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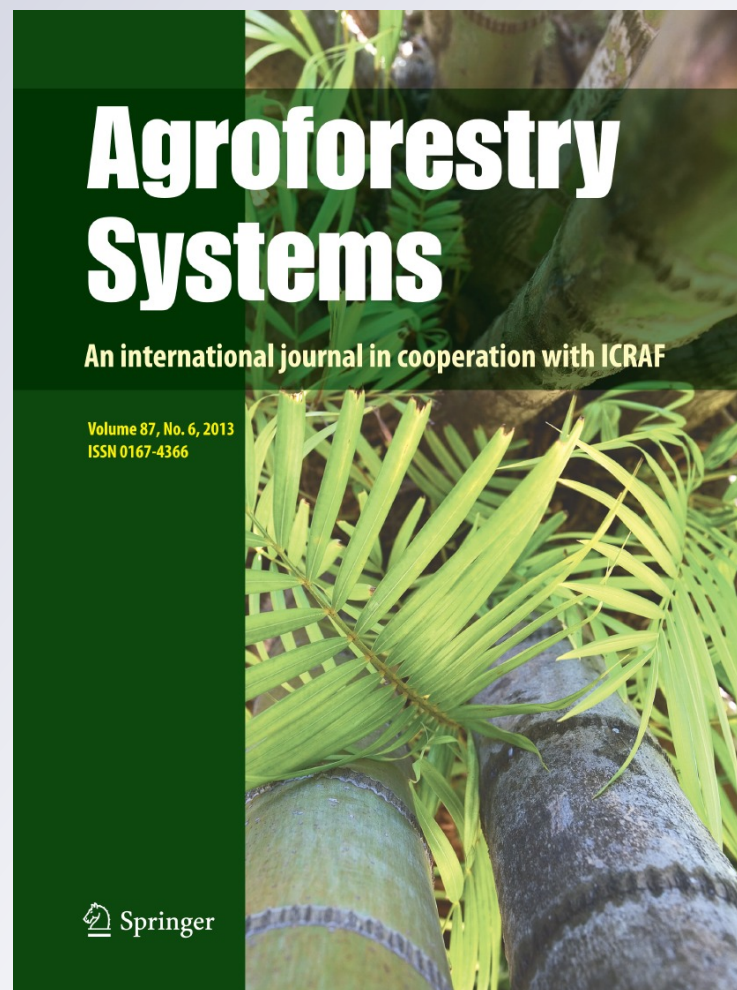
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Are silvopastoral systems compatible with forest regeneration? An integrative approach in southern Patagonia

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Abstract We used an integrated approach to analyze the influence of silvopastoral management on the biotic and abiotic factors influencing on the natural recruitment of native forests in Tierra del Fuego (Argentina). The probabilities of transition from flowers to seeds to seedlings were estimated in forests with silvopastoral management (i.e., stands that had been both grazed and thinned), secondary growth stands, and unmanaged old-growth areas. Pre-dispersal losses were caused by microclimate and insect predation acting on flowers and immature fruits. Post-dispersal losses resulted from the impact of reduced litterfall and microclimate. But the most critical stage of the overall cycle was seedling establishment. Silvopastoral practices and stand age modified the main drivers of regeneration. While flowering was unaffected by management, fruiting and seed production were more successful in unmanaged forests. Seedling establishment and survival were favored by canopy cover reduction in silvopastoral stands. The

increase of solar radiation and soil moisture in managed forests positively influenced the seedling establishment and survival, while in second-growth forests it was limited by suitable micro-site availability. Thinning practices aimed at increasing the under-story heterogeneity in mature forests and restoring canopy complexity of second-growth stands could be suitable for sustainable management of these temperate forests.

Keywords Flowering · Forest management · Recruitment · Reproductive losses · Seed predation · Seedling survival

Introduction

One of the main challenges of managing natural ecosystems is to find a balance between economic and ecological sustainability (Jose 2009). For example, the integration of native forests within livestock grazing areas is an advantageous management alternative in terms of both biodiversity and productivity, compared to traditional grazing systems in open grasslands (Sánchez-Jardón et al. 2010). Although livestock and forests have long co-existed in the rural areas of southern Patagonia, traditional practices in the past (e.g., fires) have led to the replacement several of the original old-growth forest by rangelands or secondary stands (Roig 1998). Currently, silvopastoral management systems are being promoted in the region as a

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novel strategy for a sustainable use and conservation of *Nothofagus antarctica* forests (Peri et al. 2009a). This proposal involves livestock feeding on natural pastures that grow in the understory of thinned forests, where forest regeneration occurs naturally (e.g., seeds or sprouts), not through planting. Since there are positive and negative interactions among trees, pastures and livestock (Adler et al. 2001; Romanya et al. 2005), silvopastoral systems aim to encourage the positive interactions to ensure tree regeneration and long-term viability (Peri et al. 2009a).

Forest regeneration is a dynamic process which includes multiple transitions among different reproductive stages (flowers, seeds, seedlings, and saplings). These stages are in turn influenced by abiotic and biotic factors that determine the number of recruits established (Pulido et al. 2010). *N. antarctica* (Forster f.) Oersted 1871 is a deciduous anemophilous and anemorous broadleaved species found in the temperate forest of Argentina and Chile, capable of both sexual and asexual regeneration (Premoli 1991; Donoso et al. 2006). Due to its widely recognized sprouting potential, the natural recruitment of new individuals (sexual reproduction) has been often overlooked. Some attention has been paid to the annual variability and viability of seed production (Bahamonde et al. 2011) or seed germination capacity (Premoli 1991). However, climatic conditions (Bahamonde et al. 2009), soil moisture content (Heinemann et al. 2000; Martínez Pastur et al. 2011), and seed predation (Sullivan et al. 1995; Burgos et al. 2008) have also been suggested to influence the natural recruitment of *Nothofagus* forests in several stages. Nevertheless, a whole-cycle approach that integrates the combined effects of multiple interactions among factors at each reproductive stage is needed for a complete understanding of this process (Pulido et al. 2010).

