Biological Invasions **4:** 55–72, 2002.

Original article

Woody plant invasion in relictual grasslands

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Received 19 September 2001; accepted in revised form 26 May 2002

Key words: alien, biological invasions, grassland, management, nature reserve

Abstract

Invasion by alien plants is one of the greatest and most widely distributed causes of man-made changes in ecosystems. One of its most conspicuous variants is the invasion of natural grasslands by exotic trees, which not only means the addition of new taxa to the native biota, but also the introduction of completely new life-forms. In Argentina, the Pampean plain is one of the most highly altered regions and its natural vegetation is only partially conserved in the coastal dunes, swampy lowlands, mountainous areas, riparian habitats, field edges, roadside verges and railway tracksides. Nevertheless, all these habitats are undergoing severe invasions by woody aliens that jeopardize their conservation. We present a preliminary survey of the alien woody plants affecting the last remaining natural grasslands of the Argentine Pampas, the history of their colonization and the phase of the invasion process in which they presently occur. We construct an index of invasion severity to evaluate which woody exotic species should be considered invasive and therefore targeted for control, and to set priorities for the application of management practices according to the seriousness of the threat posed to biodiversity conservation.

Introduction

The impact of tree invasions

Exotic species probably pose the greatest, most insidious and fastest-growing threat to global biodiversity (Williamson 1996), with alien terrestrial plants being responsible for extensive and far-reaching changes in natural ecosystems (Cronk and Fuller 1995; Higgins et al. 1999; Vitousek 1990). In particular, there are many examples of exotic trees introduced for commercial exploitation, wind protection or ornamental purposes that subsequently became noxious invaders, often in response to alterations in natural disturbance regimes, such as natural fire suppression, replacement of native herbivores and overgrazing (Calder et al. 1992; Hobbs 1991). Under certain conditions, any species of exotic tree widely planted in an alien environment may become naturalized and expand over native ecosystems (Richardson 1998). Invasions of pines, for instance, have affected enormous areas of grassland and shrubland in the southern hemisphere, changing the dominant life-forms, reducing the structural diversity and modifying vegetation patterns and nutrient cycles (Chilvers and Burdon 1983; Macdonald and Jarman 1985; Macdonald et al. 1989; Richardson et al. 1994; Richardson and Bond 1991). In the case of grasslands, the expansion of tree or shrub species generates a significant impact because it represents not only a taxonomic addition, but also the introduction of a life-form completely new to the ecosystem (Richardson 1998).

Natural grasslands are among the ecosystems that have been most disturbed by humans (Hannah et al. 1995); they have also received much less attention from the conservation point of view than other ecosystems such as the temperate and tropical forests. The problem of the expansion of alien woody plants is growing with the increase of forested areas and the maturity of plantations, which in turn produce an increase in the propagule pressure on the scarce relicts of native grasslands (Richardson 1998; Richardson et al. 1990). The magnitude of this problem requires urgent actions based on objective rankings of the alien species.

In the first part of this paper, we present a preliminary survey of the alien woody plants affecting the last remaining grasslands of the Argentine Pampas, the history of their colonization and the phase of the invasion process in which they presently occur. In the second part, we present an index of invasion severity (IS) to evaluate which woody exotic species should be considered invasive and therefore targeted for control, and to establish an order of priority for the application of management practices according to the seriousness of the threat posed to biodiversity conservation. This last section is presented as a case study for the main Pampas grassland conservation area.

Alien woody plants in Pampean grasslands of Argentina

The Pampa's region comprises ca. 468,000 km^2 of flat to moderately rolling lands in east-central Argentina. The climate is humid to sub-humid temperate, with precipitation ranging from 600 mm in the southwest to 1100 mm in the northeast (Burkart et al. 1999). Typical vegetation is the temperate grassland with a predominance of species of the genera *Stipa*, *Piptochaetium*, *Bromus*, *Aristida*, *Briza*, *Setaria*, *Melica*, *Poa*, *Paspalum* and *Eragrostis* (Cabrera 1971).

Most of the area formerly occupied by natural grassland has been highly transformed, especially by agriculture, which has led to increased erosion and intensification of agrochemical use, and urbanization (Bertonatti and Corcuera 2000; Kufner et al. 1998). This in turn has led to the almost complete disappearance of the original plant communities (Burkart et al. 1991; Cabrera 1971; León et al. 1984; Lewis et al. 1985; Soriano 1992).

The presence of cattle in the region has deeply modified the nature of the native vegetation, and the changes 'from a coarse herbage to a carpet of fine green verdure' (Darwin [1898] 1967) were readily perceived by travellers and naturalists visiting the area. Early on during the colonization of the Pampas, European species were added to the native flora, such as *Bromus hordaceus*, *Briza minor*, *Cristaria rostrata*, and *Carduus* spp. The success of these species can be attributed to the development of cattle management techniques (Parodi 1930) combined with the previous lack of herds of large-hoofed mammals in the Holocene, and the dominance of tussock grasses (Mack 1989). Probably as a consequence of this, the highest levels of diversity of alien species in Argentina are found in the Pampean region (Zuloaga et al. 1999).

