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Invasion of *Pinus halepensis* Mill. following a wildfire in an Argentine grassland nature reserve

Sergio M. Zalba^{a,*}, Yannina A. Cuevas^a, Roberto M. Boó^b

^aGEKKO, Grupo de Estudios en Conservación y Manejo, Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur (UNS), San Juan 670 (8 000), Bahía Blanca, Argentina

^bDepartamento de Agronomía UNS, Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, Centro de Recursos Naturales Renovables de la Zona Semiárida (CERZOS), Argentina

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Abstract

The Ernesto Tornquist nature reserve is a relict of native Pampas vegetation in Argentina. Alien trees were introduced to the reserve in the 1950s, mainly to “improve” the natural landscape, resulting in the arrival of a totally new life form. In 1987, a fire affected an area planted with *Pinus halepensis* resulting in its massive expansion. In 1999, we removed trees from 17 circular plots of 10 m diameter placed systematically within the area that was colonized after the fire. Trunks were cut 20 cm from the ground and growth rings were counted. We studied the age structure of the population in order to reconstruct the colonizing events after the fire. We found that recruitment occurred throughout this period, except in the three years after the disturbance. We suggest that this delay in recruitment might be caused by low seedling survival under water stress conditions due to low rainfall, combined with scarce vegetation cover after fire. This could have been associated with an initial reduction in propagule pressure due to the scarcity of surviving trees in the vicinity and with the fact that fire occurred after the peak of seed release, during an extremely dry summer, probably killing a great number of seeds that were already in the soil. In the following years, recruitment was probably aided by pioneer trees and later by seeds shed from established pines. Alien trees had been allowed to reach maturity due to wildfire prevention and control in the years preceding the fire and the accumulated dry matter resulted in increased fire intensity that reduced the ability of grasses to re-sprout. As a consequence, the invasion window that allowed the expansion of pines remained open for at least 12 years.

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Keywords: Age structure; Conservation; Disturbance; Invasion window; Invasive alien species

1. Introduction

Biological invasions are among the most important human-driven agents of change in natural environments around the world, and are usually associated with significant impacts on economy, culture and biodiversity (Baskin, 2002; Williamson, 1996). Historically human activities have caused the accidental or planned dispersal of many species beyond their original distribution ranges and this process is presently at its highest expression. According to Williamson (1996) only a small percentage of species introduced into a

new area are able to establish self-sustaining populations, and only a small number of them become invasive. Nevertheless, the probability of invasion success increases significantly according to three main factors: previous selection of species ecologically suited to the new location, propagule pressure and the degree of “human assistance” the species receives during the immediate post-introduction phase, when it is especially susceptible to environmental and demographic stochasticity. Forestry species have a particularly high frequency of introduction and huge efforts are directed towards getting them acclimatized to new localities. They have been introduced for a variety of purposes including firewood, food production, timber, land stabilization, wind-breaks or for “improving” the landscape (Mack et al., 2000; Richardson, 1998; Richardson and Bond, 1991).

*Corresponding author. Tel.: +54 291 4595100x2420; fax: +54 291 4595130.

E-mail address: szalba@criba.edu.ar (S.M. Zalba).

Tree species, such as pines and eucalypts, have been introduced all over the world, covering millions of hectares. Eucalypts have shown poor invasive potential, but the genus *Pinus* includes some of the species with the greatest invasive potential. Species such as *P. radiata*, *P. elliotti*, *P. halepensis*, *P. patula* and *P. pinaster* have invaded extensive regions in Argentina, Australia, Brazil, Chile, Colombia, New Zealand, South Africa, Uruguay and Venezuela (GISP, 2005; Richardson and Rejmánek, 2004). They have modified huge areas of grassland, shrubland and woodland, replacing dominant life forms, changing structural diversity and altering the frequency and intensity of fires (Chilvers and Burdon, 1983; Macdonald and Jarman, 1985; Richardson and Bond, 1991). Three species of pines, *P. radiata*, *P. halepensis*, and *P. pinaster* have been cited as aggressive invaders in Argentina (Inbiar, 2005; Simberloff et al., 2002; Zalba and Villamil, 2002) and the first two are considered as major threats to biodiversity conservation in the last relicts of native grassland in the Pampas phytogeographic province (Zalba, 2000).