Previous studies in southern Patagonia have shown how forest management induces changes to the abiotic environment in forests (Caldentey et al. 2001; Bahamonde et al. 2009; Promis et al. 2010) and on biodiversity components, such as birds and insects (Deferrari et al. 2001; Spagarino et al. 2001; Lencinas et al. 2009, 2011). These modifications may influence the success of flowering, fruiting, seed dispersal, and seedling survival (Martínez Pastur et al. 2008; Soler et al. 2010), and, consequently, the overall levels of natural regeneration. In this paper, we used an

integrated approach (Fig. 1) to analyze the influence of silvopastoral practices (grazing livestock under thinned forest stands) on the biotic and abiotic factors driving natural regeneration in native *N. antarctica* forests. We compared regeneration traits among unmanaged; secondary-growth; and previously thinned, grazed forests (silvopastoral). Secondary-growth forests (SF) (50–100 years) were included because they are currently one of the most prevalent *N. antarctica* forest types in Tierra del Fuego (Peri 2009), and they have a high potential as silvopastoral systems in the near future. Specifically, the following questions were addressed: (i) What is the critical stage explaining the final reproductive output of *N. antarctica*? (ii) What is the relative importance of abiotic and biotic factors along the reproductive cycle? (iii) Does stand age modify the main drivers as compared to primary forests?, and (iv) Do silvopastoral systems allow the maintenance of the main natural reproductive processes operating in the primary forests?

Methods

Study sites and forest structure

The study was conducted from September 2007 to January 2012 in pure *N. antarctica* forests located at Los Cerros Ranch (54°20' S, 67°52' W), Tierra del Fuego, Argentina. Within an area of 1,500 ha, we selected three different forest types and four replicates in each: (i) silvopastoral systems (SIL) had mature forests (130–180 years old) that have been managed by selective cutting and thinning (reducing about 50 % of the original cover) about 5 years before the onset of this study (Soler 2012). This canopy management improves the understory biomass (annual increase of 1,400 kg ha⁻¹ of dry matter, according Peri et al. 2009a), which is used as forage for cattle grazing; (ii) SF had young overstocked stands (50–70 years old) that originated after irregular fires in the '40 s (Roig 1998), which generated the whole conversion of the original forest structure. These forests are not currently used for grazing livestock, but it represent potential sites for future interventions (e.g., thinning) that benefit the growth of high-quality individual, making it possible to implement of silvopastoral management; and (iii) primary forests (PF) had unmanaged old-growth stands (150–200 years

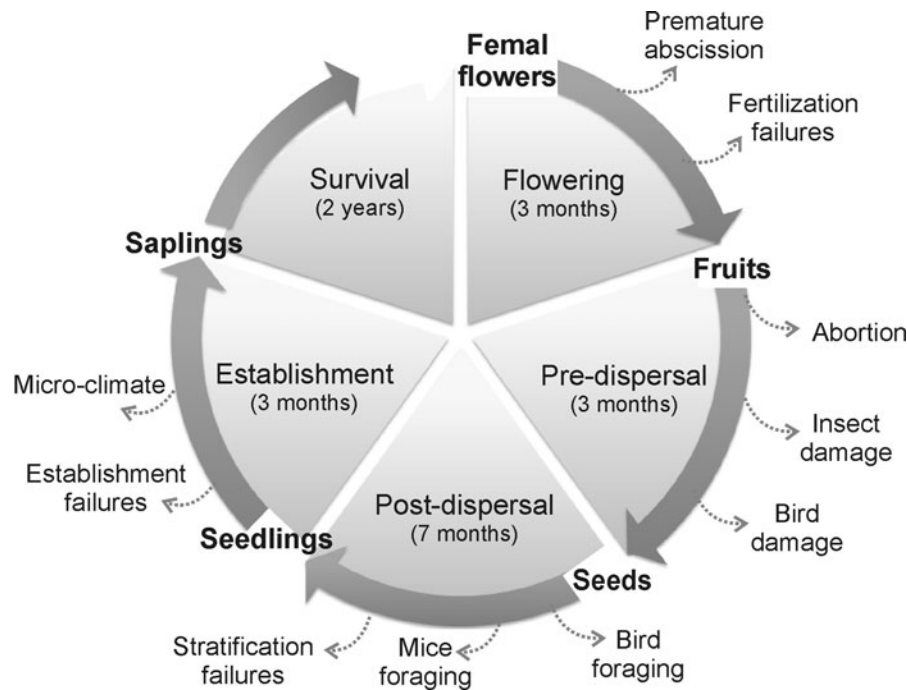


Fig. 1 Model structure for the natural regeneration cycle of *Nothofagus antarctica*. This process consists of different stages (shown as pie wedges within the circle), each of which comprises different reproductive structures: female flowers, fruits, seeds, seedlings, and saplings. At every stage, there are specific biotic and abiotic factors (indicated outside the circle)

that influence the probability of transition from one stage to the next. These effects include interactions with animals (e.g., herbivores) and with the abiotic environment (e.g., light, water). Any of these factors is limiting if independently of other effects it reduces the likelihood of successful recruitment in one stage to a value close to zero

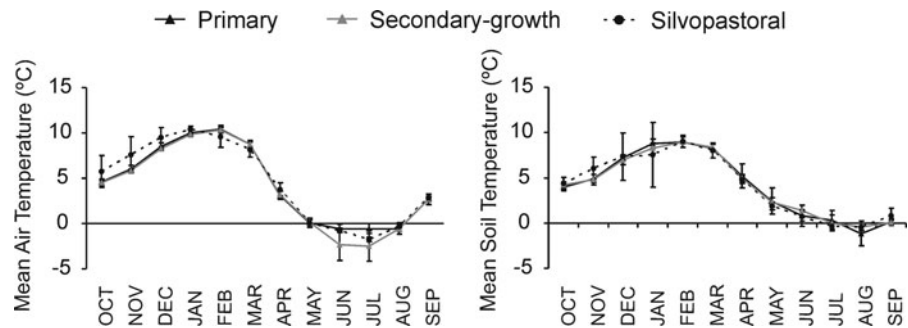
old), which have no previous forestry intervention. Currently, the forest structure in these stands (large trees, multilayered canopy, and big coarse woody debris) is the result of two centuries of natural disturbances (e.g., wind throws).

