PROCESOS DE REGENERACIÓN EN UN BOSQUE TEMPLADO FRAGMENTADO: COMPARANDO ESPECIES ARBÓREAS CON DISTINTO NICHO REGENERACIONAL

Tesis

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Summary

1- The purpose of this study was to assess the regeneration responses of four tree species with different regeneration niches in a fragmented temperate forest which is surrounded by pine plantations. In order to do that, we assessed natural regeneration of native trees, and experimental seed germination and seedlings establishment processes of four native species: *Cryptocarya alba* (shade-tolerant) and *Aristotelia chilensis*, *Nothofagus glauca* and *N. obliqua* (shade-intolerants). We worked at the Coastal maulino forest at three habitats types: the protected forest of Reserva Nacional Los Queules (RNLQ), four small forest fragments and two pine plantations. We also evaluated soil moisture and canopy openness across habitats.

2- The pattern of natural regeneration was estimated through assessment of seedling and sapling densities across the three habitat; The hypothesis was that regeneration of shade-tolerant trees (*Cryptocarya alba*) should be higher in RNLQ than in forest fragments, while in shade-intolerant trees (*Aristotelia chilensis*, *Nothofagus glauca* and *N. obliqua*) should decrease at the RNLQ compared to the forest fragments.

3- Experimental seed germination P (G) and seedling establishment P (E) were evaluated from seeds disposed at random across habitats (28 replicates per habitat). The canopy openness evaluated under seed replicates was evaluated as well as a covariate.

4- Small remnants forest and surroundings pine plantations had greater canopy openness and decreased soil moisture in relation to RNLQ.

5- Natural seedlings and saplings were detected only for *C. alba, A. chilensis* and *N. glauca*. The shade-tolerant, *C. alba* tree, presented greater seedling and sapling densities

in RNLQ compared to forest fragments, while *A. chilensis* and *N. glauca* presented more seedlings and saplings in small forest fragments.

6- P (G) of *C. alba* and *N. obliqua* did not varied among habitats, while the shade-intolerant trees, *A. chilensis* and *N. glauca*, decreased their P (G) in RNLQ compared to small forest fragments. Only *C. alba* became established in the experimental essay and it P (E) did not varied among habitats. In the other hand, P (G) of *C. alba* was negatively correlated with canopy openness, whereas *C. alba* P (E) was marginally related with canopy openness. The P (G) of *A. chilensis* and *N. glauca* were positively correlated with canopy openness, while P (G) of *N. obliqua* was unrelated with canopy openness.

7.- Our result suggest that natural regeneration is severely limited for some species (shade –intolerant trees) but not for others (shade-tolerant trees) at RNLQ. These results suggest that regeneration dynamics should be affected in the long term becoming *C. alba* the dominant species in the future.

Key-words: Forest fragmentation, soil moisture, canopy openness, shade tolerance, seed germination, seedling establishment, Chile.

Introduction

Seed germination and seedling establishment are critical stages in the life cycle of terrestrial plants (Harper 1977). These demographic processes are strongly dependent on the abiotic environment where plants occur (Harper 1977; Baskin & Baskin 1998). In tropical forests, changes in abiotic factors such as luminosity and soil moisture following forest fragmentation have affected the patterns of seed germination and seedling establishment (Kapos 1989; Kapos *et al.* 1997; Bruna 1999), altering plant regeneration processes and forest community structure (Laurance *et al.* 1998; Benitez-Malvido 1998; Benitez-Malvido & Martinez-Ramos 2003; Bruna 1999; 2002, 2003). Moreover, the sign and magnitude of such effects are dependent on the regeneration requirements of woody plants (regeneration niche *sensu* Grubb 1977), which have evolved to respond differentially to habitat heterogeneity within forest (Denslow 1987; Chen *et al.* 1992). For instance, shade-intolerant, pioneer trees may have higher recruitment probability relative to shade-tolerant in luminous and drier habitats such as small forest fragments (Benitez-Malvido 1998; Laurance *et al.* 1998; Restrepo & Vargas 1999; Sizer & Tanner 1999; Bruna 1999; 2002; 2003).

The Coastal Maulino forest (*sensu* San Martín & Donoso 1996) has a long history of anthropogenic disturbance. The current annual deforestation rate (8.15%) is one of the highest documented values for Chilean forests (Bustamante & Castor 1998). Anthropogenic disturbances have been mainly a consequence of the expansion of agriculture and forestry activities (Donoso & Lara 1996), thus changing significantly the landscape structure and species composition in native forests (Bustamante & Castor 1998; Estades & Temple 1999). Exotic tree plantations of *Pinus radiata* (D. Don) and

Eucalyptus globulus (Labille.) cover ~ 76 % of the coastal range of the Maule Region (Estades & Temple 1999). In consequence, native forest remains highly fragmented and immersed in a matrix of pine plantations (Bustamante & Castor 1998; Estades & Temple 1999). The largest remaining patch of Coastal Maulino forest (~ 600 ha) includes the "Reserva Nacional Los Queules" (RNLQ) (147 ha), which provide protection to about 25 % of mature extant old-growth forest in the region. Studies on the regeneration processes of the native tree species in the Coastal Maulino forest are urgently needed to promote conservation strategies in this forest-type.

The purpose of this study was to evaluate whether changes in abiotic conditions, induced by forest fragmentation affects regeneration responses of native trees of the Coastal Maulino forest. We tested the hypothesis that regeneration of a shade-tolerant tree (such as *Cryptocarya alba*) will be reduced at small forest remnants relative to RNLQ (shaded habitat) while, in shade-intolerant trees (such as *Aristotelia chilensis*, *Nothofagus glauca* and *N. obliqua*), it will be increased (Table 1). In order to do that, we assessed natural seedling and sapling abundance of the studied species in the forest of RNLQ and forest fragments. Secondly, seed germination and seedling establishment were experimentally assessed across these habitat types. Additionally, seed germination and seedling establishment were associated to canopy openness. Evaluations were also made in pine plantations, because it represents the largest component of the landscape.

Materials and methods

STUDY SITE

The study was conducted at the forest of Reserva Nacional Los Queules (RNLQ) and its surrounding landscape, located in central Chile (35° 58′ S - 72° 42′ W) (Fig. 1). Precipitations are concentrated during winter and spring (di Castri & Hajek 1976), the nearest meteorological station is located at the locality of Chanco at 35 km of RNLQ, it shows that precipitation during the years 2002 and 2003 also concentrated during winter and spring i.e. June, July, August, September and October with 116.2, 129.5, 377.1, 75.6, 90.5 mm respectively (Dirección Meteorológica de Chile, unpublished data). Temperatures during 9 months of the year reach over the 10°C, while the coldest moths are among June, July and August (di Castri & Hajek 1976).