One of the most conspicuous factors of landscape transformation, however, took longer to become evident: until early in the nineteenth century, trees were virtually absent from the region and shrubs formed only a minor component of the vegetation (Darwin [1898] 1967; Spegazzini 1896), to the point that the shortage of firewood was one of the main restrictions for travellers in the Pampas (Doëring and Lorentz 1916), and settlers in the region were forced to use dry thistle culms as fuel (Hudson [1918] 1963). The explanation for this lack of native trees in the Pampas has been the subject of debate among scientists, varying from those who considered the grasslands to be a response to prehispanic human settlement in the area to theories based on precipitation, soil conditions, competition by grasses or natural fires (Parodi 1942). More recent studies confirm the importance of the interference of herbaceous vegetation upon germination and establishment of woody plants and the role of propagule pressure and disturbances for the success of the invaders (Facelli and León 1986; Mazia et al. 2001; Zalba et al. 2000). The only native trees present in the interior of the Pampas before European settlement were the 'ombú' (*Phytolaca dioica*), which grew scattered throughout the grassland and the 'sauce colorado' (*Salix humboldtiana*), which was restricted to riparian areas. The establishment of the 'estancias' (the local name for ranches) was accompanied by afforestation using foreign species for timber, shade or as shelter belts; some of the most commonly planted genera include *Acacia*, *Robinia*, *Gleditsia*, *Populus*, *Melia*, and *Ailanthus*, as well as orchard trees such as peach, cherry and quince (Hudson [1918] 1963). Later on, several species of *Eucalyptus* and *Pinus* became the dominant components of woods planted by man. At the present time, the landscape of the Pampas is covered with scattered, wooded areas near urban areas, roadsides and rural dwellings.

The last relicts of the original Pampas grasslands are restricted to habitats unsuitable for agriculture (Figure 1), such as coastal dunes, swampy lowlands,

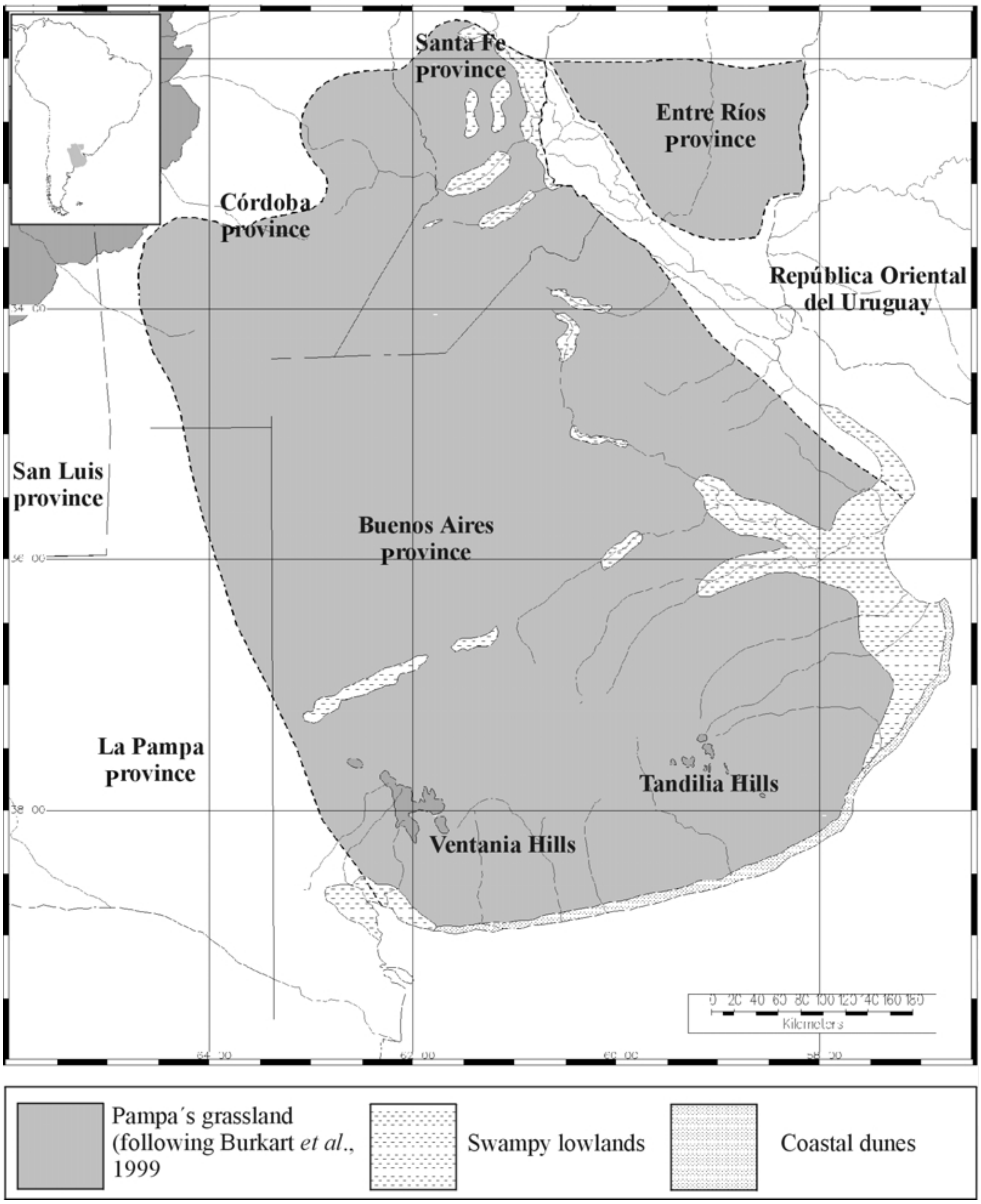

Figure 1. The Pampean region with the habitats concentrating on the last remains of natural grassland.