The ecological features that increase the ability of serotinous pines to colonize and invade new areas are related to their life-trait attributes (Rejmánek and Richardson, 1996). They are self-compatible, rapidly maturing plants that produce a large quantity of small, light, winged, wind-dispersed seeds (Cronk and Fuller, 1995; Richardson et al., 1994). Their cones remain closed for long periods, thus maintaining a persistent canopy seed bank (Daskalidou and Thanos, 1996; Izhaki et al., 2000; Thanos and Daskalidou, 2000). Fire promotes the opening of serotinous cones and favours seedling establishment due to the addition of nutrients to the soil and the elimination of vegetation cover (Rejmánek, 1999; Rejmánek and Richardson, 1996; Thanos, 1999). Therefore, fire is a key factor for the establishment of spontaneous populations of serotinous pines. Knowledge of the relationship between the alien invasive species and this disturbance constitutes a powerful tool for managing the invasion problem. *P. halepensis* is well known as a naturalized or invasive species in Australia, Israel, New Zealand, South Africa and USA (Richardson and Higgins, 1998; Richardson and Rejmánek, 2004), but its invasion dynamics have not been studied in any part of South America. In this study, we analyse the age structure of an Aleppo pine population that is invading natural grassland in the Argentine Pampas in order to determine the effect of fire on its recruitment. We also evaluate whether fire is responsible for opening an invasion window that favours the advance of the alien species.

1.1. Study area

The work was carried out in a *P. halepensis* stand located on the south-western slopes of the Ventania mountains, in the Ernesto Tornquist Provincial Park, Buenos Aires province, Argentina (Fig. 1). The Ventania mountains are found from 38°10'S to 62°8'W in a general NW–SE direction, and they include the highest peaks of the Pampas

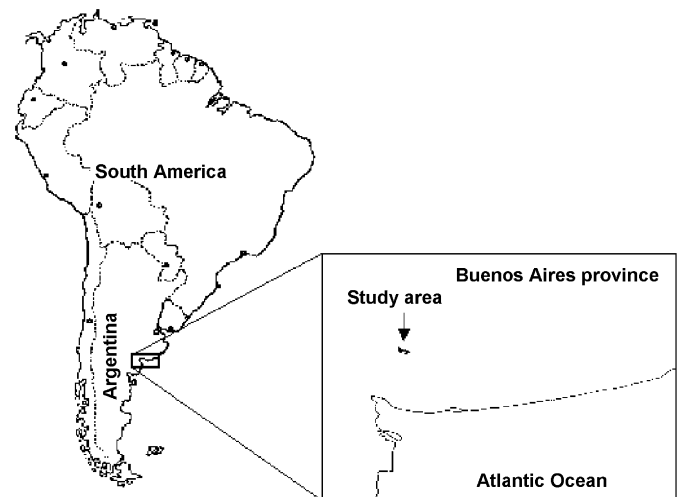


Fig. 1. Location of the study area. Ernesto Tornquist Provincial Park includes part of a mid-height mountain range in the south of Buenos Aires province, Argentina (38°04'S, 61°58'W).

region, which barely exceed 1200 m above sea level (Kristensen and Frangi, 1995).

The climate is temperate, with a mean annual temperature of 14.6 °C. Average annual rainfall ranges from 600 to 800 mm, concentrated in the spring and part of summer (Frangi and Bottino, 1995). The region belongs to the Southern District of the Pampas Phytogeographic Region, where grass steppe is the dominant vegetation (Cabrera, 1976) and *Stipa*, *Piptochaetium*, *Festuca* and *Briza* are among the most common grass genera. There are also some shrub communities mainly dominated by *Eupatorium buniifolium*, *Discaria longispina* and *Geoffroea decorticans* (Kristensen and Frangi, 1995).