Stocking rate is about 7–8 ind km⁻² (cattle) in the study area, correspond mainly to Hereford breed. The traditional grazing management is based on winter and summer extensive grazing paddock (400–1,000 ha approximately), where each paddock includes mixed habitat types (*N. antarctica* forests, grasslands, and peatlands) (Ormaechea et al. 2009). Livestock movements depend on ranching management decisions, but usually are free-ranging because the pastures here are not wire delimited. Cattle grazed on grasslands during summer-autumn, but they also use *Nothofagus* forests in winter-spring (Soler et al. 2012). In this region, natural populations of guanaco (*Lama guanicoe*) occur at about 2 ind km⁻² (Montes et al. 2000). Native and domestic herbivores overlapped in the use of grasslands and silvopastoral forests as feeding and shelter sites.

Microclimate within these forests has been characterized over a year (2008) by Soler (2012). In general, climate is defined by short, cool summers and long, snowy and frozen winters, while the growing season extends from November to March (Fig. 2). Mean monthly air temperatures varied from −0.6 °C (July) to 10.2 °C (February) in mature forests, but during winter, minimum temperature significantly decreased (−1.7 °C) under silvopastoral practices. Secondary-growth stands are cooler (−2.5 to 10.2 °C) than the others. Soil temperature (at 0.20 m depth) varied from −0.3 to −1.1 °C (August) to 9.0 °C (March) (Soler 2012).

Forest structure of each stand was characterized through five plots using the point sampling method (BAF 6) (Bitterlich 1984). In each sampling point, total height and quadratic mean diameter of each tree were measured, and dominant height, tree density, basal area, and total over bark volume were calculated as per Lencinas et al. (2002). To characterize canopy structure and solar radiation transmission to the understory, we used hemispherical

Fig. 2 Mean temperature values (air and soil) registered during 2008 in different forest types (silvopastoral systems, secondary-growth and primary unmanaged) of *Nothofagus antarctica* forests. Bars indicate \pm standard deviation



photographs (see Martínez Pastur et al. 2011). Then, we estimated canopy cover, effective leaf area index (Stenburg et al. 1994), and global radiation at the understory level (the sum of direct and diffuse radiation transmitted through the canopy) throughout the growing season (November to March). Also, volumetric soil water content in the first 0.20 m depth (%) was recorded using a MP406 moisture probe (ICT, Australia), taking five measures in each stand.

Flower and fruit production during the pre-dispersal stage

In each of the 12 study stands, 10 biomass traps (plastic recipients of 0.06 m² in area and 30 cm deep) were installed ($n = 120$). The traps were perforated for water drainage, and then placed along a 50 m transect in each stand. Fallen reproductive structures were collected monthly from the traps and transported to the laboratory. Propagules were classified as male flowers, female flowers, abscised female flowers, and female flowers resulting in empty fruits (fertilization failures). Fruits were classified as those damaged by insects or by birds, abscised immature fruits (abortion), and sound fruits. Insect damage was deduced from the deformation due to dehydration of the reproductive organs, whereas bird damage was assigned on the basis of uneaten fruit parts rejected after foraging. Classified plant material was oven-dried at 70 °C to constant weight and subsequently weighted to the nearest 0.0001 g. During the dispersal months (March, April and May), seeds collected into the traps were assessed by means of internal inspection. Subsequently, the tetrazolium test (2,3,5-triphenyltetrazolium chloride) was applied to full seeds to assess their viability (Moore 1985).

Seed production and losses during the post-dispersal stage

In the post-dispersal stage, we quantified the number of sound seeds, seeds predated by birds and by mice at the forest floor, and non-predated seeds that died during winter stratification. In each stand, one wire cage (0.4 m² with a 30 × 30 mm mesh size) was deployed from April to October to exclude bird foraging but at the same time allowing mice activity. Seeds were marked with 2 cm pale yellow nylon thread attached to the nuts. Five groups of 25 marked seeds were placed inside the cages (exposed only to mice foraging), and five groups of 25 marked seeds were placed outside close to the cages (exposed to both mice and bird foraging). Marked seeds were placed aboveground mixed with the litter at the first 5 cm layer of the forest floor (organic layer), but were not randomly scattered to prevent loss of sample and to avoid counting errors. Seeds remaining after winter (October) were recovered and counted at the end of the experimental period each year, when the snow had disappeared almost completely. Another assay was established close to the aforementioned to analyze losses of seed viability during winter. Five bags of 2 × 2 mm mesh size containing 25 seeds recently collected were placed aboveground mixed with the litter at the first 5 cm layer of the forest floor of each stand. Seed quality was determined as described in the preceding section, at the beginning (April) and at the end (October) of the assay each year.

Seedling emergence and survival

Five permanent seedling transects of 1 m² (5.0 × 0.2 m) were established at the beginning of the study in each stand. In the mid-summer (late January), each

emerged seedling was identified with its coordinates (x, y) within transect. The survival of each seedling cohort was monitored along the following two seasons. Thus, we determined the number of potential seedlings (number of seedlings surviving after post-dispersal losses, in million ha⁻¹), establishment success (emerged seedlings that developed fully expanded leaves; in %), seedling survival after 1 year (%), and seedling survival after 2 years (%).

Summarizing, in all stands the transitions between life stages were monitored in three consecutive reproductive cycles and cohorts (hereafter year 1: from flowering and seeding 2007 to seedling survival to the second growing season in January 2010; year 2: from flowering and seeding 2008 to January 2011; and year 3: from flowering and seeding 2009 to January 2012).

Statistical analyses

We compared the structural traits of the stands by means of one-way ANOVA with forest type (silvopastoral, second-growth and primary forest) as the factor. The number of female flowers was computed as the sum of all types of propagules fallen into the traps (either fertilized, non-fertilized, predated or sound). From these data we calculated the probabilities of transition (%) from any given stage to the next were used as response variables (Pulido et al. 2010). General linear models (GLM) on a mixed model nested ANOVA design has been used to test for the effect of year and forest type (fixed factors) and stand as a random factor nested within forest type. Normality and homoscedasticity were tested, and variables were log transformed when the assumptions were not accomplished. Differences were evaluated with a post hoc Tukey test at $p < 0.05$. Statistica 7.0 package (StatSoft Inc., Tulsa, USA) was used for all statistical analyses.

