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# Flowering and seeding patterns in unmanaged and managed *Nothofagus pumilio* south Patagonian forests

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**Abstract:** Regeneration is the success key for the silvicultural treatment implemented in natural seed produced forests. Most of the studies assumed that regeneration is limited by environmental factors and herbivory, but few considered other limiting factors, such as limitants during the flowering and seeding process as bird or insect foraging. It is necessary a whole cycle approach study to understand the bottlenecks in the full regeneration processes. The aim of this work was to analyze the flowering and the seeding patterns in managed and unmanaged stands of *Nothofagus pumilio* forests, including the pre-dispersion insect and bird foraging analysis, and the abscised biomass production along one growing season. Our results showed that a high percentage of pollinated flowers success in produce fruits (68-79%), independently to the seed rain production and the forest management of the stand (2.2 to 14.7 million.ha$^{-1}$). The premature abscission of fruits was the main loss factor (13-25%), while biotic factors (insect and bird foraging) was not greatly (less than 5%). The other important loss factor was the large percentage of empty seeds observed in all the treatments (21-32%), which was significantly greater in primary unmanaged stands. More studies are necessary to explain the causes of these two main loss factors, and self-incompatibility studies to quantify its influence in empty seed production, as well as to extend this kind of studies in long periods of time to include seeding years with different seed rain production.

**Key words:** silviculture, aggregated retention, dispersed retention, masting; regeneration cycle

## 1 Introduction

Several regeneration methods have been proposed for Southern Patagonian forests (Schmidt and Urzúa 1982, Martínez Pastur et al. 2000, Martínez Pastur and Lencinas 2005) based on natural regeneration of the harvested stands from seed their own production (Martínez Pastur et al. 1999a, Rosenfeld et al. 2006). These forests have been mainly managed through selection cuttings or clear-cuts (Gea et al. 2004), and by shelterwood cuts in southern Chile (Schmidt and Urzúa 1982, Rosenfeld et al. 2006). This last method significantly affects the original diversity of the system under management (plants, birds, insects, fungi and mammals) (Martínez Pastur et al. 1999b, 2002a, Pulido et al. 2000, Deferrari et al. 2001, Spagarino et al. 2001, Ducid et al. 2005). Thus, a new alternative silviculture method, which proposes to leave 30% of the timber quality forest area as aggregated retention and 10-15 m² basal area as dispersed retention (Martínez Pastur and Lencinas 2005) was defined to conserve the original biodiversity affected by the forest management (Vergara and Schlatter 2006, Martínez Pastur et al. 2007a). Retention was defined as the portion of the overstoy (dispersed or aggregated) that was leaves in homogeneous pattern for a full rotation cycle throughout the harvested area, enhancing structural diversity and aesthetics (Franklin et al. 1997, Hickey et al. 2001). This retention provides natural seed source with benefits for gene conservation, better conservation of tree hollow dependent species, and coarse woody debris, which is important for ecosystem functioning and invertebrate conservation (Harmon et al. 1986).

The success of one proposed regeneration method is analyzed through their economical feasibility implementation, the establishment of the natural regeneration and the biodiversity conservation capacity. Forest regeneration is a dynamic process where new trees are recruited into the adult population, compensating the losses due to self-thinning (Harper 1977) or harvesting. This process includes a transition of different reproductive stages (flowers, seeds and seedlings) that depends on abiotic and biotic factors by affecting the numbers of seedlings established (Pulido 2002, Pulido and Díaz 2005). For this, a whole-cycle study of the regeneration allows to understand the contribution of each stage and each factor to the final reproductive output.

Regeneration of *Nothofagus pumilio* has been largely studied (Martínez Pastur et al. 1999a, b, 2007a, b, Cuevas and Arroyo 1999, Cuevas 2002, Pulido et al. 2000, Heinemann et al. 2000, Gea et al. 2004, Rosenfeld et al. 2006). Most of them assumed that regeneration is limited by environmental factors or grazing by *Lama guanicoe*, but few works analyzed other limiting factors as flowering and seeding process (Cuevas 2000), or bird and insect foraging (Díaz and Kitzberger 2006). Therefore, to address this subject in this study we ask the following questions: (1) Is female flower production or its fecundity effectiveness affects seed production?, (2) What is the effect of predation on seed production?, (3) How is the impact of forest management on seeding cycle?, and (4) What is the bottlenecks along the seeding cycle? For these, the aim of this work was to analyze the flowering and the seeding patterns in aggregated and dispersed retention silvicultural system compared with unmanaged stands of *Nothofagus pumilio* forests, including the pre-dispersion insect, bird foraging analysis, and the abscised biomass production along one growing season.