The Coastal Maulino forest is composed by a mixture of species of different biogeographic origin: (i) sclerophyllous elements such as *Cryptocarya alba* (Lauraceae) and *Kageneckia angustifolia* (Rosaceae); (ii) Valdivian elements such as *Gevuina avellana* (Proteaceae) and *Pseudopanax valdiviensis* (Araliaceae) and (iii) endemic elements of this forest-type such as *Gomortega keule* (Gomortegaceae), *Pitavia punctata* (Rutaceae) and deciduous tree species such as *Nothofagus obliqua and N. glauca* (Fagaceae) (San Martín & Donoso 1996).

This study was conducted in the RNLQ (the large patch forest), in four small forest fragments (ranging from 2 to 6 ha in size, 2 km apart each other and 0.2 to 2 km distant from the RNLQ) and in two pine plantations which surrounded the RNLQ (Fig. 1).

THE SPECIES

The four tree species selected for this study, i.e. *Aristotelia chilensis* (Elaeocarpaceae), *Nothofagus obliqua* and *N. glauca* (Fagaceae) and, *Cryptocarya alba* (Lauraceae), are common component of the forests of the Coastal Maulino forest (Table 2). *Aristotelia chilensis* is a pioneer, shade-intolerant tree of 3-4 m of height which frequently occurs in opened and disturbed areas (Rodríguez *et al.* 1983). Flowering occurs from September to December (Hoffmann 1997). Fruits are berries with 2-3 seeds per fruit, dispersed by birds and foxes from December to February (Rodríguez *et al.* 1983); seed germination occurs from March to June. *Nothofagus obliqua* and *N. glauca* are shade-intolerant species, endemic of southern temperate forests, (Rodríguez *et al.* 1983; Donoso 1997). Flowering occurs in September and each fruits possess 3 nuts; in *N. obliqua* individual nuts are ~ 8 mm long, whereas in *N. glauca*, ~ 17 mm long. Dispersal occurs from March to the end of April, and germination occurs from July to September (Donoso 1975). *Cryptocarya alba* is an endemic, shade-tolerant tree that lives in mesic habitats of central Chile (Armesto & Pickett 1985). Flowering occurs during spring and summer (from October to January) (Hoffmann 1997). Fruits are red one-seeded drupes that ripe from March to July and are dispersed by birds and foxes; seed germination and seedling establishment occur from September to December (Bustamante & Simonetti 2001).

ABIOTIC ENVIRONMENT

Soil moisture was assessed through a gravimetric method to determine moisture variations across the three studied habitats. Each soil samples (200 cc) was collected from one meter of a experimental unit, in the RNLQ samples were taken from the first 20 experimental units, in small forest fragments from the first five experimental units per fragment (20 in total) and from the first 10 experimental units per pine plantation (20 in total). These measures were conducted during 12 consecutives months: from March 2003 to March 2004 (except April).

Canopy openness was operationally defined as the percentage of the area of the field of view not cover by vegetation when viewed from a single point (*sensu* Jenings *et al.* 1999), and was estimated in March 2003 by digital photographs, using a Canon Powershot G2 digital camera, with a diagonal field of view of ~ 53° (for methodological details see Bunnell & Vales 1990; Jenings *et al.* 1999). The camera was installed in a tripod with a bubble level to control horizontal deviation. One photo was taken in each of the experimental units selected for the germination and establishment essay. Photographs analyses were conducted using the software Scion Image 4.02 for Windows.

NATURAL REGENERATION

Seedling (height ≤ 50 cm) density of four species, *A. chilensis*, *N. glauca*, *N. obliqua* and *C. alba*, were estimated within 25 plots of 1 x 2 m = 50 m^2, separated 1 m from each other. Plots were placed along 12 transects of 50 m each in the forest of RNLQ, 12 transects in small forest fragments (three transects per fragment) and 12 transects in the two pine plantations (six per plantation). Transects were disposed approximately 50 m apart. For statistical analyses the 25 plots per transect were pooled, thus obtaining 12 replicates per habitat.

Sapling (height > 50 cm; DAP < 10 cm) densities of the studied species were estimated along the same transects used in the seedlings density estimation. Sapling of trees were counted along transects of 50 x 2 m.

SEED GERMINATION AND SEEDLING ESTABLISHMENT

Seed germination and seedling establishment of the four species of study were estimated through a field experiment which was initiated during June 2002 (beginning of winter) and finished by March 2003 (end of summer). 28 experimental units (replicates) were used, randomnly distributed in the interior of RNLQ (each 20 m apart), seven in each of the four forest fragments and 14 in each of the two pine plantations. Thus, a sample size of 84 replicates was obtained. Each experimental unit comprised 10 seeds per specie sowed in soil and covered with litter, inside transparent circular plastics cups (10 cm diameter) with holes in the bottom, to allow water run-off. They were excluded from seed predators (birds, foxes and rodents) using circular wire mesh 1 m diameter and 1 meter height). Seeds were acquired at the Centro de Semillas Facultad de Ciencias Forestales (CESAF), Universidad de Chile (each species 95 % viability; CESAF 2003).

A seed was considered as germinated when the radicle emerged at least 1 cm. Germination probability, P (G), was defined as the total number of germinated seeds, divided by the total number of seeds initially placed in a plastic cup (i.e. 10 seeds). Seedling establishment, P (E), was defined as the total number of seedling that survived by March 2003, divided by the total number of germinated seeds.

DATA ANALYSIS

Differences in soil moisture across habitats (RNLQ, small forest fragments and pine plantations) were assessed using a two-way ANOVA, with time (months) as a repeated measure and habitat as a random factor. A one-way ANOVA was used to compare canopy openness among habitats, being habitat a random factor. A mixed two-way ANOVA was used to compare seedling and sapling abundance among species and habitat, being species a fixed factor and habitat a random factor. A mixed two-way ANOVA was used to compare P (G) among species and habitats, being species a fixed factor and habitat a random factor. A one-way ANOVA was used to compare P (E) among habitats, being habitat a random factor. Species effect on establishment was not evaluated as *C. alba* was the only species where seedling establishment was recorded. For P (G) and P (E) ANOVAs, the canopy openness was included as a covariate. Also, planned comparisons were used to compare natural regeneration patterns (seedlings and saplings density) and experimental P (G) and P (E) between pairs of habitats such as RNLQ vs. small forest fragments. To satisfy normality assumptions (Zar 1999), soil moisture, P (G) and P (E) values were arcsine transformed while seedling and sapling abundance was log (x+1) transformed. Spearman rank test was used to evaluate the relation between P (G) and P (E) and the percentage of canopy openness measured at each experimental unit.

Results

SOIL MOISTURE

Soil moisture varied significantly among habitats, being significantly higher at the RNLQ (Table 3; Fig.2). Soil moisture of small forest fragments and pine plantations did not differ significantly (Table 3; Fig.2). The greater soil moisture was detected during the interphase autumn - winter (May and June) and during spring (October and November). During summer months (March 2003 and January 2004) we detected the lowest soil moisture levels (Table 3; Fig.2).