areas with insufficient precipitation or with rocky outcrops, riparian habitats, roadside verges and the edges of fields and railway lines (Bonaventura and Cagnoni 1995; Covas 1982; León et al. 1984; Parodi 1930). These relicts are, nevertheless, far from being protected from human influences, as they are subject to grazing by domestic cattle, in some cases for more than three centuries (Burkart et al. 1990; Ragonese 1967; Vervoorst 1967), and more recently by the spontaneous expansion of exotic trees and shrubs (Table 1).

Pampean coastal dunes, which include the most popular resort areas of the country, are located in this

Table 1. Phases of invasion (following Richardson et al. 2000b) of alien woody plants growing in remnants of Pampean grasslands.

Exotic woody plants	Grassland remnants				
	Coastal dunes	Lowlands	Mountains	Riparian habitats	Roadsides and fences
Acacia dealbata			I		
Acacia longifolia	I		I		
Acacia mearnsii			I		
Acacia melanoxylon			N		
Acer negundo			C		
Ailanthus altissima	N		N		
Amorpha fruticosa			N		
Broussonetia papyrifera				N	
Cedrus deodara			C		
Crataegus monogyna			N		
Cupressus sempervirens			N		
Cytisus monspessulanus			I	I	
Eleagnus angustifolia					
Eucalyptus camaldulensis			I	C	
Eucalyptus viminalis			I		
Gleditsia triacanthos	I	I	I	I	I
Juniperus virginianus			C	C	C
Ligustrum lucidum			I	I	I
Malus domestica			C		
Melia azedarach				I	
Morus alba				I	
Pinus halepensis			I		
Pinus pinaster	I		C		
Pinus radiata			I		
Populus alba			I	I	
Quercus robur			C		
Robinia pseudoacacia			N		
Rosa spp.			I	I	I
Rubus divaricatus			I		I
Rubus ulmifolius			I	I	I
Salix fragilis			I	I	
Salix viminalis			I	I	
Spartium junceum			I	I	
Tamarix gallica	N			I	
Ulex europaeus			N		
Ulmus pumila			N		

C represents casual alien plants (may flourish and even reproduce occasionally in the area, but do not form self-replacing populations); N, naturalized alien plants (reproduce consistently but their offspring usually remain close to parent plants) and I, invasive alien plants (spreading over a considerable area and colonizing natural or semi-natural ecosystems).

region. Historically, this has led to important afforestation projects in order to increase the touristic appeal. Some of the species most commonly used for this purpose are capable of dominating the natural vegetation and represent one of the main conservation problems faced by coastal reserves (Moschione 1992).

Lowlands and salty wetlands are scattered over different sectors of the pampean formation, associated with stream flood plains and depressions (Cappannini 1968; Faggi 1986). Numerous authors have evaluated the impact of invasive exotic woody species on the gallery forests along the lower course of the Paraná and Uruguay rivers and their prolongation into the de la Plata River coastal communities. Exotic tree species are progressively replacing the indigenous species (Chichizola 1993; Franceschi and Lewis 1990; Montaldo 1993), among which *G. triacanthos* stands out, due to its ability to extend beyond the limits of the native forest and to colonize patches of grassland that are interspersed within the wooded areas (Boffi Lissin et al. 1999; Haene 2000). It also invades wet lowland communities dominated by *Paspalum quadrifarium* in the center of the province of Buenos Aires (P. Laterra, pers. com.).

The mountainous areas of the Pampas include the systems of Ventania (Sierras de la Ventana) and Tandilia (Sierras de Tandil), reaching 1200 m and 500 m, respectively. It is perhaps in these environments where the invasion by woody species shows the highest intensity, as will be discussed later in the case study of the E. Tornquist Provincial Park. These mountainous areas were totally free of trees at the end of the nineteenth century (Spegazzini 1896), but at the present time they are populated by numerous exotic tree and shrub species (Table 1). The area also shows an increase in the abundance of native shrubs, probably in response to changes in the frequency of fires and overgrazing (Barrera 1991; Frangi 1975; Frangi and Bottino 1995).

The riparian habitats in Ventania, where originally *Salix humboldtiana* was the only tree species present, have now undergone an intense process of colonization by exotic species to such an extent that the populations of the native willow species became relictual (S. Zalba and C. Villamil, pers. obs.). Similar situations have been recorded in the mountainous ranges of southern Córdoba (Bianco et al. 1987), and in the northeastern portion of the Pampas (Ghersa and León 1999).

Roadside verges and the edges of fields and railway lines do not escape colonization by exotic species either, which, according to Ghersa and León (1999) are favored by sporadic fire events and seed dispersal by birds perching on wire fences. In Ventania, the proliferation of woody species dispersed by wild birds and mammals has been reported in close association with wire fences, forested areas and shelter belts (Zalba 2001). It seems predictable that in the near future there will be a great increase in the intensity and the extension of this process, taking into account the positive feedback stemming from interactions between populations of trees and shrubs and their dispersal agents.