## 2 Methods

### 2.1 Natural history of *Nothofagus pumilio* forests

*Nothofagus pumilio* forests (commonly named “lenga”) are the main commercial woodlands in southern Argentina and Chile. It is a deciduous broadleaved species that grows mainly in pure stands, but also in mixed stands with the evergreen *Nothofagus betuloides* species (Cruz et al. 2007). Lenga is a medium-high tree reaching up to 30 m in height (Martínez Pastur et al. 1997) and up to 1.7 m in diameter in the better site qualities. Lenga is a monoecious species, with solitary male flowers appearing first at the base of the shoots, and solitary female flowers growing later at the distal extremes. Budburst occurs in late spring (November) pollinated by wind and fruit development is produced during summer. The fruit has two nuts per cupule reaching maturity in March. Flowers, immature fruits and seeds are exposed to predation of insect and birds, and when they fall to the forest floor, they could be consumed by rodents (*Akodon*, *Euneomys* and *Oligoryzomys* species) or birds. Surviving nuts germinate in November-December. There is no seed bank, but seedlings can persist up to 25 years (Cuevas and Arroyo 1999).

### 2.2 Study sites and forest structure characterization

An old-growth *Nothofagus pumilio* forest were selected in Los Cerros Ranch, Tierra del Fuego - Argentina (54°20' S, 67° 52' W) where *Kareken* Sawmill carries out tree harvesting. Studied forests were harvested through the variable retention silvicultural method (Martínez Pastur and Lencinas 2005), which was largely applied in Tierra del Fuego to improve the biodiversity conservation of the managed forests since 2001 (Martínez Pastur and Lencinas 2005, Martínez Pastur et al. 2007a) (Figure 1). This system proposes to leave aggregated (one circular island per hectare of original forest with 30 m radius) and dispersed (10-15 m².ha$^{-1}$ basal area of the most dominant trees distributed between aggregates) retentions for more than one forest term.

Three aggregates on different stands in the harvested forest, three sectors of dispersed retention on the harvested forest far away to the aggregates influence, and three unmanaged stands without previous forest management were selected. Forest structure of each sector was characterized through four forest plots using the point sampling method (BAF 6) (Bitterlich 1984). The plots were systematically located 30 m apart of the sampling collection points, and dominant height, density, quadratic mean diameter, basal area, total over bark volume and site class were measured (for equations and methodologies see Martínez Pastur et al. 1997, 2002b).

Climate was measured in the study area with two weather stations (Davis Weather Wizard III and accessories - USA) placed in an old growth forest and in a harvested one during years 2002-2004. Climate was characterized by short, cool summers and long, snowy and frozen winters. Mean monthly temperatures varied from about -0.2 °C to 10.4 °C in the old growth forests, while in the harvested stands varied from about -1.0 °C to 10.6 °C. Only three months per year were free of mean temperatures under 0°C, and the growing season extended for approximately five months. Soil temperature (30 cm deep) never froze in the old growth forests, but soil freezing was observed in the harvested stands (-0.2 to -0.6 during June-July). Rainfall reaching the forest floor was 382 mm yr$^{-1}$ inside the old-growth forests, while it was 639 mm yr$^{-1}$ in the harvested stands. The average wind speed outside the forest was 8 km.h$^{-1}$, reaching up to 100 km h$^{-1}$ during storms.

### 2.3 Abscised biomass sampling in unmanaged and managed stands

In each of the nine studied sites, ten biomass trap of 0.06 m² and 30 cm deep were used, which were perforated to allow rain and snow-water drainage. In the primary unmanaged and in the dispersed retention forests, the traps were established along a 50 m transect, while in the aggregates the traps were established in the half medium area close to the centre. All the abscised biomass material were monthly collected, and manually classified in the reproductive (male and female flowers, immature fruits and seeds) and litter (leaves, fine branches less than 1 cm diameter and miscellaneous) components. Reproductive organs were counted and classified according to insect or bird damage, or without evident damage. Insect damage could be identified by the deformation on the reproductive organs, while bird damage were quantify trough the non-comestible parts rejected during the foraging.