Ernesto Tornquist Provincial Park is one of the last relicts of native vegetation in the Pampas region (Bertonatti and Corcuera, 2000; Bilenca and Miñarro, 2004) and has an area of ca. 6700 ha. More than 50% of the vascular flora belonging to this ecosystem is found in the reserve, including 37 endemic taxa (Long and Grassini, 1997), which highlights the role of this park as the most valuable unit for biodiversity conservation in the region as a whole (Kristensen and Frangi, 1995).

The reserve is undergoing severe invasion by Aleppo pine. The species occurs in a high priority area for conservation, causing significant reductions in native plant species diversity and richness, and allowing the introduction of other alien plants and the establishment of opportunistic bird species (Zalba, 1994, 2001). This species was originally planted in the park in the 1950s, with trees clustered in small plantations and also scattered along trails and roadsides. Data from aerial photographs 1:10 000 revealed that pines covered an area of ca. 10 ha in 1981 (Zalba 1994). In January 1987, a fire affected 80% of the area covered by pines. Unfortunately, there are no specific records about the extent of the fire or its intensity, or the percentage of trees that were killed by fire. We can infer,

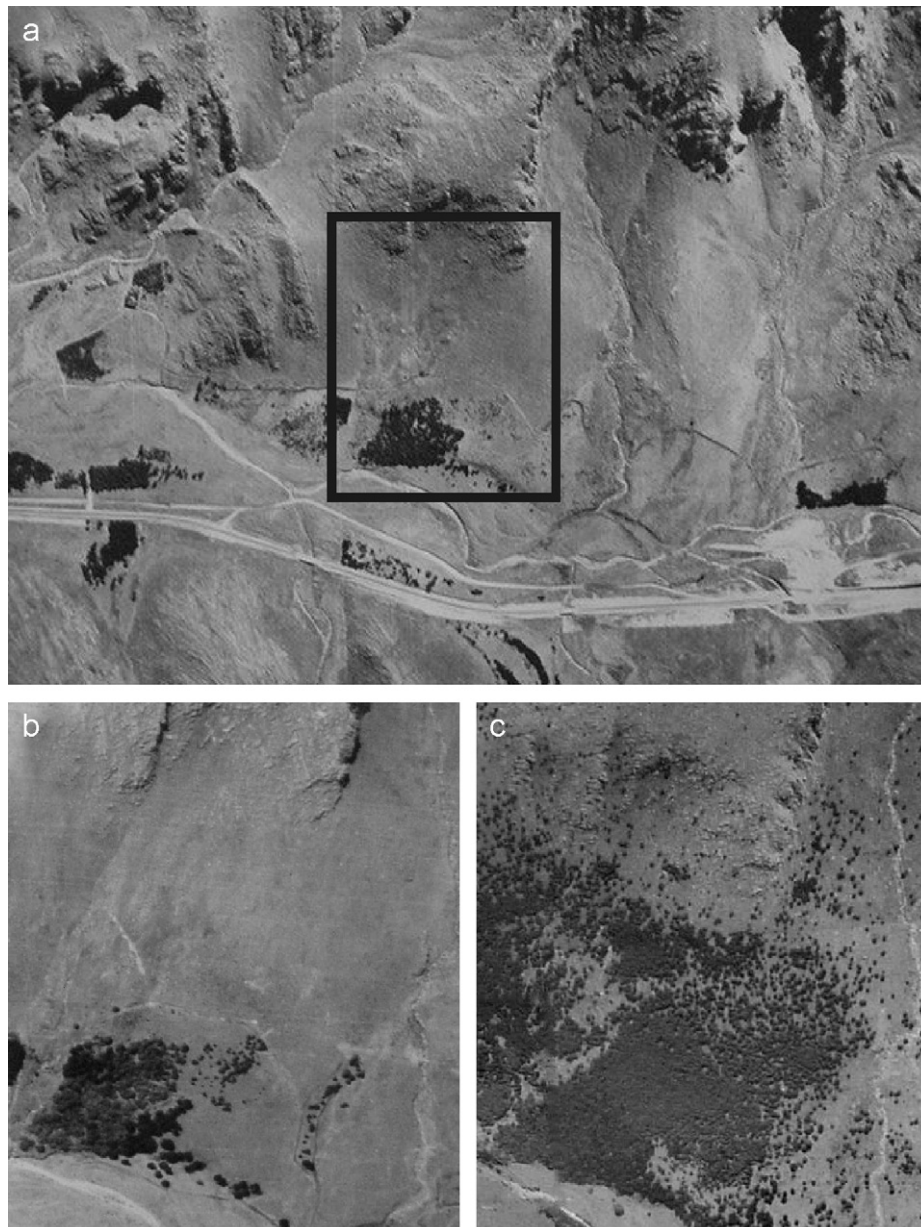


Fig. 2. Expansion of Aleppo pines in Ernesto Tornquist Provincial Park: (a) 1967 (scale 1:10 000); (b) 1981; and (c) 2003 (scale 1:6000).

from interviews with people that lived in the area at the time of the fire and also by considering the age of the oldest trees in this sector, that fire killed most of the pines in the area directly affected, leaving unburnt clusters at distances ranging from 250 to 400 m from the burnt area. A twenty-fold increase in the area of occupancy of *P. halepensis* was recorded following this fire (Zalba, 1994) (Fig. 2).

2. Materials and methods

In June 1999, 17 circular plots of 10 m diameter were established at two different altitudes (500 and 700 m above sea level) in a dense stand of Aleppo pine, as part of a control strategy implemented in the reserve to restore natural environments invaded by pines. Aerial photo-