At the present time, the remaining natural grasslands located in the western and southwestern sectors of the Pampas, where the advance of agriculture has not progressed due to insufficient rainfall, seem to be the only exception to this process of exotic species colonization. Nevertheless, these areas are undergoing an expansion of shrubs native to the neighboring Espinal and Monte phytogeographical regions (Bianco et al. 1987; Cano and Movia 1967; Dussart et al. 1998; León and Anderson 1983; León and Marangón 1980).

As we have shown, the advance of exotic species over the remaining natural grasslands of the Argentine Pampas is a widespread and severe process that needs the implementation of control measures. Nevertheless, due to the number of exotic species present in the area and to the variety of invasive phases in which they presently occur, it is necessary to develop rational systems that can detect those cases needing the most urgent attention. In the following section, we present a case study relating the application of such a ranking system to a grassland nature reserve.

Case study: alien trees in Ernesto Tornquist Provincial Park

Study area

The Ernesto Tornquist Provincial Park, which covers an area of approximately 6700 ha, is one of the few protected natural reserves of the Pampean region (Bertonatti and Corcuera 2000). It is located in the Sierra de la Ventana range (38° S, 61° W), and includes the highest point in the Pampas (slightly over 1100 m). The climate is temperate, with an average annual temperature of 14 °C, and the annual precipitation ranges from 500 to 800 mm (Burgos 1968).

Phytogeographically, the reserve corresponds to the Austral Pampean district (Cabrera 1976), with grass steppes as the dominant vegetation (Frangi and Bottino 1995). Due to differences among authors regarding the geographic delimitation of the Pampean province (Biani et al. 2001; Burkart et al. 1999; León and Anderson 1983), it is difficult to estimate what percentage of its plant diversity is represented within the reserve. However, if Parodi's (1947) estimates are taken into account, we can conclude that more than 50% of the Pampean vascular flora occurs within the Park (Long and Grassini 1997). The presence of 37 endemic taxa should be added to this exceptional diversity. This unusual concentration of endemisms, added to the above mentioned insufficient protection afforded to natural areas of the Pampean region, enhances the value of the Ernesto Tornquist Provincial Park as the most representative biodiversity conservation unit of the whole region.

The presence of numerous species of exotic trees and shrubs, some deliberately introduced to improve the landscape and others having entered spontaneously from neighboring areas, is one of the most conspicuous modifications of this reserve (Fiori et al. 1997; Zalba 1994).

Methods

Our study comprised all the exotic trees presently growing in discrete stands inside the reserve. We defined a stand as a planted group of trees, plus their offspring that were growing in the same clump. We studied a total of fifteen stands, one each of *Acacia dealbata*, *Cupressus sempervirens*, *E. camaldulensis* and *Ulmus pumila*; two each of *Cedrus deodara*, *E. viminalis*, *Populus alba* and *Robinia pseudoacacia*; a mixed stand of *E. camaldulensis* and *E. viminalis* and two mixed stands of *Pinus halepensis* and *P. radiata.* The stands were growing in five different habitat types: edges of streams, flooded lowlands, northeast and southwest facing slopes, and valleys to the northeast of the main hills.

Following the most accepted criteria defining invasive species (Cronk and Fuller 1995; Daehler 2001; Macdonald et al. 1989; Richardson et al. 2000b), the ranking system developed in this work was aimed at selecting, among the alien trees growing in the reserve, those able to advance over natural or semi-natural portions of the reserve and establish self-replacing populations there without any direct human intervention, using data about the area covered (AC) and the population structure of each stand. These variables were complemented with others regarding the dispersal strategy and the impact of each stand on the native flora in order to rank the seriousness of the threat posed by each invasive species stand in the reserve. Each variable was translated into an index ranging from zero (no threat) to one (maximum threat), and then combined in a final formula.

Area covered

In order to evaluate the historical expansion of each stand, we measured the area covered using aerial photographs (1 : 10,000) taken in 1967 and 1981 and a survey of oblique photographs from 1994. This information was incorporated into the GIS Camris (Palminteri 1998), where the area measurements were made.

We calculated an area index (AI) using the following formula:

$$\mathrm{AI} = \mathrm{A}/\mathrm{MA} \tag{1}$$

where AI is the area index for each stand, A the area covered by the stand at the present time, and MA the area covered by the largest tree stand at the present time. With AI reaching a maximum of 1 for the biggest stand.

We used an index of change in the area covered (AC) by each stand to compare all the stands by means of their growth rate over the period considered:

$$\mathrm{AC} = [(\mathrm{FA} - \mathrm{SA})/(\mathrm{SA} \times \mathrm{T})]/\mathrm{MC} \tag{2}$$

where AC is the index of change in the area covered by each stand, FA the area covered by each stand at the end of the period, SA the area covered by each stand at the start of the period, T the duration of the period in years, and MC the maximum area change recorded for all the studied stands. We started by calculating the numerator of the formula for each stand and then divided all of them by the maximum obtained (MC). According to this formula, AC will be zero for stands showing no growth in the period under consideration and one for the stand with the greatest increment of size per time unit. We considered the variations between 1967 and 1994, for the stands that were already present when the oldest photographs were taken; and between 1981 and 1994 for those established more recently.