Reproductive and litter components were dried in an oven at 70 °C until constant weight, before they were weighted with at precision of 0.0001 g. Seeds quality were analyzed prior to dried trough the manual opening of each seed, classifying them in empty or full seed. Immediately, the tetrazolium test (2,3,5-triphenyltetrazolium chloride) was conducted to quantify 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). When the solution turn to red due to hydrogen reduction derived from enzymes it was considered viable seed. Seed were no reacted to the test, dead seeds and seeds with immature embryos were considered as non-viable seeds.

### 2.4 Data and Statistical analysis

Data of reproductive components in the traps in each treatment were expressed as million ha$^{-1}$, while biomass was expressed as ton ha$^{-1}$. Comparisons of main factors were carried out by analysis of variance with F test. Significantly different averages were separated with a post-hoc Tukey (honestly significant difference) test ($p < 0.05$).

Figure 1. Study sites with primary unmanaged forests in the backside of the image, the aggregated retention (unmanaged patches) and the dispersed retention among them, in *Nothofagus pumilio* forests of Tierra del Fuego (Argentina).

## 3 Results

### 3.1 Forest structure of managed and unmanaged stands

Forest structure was significantly different in managed and unmanaged stands (Table 1), with no significant differences inside the aggregates and the primary unmanaged forests. Quadratic mean diameter increase 35% in the dispersed retention due to larger trees were selected for the retention. The basal area and the number of trees were reduced to 17% and 8% respectively in the dispersed retention, while total over bark volume decreased to 18%. Site quality of the selected stands was smoothly higher in the harvested sectors (site quality II-III) than in the primary unmanaged sectors (site quality III), with a difference of 2.2 m in the total height.

Table 1. Analysis of variance of the forest structure for different retention types and unmanaged forests, considering the dominant height (m) (DH), site class (S), quadratic mean diameter (cm) (QMD), number of trees (n ha$^{-1}$) (N), basal area (m$^2$ ha$^{-1}$) and total over bark volume (m$^3$ ha$^{-1}$) (TOBV).

| Factor | DH | S | QMD | N | BA | TOBV |
|---|---|---|---|---|---|---|
| DR | 23.4b | II-III | 74.2b | 42.4a | 13.0a | 157.9a |
| AR | 23.8b | II-III | 56.1a | 505.2b | 78.5b | 953.8b |
| PF | 21.4a | III | 53.5a | 510.5b | 71.5b | 788.8b |
| F | 7.18 | | 11.30 | 42.71 | 91.51 | 98.45 |
| p | 0.002 | | 0.001 | 0.000 | 0.000 | 0.000 |

DR = dispersed retention; AR = aggregated retention; PF = primary unmanaged forest; F = Fisher test; p = probability.
Site class was defined according to Martínez Pastur et al. (1997). Different letters showed differences by Tukey test at $p < 0.01$

## 3.2 Flowering patterns and reproductive organs abscission

Male and female flowers were higher in the primary unmanaged stands when it was compared to the aggregated and dispersed retention (eight and four folds higher, respectively) (Table 2). The flowering production presented different male-female flower ratio being higher in the primary unmanaged forests (ratio of 2.2) than in the managed stands (ratio of 0.9). Along the growing season it were observed abscission of reproductive organs (female flowers and immature fruits), being higher in the primary unmanaged forests (0.8 and 3.3 million ha$^{-1}$, respectively) than in the aggregates (0.2 and 1.3 million ha$^{-1}$, respectively) than in the harvested sectors (0.1 and 0.4 million ha$^{-1}$, respectively) (Table 2). However, there was no significant difference of abscised flowers represented as a percentage of the total flower production between the treatments (3.6% to 5.2%). In contrast, the immature fruits abscission was significantly higher in the harvested stands (19% to 25%) than in the primary unmanaged forests (13%).

## 3.3 Seeding patterns

Seeding was related to female flower production, being significantly higher in the primary unmanaged stands (14.7 million ha$^{-1}$) than inside the aggregates (4.6 million ha$^{-1}$) or the harvested sectors (2.3 million ha$^{-1}$) (Table 3). Beside this, the effectiveness of seed production, as the percentage of female flowers that reaches to a full well developed seed, did not presented significant differences between the studied treatments (68.2% to 78.6% of effectiveness). However, it was observed a different seed quality production between the studied stands. Empty, viable and non-viable seed numbers presented a similar pattern than the total seed numbers, being higher in the primary unmanaged stands than in the harvested stands. However, the percentage of empty seeds in the primary unmanaged stands (32%) was higher compared to the harvested sectors (21%) (Table 3). On the other hand, the viability was higher (63%) in the harvested sectors than in the primary unmanaged stands (49%) with intermediate values inside the aggregates. Finally, non viable seeds did not showed significant differences between treatments (12% to 15%).

