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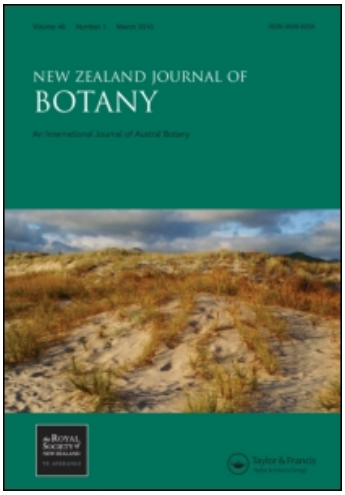

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Flowering and seeding patterns in primary, secondary and silvopastoral managed *Nothofagus antarctica* forests in South Patagonia

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The success of the reproductive process in trees depends on abiotic and biotic factors that determine the final outcome of natural regeneration. Silviculture alters biotic and abiotic factors and results in secondary forest structures. To effectively manage these forests, it is necessary to understand the bottlenecks in reproductive stages using a whole-cycle approach study. The aim of this study was to analyse flowering and seeding patterns in primary, secondary and silvopastoral managed *Nothofagus antarctica* forests, including investigating the pre-dispersion foraging of insects and birds, as well as abscised biomass production. A high percentage of female flowers produced fruits (95–96%) in which the main loss factor before seeding was the abscission of immature fruits (11–14%). Seeding was greater in secondary forests (11.4 million ha^{-1}), but managed stands presented a higher percentage of flowers resulting in seeds (82%). However, secondary forests had a better seed quality (17% viable seeds), where the main loss factor was empty seeds in all treatments (39–50%). Biotic factors (foraging by insects and birds) were higher in disturbed than primary forests. *Nothofagus antarctica* produce large quantities of seeds, but abscised immature fruits and empty seeds due to self-incompatibility mechanisms appeared as the major loss factors.

Keywords: silviculture; silvopastoral management; insect foraging; bird consumption; seed quality; regeneration cycles

Introduction

Seedlings of *Nothofagus* species in South Patagonia are often associated with canopy gap areas (Cuevas & Arroyo 1999; Rebertus & Veblen 1993). However, inadequate seedling establishment can occur and may be associated with natural (e.g. climatic conditions) or anthropic (e.g. grazing) disturbances by changing the original forest characteristics (Martínez Pastur et al. 2008; Peri et al. 2009). *Nothofagus antarctica* (commonly named 'ñire') presents a wide ecological distribution along all Patagonian forests from Neuquén at 36 °S to Cabo de Hornos at 56 °S (Donoso et al. 2006; Ramírez et al. 1985; Vidal & Premoli 2004). In South Patagonia, these forests grow in the ecotone between rangelands and *Nothofagus pumilio* woods (Roig 1998). In some stands, the tree canopy is re-established from existing seedlings following a canopy-opening disturbance, however, there is a lack of regeneration from germinating seeds in other stands. In this case, forests can recover their structure through root or stump sprouting (Peri 2005; Premoli 1991).

Ñire woods have been largely impacted in the past by fire with little or no active management, resulting in over-stocked secondary forests, while the remnant old-growth stands have been used for cattle grazing without any

