Forest Ecology and Management 384 (2017) 236–247

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Thinning of loblolly pine plantations in subtropical Argentina: Impact on microclimate and understory vegetation ☆

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ARTICLE INFO

Article history:
Received 20 July 2016
Received in revised form 9 October 2016
Accepted 15 October 2016

Keywords:
Atlantic Forest
Life form
Light demanding species
Litter removal
Species richness

ABSTRACT

During the last three decades, the area dedicated to tree plantations in northeast of Argentina has increased five-fold at the expense of the native semideciduous Atlantic Forest. Silvicultural practices such as thinning affect the understory and forest floor incrementing vegetation cover and diversity that may impact ecological functions such as carbon and nutrient cycling and provide food and shelter for wildlife. The aim of this study was to assess the effects of two thinning intensities (50% and 30% of individual removal), and litter removal in the 50% thinning treatment on the understory vegetation of loblolly pine (*Pinus taeda* L.). The high thinning intensity and the control without thinning were intended to recreate existing management practices in the region. The study was carried out in three *Pinus taeda* plantations (replicates). Environmental conditions and cover of native understory vegetation were measured during two years after thinning. Canopy openness, solar radiation, air temperature and soil bulk density were higher in thinning treatments than in control plots while soil water content was lower. Vegetation cover and richness increased with intensity of the thinning treatments. Tree saplings differed in the responses according to light requirements and height. Light-demanding species and individuals taller than 0.5 m were responsive to thinning increasing coverage, abundance and height, while smaller saplings were more abundant in control plots. No effects of litter removal were observed in understory species richness and plant cover. This study provides evidence that thinning on pine plantations in Northeastern Argentina can contribute in maintaining biodiversity and related ecosystem functions of subtropical forests. Management practices involving lower plantation densities and fewer interventions should be developed to achieve more positive effects.

1. Introduction

Species loss and simplification of ecosystem function and structure have become a major concern worldwide. Despite the goals proposed in the 2010 Convention on Biological Diversity, replacement, fragmentation and degradation of natural areas are still increasing (Secretariat of the Convention on Biological Diversity, 2014). Thus, sustainable management practices that foster biodiversity are needed (Brunet et al., 2000; Gilliam, 2007; Odion and Sarr, 2007; Roberts and Gilliam, 1995). Forest plantations offer an opportunity to maintain biodiversity if sustainable practices are implemented (Carle and Holmgren, 2008).

Silvicultural practices that increase forest understory vegetation may assist in conserving plant species populations. Understory vegetation provides food and shelter for animal species (Dracup et al., 2015; Luck and Korodaj, 2008; Seiwa et al., 2012; Taki et al., 2010; Thompson et al., 2003; Verschuyl et al., 2011), and maintains soil physico-chemical properties and biological activity (Baba et al., 2011; Fu et al., 2015). Understory vegetation contributes little to stand biomass and carbon stores (Ares et al., 2007; Gonzalez et al., 2013), but can enhance carbon and nutrient cycling because of high turnover rates and litter production (Elliott et al., 2015; Poirier et al., 2016).

Silvicultural practices such as thinning have direct and indirect effects on the understory and forest floor. The response of ground vegetation depends on changes in the environmental conditions and available resources, the species composition before thinning,

☆ CPT and PIC designed research and the analytical tools; CPT performed experiments, implemented analytical tools and analyzed the data; CPT, PIC, MV wrote the paper; LR identified plant species and helped in data collection; CPT, PIC, MV, AA, GG contributed to data interpretation and manuscript revision.

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http://dx.doi.org/10.1016/j.foreco.2016.10.040

and reproductive and functional traits of plants that allow them to colonize the understory (Ares et al., 2009; Bartemucci et al., 2006; Wilson et al., 2009). The increment of resources availability after thinning is in general associated with increasing plant biomass and vegetation cover (Muir et al., 2002; Thomas et al., 1999). Plant species richness may increase during the rotation period because of the continuous establishment of species (Gilliam and Roberts, 2003; Muir et al., 2002; Thomas et al., 1999). However, increased radiation after intense basal area reductions during thinning may increase the abundance of species typical of disturbed environments (Reich et al., 2012; West and Osier, 1995; Wilson and Puettmann, 2007), some of which can be very aggressive competitors (Franklin et al., 2002; Gray, 2005). Resprouting ability typical of some life forms may enhance understory colonization by a few species decreasing richness (Kruger and Midgley, 2001).

The Atlantic Forest of South America is considered one of the eight most important biodiversity 'hotspots' in the world (Myers et al., 2000). This ecoregion extends along the Atlantic coast of Brazil and penetrates into southeastern Paraguay and Argentina. The subtropical forests in northeastern (NE) Argentina are the southern portion of the Atlantic Forest. About 93% of the original forest has been lost due to human activities. Only small fragments of the subtropical semideciduous Atlantic Forest remain in Brazil and Paraguay (Galindo-Leal and Câmara, 2003), while the largest remnants are in Argentina. During the last three decades, the area dedicated to tree plantations in Argentina has increased five-fold (Izquierdo et al., 2008), reaching 1,181,130 ha nowadays (MA, 2016). Large portions of the subtropical forests have been replaced recently by high-yield tree plantations of loblolly pine (*Pinus taeda* L.).

We studied the effect of two thinning intensities and pine litter removal on understory species richness, structure and function under pine plantations in Northeastern Argentina. Particularly, we assessed the effects of thinning on: (1) canopy openness, air temperature, soil bulk density and soil water content, (2) understory vegetation cover and species richness, (3) the composition and abundance of different life-forms, and (4) establishment and growth of tree seedlings with different light requirements. We replicated a thinning experiment in three forest stands. One of the treatments applied corresponded to severe thinning (50%) normally carried out in stands for saw timber harvesting, while the control treatment (no thinning) simulated stands planted for pulp production. We also carried out a moderate thinning (30%) in which we expected to promote vegetation development as in 50% thinning while enhancing species richness by reducing the rapid colonization and dominance of the understory by fast growing invasive species. Low vegetation cover and species richness was expected in control plots. An experiment consisting in a litter removal treatment combined with severe thinning was also carried out in the three stands to assess if needle accumulation on the forest floor was limiting tree regeneration.

2. Materials and methods

2.1. Study area

The study was carried out in three pine plantations (*Pinus taeda* L.) and in adjacent subtropical native forests in Misiones, Northern Argentina. Mean annual rainfall in the area is about 2000 mm and is evenly distributed throughout the year. Mean annual temperature is 21 °C, and frost seldom occurs in winter. The soils, which are derived from basaltic rocks containing high concentration of Fe, Al and Si, correspond to the 9a soil complex (Ligier et al., 1990) that includes Alfisols, Molisols and Inceptisols (Soil Survey Staff, 1992).