graphs showed that the area under study was devoid of trees before the 1987 fire, and this was confirmed by the lack of trees older than 12 years in this site. All the trees inside these plots were cut down. Pines with trunk diameters of more than 1 cm were cut with hand and chain saws 20 cm above ground level, while the smaller ones were pulled by hand. The number of pines taken from each plot was recorded, the diameters of cut trunks measured, and the number of growth rings counted. For the smaller trees, the number of growth rings recorded in the field was confirmed by looking at cross-sections dyed with safranin under the microscope. In the case of larger trees, growth rings were counted in the field, and trunks were treated with bleach (sodium hypochlorite) when rings were difficult to define.

The age structure of the population was inferred from data on the density of each age class and changes in recruitment were analysed taking into account the time elapsed since the fire. Age structure was evaluated in the light of information on rainfall during the main recruitment season (March–May) (Cuevas and Zalba, 2004).

Density and basal area were calculated when the trees were felled. Differences in density, basal area and mean age between pines in the sites at different altitudes were assessed by means of “*t*” tests. Linear regression analyses were used to evaluate the relationship between the diameter of the trunks at a height of 20 cm and the number of growth rings at the different altitudes. Both regression curves were compared in order to determine if there were differences in growth rates at different altitudes.

3. Results

3.1. Age structure

A total of 199 pines were felled in the 17 plots. The mean age for all measured trees was 5.16 years (SE = 0.17) and the mode was between 5 and 6 years, corresponding to trees that recruited in 1994 and 1993, respectively. As the sampling was undertaken at the time when most of the germination takes place in the region (Cuevas and Zalba, 2004) we were not able to record seedlings corresponding to the last peak of seed release (summer 1998–1999) and so the youngest plants recorded belonged to the recruitment peak of the year preceding the cut (1998). The oldest pines were 10 years old in the higher (700 m) site and 12 years old in the lower (500 m) one, coinciding in the latter case with the fire that affected the area in 1987.