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rational planning or sustainable management (Peri 2006; Reque et al. 2007). Beside this, a silviculture based on silvopastoral practices has been proposed combining trees, pastures and cattle (Peri 2005; Reque et al. 2007). The success of this recently proposed silvicultural practice must be assessed based on its economic feasibility, biodiversity conservation capacity and the establishment of natural tree regeneration to continue the production cycle (Martínez Pastur et al. 2008, 2009; Peri 2005). The silvopastoral system is designed to reduce the original canopy cover by 30–50%, thus enhancing the herbaceous component and increasing the potential cattle stock (Peri 2005, 2006). In unmanaged secondary forests, trees growing under full canopy cover (high intraspecific competition), allocated more resources to competition for survival, rather than reproduction (Oliver & Larson 1996). These changes in the original forest structure (reduction or extreme closure of canopy) have large impacts on the abiotic components (e.g. microclimate and nutrient cycles) and biodiversity (Caldentey et al. 2001, 2005, 2009; Frangi & Richter 1994) which can potentially affect flowering and seeding processes, and consequently the success of the natural regeneration. In general, studies on the regeneration of *Nothofagus* species tend to evaluate the effect of a single critical factor, such as seed dispersal, climatic stress on seeding or seedling mortality due to competition (Cuevas 2000; Heinemann et al. 2000; Martínez Pastur et al. 1999a, 1999b, 2007, 2009; Pulido et al. 2000). In the case of *N. antarctica* in Tierra del Fuego, the combination of young forest stands, primary forest remnants and the recent implementation of silvopastoral systems, represents a spatial mosaic of reproduction opportunities and limitations, with several factors associated with flowering, seed production and germination determining the likelihood of generating a new individual. For this, a whole-cycle study of the regeneration process allows understanding of the contribution of each stage and each factor to the final reproductive output (Martínez Pastur et al. 2008).

To address this, we ask the following questions:

1. Does female or male flower production affect seed production?
2. What is the degree of predation on seed production?
3. To what extent does silvicultural stand thinning affect flowering and seeding processes?
4. What are the main loss factors during the reproductive cycle?

The aim of this study was to analyse the flowering and seeding patterns in primary, secondary and managed stands of *N. antarctica* forests. The study includes analysis of seed foraging by insects and birds prior to seed dispersal, and the abscised biomass production during one growing season.

Despite a lack of knowledge about the reproductive biology of *N. antacrtica*, on the basis of previous studies (Lencinas et al. 2005; Martínez Pastur et al. 2008; Peri 2005; Premoli 1991), a negative relationship between the structural modifications caused by silvopastoral systems and the production of flowers (female and male) and seeds due to the post-harvesting stress of the remnant overstory is expected. However, we expect low-quality seeds in young forests because of a limited allocation of some critical resources for reproduction, and also a greater influence of biotic factors (e.g. foraging by insects and birds) during the whole reproductive cycle.

Methods

Natural history of Nothofagus antarctica *forests*

Ñire is a deciduous broadleaved species that grows in pure stands, reaching up to 17 m total height and more than 1 m in diameter at the better sites (Lencinas et al. 2002). It is a monoecious species, with solitary male flowers appearing first at the base of the shoots, while female flowers with tricarpelar ovaries grow later at the distal extremes. Pollination is mediated by wind. Budburst occurs in late spring and fruits develop in early summer. The fruit has three seeds per cupule, reaching maturity in late March. Flowers, immature fruits and seeds are exposed to predation by insects and birds, and when they finally fall to

the forest floor, they may be consumed by rodents (*Akodon*, *Euneomys* and *Oligoryzomys* species) or birds. Surviving seeds germinate in November–December. There is no seed bank, but seedlings can persist up to 10 years in some stands.

Study sites and forest structure characterisation

An area of 1500 ha of *N. antarctica* forests were selected in Los Cerros Ranch, Tierra del Fuego, Argentina (54° 20′ S, 67° 52′ W). These forests were used for cattle and sheep grazing, and have been affected by large fires during the last 60 years (Roig 1998). Three treatments (four replicates each) were established according their previous management history and their conservation status: 1. four old-growth primary forests without management (PF), 2. four secondary stands (SF) produced by fire with ages of 54 ± 7 years (average $\pm$ SD) without management, and 3. four managed, thinned, old-growth stands, used as silvopastoral systems. The forest structure of each stand was characterized through five forest inventory plots. The point sampling method (BAF 6) was used, and number of trees (N), dominant height (DH), density, quadratic mean diameter (QMD), basal area (BA) and total over bark volume (TOBV) were measured (details of equations and methodologies are given in Lencinas et al. 2002). Sixty hemispherical photographs of forest canopy were taken at 1 m above the ground with a Sigma (Japan) 8 mm fish-eye lens mounted on a 35 mm Nikon (Japan) digital camera. Gap Light Analyzer v.2.0 (Frazer et al. 2001) was used to define crown cover (CC) as a percentage of open sky relative to forest canopy, and effective leaf area index (LAI) integrated over the zenith angles 0–60°.