2.2. Experimental design

The experiment sites were Palmital 16 (P16, 26°09′59″S 54°26′27″W), Palmital 17 (P17, 26°09′43″S 54°26′35″W) and Campo San Juan (SJ, 26°05′40″S 54°26′48″W) located between 1 km and 5 km apart from each other. All the pine plantations were established in 2006, with an initial density of 1667 individuals per hectare, and were located next to native forest strips (NF). Pine plantations replicates had the same forest management but differed slightly in land use history. The Pamital 16 site has previously had a 38-year old pine forest that was cut down and remained abandoned during four years until the planting in 2006. The Palmital 17 site before the current plantation was occupied by a 35-year old pine forest with a very low density (150 individuals per ha) which allowed the development of a profuse understory. The Campo San Juan site was a disturbed native forest subjected to selective logging. The last two plantations were clear cut in 2006 and immediately planted. The usual management of pine stands in Misiones involves three successive thinning at ages seven, eleven or twelve and fifteen approximately, and a rotation cycle of about eighteen years. Thinning is often carried out by removing the seventh row of pines (hauling roads) every 20 m and then cutting remnant trees until reaching the desired percentage (generally 50%). In this study thinning effects were studied between the first and the second cut (from years seven to ten after planting).

A randomized complete block designed was used in the study. Three 65 × 65 m plots were installed within each pine plantation and thinning treatments were randomly assigned in each block: (1) control (without thinning), (2) T30 (removal of 30% of the pine individuals), (3) T50 (removal of 50% of the pine individuals). A fourth 65 × 45 m plot with 50% thinning was installed in each stand to test the effect of litter accumulation on plant regeneration. In these plots the litter layer was removed (5.6 ± 0.82 cm in depth). The effect of this treatment (T50 + R) on vegetation was compared to the results obtained in T50 treatment. Inside each plot, nine and six (in T50 and T50 + R, respectively) 15 × 15 m subplots were installed for microclimate and vegetation measurements, avoiding hauling roads.

2.3. Stand structure

Total height (H) and diameter at breast height (dbh) were measured in 102 and 130 pine individuals per plot, respectively, before thinning. Plots did not differ in H (13.1 ± 0.08 m) and dbh (0.17 ± 0.001 m) average of pine trees before thinning. Pine density and basal area (BA) did not differ among treatment plots, however, mean tree density in T50 was slightly lower and mean dbh was slightly higher than the other treatment plots (Table 1). Band dendrometers were installed in 36 randomly selected individuals per plot after thinning to measure increment in dbh and monitor changes on stand basal area throughout the duration of the experiment.

Stand structure of the strips of NF remnants next to the plantations was also characterized in order to describe the condition of these forests as potential propagule sources for each stand and thus helped to explaining diverse results among replicates. Plots were installed next to those strips because the distance to native forest is a key factor explaining seed rain and thus potential regeneration (Vespa et al., 2014). All trees ⩾10 cm dbh were measured and species determined in three 10 × 100 m plots in each block; also tree regeneration, vines basal area (Gerwing et al., 2006; Schnitzer et al., 2008) and bamboo cover, were estimated. Strips differed in BA, tree species richness and bamboo abundance, being the SJ and P16 sites the least and most disturbed strips according to these parameters (Table S1). Bamboo abundance is usually high in

Table 1
Stand density (D; ind/ha), height (H; m), mortality of pines (M; ind/ha), basal area (BA; m^2/ha) and diameter at breast height (DBH; m) measured just before thinning, and at 6, 12, 20 and 27 months thereafter. Values are means ± one standard error. Different letters indicate significant interactions or treatment main effects ($^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

		Treatment					
	Time (months)	Control		T30		T50	
D (ind/ha)	0	1279 ± 81		1257 ± 81		1168 ± 81	
H (m)	0	13 ± 0.29		13.28 ± 0.29		13.21 ± 0.29	
M (ind/ha)	27	185 ± 40		75 ± 25		22 ± 5	
	0	0.17 ± 0.004	E	0.17 ± 0.004	E	0.18 ± 0.004	E
DBH (m)	6	0.17 ± 0.003	E	0.18 ± 0.003	D	0.2 ± 0.003	C
Treat*	12	0.18 ± 0.003	E	0.19 ± 0.003	D	0.2 ± 0.003	C
Time^{NS}	20	0.18 ± 0.003	D	0.19 ± 0.003	C	0.21 ± 0.003	B
Treat × Time^{NS}	27	0.19 ± 0.003	D	0.20 ± 0.003	C	0.22 ± 0.003	A
	0	35.7 ± 1.5	B	36.9 ± 1.5	B	34.9 ± 1.5	B
BA (m^2/ha)	6	34.7 ± 1	B	27.2 ± 1	D	25.9 ± 1	D
Treat*	12	35.8 ± 1	B	28.4 ± 1	D	27.5 ± 1	D
Time^{NS}	20	37.1 ± 1	B	30 ± 1	D	29.6 ± 1	D
Treat × Time^{NS}	27	39.4 ± 1	A	32.3 ± 1	C	32.6 ± 1	C

highly disturbed forests in the semideciduous Atlantic Forest (Campanello et al., 2007).

2.4. Environmental conditions

2.4.1. Air temperature

Air temperature was measured with HOBO T loggers (Onset Computer Corporation, Bourne, USA) under the tree canopy at ground level in the thinning treatments, control plots and NF. Temperature values were simultaneously recorded every 10 min over approximately five days in plots of each plantation. Daily average values were calculated as well as the average of the maximum and minimum temperatures for the period. The data were taken 16 months after thinning in February 2014.

2.4.2. Canopy openness and solar radiation

Hemispherical photos were taken with a digital camera (Camera Nikon Coolpix 950, Nikkor 8-mm lens) on a self-leveling mounting to assess changes in canopy openness (CO) and solar radiation (SR) in the experimental plots before treatments (0) and at 1, 6 and 12 months after thinning. Photos were taken in the center of three 15 × 15 m subplots inside each plot, 1 m height, processed with the software Sidelook (Nobis, 2005) to optimize contrast (Nobis and Hunziker, 2005), and analyzed with the program Gap Light Analyzer (Frazer et al., 1999) to estimate both CO and SR. They were not measured in NF.

2.4.3. Soil water content and bulk density

Samples of top soil (0–5 cm) were taken after two dry spells of 20 days without rainfall. Five and seven undisturbed soil cores (80 cm^3) were taken in each plot and in NF 23 and 27 months after thinning, respectively. Soil samples were weighted in the laboratory and dried at 105 °C until constant weight. Soil water content (SWC) was calculated as the difference between weight of moist and dry samples divided by weight of moist samples. Bulk density (BD) was estimated by calculating dry weight divided by sample volume.

2.5. Understory vegetation

A pre-thinning sampling was conducted in 20 2 × 2 m quadrats that do not strictly corresponded to the locations of the quadrats sampled after treatments due to disturbances during thinning, but were located inside the 65 × 65 m plots. Sampling effort after thinning was increased to 27 quadrats in order to augment the sample coverage per plot (Chao and Jost, 2012). Thus, changes in plant cover were monitored in 27 2 × 2 m quadrats per plot at 6, 12, 20 and 27 months after treatment.