The age structure of the population shows a multi-modal profile, with several peaks of recruitment during the period under consideration (1987 to 1999) (Fig. 3). One of the peaks corresponds to young trees one year old, representing 8.5% of the population, the majority of which showed

evident signs of weakness, with dry needles and branches. The other two peaks coincide with trees aged five and six years, and eight years, respectively. Only 3.7% of the studied pines (trees that were 10–12 years old at the time of felling) were recruited in the first three years after the fire. A good correlation can be seen between the density of trees of different ages and the amount of rain during the recruitment period (March–May). Rainfall during the recruitment periods corresponding to the first four years after the fire were slightly below the historical average of the area (212 mm, SE = 9.8). In addition, precipitation during the 1986–1987 summer was only one third of the average since 1915, probably determining extremely low water runoff and soil humidity at the moment of the fire.

3.2. Density, basal area and trunk diameter–age relationship

Mean pine density in 1999 was 0.55 trees/m² (SE = 0.20), with no significant differences in this variable between the 500 and 700 m sites ($t = 1.7$, $p = 0.12$). However, a great variation in density was observed within each site, especially at the lower altitude, with densities two and four times higher than the mean value for the site in the two plots located close to the border of the stand. When these two plots were excluded from the analysis, the consequent reduction in variability allowed the detection of a significantly higher density at the lower altitude (0.32 ± 0.04 plants/m²) compared to the higher one (0.21 ± 0.04 plants/m²) ($t = 2.074$, $p = 0.05$).

Mean basal area was 35.27 m²/ha (SE = 4.01), with no significant differences between altitudes ($t = 0.82$, $p = 0.425$) and there was still no difference even when the outer plots of the lower site were excluded ($t = 0.58$, $p = 0.57$).

Highly significant linear relationships were detected between trunk diameter and age (number of growth rings) for all the trees considered together and at the different altitudes separately (Fig. 4). The curves belonging to these

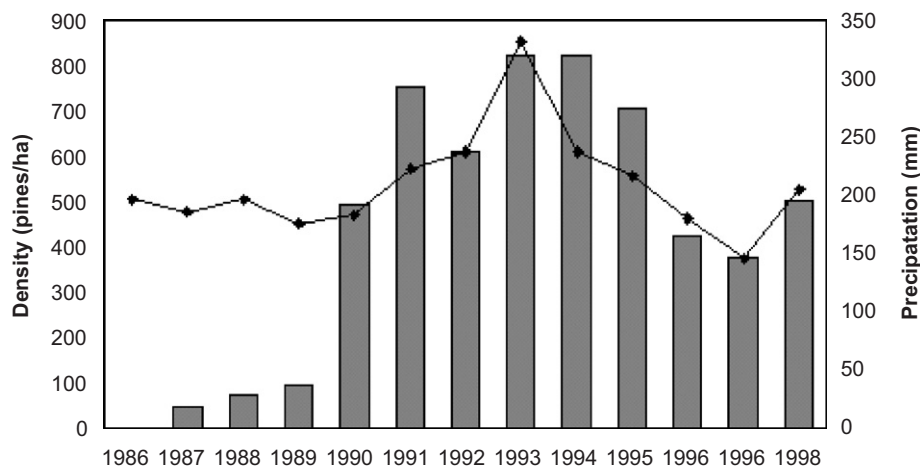


Fig. 3. Age structure in a stand of *Pinus halepensis* Mill. determined by counting growth rings on 199 trees (columns) and rainfall measured during the recruitment period (March–May) (line).

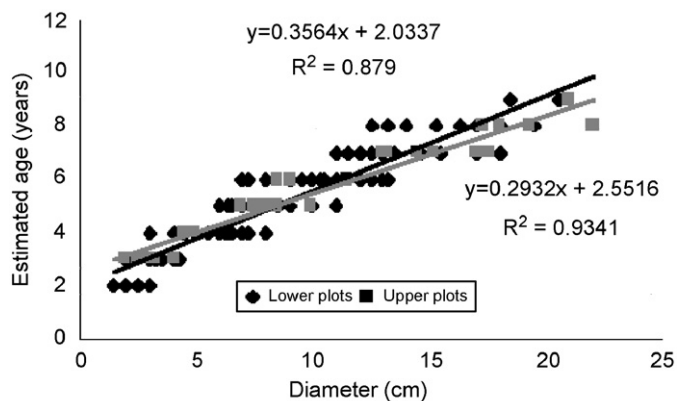


Fig. 4. Linear regression curves corresponding to pines growing at 500 (black line) and 700 (grey line) m above sea level.