Climate was measured with a weather station (Davis Weather Wizard III, USA) during the years 2006–2009, and is characterized by short, cool summers and long, snowy and frozen winters. Mean monthly temperatures varied from about -0.2 to 10.4 °C in the forests. Only three months per year had mean temperatures below 0 °C, and the growing season extended for approximately five months. Soil (at 30 cm depth) never froze below closed canopies in the forests. Rainfall without canopy cover was 639 mm year^{-1}. The average wind speed outside the forest was 8 km h^{-1}, reaching up to 100 km h^{-1} during storms.

Abscised biomass sampling

In each of the 12 studied stands, 10 biomass traps of 0.06 m^2 and 30 cm depth were used, which were perforated to allow rain and snow-water drainage. Traps were established along a 50 m transect, covering the landscape heterogeneity in each stand. All the abscised biomass material was collected monthly, and manually classified into reproductive (male and female flowers, immature fruits and seeds) and litter (leaves, fine branches <1 cm diameter and miscellaneous) components. Reproductive organs were counted and classified as having been subject to insect or bird foraging, or without evident damage. Insect foraging could be identified by deformation of the reproductive organs, while bird damage was evidenced through the non-comestible parts having been rejected during foraging (Martínez Pastur et al. 2008). Using this methodology it was not possible to estimate whole flower or fruit consumption by birds.

Reproductive and litter components were dried in an oven at 70 °C until constant weight, and weighed with a precision of ± 0.0001 g. Seed quality was analysed prior to drying by manually opening each seed, and classifying them as empty or full. Immediately after opening, the tetrazolium test (2,3,5-triphenyltetrazolium chloride) was conducted to determine seed viability. For this, embryos were incubated for 24 h in a water dilution of 0.1% solution in darkness at 25 °C (Cuevas 2000). If the solution turned to red, due to hydrogen reduction derived from enzymes, it was considered viable seed. Non-viable seeds included those wich had not reacted to the tetrazolium test, with immature embryos or dead seeds.

Data and statistical analysis

Reproductive components were expressed as million ha^{-1}, while biomass was expressed in ton ha^{-1}. Total female flower production (FF) was calculated as the sum of abscised female

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flower (AFF), immature fruits (IF) and seeds (S). The percentage of reproductive components (AFF, IF and S) was related to the number of potential seed production (PSP) calculated as the number of female flower $\times 3$ (each female flower presented a tricarpelar ovary). Comparison of main factors was carried out by analysis of variance with the *F*-test. Variables not fitting a normal distribution (e.g. percentages) were arcsin (square root)-transformed prior to statistical analyses. Significantly different averages were separated with a post-hoc Tukey's HSD (Honestly Significant Difference) test ($p < 0.05$).

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Results

Forest structure

Forest structure changed significantly when primary, secondary and managed stands were compared (Table 1), except for dominant height which varied between 10.1 and 13.6 m. Secondary forests recovered some of the original structure characteristics (e.g. BA) and presented significantly higher values for CC (86%) and LAI (2.1) compared with primary forests (79% and 1.7) and managed stands (66% and 1.1); however, as expected, QMD was lower and N was higher than primary forest values. Silvopastoral managed stands showed reduced values for BA, N, TOBV, CC and LAI compared with primary forests (26, 24, 29, 16 and 36%, respectively).

Flowering patterns and reproductive organs abscission

Male flowers were more numerous in secondary forests than in primary forests and managed stands (1.5 and 2.5 times higher, respectively) (Table 2). Female flowers did not show significant differences among treatments (3.4–5.2 million ha^{-1}). The flowering production had different male–female flower ratio (M/F), being higher in the secondary forests (5.2) than in primary and managed stands (3.2 and 3.9, respectively). Through the growing season there was significant abscission of reproductive structures (0.11–0.24 million ha^{-1} of female flowers, and 0.38–0.74 million ha^{-1} of immature fruits), representing 3–6% and 8–14% of the total female flower production with significant differences in percentages among treatments.