Canopy openness varied significantly among habitats (Table 4). At forest fragments this variable was 30.4 $\pm$ 5.4 % (average $\pm$ 2 se), in pine plantations it was 28.2 $\pm$ 1.7 % and at RNLQ it was 17.7 $\pm$ 2.1 %. Clearly, the lowest values were observed at RNLQ, being no different between forest fragments and pine plantations (Table 4).

SEEDLING AND SAPLING DENSITIES

Seedlings of *C. alba*, were observed across the three habitats types; seedlings of *A. chilensis* were detected in forest fragments and pine plantations; seedlings of *N. glauca* was detected only in forest fragments; no seedlings of *N. obliqua* were observed across habitats (Fig. 3). Seedling densities varied significantly among habitats (two-way ANOVA; $F_{6,87} = 9.35$, $P < 0.0001$), with the highest numbers at RNLQ. Seedling abundance varied significantly among species ($F_{2,12} = 120.92$, $P < 0.0001$), being *C. alba* the specie with the highest values (Fig. 3). A significant interaction between species and habitat was detected ($F_{12,87} = 41.88$, $P < 0.0001$), as in the case of *C. alba*, where seedlings were more abundant at RNLQ but in the case of *A chilensis*, seedlings were more abundant at the pine plantations (Fig. 3). Seedlings of *C. alba* tree were more abundant at RNLQ, followed by forest fragments and finally at pine plantations (Table 5; Fig. 3). In contrast, seedlings of the shade-intolerant species (*A. chilensis* and *N. glauca*) were more abundant in pine plantations followed by forest fragments and were absent in the RNLQ (Table 5; Fig. 3).

Saplings of *C. alba* and *A. chilensis* were observed in the three habitats of study; saplings of *N. glauca* were present in RNLQ and small forest fragments; no saplings were detected for *N. obliqua* (Fig. 4). Sapling abundance varied among species (two-way ANOVA; $F_{2,87} = 48.90$, $P < 0.0001$), and among habitats ($F_{6,12} = 4.04$, $P = 0.001$). A significant interaction between species and habitats was detected ($F_{12,87} = 8.15$, $P < 0.0001$) such expressed in the case of saplings of *C. alba* which were more abundant in the RNLQ. Saplings of shade-tolerant species were more abundant in the RNLQ, followed by forest fragments and less abundant in pine plantations (Table 5; Fig. 4). In contrast, shade-intolerant saplings were more abundant in forest fragments compared to the RNLQ (Table 5; Fig. 4). In pine plantations, saplings of *A. chilensis* presented it largest sapling abundance and, *N. glauca* did not present saplings at all (Table 5; Fig. 4).

GERMINATION AND ESTABLISHMENT PROBABILITIES

Seed germination differed significantly among species and habitats (two-way ANOVA; $F_{3,18} = 18.64$, $P < 0.0001$ and $F_{6,307} = 2.32$, $P = 0.03$; for species and habitat respectively). *Aristotelia chilensis* and *C. alba* were the species with the highest levels of germination (Fig. 5). A significant interaction among habitat and species was detected

($F_{18,307} = 2.59$, $P = < 0.0005$). No differences in P (G) of shade-intolerants were detected between small forest fragments and pine plantations (Table 6).

Seedling establishment was observed only for *C. alba* (Fig. 6). In this species, P (E) was not statistically different among habitats (one-way ANOVA; $F_{6,76} = 0.46$, $P = 0.83$).

In *A. chilensis* and *N. glauca*, P (G) was positively correlated with canopy openness (Table 7; Fig 7), however no significant relationship between P (G) and canopy openness was observed in *N. obliqua* (Table 7; Fig 7). In *C. alba* P (G) was negatively correlated with canopy openness (Table 7; Fig 7). P (E) of *C. alba* tended to be negatively associated with canopy openness, however this relationship was marginally significant (Table 7; Fig. 8).

Discussion

The aim of this study was to asses whether forest fragmentation affects regeneration responses on native trees species, through alterations in abiotic conditions. Firstly regeneration patterns of four tree species with contrasting regeneration niche was assessed, in order to do that natural densities of seedlings and saplings were compared among the three habitat-types: RNLQ, small forest fragments remnants and pine plantations. Experimental comparisons of seed germination and seedling establishment were assessed across the three habitats-types. Results obtained in this study indicated that, as expected, natural regeneration patterns varied according to the regeneration niche of species and the luminosity of habitats, with an increase of seedling and sapling abundance of shade-intolerant species in small forest fragments compared to RNLQ and, a decrease of seedling and sapling abundance of the shade-tolerant tree in small forest fragments. This result suggests that tree species composition in small forest fragments may be modified by forest fragmentation, tending to a tree composition dominated by shade-intolerant species (Bustamante *et al.* in press). However, the experimental germination and establishment results revealed more complex responses of tree species, not always concordant with the observed regeneration patterns: these demographic processes varied depending on (i) the particular stage of plant life cycle (i.e. seed - seedling) and (ii) the spatial scale of analysis. In the next paragraphs, these issues will be discussed in more detail.

In studying regeneration dynamics of plants, it is interesting to ask whether there is a concordance in regeneration requirements along different stages of a plant's life cycle

(Schupp 1995). In terms of seedling and sapling stages, samplings of natural densities showed that *C. alba, A. chilensis* and *N. glauca* presented equivalent tendencies across habitats, thus seedling performance may be expressed in sapling performance. These results suggest that seedling natural abundance could be a good predictor of sapling densities and eventually of its regeneration dynamics in a long term.

Field experiments showed that *C. alba* was the only specie, where it was possible to compare P(G) and P(E) as in the other tree species P(E) was zero in all cases. When we compare P(G) and P(E) both variables did not differ among habitats. The comparisons between P(G) and P(E) within habitats, showed that they responded statistically different: a negative correlation in the case of P(G) and no correlation in the case of P(E). Nevertheless, the relation of P(E) must be studied further, because in this study this relationship could be interpreted as a negative statistical marginal relation due the tendency observed. These results are interesting, because this couple relation between germination and establishment requirements is not a common attribute among tree species of Chilean temperate forest (Figueroa & Lusk 2001).

The absence of seedling establishment in *A. chilensis, N. glauca* and *N. obliqua* during the course of field experiments suggest the existence of demographic bottleneck acting on early stages of the life cycle of these species. One of the main causes of this regeneration constraint is the extreme water stress suffered by plants during summer in central Chile, which produces massive mortality of woody seedling (Fuentes *et al.* 1984; Fuentes *et al.* 1986). Despite of the absence of seedling establishment in *A. chilensis, N. glauca* in the experimental essay, natural regeneration was observed for *A. chilensis* and *N. glauca* suggesting that under a changing climatic scenario, expressed by variable interannual precipitation regimes, regeneration process of plants in the Maulino forest turns episodic similar to regeneration processes observed in the Chilean Mediterranean matorral (Fuentes *et al.* 1984; Fuentes *et al.* 1986; Jiménez & Armesto 1992). In the case of *N. obliqua* (with no seedling establishment observed either from experiments and from the natural regeneration assessments), regeneration constraints should be more severe, thus requiring higher levels of precipitations levels similar to those observed in the southern geographic distribution of this species.