Results

Forest structure

All selected stands corresponded to the higher site class according to Lencinas et al. (2002), and height of dominant trees was similar among forest types (Table 1). However, forest structure parameters showed significant differences depending on management and stand age. As expected, silvopastoral

practices significantly decreased the basal area (26 % reduction), total over bark volume (29 %), canopy cover (20 %) and effective leaf area index (19 %) compared to PF, as well as tree density (24 %), but with no significant differences. On the other hand, the structure of SF stands showed the highest tree density (7 times more than mature forests), but with tree diameters being significantly smaller than those of mature stands (Table 1). As a consequence, the SF stands had the highest canopy cover and leaf area index values, which gave way to the lowest irradiance values at the understory level. Finally, all these structural changes caused differences in soil moisture, which was significantly greater in the more open stands (SIL), compared to the other closed forests (PF and SF).

Flower production and fruit set

The annual flower production varied among forest types and years during the study period (Table 2). While the number of male flowers was significantly greater in SF, the greatest number of female flowers was recorded in PF. On the other hand, the flowers number significantly increased since year 1 $< 2 < 3$. However, forest type \times year interactions were noted due to a different trend of male and female flower production in SIL (year 2 $> 3 > 1$). Losses in female flowers caused by abscission were not affected by silvopastoral practices, and greater losses were consistently found in unmanaged stands (PF and SF). Female flowers deriving in empty seeds were the main source of loss in the flowering stage, reaching almost 50 % of losses. Moreover, this percentage was similar among forest types and years. As a consequence, the percentage of undamaged flowers that were successfully fertilized (fruit set) did not varied among PF, SF and SIL. Inter-annual variability of female flower losses was not detected, although year 1 presented the highest values of fruit set. Finally, the nested factor (stand within forest type) significantly affected the flowering stage (Table 2), since both flower numbers and percentage of losses were more homogeneous among SIL stands than in SF and PF (data not shown).

Fruit development and fruit damage

Fruit production was significantly reduced in SIL and SF, compared to PF, while values recorded during year 3 doubled those for years 1 and 2 (Table 3). Interaction

Table 1 On one-way ANOVA-type design to compare the forest structure of silvopastoral systems (SIL), secondary-growth (SF) and primary unmanaged *Nothofagus antarctica* forests (PF)

Forest type	DH	QMD	TD	BA	TOBV	CC	LAI	GR	SM
PF	13.6	47.6 b	476 a	46.5 b	357.7 b	78.9 b	1.6 b	10.6 b	30.6 a
SF	10.1	16.1 a	3,406 b	39.6 ab	245.5 a	85.5 c	2.2 c	7.7 a	27.8 a
SIL	12.4	43.9 b	364 a	34.5 a	252.5 a	66.1 a	1.3 a	16.7 c	37.6 b
F	3.48	117.29	41.24	5.97	4.67	61.51	71.99	73.43	8.87
<i>p</i>	0.076	<0.001	<0.001	0.004	0.040	<0.001	0.015	<0.001	0.001

DH dominant height (m), QMD quadratic mean diameter (cm), TD trees density (trees ha⁻¹), BA basal area (m² ha⁻¹), TOBV total over bark volume (m³ ha⁻¹), CC canopy cover (%), LAI effective leaf area index, GR global radiation at the understory level transmitted through the canopy (W m²), SM soil moisture (%), F fisher statistic, *p* probability

Different letters in each column denote differences by Tukey test at *p* < 0.05

Table 2 GLM analysis on a mixed model, nested ANOVA-type design testing for the effect of forest type, year (fixed factors) and stand (random factor) on the production of male flowers (million ha⁻¹), female flowers (million ha⁻¹), abscised female flowers (%), empty female flowers (%), and fruit set (%) of *Nothofagus antarctica* forests

Source of variation	Male flowers	Female flowers*	Abscised female flowers	Empty female flowers	Fruit set
Forest type					
PF	27.20 a	7.99 b	6.60 b	47.63	45.76
SF	35.18 b	5.90 a	6.30 b	48.36	45.32
SIL	24.44 a	5.36 a	4.22 a	49.91	45.87
Year					
1	18.54 a	4.35 a	4.75	46.23	49.01 b
2	28.94 b	4.14 a	6.14	49.80	43.96 a
3	39.34 c	10.76 b	6.22	49.87	43.98 a
Source of variation (df)					
Forest type (2, 39)					
F	15.72	230.47	4.26	0.88	0.05
<i>p</i>	<0.001	<0.001	0.010	0.412	0.948
Year (2, 312)					
F	54.63	81.06	1.74	2.85	5.52
<i>p</i>	<0.001	<0.001	0.177	0.059	0.004
Type × year (4, 312)					
F	6.87	18.49	1.27	0.77	1.45
<i>p</i>	<0.001	<0.001	0.278	0.544	0.215
Stand (type) (39, 312)					
F	1.88	1.50	1.28	1.98	1.54
<i>p</i>	0.001	0.03	0.127	0.001	0.025

Percentages refer to the absolute number of female flowers

F fisher statistic, *p* probability, PF primary forest, SF secondary-growth forest, SIL silvopastoral systems

Different letters in the same column showed differences by Tukey test at *p* < 0.05

* Log-transformed variable

(forest type × year) was related to the annual variability between SF (maximum production in year 1) and PF (year 3). The nested factor (stand) affected fruit

production mainly due to the fact that the numbers among PF stands were more heterogeneous than those in SIL and SF.