Population structure

In order to assess the self-sustaining capacity of each stand, we studied their population structures, measuring the height of the smaller trees and the diameter at breast height for the larger ones. Sampling changed depending on the size of each stand. In the larger stands, we used 3 m-wide strips placed systematically and covering ca. 10% of their area, whereas we measured all the individuals up to a minimum of 200 trees in the smaller stands. In order to avoid an underestimation of the individuals belonging to the smaller size classes, which are actually more difficult to find, we developed a sub-sampling procedure comprising 20 plots of 1 m^2 in area randomly placed inside each stand. We calculated the frequency of individuals in each size class and their distribution was displayed using histograms. The stands were classified in the following three categories according to their population profiles: (a) stands apparently stable or growing, with a high proportion of young individuals and showing population curves with more or less concave or negative exponential, (b) stands with high frequencies of young trees, but with bi- or multi-modal population profiles and (c) stands in apparent decline, with very low representation of young trees (Burdon and Chilvers 1977). We ascribed a population structure index (PS) for each category, considering the function of each structure type in terms of the potential evolution of the stand in the future. The maximum value of 1 corresponded to those stands in category (a); we assigned a value of 0.5 to the stands belonging to category (b) and finally, stands included in category (c) received a score of 0. These indexes were arbitrarily ascribed for comparative means only.

Dispersal strategies

We ascribed a dispersal strategy index (DS) for wind or animal-mediated dispersal or vegetative reproduction, considering their relative importance in terms of the colonization of new sectors of the reserve. It is well known that many aggressive exotic trees and shrubs are dispersed by animals (Richardson et al. 2000a), nevertheless, we decided to assign the maximum value of dispersal index (DI) to those species with anemophilous dispersal. This decision is addressed in more detail in the discussion section and was based on the *a priori* importance of an autonomous dispersal strategy, and the presence of strong winds throughout the year in the study area. We made the distinction between plants with winged seeds ($DS = 0.50$) and those with seeds lacking specific dispersal structures, which are spread by the wind because of their small masses ($DS = 0.30$). We gave a score of 0.35 to those trees propagated by animals and, finally, a score of 0.15 to the exotic species that depend entirely on vegetative mechanisms, considering the restrictions in time and space of this last dispersal strategy. We added the corresponding scores in the case of trees showing multiple strategies with more than one dispersal mechanism. In this way, a hypothetical species with winged seeds, animal dispersal and vegetative reproduction would obtain the maximum score of 1. The DS for each dispersal strategy was arbitrarily ascribed, trying to reflect the relative importance of each one for the potential expansion of the species, and conserving the 0–1 variation range of the other indexes.

Impacts on the native flora

As a measure of the impact posed by invasive woody plants on the native flora, we evaluated the changes in plant communities associated with the presence of the tree stands, considering changes in plant species richness, the native *versus* exotic plants ratio, and the frequency of appearance of each plant species. We randomly placed twenty 1-m^2 quadrats inside each stand and in three grassland controls free from the direct effect of the trees, that were randomly chosen in each of the five habitat types colonized by the exotic species. We recorded the plant species present in each quadrat and calculated their frequency and the ratio between native and exotic species for each stand and the controls. Mean plant species richness was compared between each stand and the corresponding grassland controls with analysis of variance (Sokal and Rohlf 1981).

In order to assess an eventual effect of the alien trees facilitating the invasion of other exotic species, we calculated an index of variation in the native *versus* exotic plant species ratio for each stand with respect to grassland controls in this habitat, using the following formula:

$$\mathrm{RV} = (\mathrm{RC} - \mathrm{RS})/\mathrm{RC} \tag{3}$$

where RV is the index of change in native *versus* exotic species ratio, RC the native *versus* exotic species ratio in grassland controls and RS the native *versus* exotic species ratio in the exotic trees stand. From previous studies (Zalba 1994), we knew that the presence of trees in the area produces an increase in exotic species in the understory and so we expected the native *versus* exotic species ratio in the controls to be larger than in the exotic trees stand. In this way, RV would range between zero (for stands producing no changes in the percentages of native species) and one (for the hypothetical case of a complete disappearance of native species in association with the stand).

Using G, goodness of fit tests (Sokal and Rohlf 1981), we measured the changes in the frequency of each plant species between grassland controls and exotic trees stands. For each stand, we then calculated the proportion of species showing significant changes in their frequency or being exclusively of grasslands or of exotic stands (FC).

As a complementary measure of impact, we used data from floristic and vegetational studies conducted in the reserve (Frangi and Bottino 1995; Long and Grassini 1997) to map the potential habitats of nine endemic plant species for which conservation is a management priority within this reserve. The endemisms selected were *Grindelia ventanensis* and

Senecio ventanensis (Asteraceae), *Rorippa ventanensis* (Brassicaceae), *Festuca pampeana*, *F. ventanicola* and *Poa iridifolia* (Poaceae), *Lupinus aureonitens* (Fabaceae), *Plantago bismarckii* (Plantaginaceae) and *Polygala ventanensis* (Polygalaceae), and they were chosen considering the data availability of their habitat requirements and their distribution in the area, as well as their conservation value. We recorded how many of them overlap with the present distribution of each stand of exotic trees and calculated an overlap index (OI) using the following formula:

$$\mathrm{OI} = \mathrm{SO}/n \tag{4}$$

where OI is the index of overlap with endemic species, SO the number of overlapping endemic species for a given stand and n the total number of endemic species considered ($n = 9$ in our study). According to this formula, a stand for which there is no overlapping with the habitats of any of these endemisms will have an OI of zero, meanwhile overlapping with the habitats of all 9 species will reach the maximum value of one.