Seeding patterns

Seeding was related to female flower production. Higher seed production was found in secondary stands (11.4 million ha^{-1}) than in primary (10.2 million ha^{-1}) and managed stands (7.6 million ha^{-1}), although there were no significant differences among treatments (Table 2). However, seeding effectiveness, as

Table 1 Analysis of variance of the forest structure for primary (PF), secondary (SF) and silvopastoral (SIL) managed stands, considering basal area (BA; $m^2\ ha^{-1}$), dominant height (DH; m), quadratic mean diameter (QMD; cm), number of trees (N; trees ha^{-1}), total over bark volume (TOBV; $m^3\ ha^{-1}$), crown cover (CC;%) and effective leaf area index (LAI)

	Stands			
Factor	PF	SF	SIL	*F* (*p*)
BA	46.5 [b]	39.6a [b]	34.5 [a]	5.97 (< 0.01)
DH	13.6	10.1	12.4	3.48 (0.07)
QMD	49.1 [b]	17.4 [a]	46.8 [b]	117.29 (< 0.01)
N	476 [a]	3406 [b]	364 [a]	41.24 (< 0.01)
TOBV	357.7 [b]	245.5 [a]	252.5 [a]	4.67 (0.04)
CC	78.9 [b]	85.5 [c]	66.1 [a]	61.51 (< 0.01)
LAI	1.67 [b]	2.13 [c]	1.07 [a]	71.99 (< 0.01)

Note: *F*, Fisher's test; *p*, probability. Different superscript letters in each row showed differences by Tukey's test at $p < 0.01$.

Table 2 Simple ANOVA for the effects of forest type (primary, PF; secondary, SF; silvopastoral, SIL) on flowering and seeding patterns. Means and standard error (SE) of number (million ha^{-1}) of male flowers (MF), total female flowers (FF), potential seed production (PSP), abscised female flowers (AFF), immature fruits (IF), seeds (S), empty seeds (ES), viable seeds (VS) and non-viable seeds (NVS)

	Stands			
Factor	PF ± SE	SF ± SE	SIL ± SE	*F* (*p*)
MF	17.69 ± 1.68 ^{b}	27.15 ± 2.03 ^{c}	10.81 ± 1.72 ^{a}	20.29 (< 0.01)
FF	4.56 ± 0.43	5.19 ± 0.53	3.39 ± 0.61	2.90 (0.06)
PSP	13.68 ± 1.31	15.55 ± 1.60	10.19 ± 1.83	2.90 (0.06)
AFF	0.24 ± 0.039	0.18 ± 0.036	0.11 ± 0.037	2.70 (0.07)
IF	0.54 ± 0.07	0.74 ± 0.18	0.38 ± 0.08	2.12 (0.12)
S	10.28 ± 1.18	11.43 ± 1.10	7.64 ± 1.82	2.52 (0.08)
ES	5.77 ± 0.60	5.61 ± 0.54	4.40 ± 0.75	1.38 (0.25)
VS	1.85 ± 0.29 ^{a}	2.36 ± 0.24 ^{b}	1.01 ± 0.21 ^{a}	6.83 (< 0.01)
NVS	1.94 ± 0.26 ^{ab}	2.25 ± 0.21 ^{b}	1.35 ± 0.25 ^{a}	3.70 (0.03)

Note: *F*, Fisher test; *p*, probability. Different superscript letters in each row showed differences by Tukey's test at $p < 0.01$.

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the percentage of PSP that became a full, well-developed seed, presented significant differences among treatments, being higher in managed stands (82%) than primary stands (71%), while intermediate values were found in secondary forests (78%). When seed quality was analysed, it differed among the studied forests. Viable seed production was higher in secondary stands (2.3 million ha^{-1} representing 19% of PSP) than in primary (1.8 million ha^{-1} representing 12% of PSP) and managed stands (1.0 million ha^{-1} representing 11% of PSP). High numbers of empty seeds were found in all treatments (4.4–5.7 million ha^{-1}), but were greater in the managed stands (50%) than primary (42%) and secondary forests (38%). Finally, the number of non-viable seeds (dead, aborted and non-viable embryos) showed significant differences among treatments, being higher in secondary (2.25 million ha^{-1}) than managed stands (1.35 million ha^{-1}), and similar to primary forests (1.94 million ha^{-1}) (Table 2).

