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Variable retention harvesting influences biotic and abiotic drivers of regeneration in *Nothofagus pumilio* southern Patagonian forests

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ABSTRACT

Understanding regeneration processes is important for implementing new silvicultural treatments that rely on natural regeneration from seed. Nevertheless, integrated, flower-to-sapling studies of the regeneration cycle evaluating the effect of management factors operating at each reproductive stage are scarce. We analyzed the influence of variable retention harvesting on the biotic and abiotic drivers of regeneration of *Nothofagus pumilio* forests of Southern Patagonia (Argentina). We quantified losses in reproductive potential caused by biotic and abiotic factors within the landscape mosaic generated by variable retention, including harvested stands with aggregated retention and dispersed retention, and in primary unharvested forests. Overall, pre-dispersal losses were caused by wind and insect predation acting on flowers and developing fruits, whereas post-dispersal losses resulted from stratification during winter, and impact of microclimate and rodent predation upon seeds. Dispersed retention areas modified the main drivers of regeneration as compared to aggregates and control areas. Flowering and fruiting was favored in the dispersed retention treatment, whereas seed and seedling survival were more successful in aggregates and control stands. Aggregates retained within harvested areas maintained most of reproductive processes of primary unharvested forests. The most critical step of the reproductive cycle is associated with the seedling stage to the extent that complete regeneration failure can occur in certain years independently of flower and seed crops.

1. Introduction

The success of any regeneration method depends on its economic feasibility, its impact on biodiversity, and the potential recovery after harvesting. Forest regeneration is a dynamic process whereby new trees are recruited into the adult population, thus compensating for the losses derived from gradual mortality (Busing and Mailly, 2004), wind-throws (Rebertus and Veblen, 1993), or harvesting (Gea et al., 2004). The full regeneration process includes multiple transitions among different reproductive stages (flowers, seeds, seedlings, and woody saplings) that depend on abiotic and biotic factors affecting the final reproductive output in terms of the number of new juvenile trees established (Pulido, 2002; Pulido and Díaz, 2005). In Patagonian forests, harvesting greatly modifies the forest environment (e.g., microclimate and nutrient cycles) (Frangi and Richter, 1994; Caldentey et al., 2001, 2009; Promis et al., 2010) and impact on most of their biodiversity components (e.g., Deferrari et al., 2001; Spagarino et al., 2001). These changes potentially influence the success of flowering, fruiting, dispersal, recruitment, and, consequently, the overall levels of natural regeneration (Soler Esteban et al., 2010).

Several methods have been proposed to manage southern Patagonian forests based on their sexual regeneration, e.g., high-grading cuttings, clear-cuts (Gea et al., 2004), shelterwood cuts (Rosenfeld et al., 2006), and, recently, a variable retention system (Gustafsson et al., 2012; Lindenmayer et al., 2012) was proposed for these austral forests (Martínez Pastur et al., 2009, 2011a). This method proposes to keep 30% of the timber quality forest area as aggregated retention in 60 m diameter patches and 10–15 m^2 basal area as dispersed retention among aggregates, thus enhancing biodiversity conservation of the harvested stands (Vergara and Schlatter, 2006; Lencinas et al., 2009, 2011).

Regeneration of *Nothofagus pumilio* forests has been intensively studied (e.g., Heinemann et al., 2000; Cuevas, 2000, 2002; Gea et al., 2004; Rosenfeld et al., 2006; Heinemann and Kitzberger, 2006; Martínez Pastur et al., 2011a,b). Most previous reports a priori assumed single factors, such as microclimate or over-browsing by guanaco (*Lama guanicoe*) (Pulido et al., 2000), as explanations of regeneration failure without considering the interactive effects of other factors along the cycle (e.g., foraging, fruit set, seed quality, frost damage during stratification) (Cuevas, 2000; Soler Esteban et al., 2010). Therefore, we lack an integrated picture of the whole

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regeneration process and of the contribution of each factor to the final reproductive output (Pulido et al., 2010). For each sequential stage (flower, fruit, seed, seedling), the reproductive potential depends on the combined effects of biotic and abiotic factors (Wang and Smith, 2002). Therefore, to develop sound silvicultural techniques for improving *N. pumilio* regeneration, we must first know the effects of these factors on the reproductive output at any given stage of the whole cycle (Pulido et al., 2010). In this paper we used an integrated approach to analyze the influence of variable retention harvesting on the biotic and abiotic drivers acting along the reproductive cycle of Patagonian *N. pumilio* forests. Transition probabilities between stages of the reproductive cycle in different harvested and unharvested forests (Pulido and Díaz, 2005; Pulido et al., 2010) were estimated to address the following questions: (i) which is the relative importance of the different abiotic and biotic drivers along the reproductive cycle?, (ii) does forest harvesting modify the main drivers as compared to primary unharvested forests?, (iii) does variable retention allow the maintenance of the main natural reproductive processes operating in the primary unharvested forests?, and (iv) what are the critical stages explaining regeneration failure along the whole process?