Final ranking

The scores assigned to each stand were combined in a final expression in order to obtain an index of IS that can be used as a baseline to establish control priorities:

$$\mathrm{IS} = \{[(\mathrm{AC} + \mathrm{PS})/2] * [(\mathrm{AI} + \mathrm{DS} + 2(\mathrm{RV} + \mathrm{FC} + \mathrm{OI}))/8]\}^{1/2} \tag{5}$$

where AC is the index of change in the area covered by each stand, PS the population structure index, AI the area index for each stand, DS the dispersal strategy index, RV the index of change in native *versus* exotic species ratio, FC the proportion of species showing significant changes in their frequency or being exclusive of grasslands or woods and OI the index of overlap with endemic species. The first portion of the formula $[(\mathrm{AC} + \mathrm{PS})/2]$ represents the condition for a species to be considered invasive. In this way, if an exotic tree has not increased its area in the reserve and shows a declining PS, it should not be considered truly invasive, with the index of IS becoming zero. The second portion of the formula $[(\mathrm{AI}+\mathrm{DS}+2\,(\mathrm{RV}+\mathrm{FC}+\mathrm{OI}))/8]$ completes the ranking criteria, differentially weighting the impact measures because they represent an objective index of the interference of the alien with the reserves conservation objectives. The values of the index of IS are expected to range between 0 (no invasion) and 1 (maximum severity).

Results

Area covered

The maximum value of covered area belongs to a mixed stand of *Pinus halepensis* and *P. radiata*, with an area that is five times larger than the next one in size, which is also of pines. The other stands grow in areas one, two and up to three orders of magnitude smaller (Table 2).

We recorded a great variation in the rate of spread of the different woody species, and also of different stands of the same species in the period of time considered (Table 2). Only one *Cedrus deodara* and the *Cupressus sempervirens* stands showed little reduction in their covered areas. As the condition defined in this study for invasiveness was ‘growing area’, we ascribed to them an index of change in the area covered (AC) of zero. All the remaining stands increased their area covered in the reserve, the maximum rate of spread corresponding to the same pine stand that showed the largest area inside the park (Figure 2). A lack of aerial photographs prevented making the calculations for stands no. 8 (*Pinus halepensis*) and no. 14 (*Robinia pseudoacacia*).

Population structure

The studied stands showed all three size structures considered. As an example, we included the graphs corresponding to populations of *Populus alba*, *Pinus halepensis* and *Cedrus deodara*, belonging to stands nos. 12, 10 and 3, respectively (Figure 3). The *Acacia dealbata* stand, a mixed pine stand (no. 9), and both *Populus alba* stands showed a high proportion of individuals belonging to the smaller size classes and population structures of the negative exponential type, and they were all given the maximum PS (PS = 1). The three *Eucalyptus* stands, both *Robinia pseudoacacia* stands and the *Ulmus pumila*, *Cupressus sempervirens* and mixed pine (no. 10) stands showed multi-modal population profiles, and thus we assigned a score of PS = 0.5 to all of them. Finally, one *Pinus halepensis* stand (no. 8) and both *Cedrus deodara* stands showed bell-shaped population profiles with an almost complete absence of young individuals, and so, despite a few exceptions, the trees present in each of these stands are probably the same ones that were originally planted and the corresponding PS is 0.

Table 2. Area covered by the stands included in the analysis and its variation between 1967 and 1994.

Stand	Species	Area 1967 (m^2)	Area 1981 (m^2)	Area 1994 (m^2)	AI	AC
1	*Acacia dealbata*	678	1,786	2,009	0.003	0.085
2	*Cedrus deodara*	14,355	16,303	15,628	0.024	0.004
3	*Cedrus deodara*	13,144	15,851	10,562	0.016	−0.008
4	*Cupressus sempervirens*	25,169	29,427	18,504	0.028	−0.011
5	*Eucalyptus viminalis*	[a]	14,619	15,262	0.023	0.001
6	*Eucalyptus viminalis*	[a]	1,703	2,385	0.004	0.008
7	*Eucalyptus viminalis – E. camaldulensis*	5,885	17,097	20,517	0.032	0.107
8	*Pinus halepensis*	[b]	[b]	8,741	0.013	—
9	*Pinus halepensis – P. radiata*	26,748	88,143	647,298	1	1
10	*Pinus halepensis – P. radiata*	[a]	110,131	130,600	0.202	0.004
11	*Populus alba*	1,109	3,416	4,147	0.006	0.118
12	*Populus alba*	2,308	7,874	12,701	0.020	0.194
13	*Robinia pseudoacacia*	[a]	4,742	17,458	0.027	0.056
14	*Robinia pseudoacacia*	[b]	[b]	11,621	0.018	—
15	*Ulmus pumila*	[a]	457	610	0.001	0.007

AI is the area index for each stand and AC, the index of change in the area covered by each stand.