Seeding was not homogeneous along the stands of the same treatment (Fig. 1). Seed mass production varied significantly among stands ($F = 10.29$, $p < 0.001$), from 40 to 198 kg ha^{-1} in primary forests, 74 to 225 kg ha^{-1} in secondary forests and 11 to 254 kg ha^{-1} in managed stands. These differences were not related to CC, LAI and BA. Ratios between seed mass production and these variables did not show tendencies that might explain these differences in the seeding production patterns.

Insect and bird foraging patterns

The number of female flowers, immature fruits and seeds foraged by insects did not show significant differences among treatments (Table 3). But when foraging was expressed as percentage of PSP, some differences were found (Table 4). The percentage of foraged female flowers was higher in the secondary stands (0.9%) than in the other treatments (0.1%). The percentage of foraged immature fruit was greater in the mature stands (9% in primary and 6% in managed) than in second-growth forests (2%). Finally, the percentage of seeds damaged by insects did not vary among stands, representing 3–10% of the total seed production.

Bird foraging was higher in secondary forests (Tables 3 and 4). The number of foraged immature fruits varied from 0.01 million ha^{-1} in primary forests to 0.28 million ha^{-1} in second-growth stands, which represents 0.1–3.0% of PSP. Also, seed foraged by birds was higher in secondary stands (0.8 million ha^{-1} representing 8% of PSP) than in primary and silvopastoralforests (0.18 and 0.07 million ha^{-1} representing 2 and 1% of PSP, respectively).

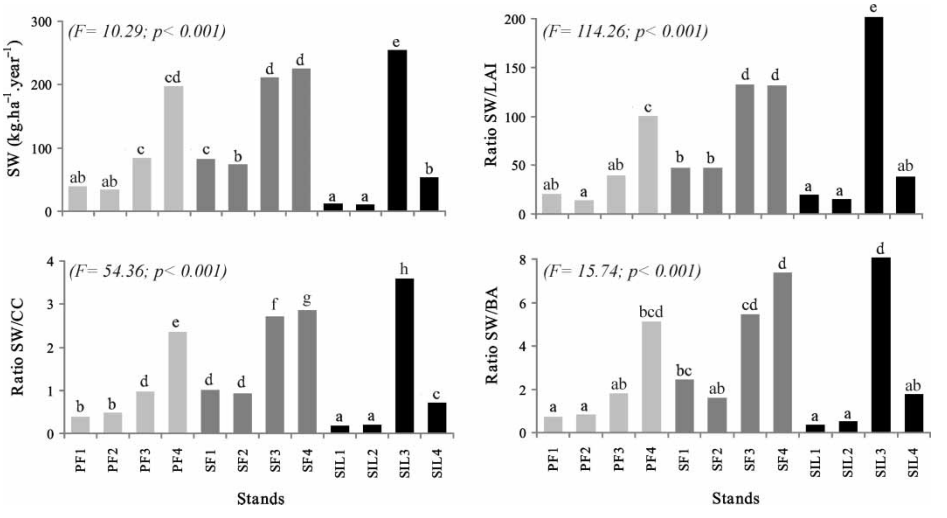

Fig. 1 Comparison with seed mass production (SW) in primary (PF, pale grey), secondary (SF, dark grey) and silvopastoral (SIL, black) managed stands, and their ratios with crown cover (CC,%), effective leaf area index (LAI) and basal area (BA, m^2 ha^{-1}). Letters a–e indicate differences by Tukey test at $p < 0.05$.