Table 2. Analysis of variance of different retention types and unmanaged forests for the number of male flowers (MF) (million ha$^{-1}$), number of female flowers (FF) (million ha$^{-1}$), ratio between male and female flowers (R), number (AFF) (million.ha$^{-1}$) and percentage (AFF%) of abscised female flowers, and number (IF) (million.ha$^{-1}$) and percentage (IF%) of immature fruits.

| Factor | MF | FF | R | AFF | AFF% | IF | IF% |
|---|---|---|---|---|---|---|---|
| DR | 1.85a | 2.75a | 0.96a | 0.09a | 5.22a | 0.40a | 19.22ab |
| AR | 8.01a | 6.08a | 0.89a | 0.22a | 3.67a | 1.28a | 25.50b |
| PF | 38.83b | 18.90b | 2.23b | 0.86b | 4.58a | 3.35b | 12.85a |
| F | 79.40 | 45.45 | 23.88 | 23.48 | 0.36 | 29.71 | 4.75 |
| p | 0.000 | 0.000 | 0.000 | 0.000 | 0.698 | 0.000 | 0.011 |

DR = dispersed retention; AR = aggregated retention; PF = primary unmanaged forest; F = Fisher test; p = probability. Different letters showed differences by Tukey test at $p < 0.01$.

## 3.4 Insect and bird foraging patterns

Large number of female flowers, immature fruits and seeds foraged by insects were observed in primary unmanaged forests (0.12, 0.13 and 0.31 million ha$^{-1}$, respectively) than in the harvested stands (inside the aggregated retention and in the dispersed retention) (0.01-0.02, 0.02 and 0.02-0.04 million ha$^{-1}$, respectively) (Table 4). This insect foraging represented a small percentage of the flower and immature fruit production (less than 0.8%) without significant differences between the treatments. However, the percentage of seeds damaged by insects was significantly higher in the primary unmanaged stands (2.6%) than the harvested sectors (0.4%) founding intermediate values inside the aggregates (1.3%).

Bird foraging patterns was similar than those described for the insects, being the amount of foraged immature fruits and seed higher in the primary unmanaged stands (0.5 and 0.2 million ha$^{-1}$, respectively) than the harvested stands (0.02-0.08 and 0.02-0.11 million ha$^{-1}$,

Table 3. Analysis of variance of different retention types and unmanaged forests for the number (S) (million ha$^{-1}$) and percentage (S%) of seeds, number (ES) (million ha$^{-1}$) and percentage (ES%) of empty seeds, number (VS) (million ha$^{-1}$) and percentage (VS%) of viable seeds, and number (NVS) (million ha$^{-1}$) and percentage (NVS%) of non-viable seeds.

| Factor | S | ES | VS | NVS |
|---|---|---|---|---|
| DR | 2.26a | 0.41a | 1.50a | 0.31a |
| AR | 4.57a | 1.44b | 2.38a | 0.60a |
| PF | 14.69b | 4.30c | 7.06b | 2.78b |
| F | 46.16 | 48.85 | 42.50 | 13.39 |
| p | 0.000 | 0.000 | 0.000 | 0.000 |
| **Factor** | **S%** | **ES%** | **VS%** | **NVS%** |
| DR | 73.03a | 21.24a | 63.44b | 12.35a |
| AR | 68.20a | 28.41ab | 56.03ab | 11.84a |
| PF | 78.66a | 31.55b | 48.78a | 15.49a |
| F | 2.28 | 3.84 | 4.89 | 1.19 |
| p | 0.107 | 0.025 | 0.009 | 0.309 |

DR = dispersed retention; AR = aggregated retention; PF = primary unmanaged forest; F = Fisher test; p = probability. Different letters showed differences by Tukey test at $p < 0.01$

Table 4. Analysis of variance of insect foraging for different retention types and unmanaged forests considering the number (FFI) (million.ha$^{-1}$) and percentage (FFI%) of female flowers, the number (IFI) (million.ha$^{-1}$) and percentage (IFI%) of immature fruits, and the number (SI) (million.ha$^{-1}$) and percentage (SI%) of seeds.