If seed germination and seedling establishment processes are critical and determinant for plant regeneration in a fragmented forest (as a consequence of altered light and water availability), then there should be a correspondence between seed germination/ seedling establishment detected in the field experiment with the natural regeneration patterns observed (Harper 1977). In absence of such relationship, other ecological processes, such as seed predation, may be important to explain plant regeneration patterns. For shade-intolerant trees, experimental seed germination was equivalent to the observed natural abundance of seedlings and saplings across habitats, being enhanced in small forest fragments compared to RNLQ. In contrast, *C. alba* expressed the same experimental seed germination and seedling establishment among habitats while, in the natural regeneration assessment, *C. alba* expressed enhanced seedling and sapling densities in the forest of RNLQ compared to small fragments, suggesting that other ecological factors such as enhanced seed predation in forest fragments may be an additional factor affecting tree regeneration (Donoso & Simonetti 2004).

Seed germination of *A. chilensis* and *N. glauca* expressed the same positive response to canopy openness both within and between habitats while, *N. obliqua* was insensitive to canopy openness at the two spatial scales. Several studies have demonstrated the importance of using different spatial scales approaches to address regeneration dynamics in forest ecosystems, as a way to capture the complexity of regeneration responses of plants occurring in heterogeneous environments (Armesto & Pickett 1985; 1986; Schupp 1992; Pickett & Cadenasso 1995; Brokaw & Busing 2000). The challenge of a hierarchical approach is to elucidate whether processes and patterns that occur at a lower level may be "scaled" to a higher level (O´ Neill *et al.* 1986). In the case of the *C. alba*, we detected different germination responses depending on the scale of analysis: no differences at a large scale (between habitat comparison) but a negative effects as a function of canopy openness (within habitat comparison). This result reinforces the basic idea to define explicitly the scale of analysis both in basic and applied studies (Pickett & Cadenasso 1995).

Tree regeneration information obtained in this study, is difficult to compare quantitatively with other similar studies conducted in tropical and temperate forests because data were different in terms of scale of analysis, experimental design, stages of the life cycle analyzed, etc. However, it is possible to corroborate the general idea that in most studies shade-intolerant tree species regeneration resulted favoured by forest fragmentation (Chen *et al.* 1992; Laurance *et al.* 1998; Benitez-Malvido 1998). Thus, it is reasonable to suggest that composition and structure of fragmented forests, either temperate and tropicals, should tend to be dominated by pioneer shade intolerant species and therefore turn to initial stages of succession (Chen *et al.* 1992; Laurance *et al.* 1998; Benitez-Malvido 1998).

In summary, in a fragmented landscape abiotic variability that occur at different spatial scales tree regeneration responses varied within and between forests patches. Moreover regeneration niche may be a good predictor of tree regeneration, at least for shade-intolerant species. For a complete understanding of forest fragmentation and its consequences on plant regeneration, it is necessary to conduct studies using a multi scale approach and also consider more than one stage in the plant life cycle.

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Table 1: Regeneration predictions for species with contrasting shade tolerance; (-) indicates lower regeneration and, (+) indicates greater regeneration, (?) unknown regeneration.

Regeneration niche	Habitat
Shade-tolerant	Large patch forest (RNLQ) > Small forest fragments; Pine plantations?
Shade-intolerant	Large patch forest (RNLQ) < Small forest fragments; Pine plantations?

Table 2: Forest composition at the Reserva Nacional Los Queules (RNLQ), four small forest fragments and two pine plantations, species abundance was estimated as the number of adult (DAP $\geq$ 10 cm) recorded in 12 transects per habitat (50 x 2 m).

Tree species	RNLQ (ind/ha)	Small forest fragments (ind/ha)	Pine plantations (ind/ha)
Aristotelia chilensis	8	208	1025
Nothofagus obliqua	58	508	0
Nothofagus glauca	58	542	0
Cryptocarya alba	392	408	0
Aetoxicon punctatum	642	58	0
Azara spp.	17	17	0
Gomortega keule	17	17	0
Pinus radiata	0	17	250
Citronella mucronata	42	0	0
Gevuina avellana	417	267	0
Luma apiculata	8	17	0
Lithraea caustica	0	17	0
Lomatia dentata	108	0	0
Laurelia sempervirens	83	8	0
Peumus boldus	0	8	0
Persea lingue	142	25	0
N°	1992	2117	1275
N° of native tree species	13	13	1
Exotic tree species	0	1	1

Table 3: ANOVA with repeated measures analyses of soil moisture at the Reserva Nacional Los Queules (RNLQ), four small forest fragments and two pine plantations.

Source of variation	d.f.	F	P
Between subjects			
Habitat	2, 57	10.87	0.0001
Within subjects			
Months	11, 627	289.52	< 0.0001
Habitat x months	22, 627	2.12	0.002
Planned comparisons			
RNLQ > forest fragments	1, 57	17.35	0.0001
Forest fragments = pine plantations	1, 57	0.07	0.79
RNLQ > pine plantations	1, 57	15.20	0.0002

Table 4: One-way ANOVA analyses of canopy openness in the Reserva Nacional Los Queules (RNLQ), four small forest fragments and two pine plantations.

Source of variation	d.f.	F	P
Habitat	6, 78	19.86	< 0.0001
Planned comparisons			
RNLQ < forest fragments	1, 78	46.13	< 0.0001
Forest fragments = pine plantations	1, 78	1.43	0.24
RNLQ < pine plantations	1, 78	31.97	< 0.0001

Table 5: Planned comparisons of seedling and sapling densities of three trees species in different habitat types: Reserva Nacional Los Queules (RNLQ), four small forest fragments and pine plantations.

Source of variation	d.f.	F	P
Seedling abundance			
Shade-tolerant: *Cryptocarya alba*			
RNLQ > forest fragments	1, 87	105.76	< 0.0001
Forest fragments > pine plantations	1, 87	99.57	< 0.0001
Reserve > pine plantations	1, 87	410.55	< 0.0001
Shade-intolerant: *Aristotelia chilensis* + *Nothofagus glauca.*			
RNLQ < forest fragments	1, 87	28.90	< 0.0001
Forest fragments < pine plantations	1, 87	4.23	0.04
RNLQ < pine plantations	1, 87	55.25	< 0.0001
Sapling abundance			
Shade-tolerant: *Cryptocarya alba*			
RNLQ > forest fragments	1, 87	12.29	0.0007
Forest fragments > pine plantations	1, 87	5.77	0.02
RNLQ > pine plantations	1, 87	34.95	< 0.0001
Shade-intolerant: *Aristotelia chilensis* + *Nothofagus glauca.*			
RNLQ < forest fragments	1, 87	7.64	0.007
Forest fragments = pine plantations	1, 87	0.44	0.51
RNLQ < pine plantations	1, 87	11.76	0.0009

Table 6: Planned comparisons of germination probabilities of four trees species in different habitat types: Reserva Nacional Los Queules (RNLQ), four small forest fragments and pine plantations.