Two sampling methods were used to measure plant cover: punctual interception (Mueller-Dombois and Ellenberg, 1974) and Braun-Blanquet (1932). Both methods were used because they provide different information to characterize cover changes due to treatments. The intercept method is a faster sampling technique and allowed us to perform quantitative analysis to detect differences in cover with statistical models. The Braun-Blanquet method offered more detail about the species composition and allowed multivariate descriptive analysis taking into account many variables at the same time to detect differences between treatments. The first was performed by placing a 2-m-tall rod in four points located 50 cm inward each side of the 2 × 2 m quadrats. All the individuals or dead branches that were in contact with the rod were quantified. The absence of any "hit" was considered as absence of vegetation. For the second method, visual cover of all the species, branches and bare soil were determined according to the classification of Braun-Banquet as follows: (1) 0–5%, (2) 5–25%, (3) 25–50%, (4) 50–75% and (5) 75–100% cover. Treatments effects on species richness and life-form cover were measured four times along two years to characterized thinning treatments and once after a year in the case of needle removal treatment (the average number of species in 15 × 15 m subplot was considered).

All the species were determined when possible and classified according to their life-form in shrubs (S), palms (P), vines (V), ferns (F), graminoids (G) -including species in Poaceae and Cyperaceae, woody bamboos (WB), perennial herbs (PH), annual herbs (AH), creeping herbs (CH), and trees. The latter were categorized for analysis taking into account light requirements (light-demanding, LDT; shade-tolerant trees, STT) (Lorenzi, 2002; Vale et al., 2013; Zugliani Toniato and Oliveira-Filhob, 2004) and height (trees <50 cm and ⩾50 cm).

2.6. Data analysis

The plantation stands determined the sample size in all analyses (n = 3). Subplots and quadrats were the units of measure depending on the analysis performed, and were included as a random factor. Differences in dbh, BA and H were tested using linear mixed-effects models (LMM). For these data a model with a normal distribution and an identity link function was used. Dbh and BA were measured before and after thinning, so time, treatment and their interaction were included as fixed factors and site as a random factor. To analyze H before thinning the model included treatment and site as fixed and random factors, respectively.

Microclimate changes were also analyzed using LMM. Treatment effects on mean, daily maximum and daily minimum temperatures, CO, SR and SWC were also analyzed using LMM with treatment as a fixed factor and site and subplot as random factors. For these data it was used a model with a normal distribution and an identity link function. As the variance of temperature differed markedly among treatments, a constant variance function structure (varIdent) was also added to the model to correct residual spreads. For CO and SRT, the model included time, treatment, and their interaction as fixed factors, and site and subplot as random factors. For BD and SWC, treatments were considered a fixed factor and site a random factor. In the last model, the varIdent function was used.

Data on plant cover, branch litter, no vegetation and life forms obtained with the interception method were analyzed using GLMM with Poisson errors and log link function. Time, treatment, and the interaction were included as fixed factors and plantation and quadrat as random factors. Quadrats were the repeated unit. Patterns of concordance in the species cover data and life forms estimated by Braun-Blanquet were examined with principal-component analysis (PCA). Species that appeared only once were not taken into account in the analysis. Pearson correlations between understory species cover and life forms and the first two PC axes were determined. Species and life forms with correlation coefficient >0.2 and 0.3 respectively, and with $P < 0.05$ were retained. This analysis allowed the selection of the most relevant species and life forms that explained the ordination of the thinning plots (see Tables S2 and S3 in supplementary material for details). To analyze density of tree individuals GLMM with Poisson distribution and log link function was used while mean height was analyzed using LMM with a normal distribution and identity link function. Both analyses included time, treatment and their interaction as fixed effects and, site and quadrat as random effects. In the LMM the varIdent function was used. The analyses were made separated by the two height categories: ⩾50 cm and <50 cm.

Data on species richness were analyzed using GLMM with Poisson errors and log link function. Time, treatment, and the interaction were included as fixed factors and, plantation and subplot as random factors.

For all models, the significance of fixed effects was assessed using likelihood ratio tests. A posteriori tests were performed by the DGC test (Di Rienzo et al., 2002). Significance levels of 5% were used. InfoStat software was used for all analysis, as an interpreter of R (Di Rienzo et al., 2015).

3. Results

3.1. Stand structure

In experimental plots, there were no pre-treatment differences in mean tree dbh, total height and in stand basal area. Mean dbh was greater in the thinning treatments (T50 > T30 > control), and differences among treatments increased over time. Stand basal area in control plots was higher in all post-treatment measurements than in thinning plots. Stand BA did not differ between thinning intensities at any time (Table 1).

3.2. Environmental conditions

Canopy openness and solar radiation increased in the thinning treatments just after imposing the treatments but no differences were found between R30 and R50 at any time. Canopy openness in control plots as did solar radiation decreased in the first two measurements but then increased after a year (Fig. 1).

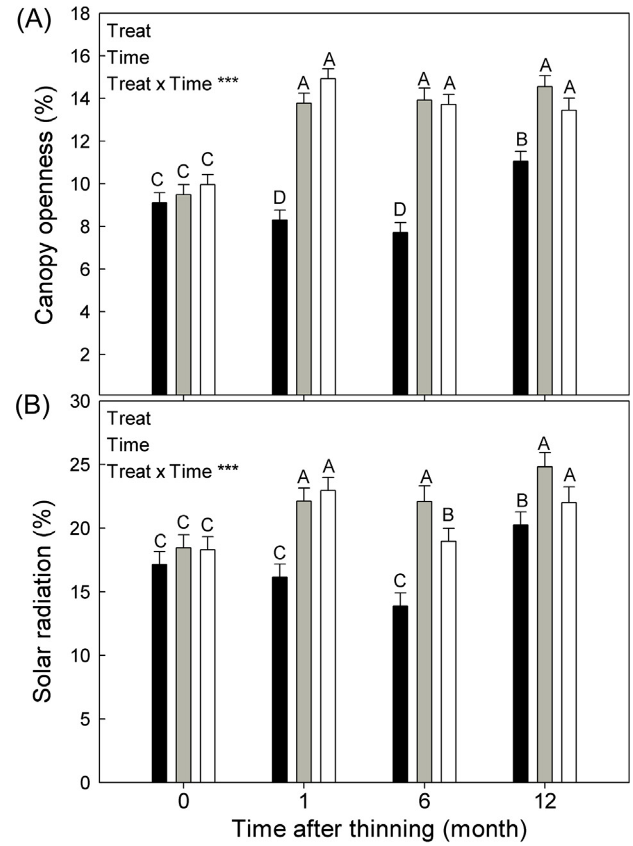

Fig. 1. Percentage of canopy openness (A) and solar radiation (B) in thinning treatments (T30 and T50), and control ( ) before thinning (0) and at 1, 6, and 12 months after thinning. Values are means ± one SE. Different letters indicate significant interactions or treatment main effects ($^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

Fifteen months after thinning, mean and maximum air temperatures measured during the summer were 1–4 °C higher in the thinning treatments than in the control and native forest, reaching 37 °C. Minimum air temperatures were higher in pine plantations compared to NF, with control plots showing the highest minimum temperatures (see Table 2).