| Factor | FFI | FFI% | IFI | IFI% | SI | SI% |
|---|---|---|---|---|---|---|
| DR | 0.02a | 0.81a | 0.02a | 0.50a | 0.02a | 0.37a |
| AR | 0.01a | 0.24a | 0.02a | 0.63a | 0.04a | 1.33ab |
| PF | 0.12b | 0.59a | 0.13b | 0.61a | 0.31b | 2.56b |
| F | 5.23 | 0.59 | 9.32 | 0.07 | 20.80 | 4.66 |
| p | 0.007 | 0.555 | 0.001 | 0.934 | 0.000 | 0.012 |

DR = dispersed retention; AR = aggregated retention; PF = primary unmanaged forest; F = Fisher test; p = probability. Different letters showed differences by Tukey test at $p < 0.01$

respectively) (Table 4). However, no significant differences were founded when these values were compared as the percentage of total immature fruits or seeds, representing the 1.2-2.7% of the immature fruits and 1.6-2.6% of the total seed production.

### 3.5 Monthly abscised biomass production

Male flowering began in October in all the stands (11% to 24% of the total production), presented the maximum during November (75% to 86%) being more homogeneous in the primary unmanaged forests (Figure 2). When the male flowering ended, the female flowering began, with a maximum abscission during December, which was more homogeneous in the harvested stands. Immature fruits abscission was mainly produced between December and March, being higher during February. Maximum seeding was observed in March (68% to 85%) being higher in the primary unmanaged stands. Finally, when the seeding ended it was observed the mass litter fall during April and May. This litter fall was more concentrated in the primary unmanaged forest (46%) and occurred one month earlier (April) than in the harvested stands (29% to 39% measured in May). Values of litter reached to 4.01 ton ha$^{-1}$ ± SE 0.35 ton ha$^{-1}$ (average ± standard error) in the primary unmanaged forests, 3.14 ton ha$^{-1}$ ± SE 0.58 ton a$^{-1}$ (average ± standard error) inside the aggregated retention, and 0.95 ton ha$^{-1}$ ± SE 0.27 ton ha$^{-1}$ (average ± standard error) in the dispersed retention of the harvested stands.

## 4 Discussion

Harvesting produces greatly changes in the forest structure of the managed stands (Martínez Pastur et al. 2000), with significant alterations in the microclimatic conditions (Caldentey et al. 2005a, b), modifying the light and water availability at the understory level (Martínez Pastur et al. 2007b). Harvesting leaves the largest tress as a remnant overstory, increasing the quadratic mean diameter of the trees (Martínez Pastur et al. 2000, Gea et al. 2004). On the other hand, the changes in forest structure and microclimatic conditions produce greatly modifications in the natural structure populations associated to the forests, on plants (Martínez Pastur et al. 2002a), birds (Deferrari et al. 2001), insects (Spagarino et al. 2001) and fungi species (Ducid et al. 2005).

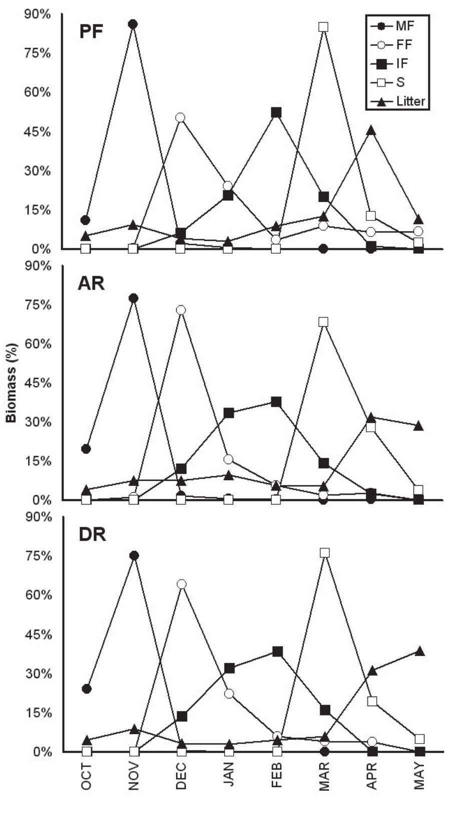

Figure 2. Monthly abscised biomass production (% of the total of each component) considering male flowers (MF), female flowers (FF), immature fruits (FF), seeds (S) and litter (leaves, fine branches and miscellaneous) as main components, in primary unmanaged forests (PF), aggregated retention (AR) and dispersed retention (DR) treatments.