Table 3 GLM analysis on a mixed model, nested ANOVA-type design testing for the effect of forest type, year (fixed factors) and stand (random factor) on the production of fruits(million ha⁻¹), fruits predated by insects (%), fruits predated by birds (%), abscised immature fruits (%), and sound fruits (%) of *Nothofagus antarctica* forests

Source of variation	Number of fruits*	Insect-predated fruits	Bird-predated fruits	Abscised immature fruits	Sound fruits
Forest type					
PF	3.81 b	21.06 b	5.63 b	28.06	45.23
SF	2.86 a	15.86 a	8.97 b	29.79	45.36
SIL	2.67 a	25.55 b	3.52 a	28.37	42.55
Year					
1	2.29 a	16.62 a	5.52 b	21.63 a	56.23 c
2	1.95 a	26.85 b	1.71 a	21.63 a	27.76 a
3	5.10 b	19.01 b	10.90 c	43.67 b	49.16 b
Source of variation (df)					
Forest type (2, 39)					
F	5.48	11.57	17.03	0.41	0.73
<i>p</i>	0.004	<0.001	<0.001	0.661	0.480
Year (2, 312)					
F	44.18	14.09	48.01	81.15	64.22
<i>p</i>	<0.001	<0.001	<0.001	<0.001	<0.001
Type × year (4, 312)					
F	13.48	6.67	7.26	4.25	5.73
<i>p</i>	<0.001	<0.001	<0.001	0.002	<0.001
Stand (type) (39, 312)					
F	1.58	1.28	1.13	1.57	1.11
<i>p</i>	0.018	0.129	0.284	0.002	0.307

Percentages refer to the absolute number of fruits

F fisher statistic, *p* probability, *PF* primary forest, *SF* secondary-growth forest, *SIL* silvopastoral systemsDifferent letters in each column showed differences by Tukey test at *p* < 0.05

* Log-transformed variable

Regarding fruit losses, fruit damage by biotic factors was higher than expected, since all predators pooled caused similar percentages (26 %) than the spontaneous abortions (28 %) at this stage. Insect damage was significantly higher in SIL and PF, compared to SF. However, bird damage was not affected by silvopastoral practices, being greater in unmanaged stands (SF > PF). Finally, there were no effects of forests type on the proportion of aborted fruits. Regarding temporal patterns, losses due to bird predation and abortions increased in year 3, while the percentage of insect predation was equally high during years 2 and 3. As a consequence, the proportion of sound fruits was greater during year 1 (Table 3). Significant interactions were observed due to: (i) the high percentage of aborted fruits in SIL during year 2,

unlike other years which were greater in PF; (ii) similar insect damage proportion between SIL and PF during years 1 and 2, but increased damage in SIL for year 3; and (iii) high birds predation percentage in SF during years 1 and 2, but similar values between PF and SF in year 3. The nested factor (stand) only affected the proportion of aborted fruits due to one of the PF stands and one of the SIL stands showed higher values than the other stands within each forest type.

Post-dispersal stage

As noted for fruit production, the absolute number of seeds was significantly reduced in SIL and SF, compared to PF (Table 4). Seed number peaked in year 3, but significant interactions were detected.

Table 4 GLM analysis on a mixed model, nested ANOVA-type design testing for the effect of forest type, year (fixed factors) and stand (random factor) on the production of seeds(S) (million ha⁻¹), seeds predated by mice (%), seeds predated by birds (%), seeds died during winter stratification (%) and sound seeds (%) of *Nothofagus antarctica* forests

Source of variation	Number of seeds*	Mice-predated seeds	Bird-predated seeds	Non-viable seeds	Frost-damaged seeds	Sound seeds
Forest type						
PF	5.76 b	0.21 a	1.66 b	8.77	8.05 b	85.19 ab
SF	3.41 a	0.85 b	1.08 a	9.04	6.83 a	87.62 b
SIL	2.81 a	0.82 b	1.29 ab	9.65	8.90 c	82.40 a
Year						
1	3.16 b	0.69 b	2.69 b	13.75 c	11.92 c	76.54 a
2	1.33 a	0.32 a	0.57 a	4.64 a	7.88 b	88.42 b
3	7.51 c	0.87 b	0.78 a	9.07 b	3.95 a	90.25 b
Source of variation (df)						
Forest type (2, 39)						
F	18.06	32.73	2.99	0.53	3.14	4.05
<i>p</i>	<0.001	<0.001	0.052	0.588	0.044	0.018
Year (2, 312)						
F	74.82	18.71	46.44	55.56	29.93	33.03
<i>p</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Type × year (4, 312)						
F	16.86	52.11	5.04	1.39	2.95	5.25
<i>p</i>	<0.001	<0.001	<0.001	0.237	0.020	<0.001
Stand (type) (39, 312)						
F	1.30	1.21	0.72	0.64	0.56	1.29
<i>p</i>	0.114	0.186	0.891	0.953	0.991	0.121

Percentages refer to the absolute number of seeds

F fisher statistic, *p* probability, *PF* primary forest, *SF* secondary-growth forest, *SIL* silvopastoral systemsDifferent letters in each column showed differences by Tukey test at $p < 0.05$

* Log-transformed variable

During year 3, seed production in PF (12.7 million ha⁻¹) far exceeded the values of SF (5.6 million ha⁻¹) and SIL (4.2 million ha⁻¹), while in years 1 (2.6–3.5 million ha⁻¹) and 2 (1.1–1.6 million ha⁻¹), PF showed similar values to SF and SIL.

We found significant effects of forest type on seed losses. The mice-predated proportion was significantly greater in SF and SIL than PF (Table 4), while the bird-predated proportion was higher in unmanaged stands. Although the non-viable seed proportion was not affected by forest type, SIL increased the percentage of dead seeds during the winter stratification as compared to unmanaged stands. Overall, the percentage of sound seeds was significantly reduced in SIL, compared to PF and SF (Table 4). Significant inter-annual variation was observed for all seed losses.

Year 3 showed the lowest percentage of seed losses and, consequently, the greatest probability of success in the final seed output. However, it depended on the forest type because in years 1 and 2 the highest percentage of success occurred in SF, while in year 3 it occurred in PF.