Monthly abscised biomass production

Male flowering began to fall in October in all stands (0.1–0.3% of the total biomass production), and reached a peak during November in the secondary forests (60%) and during December in the primary (54%) and managed stands (58%) (Fig. 2). Female flowers occurred together with male flowers. In primary forests, maximum abscission of female flowers was between November and February (26–36%), whereas secondary forests and managed stands were more homogeneous and occured mainly during January (44 and 38%, respectively). Immature fruit abscission was higher during February and March until the end of summer. Seeding began in March, which was more homogeneous in secondary forests (69% of the total fall) and managed stands (44%). In primary forests, seeding began in March and reached its maximum in April (46%). Finally, mass litter fall began together with seeding, but it reached its maximum when seeding ended during May (30–31% for all the stands) (Fig. 2). Litter biomass reached 3.45 ± 0.90 ton ha^{-1} (average $\pm$ SD) in secondary forests, 2.17 ± 1.01 ton ha^{-1} in primary unmanaged

Table 3 Simple ANOVA for the effects of forest type (primary, PF; secondary, SF; silvopastoral, SIL) on foraging patterns. Means and standard error (SE) of number (million ha^{-1}) of abscised female flowers foraged by insects (AFFI), abscised immature fruits foraged by insects (IFI), abscised immature fruits foraged by birds (IFB), seed foraged by insects (SI) and seed foraged by birds (SB)

	Stands			
Factor	PF $\pm$ SE	SF $\pm$ SE	SIL $\pm$ SE	*F* (*p*)
AFFI	0.004 ± 0.004	0.025 ± 0.01	0.008 ± 0.006	2.50 (0.13)
IFI	0.34 ± 0.06	0.14 ± 0.04	0.30 ± 0.08	2.60 (0.07)
IFB	0.01 ± 0.01 [a]	0.28 ± 0.11 [b]	0.04 ± 0.01 [a]	5.23 (< 0.01)
SI	0.53 ± 0.09	0.33 ± 0.06	0.74 ± 0.23	1.92 (0.15)
SB	0.18 ± 0.06 [a]	0.87 ± 0.21 [b]	0.07 ± 0.03 [a]	11.09 (< 0.01)

Note: *F*, Fisher test; *p*, probability. Different superscript letters in each row showed differences by Tukey's test at $p < 0.01$.

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Table 4 Simple ANOVA for the effects of three treatments analysed (primary, secondary and managed forests) on percentage of female flowers, immature fruits, and seeds (abscised, foraged by insects, FI; foraged by birds, FB)

Factor	*F*	*p*
% Flowers		
Abscised	2.84	0.06
FI	2.62	0.07
% Immature fruits		
Abscised	4.63	0.01
FI	9.38	<0.01
FB	5.87	<0.01
% Seeds		
Abscised	5.87	<0.01
empty	5.70	<0.01
viable	8.21	<0.01
non-viable	0.58	0.56
FI	1.38	0.25
FB	19.13	<0.01

Note: Variables (%) were arcsine square root transformed for the analysis of variance.

forests and 1.50 ± 0.94 ton ha^{-1} in managed stands.

Discussion

Forest structure varied according to the previous and current management of the stands. Primary forests showed an irregular structure with different microenvironments and varying crown strata. The canopy was closed (79%) but it is common to find natural openings created by tree falls that allow the seedlings to establish (Rebertus & Veblen 1993). As expected, secondary forest presented a typical structure of stands under high intraspecific competition, where high levels of CC and LAI diminished light and rainfall at the understory level (Oliver & Larson 1996). Silvopastoral systems had reduced crown cover and stand density (to 66% and 364 trees ha^{-1}, respectively in our plots) according to the proposal for South Patagonia (Peri 2005). These practices could lead to changes in the microclimatic conditions (Frangi & Richter 1994), increasing soil moisture and air temperature in summer (Peri 2005) whilst generating more extreme temperature minimums due to less canopy protection, especially during winter–spring. This kind of modification affects flowering (Pulido & Díaz