Source of variation	d.f.	F	P
Shade-tolerant: *Cryptocarya alba*			
RNLQ = forest fragments	1, 307	0.140	0.708
Forest fragments = pine plantations	1, 307	0.690	0.407
RNLQ = pine plantations	1, 307	1.383	0.240
Shade-intolerant: *Aristotelia chilensis, Nothofagus glauca* + *N. obliqua*			
RNLQ < forest fragments	1, 307	8.696	0.003
Forest fragments = pine plantations	1, 307	1.851	0.175
RNLQ < pine plantations	1, 307	19.762	< 0.0001

Table 7: Correlation analyses between germination and establishment probabilities with canopy openness. (P (G): germination probabilities; P (E): establishment probabilities). R_S = Spearman correlation test.

Species	Variable	N	r_s	$t_{(N-2)}$	P
Cryptocarya alba	P (G)	84	- 0.303	-2.876	0.005
	P (E)	84	- 0.187	-1.728	0.088
Aristotelia chilensis	P (G)	84	0.212	1.965	0.053
Nothofagus obliqua	P (G)	84	0.114	1.036	0.303
Nothofagus glauca	P (G)	84	0.291	2.759	0.007

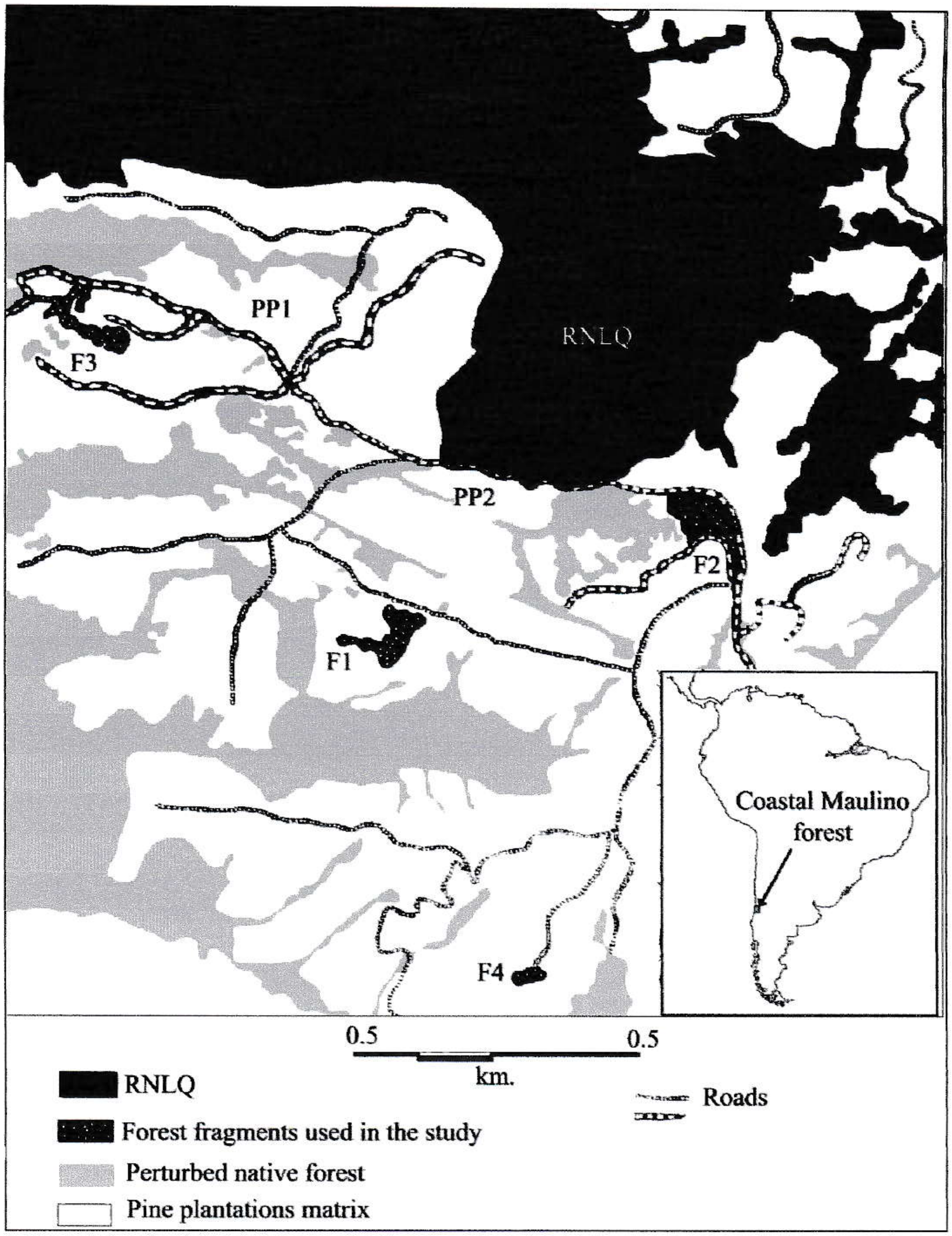

Fig. 1: Location of the study site at Reserva Nacional Los Queules (RNLQ), four small forest fragments (F 1 – F 4) and two pine plantations (PP1-PP2).