two zones showed significant differences ($p = 0.0013$). The one corresponding to the higher altitude ($Y = 0.293X + 2.551$) has a smaller slope than the one at the lower altitude ($Y = 0.356X + 2.033$). This reveals significant differences in the growth rate, favouring trees at the higher altitude.

4. Discussion

The effect of disturbance on the success of invasive species has been extensively discussed (Hobbs, 1989, 1991; Lozon and MacIsaac, 1997). In particular, the relationship between disturbance and success of alien invasive plants in the Pampas grasslands of Argentina was assessed experimentally by Facelli and León (1986) and Mazía et al. (2001) working with elm (*Ulmus pumila*), privet (*Ligustrum lucidum*), and honey locust (*Gleditsia triacanthos*) and they concluded that native grasses interfere with establishment processes and that invasion only becomes possible when grasslands are strongly disturbed by vegetation clipping or topsoil disturbance. In a similar way, our results stress the importance of fire as a key factor that triggered the invasion of *P. halepensis* in the natural grassland that we studied. This situation has already been reported by many authors working in the area where this species is native (Izhaki et al., 2000; Ne'eman and Izhaki, 1998, 1999; Ne'eman et al., 1992; Thanos and Daskalidou, 2000; Thanos et al., 1996; Tsitsoni and Karagiannakidou, 2000) and also in regions where it acts as an invasive alien (Higgins and Richardson, 1998; Richardson, 1988; Richardson and Higgins, 1998; Rouget et al., 2001). Nevertheless, some interesting features arose when the age structure of pines that invaded our study area was compared with those reported elsewhere, and this could help to fill a gap in our understanding of the invasive nature of this species.

One of these features relates to the length of the recruitment period. The 1987 fire in our study site seemed to promote massive seed release and recruitment, as happens in all the other described locations, the difference

being that in our case recruitment continued for at least the next 12 years. In South Africa Aleppo pine recruitment completely stopped seven years after fire (Richardson, 1988), whereas in Greece it started after fire with a gradual decrease during the first two post-fire years (Thanos et al., 1996). Our results indicate continuous establishment during the study period which coincides with results reported by Trabaud et al. (1985) for Montpellier, France, where Aleppo pine density increased during 15 years after fire. The soil seed bank in *P. halepensis* is ephemeral (Daskalidou and Thanos, 1996; Izhaki et al., 2000; Skordilis and Thanos, 1995; Thanos 2000; Thanos et al., 1996), so the seed source for this continuous recruitment must have come from trees that remained unaffected by fire, as well as from cones in trees that were partially burnt but not killed by fire, which in turn were able to cast seeds during the first years after fire (Trabaud et al., 1985). A few years later, newly established trees must have constituted new seed sources, as suggested below.