Natural *Nothofagus* forests in Tierra del Fuego are characterized by a permanent seedling bank in the understory and by the lack of a seed bank in the soil, due to seeds loose their viability at the end of one growing season (Cuevas and Arroyo 1999). The seedling bank can survive for long periods of time (Cuevas 2002), awaiting a canopy opening to occur in a natural dynamic process (Rebertus and Veblen 1993, Heinemann et al. 2000) or due to human harvesting (Martinez Pastur et al. 1999a, Rosenfeld et al. 2006). However, an absence of mast seeding years could produce a lack of seedling recruitment. For this, the understanding of the flowering and seeding processes could help to develop new silvicultural management strategies and to detect the bottlenecks along the full regeneration cycle.

Seeding varied along the years, presenting cycles of seven years in *Nothofagus pumilio* (Cuevas 2000). These seeding cycles have been described in several forest species (Kelly 1994, Kelly et al. 2000, Koenig and Knops 2000) and have received considerable attention in *Nothofagus* forests (Monk and Kelly 2006), because the level of variation among years is especially high (Kelly 1994, Kelly and Sork 2002). However, these cycles are not homogeneously produced at landscape level, and it is possible to observe different quantity of flowers and seeds in stands with equivalent density. The flower production was significantly higher in the primary unmanaged forests than in the managed ones, showing a higher ratio among male and female flowers. This large production of female flowers could be due to the post-harvesting stress of the remnant overstory, which could induce to produce a higher proportion of female than male flowers. The abscission of female flowers could be related to the lacking of pollination (Díaz et al. 2003), which percentage not varied between treatments, reaching a high degree of effectiveness due to the pollination strategy and the high dispersion capacity of the *Nothofagus pumilio* pollen (Cuevas and Arroyo 1999, Kelly et al. 2001). The abscission of immature fruits was severe, reaching to 25% of the fertilized female flower production. This abscission was higher in the harvested stands than in the primary unmanaged forests, and could be due to the wind effect, which is significantly intense (50%) in the harvested stands (Caldentey et al. 2005a). Pulido and Díaz (2005) founded for primary and managed *Quercus ilex* forests, a fertilization failure of 31% to 36%, with efficiency in fruit production of 18% to 28%. These values are significantly different than those described for *Nothofagus pumilio*, where the fertilization failures are lower, and the efficiency is higher. Beside this, Díaz et al. (2003) suggest that the intensity of selection is greater when environmental stress is more intense, which could explain the higher levels of spontaneous abortion in managed stands.

The seeding values indicate a mass-seed year for the primary unmanaged stands, with an average of 14.7 million ha$^{-1}$ for the three stands, and a maximum production individual stand of 23.8 million ha$^{-1}$. These values did not reach to the maximum reported for the species in Chile that ranged between 16.0 million ha$^{-1}$ in the XII Region (Schmidt et al. 1997) and 50.0 million ha$^{-1}$ at 450 m. a. s. l. in Tierra del Fuego (Cuevas 2000).

The fruit production effectiveness did not significantly varied among the managed and unmanaged forests, which indicates that the proportion of flowers and immature fruits abscission did not limited the total fruit production. The quality of the seed was better in the harvested stands. Cuevas (2000) informed changes according to the altitude (460 m. a. s. l. to timberline) and studied years, which could be related to foliage development, and to the adverse climatic conditions.

The empty seeds represents a large percentage of the seed fall (21% to 32%), being higher in the unmanaged primary stands. Cuevas (2000) informed variable percentages of empty seeds between altitudes and among studied years. During the seeding years the percentage was lower (29% to 88% between lower and higher altitudes) than during the lower seed production years (75% to 98% between lower and higher altitudes). This phenomenon was informed for other species (Wardle 1970, Manson 1974, Allen and Platt 1990). Beside this, seed viability was not related to seed rain production, observing large viability in managed forests (56% to 63%) than in primary unmanaged forests. Cuevas (2000) informed variable percentages of viability between altitudes and among studied years. During the seeding years the percentage was higher (61% to 7% between lower and higher altitudes) than during the lower seed production years (3-8% to 0% between lower and higher altitudes). The empty seed percentage was lower and the viability was higher in the dispersed than in the aggregated retention. The higher viability observed in the managed forests could be related with the canopy opening, which offers to the remnant trees higher incident light readiness and consequently large photosynthetic capacity to fill the fruits.