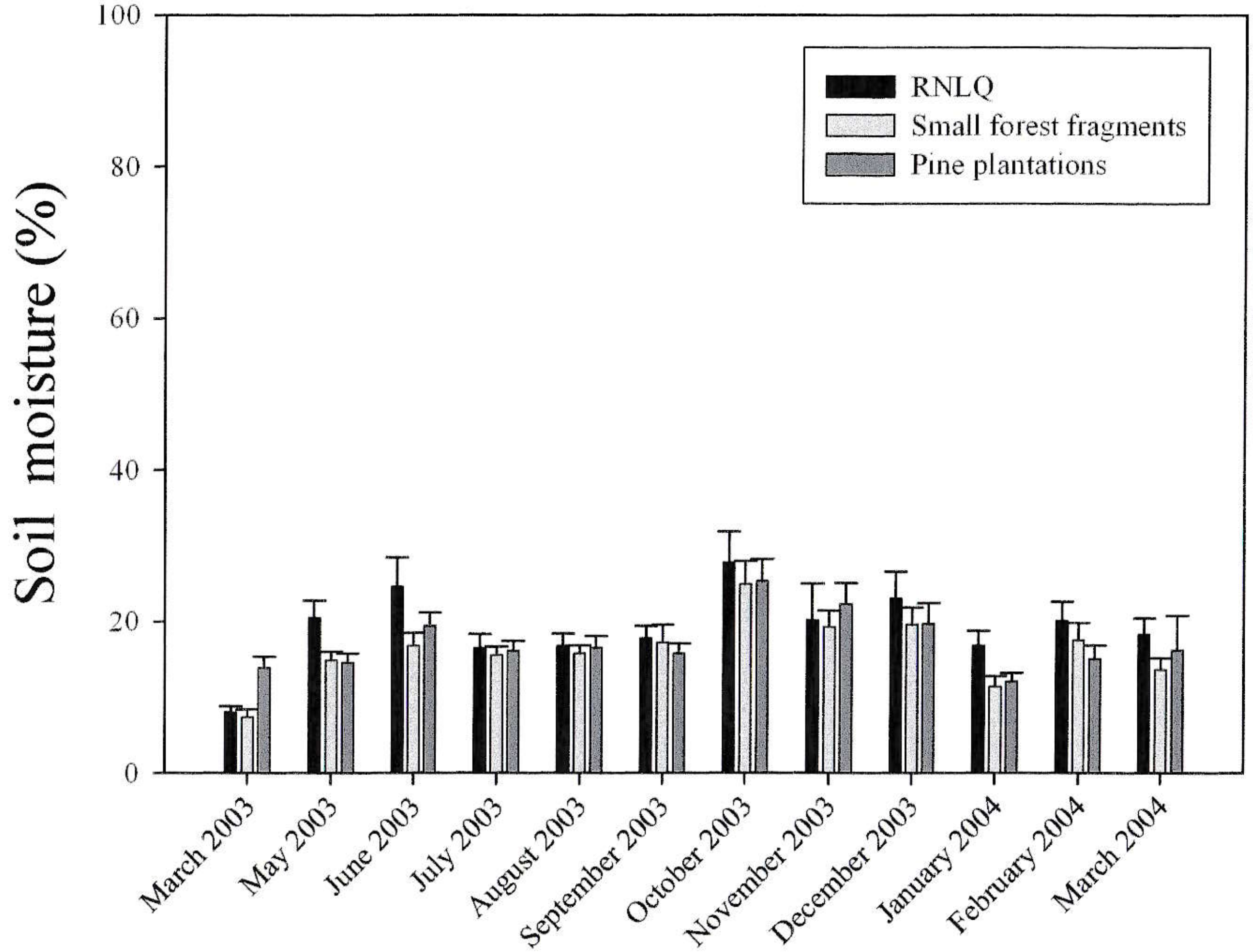

Fig. 2: Soil moisture at the Reserva Nacional Los Queules (RNLQ), four small forest fragments and two pine plantations. Bars show means ± 1.96 SE.

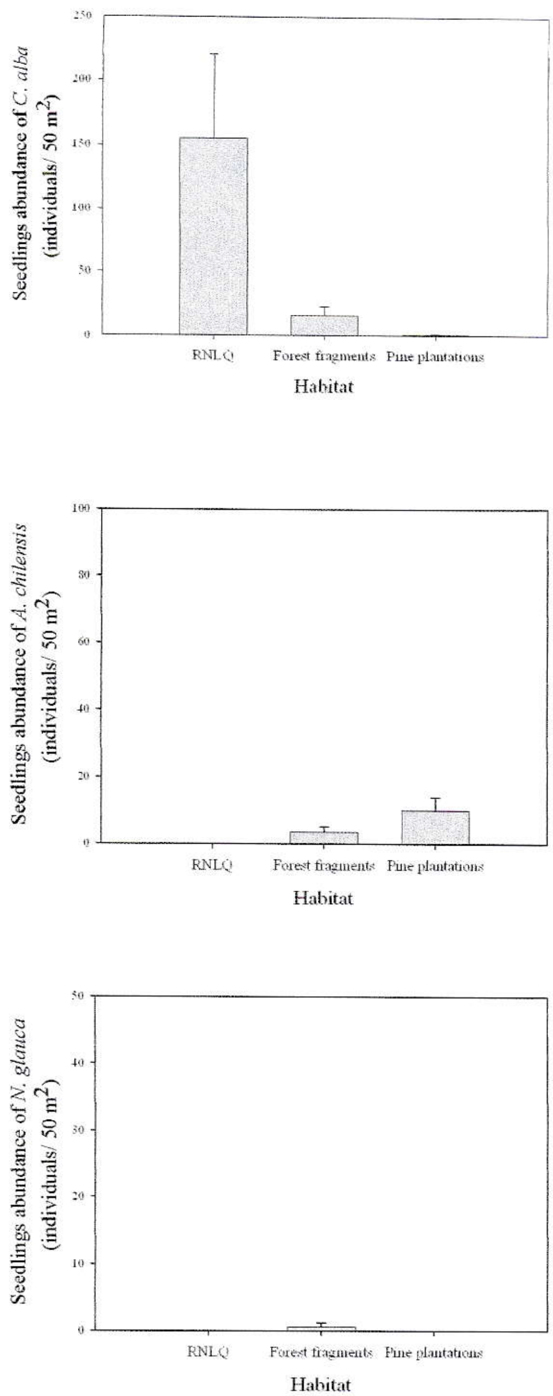

Fig. 3: Seedlings abundance at Reserva Nacional Los Queules (RNLQ), four small forest fragments and two pine plantations. Bars show means $\pm$ 1.96 SE.

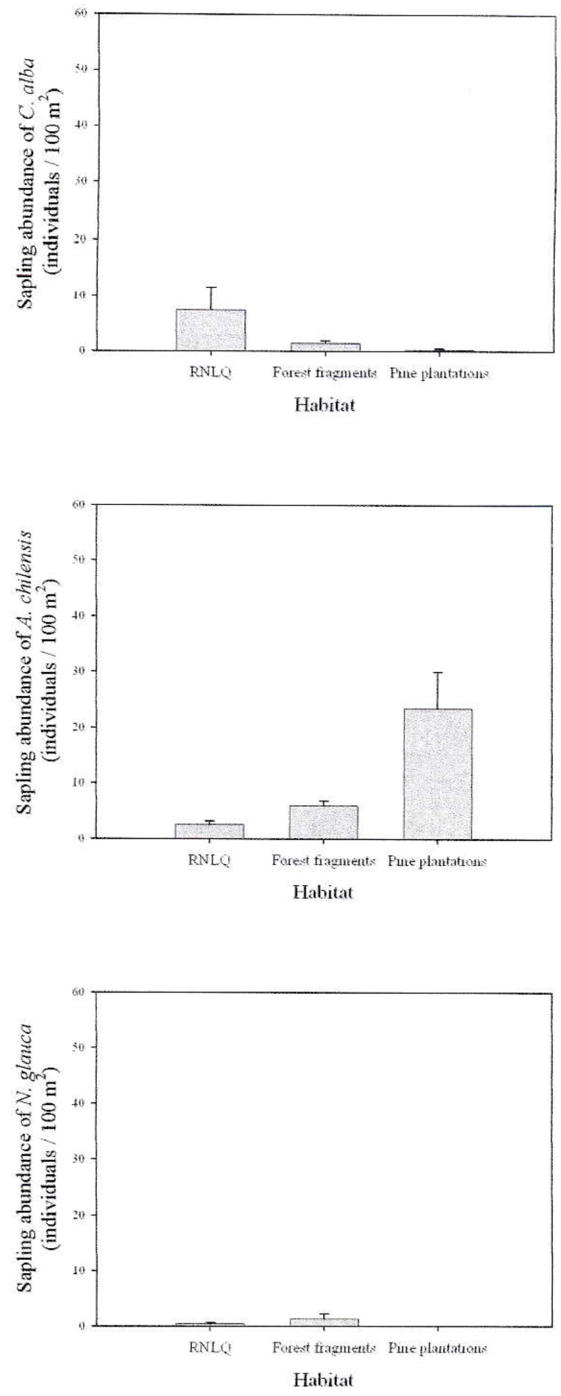

Fig. 4: Sapling abundance of three tree species at the Reserva Nacional Los Queules (RNLQ), four small forest fragments and two pine plantations. Bars show means $\pm$ 1.96 SE.