Seedling emergence and survival

The number of potential seedling was significantly reduced in SIL and SF compared to the PF, with a significant temporal variation (year 3 > year 1 > year 2; Table 5). High spatial and temporal heterogeneity was shown as a function of forest type × year interactions. The maximum number of potential seedlings for SF and SIL was during year 1, but for

Table 5 GLM analysis on a mixed model, nested ANOVA-type design testing for the effect of forest type, year (fixed factors) and stand (random factor) on the number of potentialseedlings (million ha⁻¹), establishment success (%), survival at year one (%) and survival at year 2 (%) of *Nothofagus antarctica* forests

Source of variation	Potential seedlings*	Establishment success	One-year survival	Two-year survival
Forest type				
PF	4.92 b	0.52 b	0.37 b	0.25 b
SF	2.93 a	0.09 a	<0.01 a	<0.01 a
SIL	2.30 a	0.96 c	0.37 b	0.24 b
Year				
1	2.38 b	0.76 b	0.24 b	0.17 b
2	1.22 a	0.63 b	0.47 c	0.33 c
3	6.53 c	0.20 a	0.05 a	<0.01 a
Source of variation (df)				
Forest type (2, 39)				
F	20.88	34.26	23.88	24.39
<i>p</i>	<0.001	<0.001	<0.001	<0.001
Year (2, 312)				
F	86.31	15.60	24.23	31.34
<i>p</i>	<0.001	<0.001	<0.001	<0.001
Type × year (4, 312)				
F	20.51	9.44	5.62	8.36
<i>p</i>	<0.001	<0.001	<0.001	<0.001
Stand (type) (39, 312)				
F	1.34	1.26	1.43	1.06
<i>p</i>	0.092	0.139	0.052	0.379

Percentages refer to the number of emerged seedlings

F fisher statistic *p* probability, *PF* primary forest, *SF* secondary-growth forest, *SIL* silvopastoral systems

Different letters in each column showed differences by Tukey test at *p* < 0.05

* Log-transformed variable

PF it occurred during year 3. Establishment success was significantly higher in SIL than in PF, while it was close to zero in SF. The percentage of seedlings surviving after 1 and 2 years was similar between PF and SIL. Regarding temporal patterns, establishment success significantly decreased from year 1 > year 2 > year 3. Then, the survival rate during year 2 was significantly greater than in the other years. The interaction was due to the survival rate being higher in SIL in the first 2 years, while during year 3 it was greater in PF.

Synthesis: cumulative probabilities of transition along the whole cycle

Figure 3 shows the cumulative losses during the recruitment cycle for different cohorts and forest type

are shown. From that, it is possible to observe the probability of successful transition after such losses, i.e., the proportion of reproductive structures moving to the next stage (flowers to fruit, etc.). In general, probabilities were higher for the pre-dispersal stages (flowers and fruits at the tree canopy) than for post-dispersal stages (seeds and seedlings in the under-story). In particular, pre-dispersive losses were higher for flowers than for fruits, due to the fact that almost 50 % of female flowers produced empty fruits. Similarly, the percentage of sound fruits at the end of the pre-dispersal stage was less than 50 %, mainly due to a higher percentage of insect-damaged fruits and fruit abortion (Fig. 3). The probability of transition from immature fruits to sound fruits was much reduced in cohort 2 (28 %). Once on the ground, the losses due to animal predation were very low as

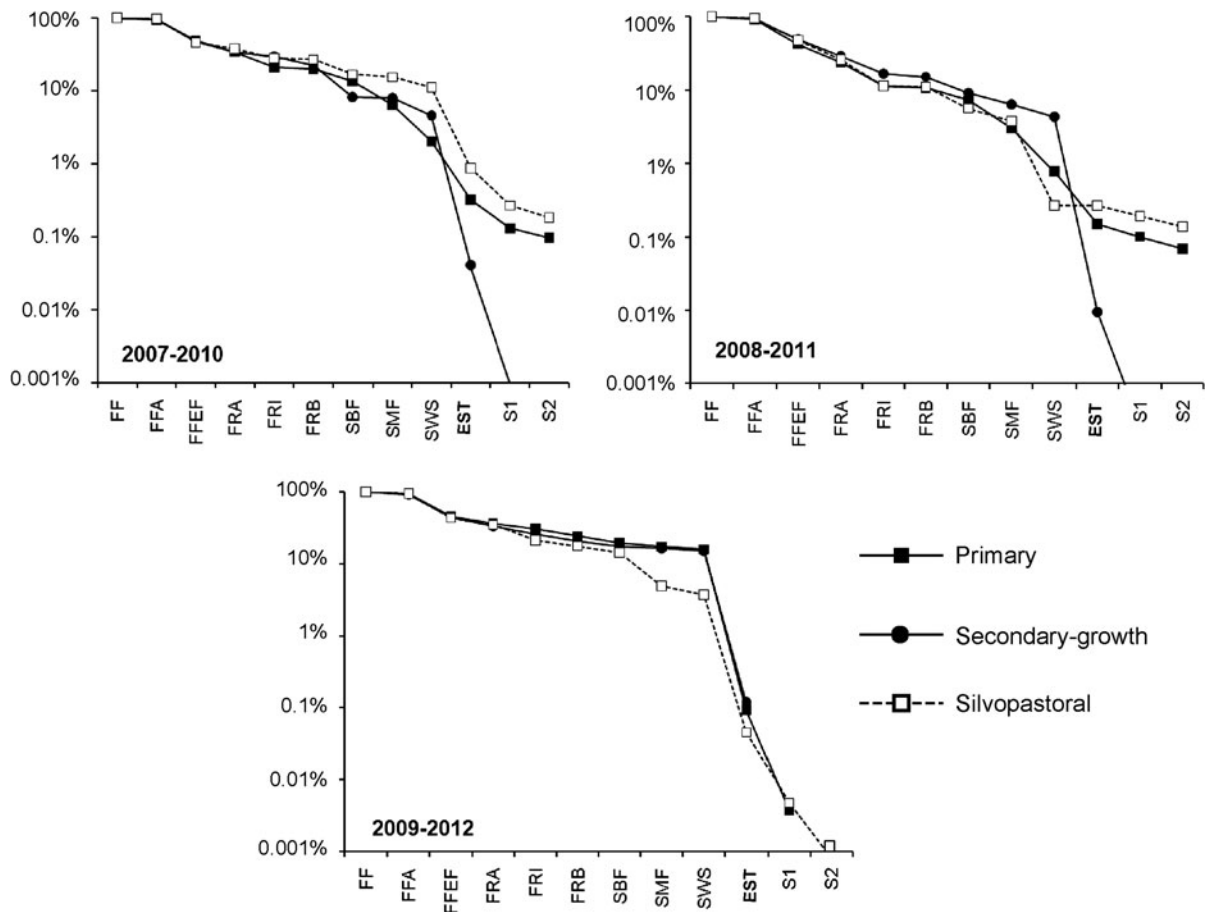


Fig. 3 Mean cumulative probabilities of transition between stages as a result of damage by biotic and abiotic factors according to forest types (silvopastoral systems, secondary-growth and primary unmanaged) and cohorts (2007–2010, 2008–2011, 2009–2012) of *Nothofagus antarctica* forests. Percentages are referred to the initial number of female flower (FF). Note the logarithmic scale of the vertical axis. Lines

crossing the horizontal axis drop to zero values. FF total female flowers, FFA abscised female flowers, FFEF female flowers derived in empty fruits, FRA abscised immature fruits, FRI fruits foraged by insects, FRB fruits foraged by birds, SBF seeds foraged by birds in the forest floor, SMF seeds foraged by mice in the forest floor, SWS seeds died during winter stratification, EST establishment, S1 survival at year 1, S2 survival at year 2

compared to winter stratification seed losses. Overall, losses at the seed stage were quantitatively less important than those in the flower and fruit stages considering all cohorts.