[a] The stand was still not planted by this year; [b] no data available.

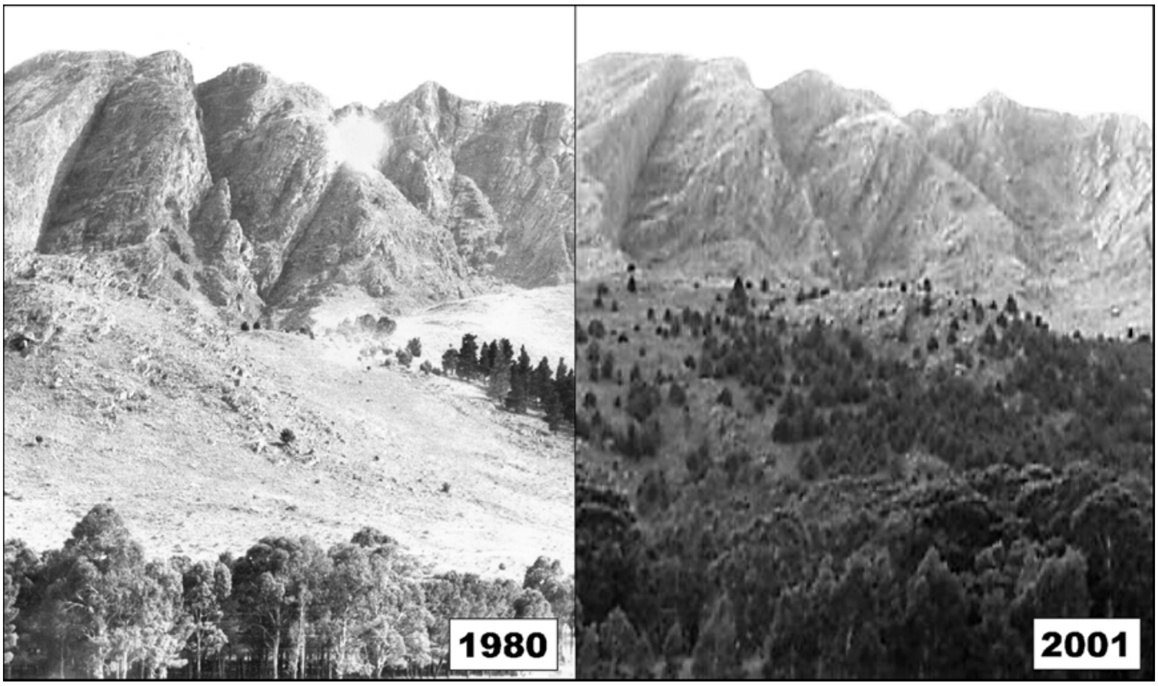

Figure 2. Mixed *Pinus halepensis* and *P. radiata* stand growing on Co. Ventana foothill (Parque Provincial Ernesto Tornquist, Buenos Aires, Argentina), and its expansion in the past 20 years.

Dispersal strategies

The most commonest dispersal strategy among the studied tree species is wind dispersal. Both pine species, *Cedrus deodara* and *Ulmus pumila* produce winged seeds and have a DI of 0.5. *Cupressus sempervirens* and both *Eucalyptus* species also depend upon wind for their dissemination, but their seeds do not have special structures to help dispersion and so their DI is 0.30. *Acacia dealbata* is dispersed by animals

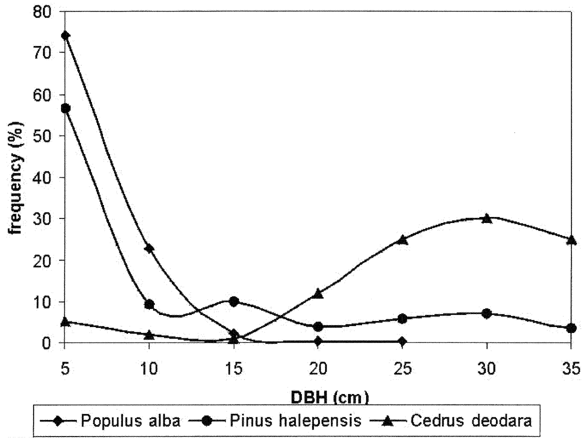

Figure 3. Size structure of three stands of alien woody plants (*Populus alba*, *Pinus halepensis* and *Cedrus deodara*) showing the three typical population profiles (concave or negative exponential, multi-modal and with almost no recruitment, respectively).

Table 3. Seed dispersal strategies for the tree species considered in this work.

Species	WD*	WD	AD	VD	DS
Acacia dealbata			0.35		0.35
Cedrus deodara	0.50				0.50
Cupressus sempervirens		0.30			0.30
Eucalyptus spp.		0.30			0.30
Pinus spp.	0.50				0.50
Populus alba				0.15	0.15
Robinia pseudoacacia			0.35	0.15	0.50
Ulmus pumila	0.50				0.50

WD* represents wind-dispersed seeds with wings or feather-like structures; WD, wind-dispersed seeds without special structures; AD, animal dispersion; VD, vegetative propagation and DS is the dispersal strategy index.