Pine plantations had significantly higher soil bulk density than NF. Thinning treatments increased bulk density compared to control plots. Soil bulk density was lower in the litter removal treatment than in T50 (Fig. 2A). Soil water content at 0–5 cm depth was higher (2–10%) in NF than in thinning and control treatments before and after the growing season (October 2014 and March 2015, respectively) measurements. At the end of the growing season, SWC was lower in T50 compared to T30 and control (Fig. 2B). Soil water content values were lower at the end of the growing season in all treatments; despite being subjected to similar dry spells. The litter removal treatment had a lower SWC than T50 only at the beginning of the growing season (October 2014).

Table 2
Mean, maximum and minimum air temperature at ground level in thinning (T30, T50) and control plots; and native forest (NF), 15 months after treatments. Values are means ± one SE. Different letters indicate significant interactions or treatment main effects ($^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

Treatment	Mean T (°C)*	Max T (°C)***	Min T (°C)**
NF	25.5 ± 0.8 B	32.3 ± 2.2 B	20.9 ± 0.5 C
Control	25.8 ± 0.8 B	32.4 ± 2.3 B	22.2 ± 0.5 A
T30	26.7 ± 0.8 A	36.7 ± 2.2 A	21.6 ± 0.5 B
T50	26.9 ± 0.8 A	37. 5 ± 2.2 A	21.5 ± 0.5 B

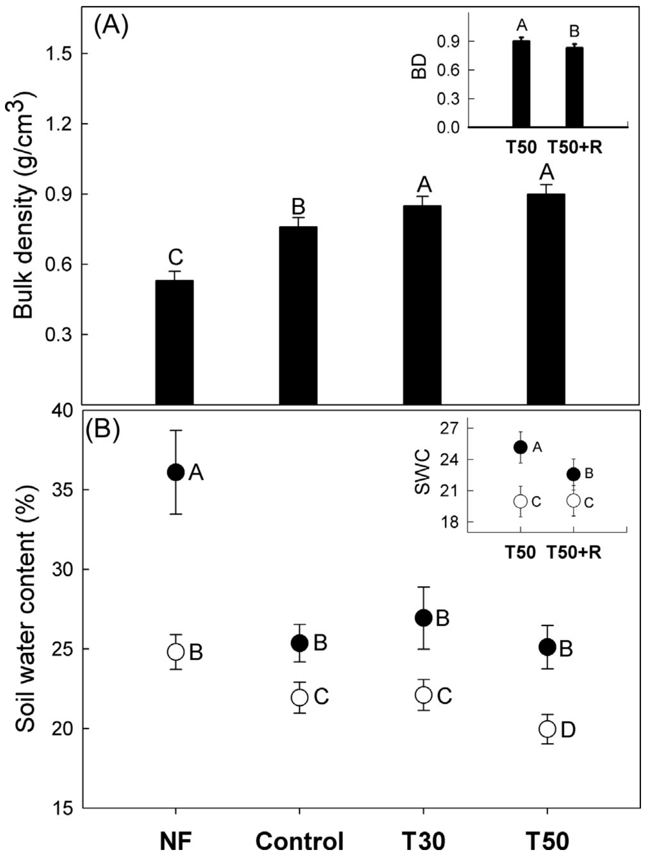

Fig. 2. Soil bulk density (BD) and water content (SWC) at 0–5 cm depth in thinning (T30, T50) and control plots, and in native forest (NF). Needle removal effects on BD and SWC (T50 + R) are shown in the upper right graphs. Soil water content was measured after moderate dry spells (20 days without rainfall) in October 2014 (●) and March 2015 (○). Values are means ± one SE. Different letters indicate significant interactions or treatment main effects ($^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

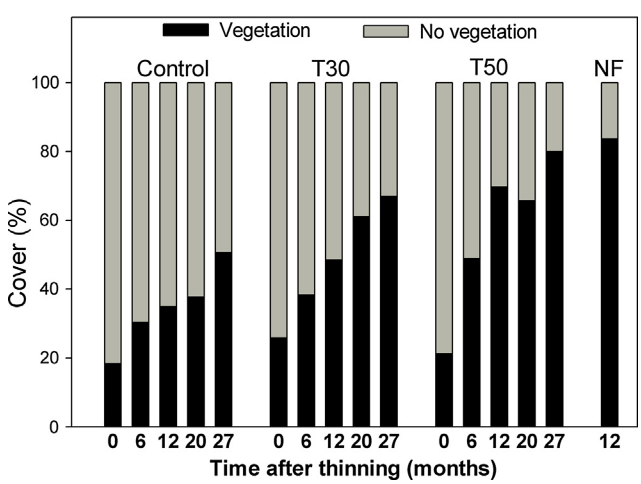

Fig. 3. Understory vegetation cover estimated as the ratio of points with at least one "touch" of vegetation by all points recorded in treatment (T30 and T50) and control plots, and native forest (NF) just before thinning, and at 6, 12, 20 and 27 months thereafter.

3.3. Understory vegetation

Understory vegetation cover estimated by the interception method, increased over time in all plots. In control plots vegetation cover was always less than 50%, while in thinning plots it reached 80% at the end of the experiment (Fig. 3).

Thinning treatments had a significant effect on vegetation cover at all measurement times, with the highest cover in the severe thinning treatment. The highest increase in plant cover was observed one year after applying the treatments in T50 (Fig. 4A). Thinning increased branch litter cover which decreased over time and returned to the initial condition two years after thinning (Fig. 4B). Areas without vegetation decreased with thinning, especially in T50. The differences among T50, T30 and control were maintained over time (Fig. 4C). The litter removal treatment had no effect on vegetation cover (data not shown).