2. Methods

2.1. Natural history of N. pumilio

N. pumilio forests are the main commercial woodlands in southern Argentina and Chile. *N. pumilio* is a deciduous broadleaved species that grows mainly in pure stands, but also in mixed stands with the evergreen *N. betuloides* (Cruz et al., 2007). It is a medium- to large-sized tree reaching up to 30 m in height and up to 1.7 m in DBH in the best site qualities (Barrera et al., 2000; Gea et al., 2004). According to Martínez Pastur et al. (2008), *N. pumilio* is a monoecious, anemophilous species, with solitary male flowers appearing first at the base of the shoots, and solitary female flowers growing later at the distal extremes. Wind pollination occurs in late spring, whereas fruit development takes place during early summer. The fruit is a nut that reaches maturity during late summer and early autumn. Flowers and fruits are exposed to pre-dispersal predation by insect and birds. After dispersal seeds are consumed by rodents (e.g., *Akodon*, *Euneomys* and *Oligoryzomys* species) or birds. Surviving seeds germinate during the subsequent growing season in late spring and early summer. There is no persistent seed bank in the forest floor, but seedlings can persist up to 25 years with suppressed growth in the understory (Cuevas, 2000, 2002).

2.2. Study sites and forest structure

We estimated the transition probabilities between stages of the reproductive cycle in different harvested and unharvested primary forests at Los Cerros ranch (54°20′SL, 67°52′WL), Tierra del Fuego, Argentina. Timber managed forests were harvested through the variable retention system (Martínez Pastur et al., 2009). Nine plots were selected within an area of 3500 ha: three aggregates (AR: dense circular patches 60 m in diameter), three areas of dispersed retention 20–30 m between the aggregates (DR), and three unharvested primary forests (PF) located in different stands. Location of the plots within the area was selected according its homogeneity and accessibility. In the harvested plots, harvesting was performed 2 years before the onset of this study. We studied three consecutive reproductive cycles (2006, 2007 and 2008) producing seedlings in 2007, 2008 and 2009. Each seedling cohort was monitored for three consecutive years until the sapling stage.

Forest structure was characterized in six plots using the point sampling method (BAF 6) (Bitterlich, 1984). The plots were systematically located 30 m apart from the biomass traps in DR and PF, and in the center of 6 different aggregates at each sampling point. In each sampling-point, total height and quadratic mean diameter (QMD) of each tree were measured, and dominant height (DH), tree density (N), basal area (BA) and total over bark volume (TOBV) were measured using methodology proposed by Gea et al. (2004). To characterize canopy structure and irradiance, we used hemispherical photographs of the forest canopy taken 1 m above ground level with an 8 mm fish eye lens (Sigma, Japan) mounted on a 35 mm digital camera (Nikon, Japan). Gap Light Analyzer software v.2.0 (Frazer et al., 1999) was used to estimate crown cover (CC), effective leaf area index (LAI) integrated over the zenith angles 0–60°, global radiation (GR) at understory level transmitted through the canopy along the growing season (November–March), and percentage of global radiation (PGR) as the ratio of GR to the amount of direct and diffuse radiation incident on a horizontal surface located above forest canopy (for details see Martínez Pastur et al., 2011a,b).

Climatic variables (air temperature, soil temperature at 30 cm depth, average maximum wind speed at 2 m height and rainfall reaching the forest floor) were measured with three weather stations (Davis Weather Wizard III and accessories, USA) placed in each treatment for 3 years (2006–2008). Climate was characterized by short, cool summers and long, snowy and frozen winters (Fig. 1). Temperatures below zero occurred all the year round, and the growing season extended for approximately 5 months (November–March). Mean monthly air temperatures were higher in PF than in AR and DR. Soil temperature was always above zero in PF and AR, but soil freezing was observed in DR during July. Wind speed was higher in DR > AR > PF. Rainfall was homogeneously distributed throughout the year, and was higher in DR > AR > PF (Fig. 1).

2.3. Flower and fruit production (pre-dispersal phase)

In each of the nine plots, we installed 10 biomass traps (plastic buckets 0.06 m^2 in area and 30 cm deep), which were perforated to allow water drainage. In PF and DR the traps were established along a 50 m transect. In AR the traps were placed close to the center of the aggregate to minimize edge effects. Flowers and fruits fallen into the traps were collected monthly and transported to the laboratory. Classified plant material was oven-dried at 70 °C until constant weight and subsequently weighed to the nearest 0.0001 g.

Flowers from traps were classified as intact male flowers (MF), intact female flowers (FF), female flowers damaged by insects (FFI), abscised female flowers (FFA), and female flowers resulting in empty fruits (FFEF). Fruits were classified as fruits damaged by insects (FRI), fruits damaged by birds (FRB), abscised immature fruits (FRA), and sound fruits (SFR). Insect damage was deduced from the deformation due to dehydration of the reproductive organs, whereas bird damage was assessed on the basis of uneaten fruit parts rejected after foraging. Seed development (full or empty) was assessed by means of internal inspection. Subsequently, the tetrazolium test (2,3,5-triphenyltetrazolium chloride) was conducted to assess seed viability. Embryos were incubated for 24 h in a water dilution of 0.1% solution in darkness at 25 °C (Cuevas, 2000). Seeds were considered viable if the solution turn red due to hydrogen reduction derived from enzymatic activity. Seeds showing no reaction and seeds with aborted embryos were considered as non-viable seeds.

2.4. Seed production and seed losses (post-dispersal phase)

In the post-dispersal phase we quantified the number of sound seeds produced (SS), seeds predated by mice (SM), seeds predated