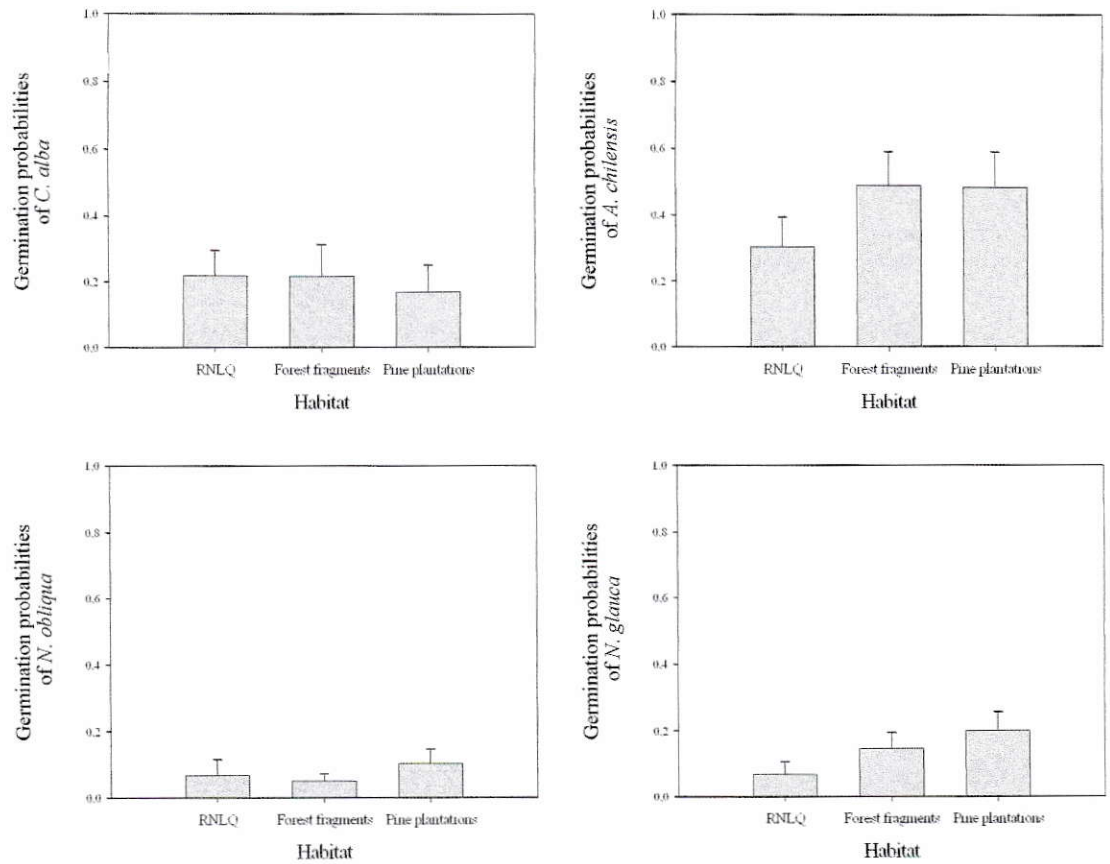

Fig. 5: Germination probabilities based on the experimental essay for *A. chilensis*, *C. alba*, *N. obliqua* and *N. glauca* at Reserva Nacional Los Queules (RNLQ), four small forest fragments and two pine plantations. Bar shows means $\pm$ 1.96 SE.

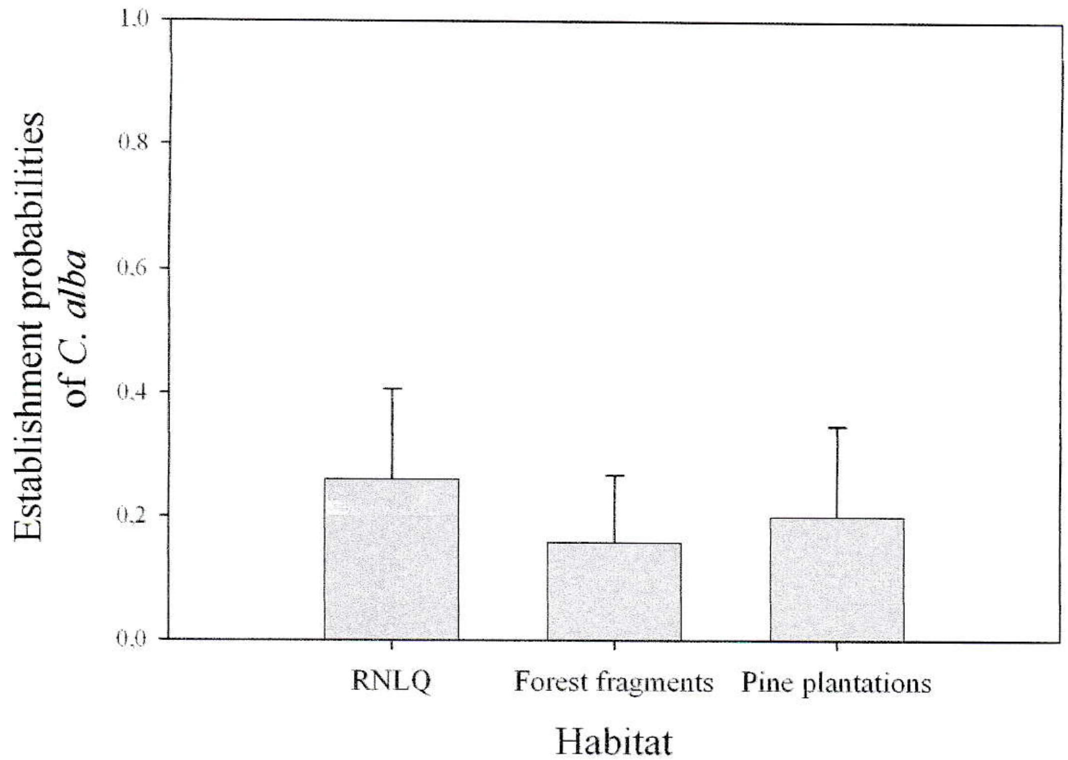

Fig. 6: Establishment probabilities based on the experimental essay at Reserva Nacional Los Queules (RNLQ), four small forest fragments and two pine plantations. Bar shows means ± 1.96 SE.