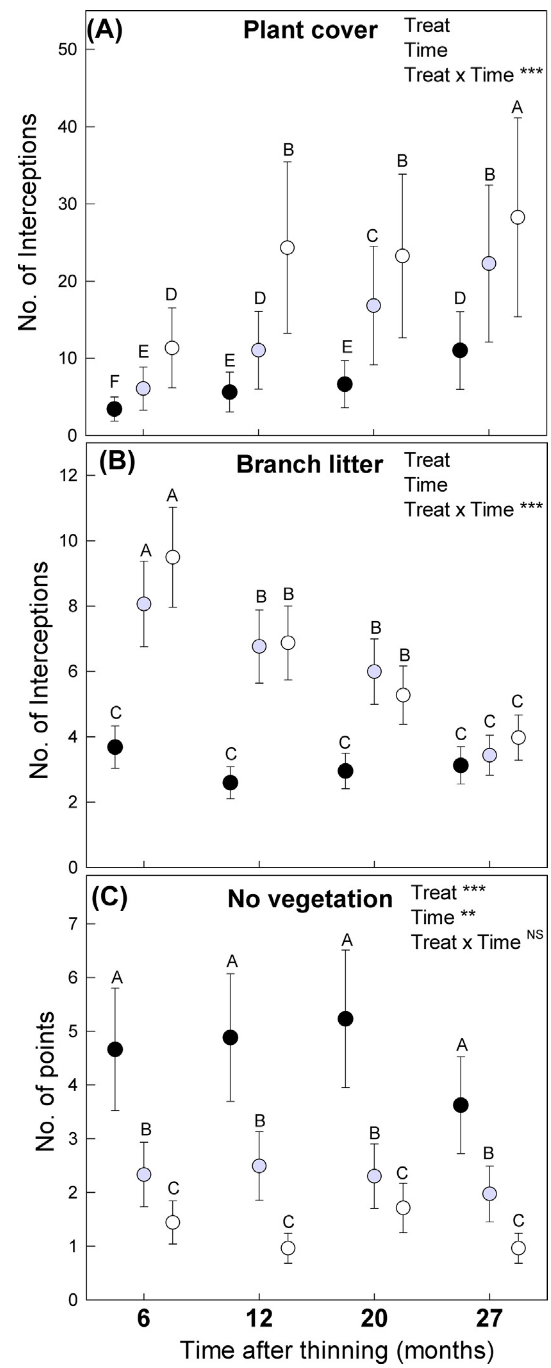

Fig. 4. Understory cover measured as number of points intercepted by plants (A), and fallen branches (B), and points without interceptions (C) in thinning (T30 ◯ and T50 ○) and control plots (●) at 6, 12, 20 and 27 months after thinning. Values are means ± one SE. Different letters indicate significant interactions or treatment main effects ($^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

There were no differences in life form cover between plots before thinning, except for perennial herbs and light-demanding trees. Perennial herbs had greater cover in T50 before thinning, but were no responsive to thinning (Fig. 5H). Light-demanding trees species reached the highest coverage in T50 six months after thinning, despite that his initial pre-thinning values were significantly higher in T30 (Figs. 5E, S1). Understory vegetation was dominated by creeping herbs, graminoids, vines and ferns. Cover of creeping herbs and vines was greater in thinning than in control plots in all measurement times after thinning (Fig. 5). Graminoids and ferns were also responsive to thinning with different patterns. Graminoids increased in T50 in two measurement periods after thinning, coincident with the growing season (Fig. 5B). The ferns cover was greater in thinning plots but increased in all plots with time, being the dominant life form in the control plots (Fig. 5D). Light-demanding trees increased in the thinning treatments but his contribution in understory cover is low (Fig. 5E). Woody bamboos and annual herbs appeared in low frequency.

The principal component analysis based on Braun-Blanquet measures was consistent with results obtained by the point

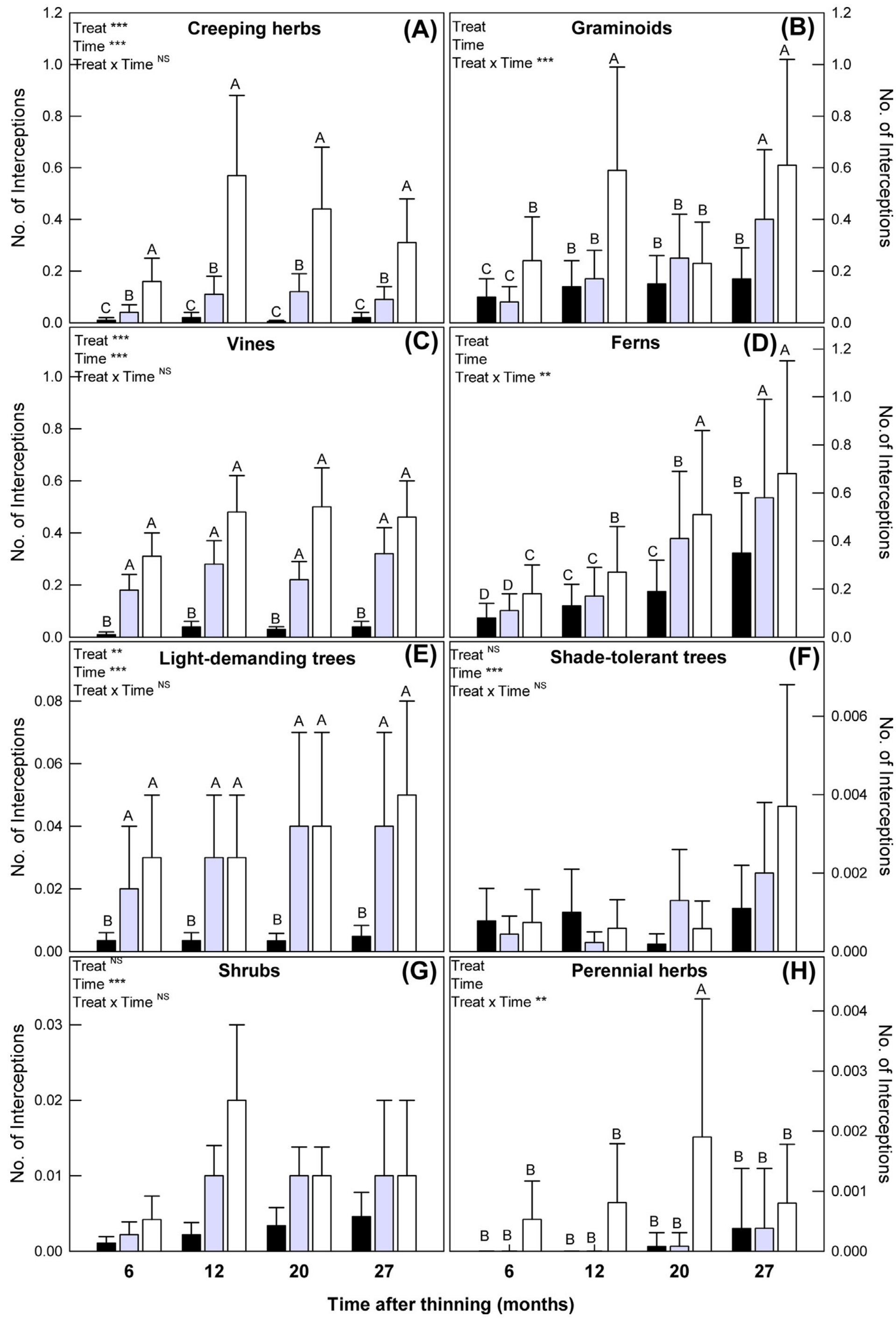

Fig. 5. Cover of life form groups estimated as number of interceptions in thinning (T30 and T50) and control ( ) plots at 6, 12, 20 and 27 months after thinning. Values are means ± one SE. Different letters indicate significant differences on interaction or main effect of treatment ($^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$). Main time effect is not shown.

interception method illustrating compositional differences between thinned and control plots (Fig. 6). The first and second principal component axes accounted for 83% and 67% of the variation in life forms and species, respectively (Figs. 6 and 7). Assemblage patterns of life forms and species in the ordination space were most correlated with time (PC1) and thinning treatments (PC2). Life forms and species composition were similar before thinning as indicated by their proximity (Squares in Figs. 6 and 7). Life forms with greater contribution to the ordination of the plots both due to time and treatments were ferns, vines, graminoids, creeping herbs, and light-demanding trees. The negative loading of ferns and the positive one of creeping herbs contributed to separate control plots from thinning plots along the PC2 axis. Life forms that drove changes in thinning plots over time were vines and creeping herbs, while shift in control plots were mainly explained by ferns and graminoids.