The probability of transition from a sound seed to a new individual was extremely low in all forest types due to failure during the establishment phase, which is the most critical stage detected in the cycle of *N. antarctica* (Fig. 2). Establishment losses were severe in SF, thus leading to virtually no recruitment in the latter. For both PF and SIL, the highest proportion of seedling establishment occurred in cohort 1 (0.3 % and 0.9 % respectively). Seedling

survival after 1 year was around or below 0.1–0.3 % for mature stands, while cumulative 2 years seedling survival was consistently higher in SIL. The crucial role of establishment was enhanced by seedling survival, which was 25.8 % in PF, 0 % in SF and 30.3 % in SIL after 2 years. Summarizing, the recruitment rate was 0.0006 in PF, 0 in SF, and 0.0011 in SIL, with some differences among years (e.g., for cohort 3, the final recruitment was virtually zero in all forest types). This was based on relative percentage of losses, and therefore does not account for differences in absolute fecundity among forest types.

Discussion

Forest types differentiation

Reduction of canopy cover in *N. antarctica* forests by reduction of tree density and basal area are intended to increase the forage biomass for domestic livestock in silvopastoral stands. In this study, the canopy reduction applied in silvopastoral stands was quite conservative, since retained canopy here was higher than proposed by Peri et al. (2009a) for southern Patagonia (e.g., high-intensity thinning leaving 30–40 % of canopy in areas with moderate water-deficit stress). Theoretical importance of these retained trees include the provision of shade and shelter for livestock, refuge for biodiversity, and maintenance of certain ecosystem services (Gregory 1995; Jose 2009).

However, the management plans should also consider the modifications of microclimate conditions affecting natural regeneration stages and therefore the sustainable use of *N. antarctica* forests. The silvopastoral stands were sunnier and moister than primary and second-growth forests. Bahamonde et al. (2009) reported how *N. antarctica* forests in Santa Cruz (Argentina) are subject to microclimate changes depending on silvopastoral practices and site quality. Also, great increases of light and soil water content in managed *N. pumilio* and *N. betuloides* forests have been described in southern Patagonia (Promis et al. 2010; Martínez Pastur et al. 2011). On the other hand, dense closed canopy determined high leaf area indexes and, consequently, low levels of solar radiation reaching the forest floor. Thus, the understory environment became darker, cooler and drier than other mature ones (with greater canopy heterogeneity), as has been reported for other deciduous forest (Grimmond et al. 2000). However, microclimatic changes will depend on the degree of canopy retention after silvicultural interventions. For example, Martínez Pastur et al. (2011) determined the influence of different levels of retained trees on *N. pumilio* recruitment by modifying the soil moisture and light availability.

Flowering stage

Usually, studies on forest dynamics considered seed production as the starting point of the cycle (Clark et al. 1999). However, the understanding of flowering and fruiting processes is crucial to determine limitations in

regeneration due to tree fecundity, losses caused by predators, or micro-climate (Jordano 2000; Ratajczak and Pukacka 2005; Pulido et al. 2010). In this study, female flower production per hectare was significantly higher in the PF than in the secondary-growth and silvopastoral stands. In contrast, male flower production was related to the overstory cover gradient analyzed here with the high tree density of SF determining a greater number than in primary and silvopastoral forests. Martínez Pastur et al. (2013) also found that flower production in *N. pumilio* forests was related to the overstory gradient originated by forest management with variable retention in Tierra del Fuego (Argentina).

Among the factors affecting *Nothofagus* fertilization, it is possible to cite the unpredictable nature of the pollinating agent (wind), as well as associated weather factors (e.g., rain, high levels of humidity), all of which decrease fertilization success (Báez et al. 2002). Following this idea we consider that the premature abscission of female flowers would be related to pollination failures. In our study, a low percentage of losses found in silvopastoral stands could be explained by enhanced pollination effectiveness likely by higher exchange of airflow (wind speed) in thinned areas (Bahamonde et al. 2009). Yet, in general, we found low percentages of aborted female flowers throughout this study, which are in agreement with Báez et al. (2002) who argued the pollen of *Nothofagus* species in Chile and Argentina is highly viable and vigorous.

On the other hand, female flowers deriving in empty seeds could be here understood as a mechanism for self-incompatibility. As noted in previous studies, *Nothofagus* species prevent inbreeding among populations with similar genetic structure through barriers to avoid fertilization (Riveros et al. 1995). These barriers would be highlighted by environmental stress (Steinke et al. 2008), as those microclimatic changes generated by forest harvesting. Although silvopastoral management in this study did not increase such losses, it is possible that the proportion of empty seeds could increase after more severe interventions (e.g., high-intensity thinning). To meet this answer, we need further studies to test and expand different thinning intensities.

Pre-dispersal stage

Aborted fruits were the main source of loss during the pre-dispersive stage. This may be explained by

extreme temperature events. For example, a late spring frost occurred in all forest types (Soler 2012). In addition, unusually high temperatures promote the abscission of immature fruits, and generally the small-size and young fruits are more susceptible to abiotic damage than older fruits (Stephenson 1981).

Elevated damage by insects in both primary and silvopastoral forests could be related to greater richness and abundance of insects in old-growth forests, as was described by Spagarino et al. (2001) for *N. pumilio* forests in Tierra del Fuego. Because the overstory retained in silvopastoral systems included in this study is still high, this could be sustaining a large insect population that influence over fruits as well as observed in PF. This would be an advantage from the point of view of biodiversity conservation, but insect damage during those years with reduced propagule production (e.g., 2009) could become a critical loss factor in silvopastoral stands.