Another interesting feature of the case reported in this study is the relative low success of cohorts recruiting in the years after fire, which determines the shape of the age structure curve. Most studies on the response to fire by *P. halepensis* report population structures that are almost even-aged, with a main peak in the first year after the disturbance (Richardson, 1988; Trabaud et al., 1985). The time of establishment of the older trees in our study (12 years) coincides with the year after the fire. Fire was probably responsible for increasing pine recruitment, either by stimulating seed release or reducing competition with grasses in the regeneration niche, or both. Nevertheless, seedling establishment in our study area was not very successful during the first three years after the fire; consequently, the main peak in the age structure curve is displaced forward. We suggest that this delay in recruitment might be caused by low germination and/or seedling survival under water stress conditions resulting from the combination of low rainfall and lack of protection due to scarce vegetation cover after fire. Thanos et al. (1996), working with a native Aleppo pine forest in Greece, pointed out high mortality, exceeding 80%, during the first three years after fire, mainly in response to competition with other plants, attacks by insects and other animals, fungal infections and water and cold stress. Also in Greece, Daskalidou and Thanos (2004) found seedling mortalities ranging from 23% to 50% of the total cohort in relation to water availability during the early establishment phase after fire and during the following drought tolerant phase when germination and early seedling development and establishment take place. Trabaud et al. (1985) also reported a high mortality of young pine classes in Montpellier, France, that was probably due to dry climatic conditions that affected seedling survival; moreover, they found two areas where there was no re-colonization during the first three and four years after fire, probably due to high mortality. Pausas et al. (2003) reported a significant decrease in seedling recruitment during the 29 months

following a fire. Survival challenges seem to be especially critical far away from the large burnt canopies, where inter- and intra-specific competition are higher, and mineral nutrition is poorer (Ne'eman et al., 1992). Trabaud et al. (1985) found that a light vegetation cover increases the survival of seedlings, especially during summer droughts when they are young. In a similar way, Pausas et al. (2004) observed that the main source of variation in post-fire regeneration was the number of branches and trunks covering the soil surface. Branches from burnt trees provide micro-climatic conditions that favour the establishment of pines, emphasising the importance of physical stress for tree establishment. As has been said, precipitation during the recruitment periods corresponding to the first four years following fire was slightly below the historical average for the area, and this, combined with the reduction in vegetation cover that followed the fire in our study site, probably increased insolation and water stress. This hypothesis coincides with results obtained in another study in the same area that showed that Aleppo pine seedlings growing in sites subjected to high defoliation levels (and so more exposed to high solar radiation and evapotranspiration) suffer from higher mortality (de Villalobos com. pers.).

Seedlings that were successfully established in the years after fire in our study site might have changed the micro-climatic conditions, increasing the probability of survival of those that germinated later. This could explain the peak in recruitment that started in the fourth year after fire. These more appropriate conditions for germination and seedling survival may have continued until the eighth year, when pine density increased to a level that generated density-dependent mortality resulting in a poorer representation of the following age classes. The observed drop in recruitment in 1992 might be the effect of unusually low precipitation (there was no rainfall in the period February–March 1992).

The following recruitment peak in 1993–1994 probably originated from the seeds produced by pines established soon after the fire. Trabaud and de Chanterac (1985) report that the juvenile period in *P. halepensis* in France lasts for more than 10 years, whereas Thanos and Daskalakou (2000) state that this period is no longer than six years in Greece where it is apparently common to see reproductive trees of 3–4 years in populations recruited after a fire (Thanos et al., 1996). This last record coincides with the reproductive behaviour of the species in our study area where seeds are released from five year old trees and 25% of the 11 year old trees have open cones (Zalba et al., 2003).

Recruitment was high again in the last two years of our study, but the majority of these new plants growing in a fully stocked population will probably die young. This negative density-dependent effect is also reflected in the lower growth rate recorded for pines growing in the lower altitude site, where tree density is significantly higher than at the higher altitude. In the study area, tree density is higher in the foot-hills, with no difference in basal area in respect to the higher altitude site, indicating that on

average pines growing higher up in the mountains are larger despite the fact that recruitment started later in this area.