3.4. Species richness and composition

There were differences in mean species richness between main effect of treatment; i.e., 17, 14, and 11 species in T50, T30 and control, respectively (Table 3). Richness increased with time mainly 12 and 27 months after thinning.

Abundance for tree individual's <50 cm in height increased almost four-fold in control plots, whereas in thinning plots increased slightly (Fig. 8A). Abundance for trees ⩾50 cm in height in thinning plots was 40% higher than in control plots (Fig. 8B). Recruitment was dominated by few species (e.g., *Nectandra megapotamica* (Spreng.) Mez and *Prunus subcoriacea* (Chodat & Hassl.) Koehne).

There were significant differences in mean height between treatments for individual's <50 cm in height at all times measured (Fig. 8C). Also, thinning significantly increased tree height compared to control treatment for individuals ⩾50 cm in height. In most measurements the heights reached in T30 were higher than in T50 (Fig. 8D).

4. Discussion

Forest plantations can sustain high levels of biodiversity (Keenan et al., 1997) particularly when they are established in lands originally covered by forests (Corbelli et al., 2015; Filloy et al., 2010). Forest management practices such as thinning offer the opportunity of increasing diversity of vascular plant species and other organisms (Ares et al., 2010; Bauhus and Schmerbeck, 2010; Huang et al., 2014). Understory species diversity and plant cover can greatly increase after thinning, thus contributing to maintaining functional and structural characteristics of forest ecosystems (Neill and Puettmann, 2013). Thinning effects on the understory of monoculture plantations has been investigated mostly in temperate regions (e.g. Ares et al., 2010; He and Barclay, 2000; Nagai and Yoshida, 2006; Papanastis et al., 1995), with fewer studies in subtropical environments. In this study, thinning contributed to a rapid development of a profuse understory of loblolly pine plantations in subtropical Argentina.

4.1. Environmental conditions

Thinning increased canopy openness (CO) in the short term, although no differences were found between thinning intensities. In control plots (CO) decreased at the beginning of the experiment due to tree growth. Decreased differences in (CO) between thinning and control plots one year after thinning were consistent with other studies (Seiwa et al., 2012), probably because of crown size increase in thinning plots and self-thinning in control plots. Indeed, tree mortality was more than eight-fold on control plots than in the thinning treatments. Also, at the beginning of the experiment hemispherical photos were taken above the height of the understory in all the treatments, while at the end of the experiment in some cases, particularly in the R50 plots, the pictures were taken below the understory, which probably contributed to a reduction in CO in that treatment compared to unthinned plots. Despite these apparent low values of CO (but see Liu et al., 2005), sound differences were observed between treatments. In a study carried out

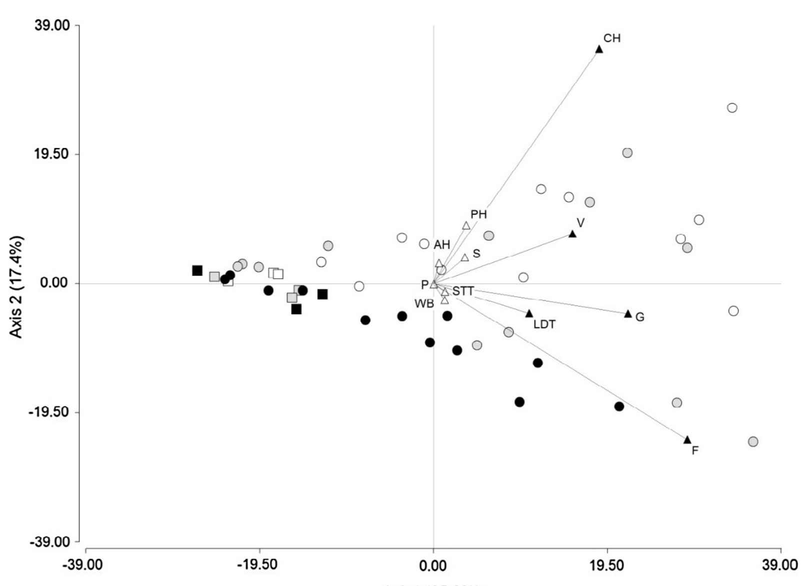

Fig. 6. Principal component analysis of life forms inT50 (○), T30 (◉) and Control (●). Points correspond to centroids of all quadrats in each treatment at 6, 12, 20 and 27 months after thinning. Pre-thinning data were included in the analysis (■, ▣, □). Life forms (▲, △) are: shrubs (S), palms (P), vines (V), ferns (F), graminoids (G), woody bamboos (WB), perennial herbs (PH), annual herbs (AH), creeping herbs (CH), light demanding trees (LDT) and shade tolerant trees (STT). Cophenetic correlation coefficient = 0.99. Life forms with a loading >|0.3| and (P < 0.05) are shown with black triangles while the others are represented with white triangles. Pearson correlations are shown in Table S2.

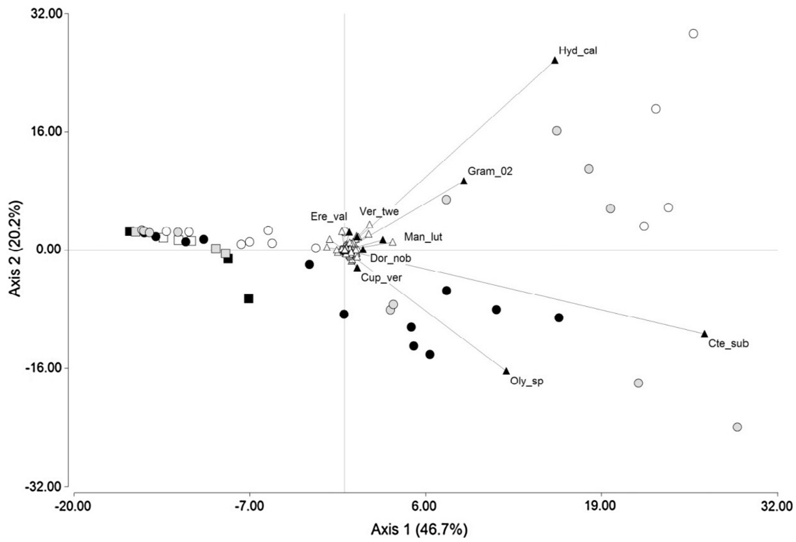

Fig. 7. Principal component analysis of species abundance in T50 (○), T30 (●) and Control (●). Points correspond to centroids of all quadrats in each treatment at 6, 12, 20 and 27 months after thinning. Pre-thinning data were also included in the analysis (■, ■, □). Principal species are: Hyd_cal (*Hydrocotyle callicephala* Cham.), Sp_02 (Poaceae), Cte_sub/The_sca (*Ctenitis submarginalis* (Langsd. & Fisch.) Ching/*Thelypteris scabra* (C. Presl) Lellinger), Oly_spp (*Olyra spp*), Ere_val (*Erechtites valerianifolius* (Link ex Spreng.) Less. ex DC. f. *valerianifolius*), Ver__twe (*Vernonanthura tweedieana* (Baker) H. Rob.), Man_lut (*Manettia luteo-rubra* (Vell.) Benth.), Dor_nob (*Doryopteris nobilis* (T. Moore) C. Chr.) and Cup_ver (*Cupania vernalis* Cambess.). Cophenetic correlation coefficient t = 0.97. Species with loading >|0.2| and P < 0.05 are shown with black triangles while the others are represented with white triangles. Pearson correlations are shown in Table S3.