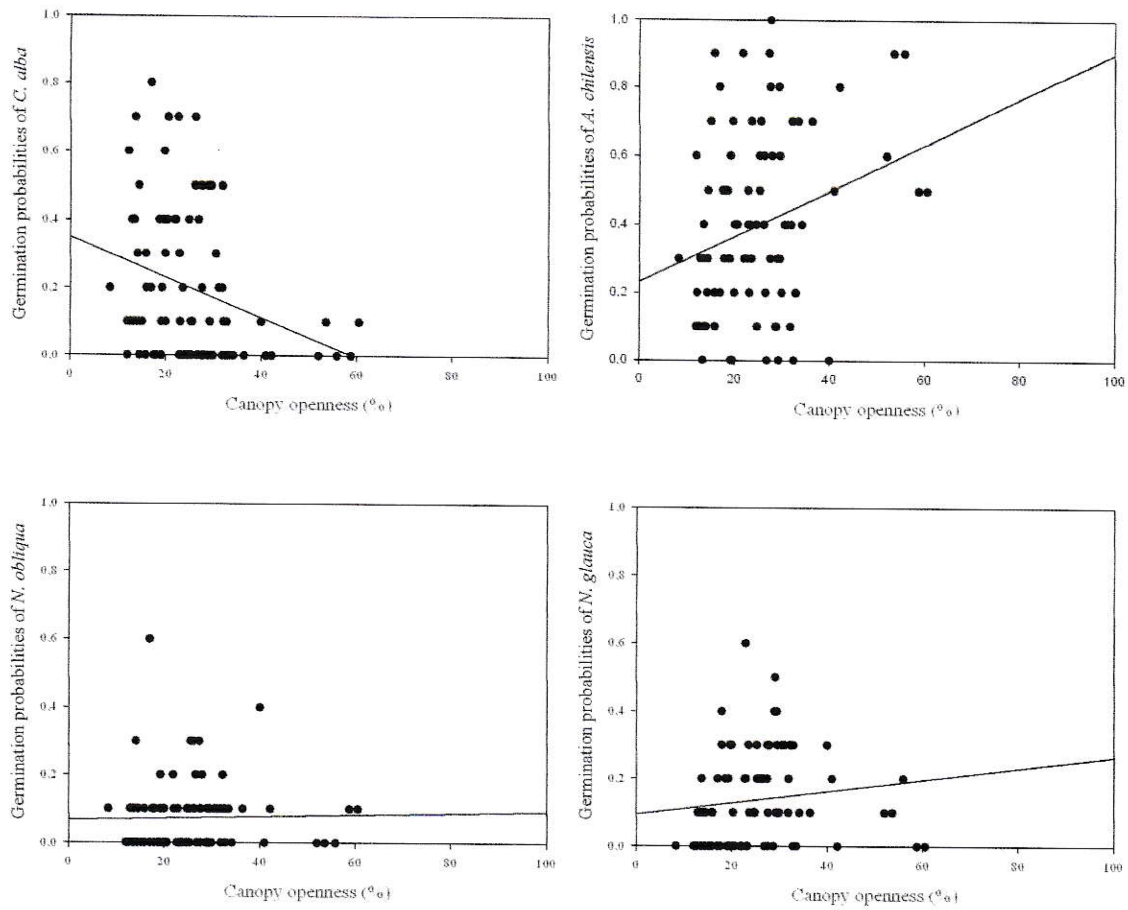

Fig. 7: Correlations between germination probabilities for four tree species with the canopy openness of the forests within the Reserva Nacional Los Queules, four small forest fragments and two pine plantations.

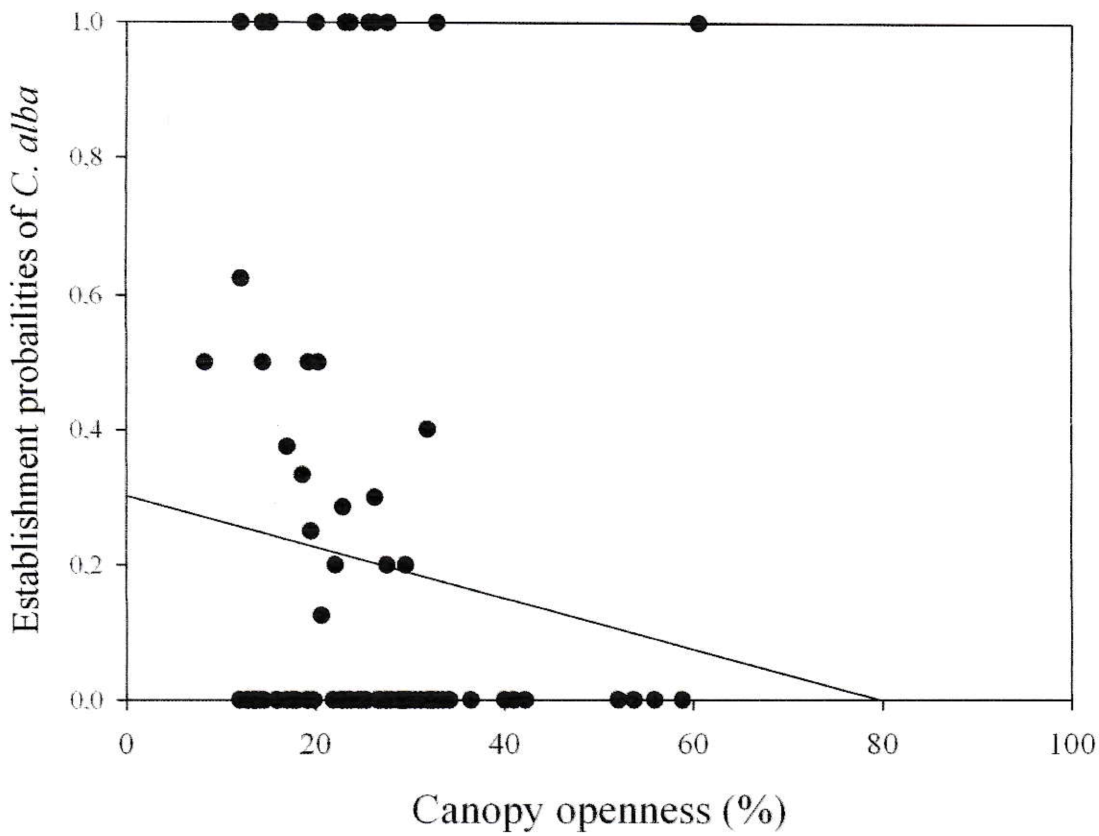

Fig. 8: Correlations between establishment probabilities of a shade-tolerant specie with the canopy openness of the forests within the Reserva Nacional Los Queules, four small forest fragments and two pine plantations.