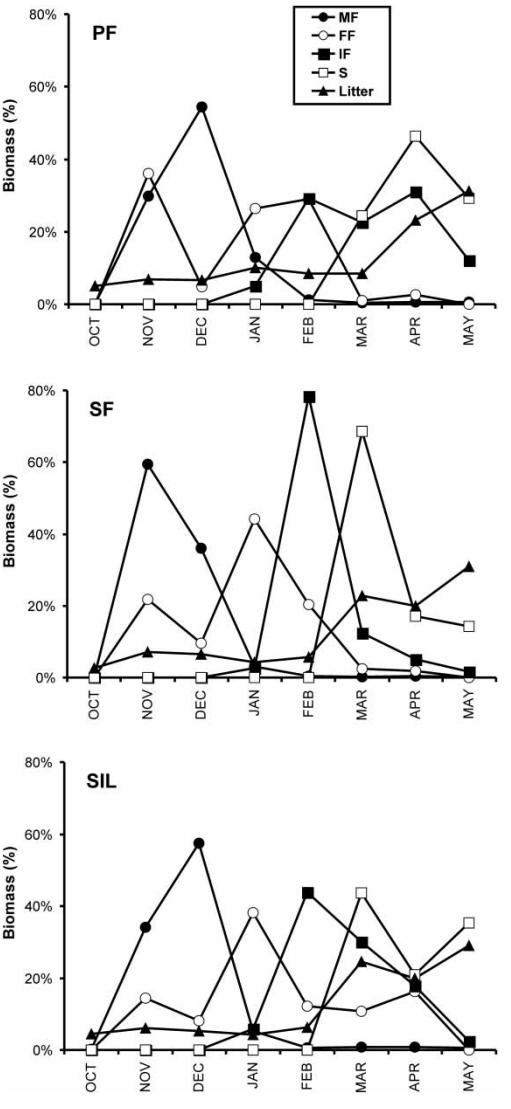

Fig. 2 Monthly abscised biomass production (% of the total of each component) considering male flowers (MF), female flowers (FF), immature fruits (FF), seeds (S) and litter (leaves, fine branches and miscellaneous) as main components, in primary (PF), secondary (SF) and silvopastoral (SIL) managed stands

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2005; Williams et al. 2006) and seeding patterns in trees (Donoso et al. 1993), and the behaviour of animals interacting with the tree species (Pulido 2002).

Although little is known about flowering process of *N. antarctica*, some authors reported that extreme environmental conditions (e.g. low temperature, winds, or nutrient shortages) affect the reproductive capabilities of the species (Premoli 1991; Ramírez et al. 1985). In this study, the number of male flowers was reduced in silvopastoral systems, possibly because of the extreme microclimatic conditions (e.g. soil and air temperature) experienced within the managed stands at the beginning of the growing season, compared with those stands with high canopy closure. However, the scarce abscission of female flowers may indicate the high effectiveness of the pollination strategy and the good dispersal capacity of the *Nothofagus* pollen (Cuevas & Arroyo 1999; Kelly et al. 2001). Similar results were reported for *N. pumilio* (Martínez Pastur et al. 2008) where primary unmanaged forest presented higher numbers of male flowers and a higher M/F ratio than managed stands. However, this does not ensure that all fertilized female flowers become full fruits, which is reflected on the high percentage of fallen immature fruits in all treatments (11–14%). This was one of the most critical loss factors in the reproduction cycle, and could be due to a fertilization failure which has been described by Martínez Pastur et al. (2008) for *N. pumilio*, as well as by Pulido & Díaz (2005) for *Quercus ilex* forests.