Table 3
Mean vascular plant richness estimated in 15 × 15 m subplots in thinning (T30, T50) and control plots 6, 12, 20 and 27 months after imposing the treatments. Values are means ± one SE. Different letters indicate significant differences on main effects of treatments and time ($^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

Treatment	Richness***	Time (months)	Richness***
Control	11 ± 2 C	6	11 ± 2 C
T30	14 ± 3 B	12	15 ± 3 A
T50	17 ± 3 A	20	13 ± 2 B
		27	16 ± 3 A

in a temperate forest no differences in CO were observed in thinned vs unthinned plots (Thomas et al., 1999). Our study system revealed a notable heterogeneity in thinning plots, which is not reflected by a relatively low mean value of CO or SR. There were microsites receiving more than 30% of solar radiation in the more sever thinning treatments which are values similar to the ones found in small to medium canopy gaps in the native forest in Northeastern Argentina (Campanello et al., 2007).

Significant changes were found on air temperatures between thinning and control plots. In addition, temperature was higher than that observed in native forest strips like in previous studies (Campanello et al., 2007). Increased medium and maximum temperatures could negatively affect the development of vegetation through combined effects on physiological processes such as photosynthesis and increased water deficit, particularly for slow-growing and shade-tolerant species (Campanello et al., 2008). Higher temperatures in thinning plots have been reported to have significant positive effects on emergence of light-demanding species (Wetzel and Burgess, 2001; Zhu et al., 2003). Consistent with other studies (e.g., Ares et al., 2010; Liu et al., 2005), relative abundance and cover of several light-demanding trees and clonal species increased, particularly after severe thinning. Therefore, successive thinning might lead to over-dominance of the understory by fast-growing species and life-forms with clonal reproduction such as vines, creeping herbs and grasses.

The lower soil water content and higher bulk density in the pine plantation compared to native forest support the idea that less water is available for understory plants in the pine stands. The level of plant's water stress was not determined, but it may be relevant particularly in second or third-rotation plantations in which bulk density is probably higher because of soil compaction. Although there is disagreement about the effect of thinning on soil compaction (Zhang et al., 2016) the effect on soil water content was also more pronounced in the severe thinning than in the other plots probably because more evapotranspiration caused by changes in soil conditions and larger trees (Breda et al., 1995). A direct relationship between bole diameter and xylem area exists in loblolly pine leading to increased water use with tree size (Rodriguez, 2015). Indeed, more water consumption was observed in the severe thinning than in control plots two years after thinning (Campanello, unpublished data). The more abundant understory vegetation may have also contributed to decreased soil water content in thinning plots. Forest floor retention is essential to conserve soil water as demonstrated by lower values after needle litter removal.

Even though the spring and summer soil water content values were obtained after a moderate dry spell, differences in thinning and control plots were only observed in summer. At the end of the growing season (March) soil moisture may have been lower due to the increased evaporative demand, as a result of very high temperatures during summer (December to March), and because a higher vegetation cover and greater tree bole diameter than in October (beginning of the growing season).

4.2. Understory vegetation

In this study, thinning increased understory vegetation cover in agreement with other studies (Ares et al., 2010; Bataineh et al., 2014). Understory plant development can increase rapidly (Weng et al., 2007) instead of showing a phase lag (Alaback and Herman, 1988). Plant cover increased more than doubled one year after imposing the severe thinning regime. In moderate thinning, the effect on cover was more gradual than in the severe thinning. The small increase in understory cover in the unthinned treatment during the second year was probably related to increased solar radiation reaching the forest understory because of tree mortality.

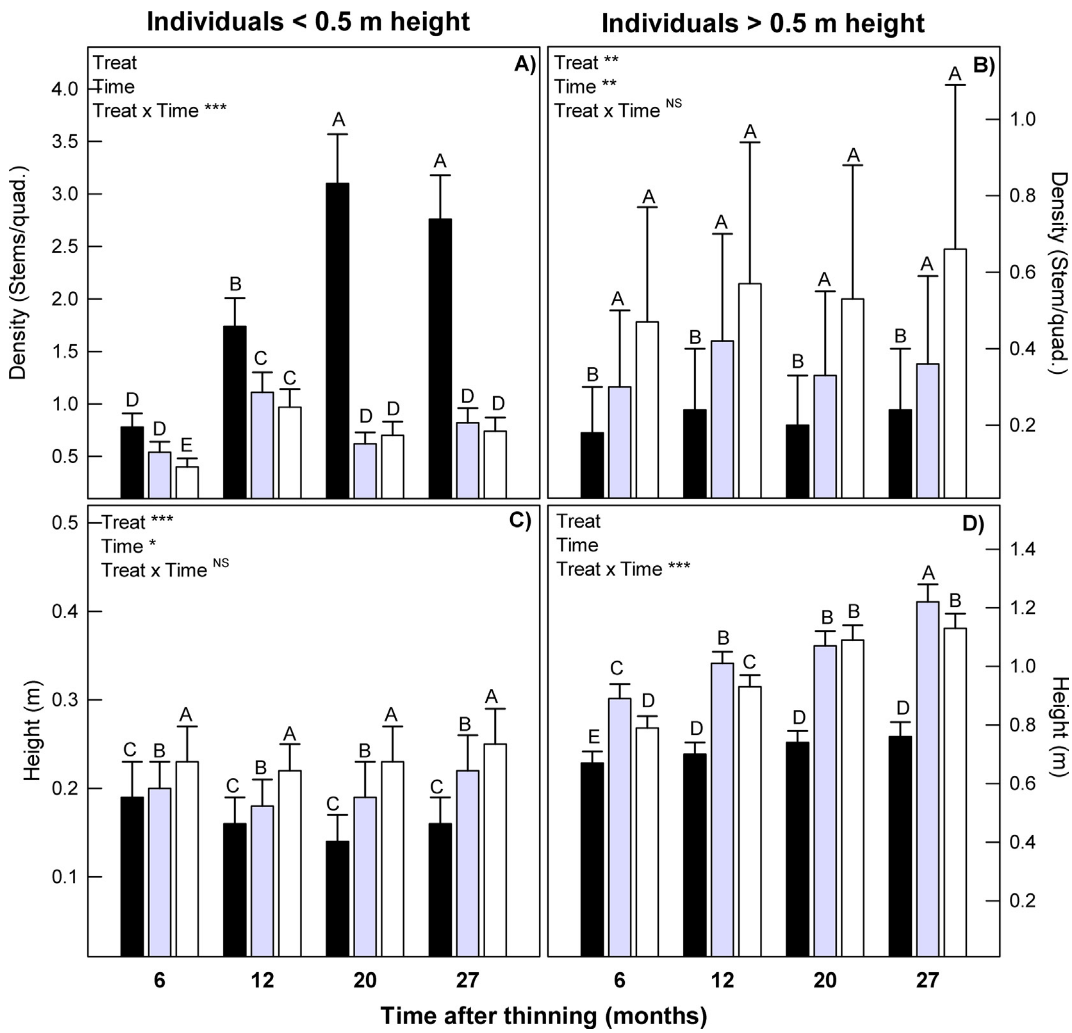

Fig. 8. Trees density (A and B) and mean height (C and D) estimate in 2 × 2 m quadrate at two categories: trees <0.5 m and >0.5 m tall, in thinning (T30 and T50) and control () treatments at 6, 12, 20 and 27 months after thinning. Values are means ± one SE. Different letters indicate significant differences on interaction or main effect of treatment ($^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