The *N. antarctica* seed production recorded in this work might relate to the basal area of each forest type, and its reduction in silvopastoral stands would explain the low quantities of seeds. However, previous studies reported similar magnitudes of *N. antarctica* seed production and inter-annual variability (Premoli 1991; Bahamonde et al. 2011), as found here. Whereas *N. antarctica* seedling variability is influenced by extreme climatic events (e.g., low temperatures during the pre-flowering stage) (Bahamonde et al. 2011), future efforts are necessary to better understand the interaction between thinning and micro-climate variations inside forests.

Post-dispersal stage

Losses after seed dispersal were negligible compared to the other stages of the reproductive cycle of *N. antarctica*. Seed mortality during winter stratification was the main loss factor acting once seeds were dispersed, being greater in forests under silvopastoral practices. These differences may be a result of (i) inadequate seed cover during stratification at the forest floor due to lower litter production than in PF and SF (Soler 2012) or (ii) freeze and snow occurrence and lower temperatures during winter in thinned areas (Ratajczak and Pukacka 2005). The magnitude of these factors varied according to years, due to microclimatic variation, causing extreme values in the rates of seed loss.

Many studies considered the post-dispersal seed predation as key process for plant recruitment (Jordano 2000; García Castaño et al. 2006), but in this study, the incidence of biotic factors was less than 2 % and highly variable among years. Closed canopies in unmanaged stands diminished the effects of birds, but increased mice foraging, perhaps as a result of habitat preferences for some mice species (e.g., *Akodon* sp.) (Kelt et al. 1994). This percentage could be related to seed availability, which was greater at high seed density, as frequently was found for other Fagaceous trees (Jordano 2000; Ueda 2000). Overall, the incidence of birds and mice in this study did not represent a critical limiting factor for seedling emergence and future establishment. Summarizing, it can be concluded that post-dispersal seed losses were mainly determined by the combined effects of litter production and microclimate. At the end of the post-dispersal stage, the probability that a dispersed seed survives is high, but significantly reduced under silvopastoral practices.

Seedling recruitment

The soil seed bank is not part of *Nothofagus* reproductive strategies in southern Patagonia (Donoso et al. 2006), but emergence and mortality in the seedling bank continuously occurs from year to year. In our study, failures during establishment of *N. antarctica* seedlings were the main source of losses at this stage in all forest types. This trend has been also reported for other North and South American deciduous species (*Betula* sp. and *Polylepis* sp.) (Clark et al. 1999; Seltsmann et al. 2007). The main alternatives explaining recruitment limitations are usually the availability of seeds or the availability of suitable microsites for germination and survival (Clark et al. 1999). *N. antarctica* was differentially affected by silvopastoral practices and stand age. In the first case, recruitment was mainly limited by the tree density reduction implying seed source limitations. But after seeding in managed stands, there was a positive influence of light and soil moisture at the understory level that improved the seedling establishment, the most critical stage for regeneration. In the second case, seedlings establishment in second-growth forests could be limited by suitable microsites for seedling establishment and light, due the high canopy closure. It has been demonstrated that both soil moisture and

light availability decrease with canopy cover, which strongly influence establishment and survival of *Nothofagus* seedlings (Martínez Pastur et al. 2011).

Survival of seedlings and saplings depends on the species' ecophysiological traits. *N. antarctica* is considered less 'shade tolerant' from a physiological perspective compared to other closely related *Nothofagus* species (Peri et al. 2009b), which provides competitive advantages to grow in open areas (Donoso et al. 2006). In our study, the success of seedling establishment and survival to the sapling stage in managed stands highlighted the advantage of *N. antarctica* for the implementation of silvopastoral systems in southern Patagonia.

Conclusion and forest management implications

By using an integrative approach, we gained insight into the influence of main factors (biotics and abiotics) driving the natural regeneration in temperate *N. antarctica* forests, identifying the most critical stages. First, it was possible to quantify the relative importance of abiotic and biotic factors along the reproductive cycle, in order to define the most critical ones. Second, regardless of forest management, failures of female flowers fertilization (resulting in empty fruit) and during the installation were the main (abiotic) factors limiting regeneration of *N. antarctica*. Third, both the number of propagules and the influence of loss factors were highly variable between years. Consequently, in years of poor seed production, silvopastoral practices narrow the reproductive success of *N. antarctica* by altering some loss factors.

Silvopastoral practices affected negatively fruiting (pre-dispersal) and seedling (post-dispersal) survival, but the last stage of the reproductive cycle seems to be enhanced leading to similar regeneration values than PF. The establishment and seedling survival were transitions more successful in silvopastoral systems, probably by improving the soil moisture and light availability (Soler 2012), increasing debris cover, and understory heterogeneity that provides favorable microsites for establishment (Martínez Pastur et al. 2011). Besides these improvements, ecophysiological plasticity (Donoso et al. 2006; Peri et al. 2009b) allows *N. antarctica* to exploit conditions created by forest thinning.

Secondary-growth forests represent potential sites to implement silvopastoral systems through overstory

management (Peri 2009). High-intensity thinning over optimal-growth phase stands enhance the growth and quality form of remnant trees (Ivancich et al. 2012), and improve the stand conditions for future regeneration establishment and growth. SF studied here revealed good reproductive performance through the natural cycle (e.g., flowers, seed quality), except for the establishment stage, likely related to the lack of favorable conditions present in mature stands (D'Amato et al. 2009). These patterns reinforce the suitability of thinning practices for increasing understory heterogeneity and restoring canopy complexity in secondary-growth stands.

There is significant potential for increasing the productivity of native *N. antarctica* forests by increasing the timber value and allowing livestock production. Proper management guidelines for these southern Patagonia forests (e.g., thinning intensity) are still being discussed (Peri et al. 2009a; Ivancich et al. 2012). Thinning intensity and the degree of retained canopy will depend on regional characteristics (e.g., precipitation regime) and stand age (Peri et al. 2008, 2009a; Ivancich et al. 2012). There is therefore a need of further research in the area, including long-term measurements and considering the specific mechanisms involved on the seedling establishment success and tree-livestock interactions.

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