Seed production in *Nothofagus antarctica* in Santa Cruz (Argentina) varied between years and was related to the site quality of stands between 2 and 52 million ha^{-1} (Peri personal commununication). In our study, seeding presented an average of 9.8 million ha^{-1} for all treatments with a maximum value of 28.1 million ha^{-1} in a primary forest stand. These values indicate an average seeding year, which was convenient to describe the flowering and seeding processes. Previous studies with wind-dispersed North American species indicate that larger trees produce larger seed crops (Greene & Johnson 1994). Against our expectations, secondary forests of ñire have a (non-statistically significant) trend for higher numbers of seeds when compared with old growth and managed forests. However, higher seeding effectiveness in managed stands, as our results show (% of PSP that became a full seed), could be related to better pollination in the open forests, where pollen dispersal could be facilitated because of the increase in wind speed in low crown cover environments (Bazzaz et al. 2000; Williams et al. 2006). Studies in *N. pumilio* forests showed that old-growth stands produced more seeds than managed stands (3.2–6.5 times), but seeding effectiveness did not vary significantly (68–78%) (Martínez Pastur et al. 2008).

Seed quality was the main loss factor throughout the cycle in all treatments. Empty seeds represent a large percentage of seeding (55–64%), being higher in managed stands. Studies in South (Peri 2005) and North Patagonia (Premoli 1991) describe high empty seed percentages in *N. antarctica* (74 and 80%, respectively), which varied among years and with the site quality of the stands. Vidal & Premoli (2004) attributed these high percentages of empty seeds to the self-incompatibility mechanisms that prevent self-fertilization of individuals in populations with a similar genetic structure. These selection mechanisms increase with environmental stress (Díaz et al. 2003; Steinke et al. 2008), which can explain some of the spontaneous abortion in managed stands.

Nothofagus antarctica had low seed viability (11–17% of the PSP), when compared with other *Nothofagus* species, such as *N. pumilio* (up to 60%) (Cuevas 2000; Martínez Pastur et al. 2008), *N. betuloides* (up to 53%) (Donoso et al. 2006), *N. glauca* (95%) (Burgos et al. 2008), *N. truncata* (62%) and *N. menziesii* (35%) (Alley et al. 1998; Wardle 1984). Contrary to our expectations, secondary forest had the best seed quality, showing a positive relationship with high LAI values in these forests. Also, the low viability in old-growth forests (with or without management) can be interpreted as a failure due to the physiological age of the old stands (Kozlowski & Pallardy 1997).

To attain an approach to the whole reproductive cycle, we considered pre-dispersal predation by insects and birds as biotic factors

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influencing this cycle. Total insect predation tends to be higher (non-statistically significant) in old growth forests (9% of PSP) than in younger forests (5% of PSP), regardless of forest management. It reflects the high insect richness and relative abundance in mature forests described by Spagarino et al. (2001). However, as expected, most of the fruits (immature and full seeds) were consumed by birds in secondary forest (5% of PSP compared with 1% in mature stands), and may be related to the greater fruit production observed in these stands. Ñire fruits may be the main food resources for granivore birds in the closed secondary forests, and acted as secondary food resources in the managed stands, where grass grains are more abundant (Lencinas et al. 2005, 2009; Martínez Pastur et al. 2002). Pulido & Díaz (2005) note losses due to biotic factors (e.g. foraging of deer, pigs and rodents) of 10–29% for primary and managed *Quercus ilex* forests, which are higher than those described here. Because the degree of infestation and foraging by predators can vary according to fruit and seed productivity and also from year to year (Sullivan et al. 1995), more studies including several years are required.

The observed phenology followed a similar trend to that described for other *Nothofagus* species in the southern hemisphere (Alley et al. 1998; Barrera et al. 2000; Martínez Pastur et al. 2008; Manson 1974; Wardle 1984). Seeding occurred abruptly at the end of the summer, prior to the mass litter fall (protection for seeds during the winter), providing the optimal regeneration conditions for the next spring. Our results showed that a high percentage of pollinated flowers of *N. antarctica* succefully produce fruits, but a small percentage of seeds were able to produce seedlings because of low viability (only 11–17% of the PSP were viable prior to the winter season). Forest management reduced the number of male flowers and the proportion of empty seeds, but apparently did not affect the seeding effectiveness. Abscised immature fruits and empty seeds appeared as the major loss factors leading to low quantities of viable seeds. Further studies are necessary to explain these loss factors to quantify its influence in seeding, as well as to extend this kind of study to longer periods of time to include seeding years with different flowering and seeding events.

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