>Erica arborea</i>	13.8	28.3	12		0.2
<i>Euphorbia</i> sp.	0.2				
<i>Galium aparine</i>	0.2				
<i>Galium parisiense</i>	0.3	0.5	0.3	0.3	0.2
<i>Galium scabrum</i>	0.2	0.3			0.2
<i>Geranium robertianum</i>	0.2	0.2		0.2	
<i>Hypericum reflexum</i>		0.2			
<i>Lotus campylocladus</i>	0.3				
<i>Micromeria varia</i>	0.2	0.3			
<i>Moehringia pentrandra</i>		0.3	1	0.2	0.2
<i>Morella faya</i>	5.5				
<i>Myosotis</i> sp.		0.2			
<i>Neotinea maculata</i>		0.3	0.3		0.2
<i>Oreganum vulgare</i>	0.2	1.02	0.2	0.2	
<i>Peridium aquilinum</i>		0.2	0.2		
<i>Pteroccephalus lasiospermus</i>		0.5			0.2
<i>Ranunculus cortusifolius</i>	0.2				
<i>Sherardia arvensis</i>	0.2				
<i>Sideritis oroteneriffae</i>		2.3		0.5	
<i>Silene gallica</i>	0.2				
<i>Silene vulgaris</i>				0.2	
<i>Sonchus acaulis</i>	0.2				
<i>Sonchus asper</i>		0.3			
<i>Sonchus oleraceus</i>	0.3				
<i>Sonchus tenerrimus</i>		0.5	0.3	0.5	0.2
<i>Stachys arvensis</i>	0.2				
<i>Tolpis lagopoda</i>		0.5	0.5	0.3	0.5
<i>Torilis arvensis</i>	0.2				
<i>Trifolium campestre</i>	0.3				
<i>Trifolium glomeratum</i>	0.2				
<i>Trifolium ligusticum</i>	0.4				
<i>Tuberaria guttata</i>	0.5				
<i>Vicia sativa</i> ssp. <i>nigra</i>	0.2		0.2		
<i>Vicia</i> sp.	0.2				

Tappeiner, 1998; Zhu et al., 2003). In our study, the understory shrub cover, grown seven years after thinning, apparently did not negatively affect plant diversity or pine regeneration.

5. Conclusions

Heavy thinning of Canary pine plantations on Tenerife improved pine seed production, natural pine regeneration, structural complexity and understory plant diversity. Thinning intensity of 60% of basal area seems to be sufficient to enhance tree growth (Pérez-de-Lis et al., 2011) and to facilitate functional regeneration of this heliophytic pine, while lower thinning intensities did not show significant effects (Arévalo and Fernández-Palacios, 2008). Therefore, different objectives of current forest management strategies on Tenerife could be achieved at the same time with only one treatment. Not only would total plant richness increase, but also the diversity of endemic species typical of Canary pine forests, without triggering plant invasion. This is of great conservation interest. Our study provides evidence that heavy thinning represents an important management tool to enhance naturalization and local biodiversity of the large areas of pine plantations on this Archipelago. Future research should also try to explore other treatments, such as creation of gaps or small clear cuttings, which could improve natural regeneration of these pine stands in the Canary Islands, as an alternative or complementary strategy to heavy thinning.

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Appendix A

See Table A1.

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