To attain an approach of the whole regeneration cycle, it is necessary to consider the pre-dispersal predation by birds and insects. Insect predation could be produced by moths or monophagous weevils (Sullivan et al. 1995), which deformed the infected flowers, fruits and seeds. It was possible to observe large quantities of insect larvae inside the fruits, but there was not taxonomically identified. In the present work, the damage by insect was greater in timber quality primary unmanaged forests. This could be due to the abundance and diversity in unmanaged forests is higher than in managed stands (Spagarino et al. 2001) or associated non-timber quality forests (Lencinas et al. 2007). Many insect species are missing in the harvested stands (Spagarino et al. 2001), but similar levels of insect populations are able to survive inside the aggregates (Martínez Pastur and Lencinas 2005) being the main biodiversity conservation advantage of this regeneration method. This is reflected in the percentage of the affected seeds where there are significant differences between the primary forests and the dispersed retention treatments.

Bird predation consumes the endosperm and discards the rest of the fruit, for this, it is easily identified into the samples collected by the traps. There were no significant differences in the percentage of foraged seeds by birds. Beside this, large number of immature fruits and seeds were consumed in the primary forests (0.76 million ha$^{-1}$) than in the harvested forests (0.04 to 0.19 million ha$^{-1}$). The main seed consumers are Passeriforms (e.g. *Carduelis barbata* or *Phrygilus patagonicus*) and Psitaciforms (*Enicognathus ferrugineus*) (Díaz and Kitzberger 2006) which inhabits both environments (Deferrari et al. 2001, Lencinas et al. 2005). However, in the managed forests, the food offer is greater than in the unmanaged primary stands, due to the increase in understory biomass (Martínez Pastur et al. 2002a). It is possible that immature fruits and seeds were one of the main food resources for the herbivore birds in the primary unmanaged forests, and acted as secondary food resources in the managed forests, where grass grains are more abundant (Martínez Pastur el al. 2002a). Beside this, Díaz and Kitzberger (2006) describe the flower foraging of *E. ferrugineus*, where could underestimate the real male flower number in the stands. In this study empty male flowers was quantify, but it is no possible to known if this species consumes only the pollen or consumes the full flower. Pulido and Díaz (2005) inform looses due to biotic factors of 10% to 29% for primary and managed *Quercus ilex* forests, which are higher than those described here.

Generally, the observed phenology presented an expected behavior than those described previously (Barrera et al. 2000). Monthly abscised biomass showed that male flowering occurred prior to female flowering, followed by a rapid fruit development. Seeding abruptly occurred at the end of the summer, prior to the mass litter fall. This litter fall was delayed in the dispersed retention compared with the aggregated retention and followed by unmanaged forests. This could be due warmer temperatures in the harvested stands at the beginning of the autumn. Litter fall after the seeding, covering and protecting seeds during winter, and bringing the optimal regeneration conditions for the next spring, due to *Nothofagus pumilio* have an absence of seed bank in the forest floor (Cuevas and Arroyo 1999).

The number of propagules produced by most organisms is exceedingly large compared to the number of successful survivors (Díaz et al. 2003). Such excessive production allows parents to adjust the numbers of survivors to that which is optimal under current environmental conditions, and adapt to fluctuating environments (Mock and Forbes 1995) make a selection through quantity and quality of reproductive organs (Kozlowski and Stearns 1989). Our results showed that a high percentage of pollinated flowers success in produce fruits, independently to the seed-fall production and the forest management of the stand. Fertilization is mainly controlled by weather factors acting in several stages for *Quercus* (Pulido and Díaz 2005, Wolgast and Stout 1977) and *Nothofagus* (Kelly et al. 2001). The premature abscission of fruits was the main loss factor, while biotic factors (insect and bird foraging) was not greatly. The other important loss factor was the large percentage of empty seeds observed in all the treatments, but significantly greater in primary unmanaged stands. It is possible that the empty fruits corresponded to auto-pollinated flowers, where the fruit formation processes was induced, but the absence of an embryo impeded the endosperm accumulation. *Nothofagus pumilio*, probably, is genetically self-incompatible (Cuevas and Arroyo 1999). More studies are necessary to explain the causes of these two main loss factors, and self-incompatibility studies to quantify its influence in empty seed production, as well as to extend this kind of studies in long periods of time to include seeding years with different seed rain production.

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