Consistent with the rapid increase in vegetation cover after thinning, most new species established the first year after the treatments were applied. The slight decrease in species richness and cover 20 months after thinning can be attributed to the loss of annual plants (i.e., *Erechtites valerianifolius* (Link ex Spreng.) Less. ex DC. *f. valerianifolius*) and shedding of leaves during the coldest season that may have decreased detectability. As expected, species richness was higher in thinning than in control plots (Cole et al., 2008). We hypothesized that the high-density thinning would lead to a rapid colonization of few dominant species potentially preventing other species from colonizing the forest understory. On the contrary, higher species richness was observed in the severe thinning compared to the moderate thinning. Canopy openness increase with thinning did not seem to be strong enough to promote the invasion of light-demanding species. Furthermore, pine growth response to thinning was high with increments in mean diameter of 2 cm per year in the severe treatment, and led to a rapid decline of solar radiation reaching the understory. Severe thinning may have a higher effect when applied later in the rotation cycle of pine plantations and much lower final tree densities are reached (i.e., between 200 and 300 trees per hectare).

Potentially invasive clonal species including graminoids, creeping herbs and vines were the most abundant life-forms and the most responsive to thinning. Vines and creeping herbs increased greatly after thinning compared to control, while creeping herbs also showed differences between thinning intensities. The decrease in creeping herbs cover at the last sampling time could be attributed to the reduction in canopy openness over time. Fern cover increased with time but at a considerably slower rate in low light environments than in openings; however, in control plots it was greater than for the other plant groups. Some fern species are known to have detrimental allelopathic effects on other plants (Fisher, 1980; Walker, 1994). Plot ordination based on species composition and life-form presented a similar pattern because few species led the vegetation response. The low loading scores of those species is because of the high species richness found in the forest understory (160 species). Life-forms were represented by small groups of dominant species (e.g., ferns were mainly represented by *Ctenitis submarginalis* (Langsd. & Fisch.) Ching and *Thelypteris scabra* (C. Presl) Lellinger).

Life-forms showed a disparate response to thinning. Woody species such shrubs and light-demanding and shade-tolerant trees contributed slightly to vegetation cover. Particularly shrubs and shade-tolerant trees did not respond to thinning treatments during the first year. However shrubs showed a greater tendency in thinning plots and shade-tolerant trees increased in thinning plots but after two years, this could be because of a late response to treatment. This trend was not observed in control plots. Cover of light-demanding tree species increased after thinning; although no significant differences were found between thinning intensities probably because of no differences in canopy openness between treatments. These scarcely represented groups in this study may contribute disproportionally to certain ecosystem functions: e.g., shrubs that promotes litter decomposition (Qiao et al., 2014) or trees that affect mycorrhizal community composition (Nantel and Neumann, 1992).

The higher density of tree's individuals <50 cm height in control plots compared to thinning plots could indicate more favorable conditions for germination such as lower air temperatures, greater soil water availability and lower soil compaction. It was possible, however, that these individuals did not grow fast enough to move up to a larger size category. On the other hand, thinning increased densities of individual's ⩾50 cm and decreased that of individuals <50 cm. Indeed, height of individual's ⩾50 cm increased over time in thinning plots while no response was observed in control plots. The increase in individual density and height in thinning treatments may be caused by increased solar radiation allowing seedling tree's development (Zhu et al., 2003).

4.3. Litter removal

Plant detritus ground cover protects soil from erosion, increments aeration, regulates temperature, and increases soil organic content (Chapman et al., 2006). Litter biomass was greater in high thinning than in the others treatments (Trentini, unpublished data) and this situation followed by increased understory plant cover can positively affect soil properties. However, litter accumulation can be detrimental to seed germination and plant establishment especially for tree species with small seed size (Messaoud and Houle, 2006; Barbier et al., 2008). In this study, no effect on understory vegetation cover of any life-form or species richness was found after removing litter in the severe thinning treatment. This was probably because most understory species established by clonal reproduction.

Branch ground cover was more than twice as high in thinning compared to control plots, and slightly higher in the severe thinning treatments than in moderate thinning. However, branch cover decreased over time reaching values similar to control plots after two years, probably because of high rates of litter decomposition in subtropical region (Yang et al., 2004). Also the high proportion of recalcitrant needle litter and high moisture levels could generate a favorable environment for the development of lignin degrading fungi (e.g., white rot) (Humphrey et al., 2000) that could be responsible for the rapid degradation of wood detritus.

5. Conclusions

Management strategies such as thinning appear valuable to promote native understory vegetation, and improve wildlife habitat (Lindenmayer and Hobbs, 2004), which in turn results in a positive feedback on understory regeneration (Roldan and Simonetti, 2001). All this changes in understory contribute to faster litter and nutrient turnover and thus tend to enhance soil productivity in the long term (Elliott et al., 2015). Although thinning can induced soil compaction and reduced soil water content as shown in this study, with potential detrimental effects on soil biota. This impact could increase after repeated thinning events.

In pine plantations in Misiones, rotation cycles are short (i.e., 17 years) and time is probably not sufficient for some life forms such as shade-tolerant species to get established, considering also that forest operations tend to damage understory vegetation. While the benefits were seen in first thinning understory vegetation, successive thinning events are likely to favor fast-growing species. Unthinned plots exhibited low vegetation cover and species richness. Thus, the contribution of high density plantations, aimed to generate large volumes of low quality wood for pulp production, is very limited for the maintenance of biodiversity and related ecosystem functions. The negative effects of thinning on some soil characteristics can be reduced by adopting low-impact operational practices. In sum, thinning can be recommended for restoring ecological functions. Forest management strategies could also involve initial stand lower densities and fewer thinning interventions.

Acknowledgments

This study was funded by the UCAR (Unidad para el Cambio Rural, Argentina) and MAGyP (Ministerio de Agricultura, Ganadería y Pesca, Argentina) through projects PIA 10101 and BIO-27. We would like to thank the forest company Pindo SA and Hugo Reis for support and permission to conduct the whole experiment on their plantations. We would also like to thank Oscar Lezcano for all the logistic support and field work, this project would not have been possible without him, and Analía Bardelás, Debora di Francescantonio, Diego Gomez Pamies, Adela Panizza, Laureano Oliva Carrasco, Marcelo Kostlin, Silvia Zaninovich and Marcio Antunez, for field and laboratory assistance.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.10.040.

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