A complementary hypothesis which would explain the delay in recruitment is an unexpected low propagule pressure following the fire due to the scarcity of surviving trees in the vicinity, and also because fire occurred after the peak of seed release, during an extremely dry summer, probably killing a great number of seeds already in the soil. Total rainfall during the summer after the fire in our study area (December 1987–February 1988) was only 74 mm, which is extremely low compared with a historical average of 226.05 mm ($DS = 87.74$) for the same months during the period 1915–2005, being the second lowest rainfall in 90 years. Recent discussions about the reproductive biology of *P. halepensis* include a shift from a traditional strong emphasis on fire as the major factor affecting regeneration (Ne'eman et al., 2004). The species has usually been considered as a post-fire obligate seeder, which regenerates only from seeds in the post-fire environment, nevertheless it is now proposed that most of the seeds of *P. halepensis* are produced in regular cones that release their seeds under dry weather conditions (Lavi et al., 2005; Nathan et al., 1999; Ne'eman et al., 2004). The unusually dry conditions prior to the fire probably stimulated seed release and those seeds were then killed by fire. Moreover, another factor is that the studied population was established in an area which was previously devoid of trees, at distances ranging from 250 to 400 m from the parent plants, and therefore the area was not directly under the canopy and seed rain was probably not as intense as in other studies of Aleppo pine regeneration. It is interesting to note that this delay in recruitment did not occur in later fires that affected different sectors of the study site in December 2001, December 2002 and February 2003 (Zucchini and Zalba, 2003) when an intense recruitment was observed in the first year after fire in all cases. The main differences between these more recent fires and the one in 1987 were that in the former recruitment occurred over previously invaded areas, and not before especially dry summers.

Both reduced initial recruitment and high mortality could explain the observed density that is among the lowest values reported for Aleppo pines recovering from fire (Pausas et al., 2004).

The Pampas grasslands were almost devoid of native trees before European settlement, with the exception of a few scattered individuals restricted to habitats protected from fire, and so alien trees are a totally new life form in this ecosystem. Wildfires, which were the main cause for the absence of trees in this ecosystem, are now a significant factor for serotinous pine expansion. The invasion window triggered by fire remained opened for at least 12 years and this might be a consequence of a fire suppression policy undergoing in this region. If fires occur at intervals that largely exceed the natural disturbance regimes in the area, it is possible that the accumulation of biomass results in fires of such intensity that the restoration ability of natural

grasslands is limited, increasing the period during which they remain vulnerable to invasion. In a similar way, the absence of fire could result in a reduction of the abundance of plant species capable of rapid recovery and growth after fire, which might be the clue to the resistance of grassland to alien woody plants. Prescribed fire has been used as a management tool for controlling invasive pines in South Africa, where management actions are directed to mimic the natural frequency of this disturbance, which in turn favours the restoration and conservation of natural plant communities (van Wilgen et al., 1992). Depending on management decisions, fire can be the initiator of an invasion, or a key factor in serotinous pines control if the frequency between successive fires is greater than the period that elapses between pine recruitment and maturation and if it helps to maintain healthier natural grasslands. Fires in the study area are known to increase green biomass and net primary productivity and to produce an initial increment in the frequency of annual exotic herbs (Frangi et al., 1980), with the recovery of natural grassland structure and composition in about two years (Kristensen, 1993). Aleppo pines in our area start to release seeds at the age of five years (Zalba et al., 2003), and so initial burning frequencies from two to five years could be appropriate for effectively controlling the invasion. Further research is needed to assess burning frequencies that are compatible with long-term conservation of grassland biodiversity and prevention of reinvasion by pines. A strategy of adaptive management might be the best option for assessing the optimal burning frequency, considering the urgent need to stop pines from spreading.

5. Conclusions

Fire appears to be a key factor for triggering the invasion of *P. halepensis* in natural Pampas grassland in Argentina.

Propagule pressure and/or rainfall during the germination and seedling establishment period (March–May) seem to be critical for Aleppo pine recruitment in the area.

Seedling established in the years after fire might increase the probability of survival of those plants that germinate later, by changing micro-climatic conditions.

Despite high seed production, density-dependent mortality reduces trees survival at the end of the study.

Burning can be an effective control method if applied with a frequency that permits grassland recovery but inhibits pine maturation and seed release. In the study area this might initially be between two and five years, but more research is needed to carefully evaluate the relationship between natural grassland, fire and invasive species in order to assess an optimal fire frequency to maintain the ecosystem's natural resistance.

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