(DI = 0.35), *Robinia pseudoacacia* has a mixed strategy with seeds that are dispersed by animals and also vegetative propagation by budding roots (DI = 0.50), and *Populus alba* depends exclusively on vegetative propagation and so received the lowest dispersal index (DI = 0.15) (Table 3).

Impacts on the native flora

We recorded significant decreases ($P < 0.05$) in total plant species richness (native and exotic) for all the studied stands relative to their corresponding controls in native grassland. The only exception corresponded to the *Cedrus deodara* in stand no. 2, which showed an increase that was, however, not statistically significant ($P > 0.1$). We also found large increases in the proportion of exotic species in the understory of all stands (Table 4). The percentage of plant species exclusive to the stands' understory or to the grassland controls, or showing significant differences in their frequency between both habitats (FC), was greater than 60% for all the stands. The greatest changes were in the *Robinia pseudoacacia* and *Eucalyptus* stands (Table 4). Regarding the overlap between the area covered by each stand and the habitats of the selected endemic plant species, the highest values belonged to a mixed pine stand, the distribution of which overlapped with the habitat of eight out of the nine endemic species considered (Table 5).

Final ranking

Among the considered stands, only a *Cedrus deodara* stand (No. 3) can be *a priori* discarded as being an invasive species posing a threat to the reserve, because it is apparently in decline, almost without saplings and young trees, not having expanded its distribution over the last thirty years (Table 6). We do not have precise references about changes in the area covered by stand no. 8 of *Pinus halepensis*, due to the lack of historical aerial photographs of the area where it grows. It has a population structure that could be ascribed to a stable population, but we think that it should not be disregarded as a potential invader, mainly because of the historical behavior of the other stands of this species. The *Cupressus sempervirens* stand showed an expansion in the first period considered in this study (Table 2) despite a decrease in its covered area between 1967 and 1994, and it currently includes a high proportion of young individuals, fulfilling at least one of the requisites in our definition of invasive species, and for this reason it should be included in the future control strategy. From the final classification of the remaining stands, it appears that the maximum invasion severity corresponds to a mixed *Pinus halepensis* and *P. radiata* stand, followed by the *Acacia dealbata*, *Populus alba* and *Robinia pseudoacacia* ones (Table 6).

Discussion

The first part of this study clearly shows that, although the areas of Pampean grassland in Argentina that are presently considered to be in the best state of conservation have escaped the advance of agriculture, they are seriously threatened by the invasion of woody exotic species.

Table 4. Changes in plant species richness and composition associated with each exotic stand.

Stand	Species	Plant species richness ([a])	Native *versus* exotic species ratio ([b])	RV	FC
1	*Acacia dealbata*	11 (39)	1.2 (37.7)	0.97	0.79
2	*Cedrus deodara*	40 (39)	2.33 (37.7)	0.94	0.70
3	*Cedrus deodara*	17 (39)	1.83 (37.7)	0.95	0.78
4	*Cupressus sempervirens*	15 (39)	2 (37.7)	0.95	0.81
5	*Eucalyptus viminalis*	33 (45)	3.12 (21.7)	0.86	0.68
6	*Eucalyptus viminalis*	32 (45)	7 (21.7)	0.68	0.63
7	*Eucalyptus viminalis – E. camaldulensis*	21 (45)	3.2 (21.7)	0.85	0.86
8	*Pinus halepensis*	16 (39)	0.78 (37.7)	0.98	0.83
9	*Pinus halepensis – P. radiata*	22 (39)	6.3 (37.7)	0.82	0.62
10	*Pinus halepensis – P. radiata*	43 (55)	4.4 (14.2)	0.69	0.70
11	*Populus alba*	21 (58)	4.2 (15.9)	0.73	0.76
12	*Populus alba*	17 (58)	4.7 (15.9)	0.71	0.72
13	*Robinia pseudoacacia*	25 (45)	2.1 (21.7)	0.90	0.86
14	*Robinia pseudoacacia*	12 (55)	1 (14.2)	0.93	0.95
15	*Ulmus pumila*	21 (27)	1.1 (7.4)	0.85	0.68

Figures in parenthesis correspond to the average plant species richness ([a]) and the native *versus* exotic species ratio ([b]) in the grassland controls for this habitat. RV is the index of change in the native *versus* exotic species ratio and FC the proportion of species showing significant changes in their frequency or being exclusive of grasslands or stands.

Most of the plant species are mentioned in this study as having invaded the Pampean grasslands, and are also known as natural-area invaders in other ecosystems. For instance, the three most invasive pine species in the Pampean grasslands (*Pinus halepensis*, *P. pinaster* and *P. radiata*) are among the top five invaders that occur in many countries in the Southern Hemisphere, such as Australia, Chile, South Africa, New Zealand and Uruguay (Richardson et al. 1990, 1994; Rouget et al. 2001). The legume species mentioned in this study have likewise shown a remarkable ability to invade the Pampean grasslands, as they have done in the rest of the world (Binggeli 1998, International Legume Database and Information Service 2001; Macdonald et al. 1991). On the other hand, species like *Eucalyptus*, which on a world scale show a reduced capacity to invade natural ecosystems compared to other intensively planted species such as pines and legumes, (Binggeli 1998; Richardson 1998; but see also Burdon and Chilvers 1983; Chilvers and Burdon 1977) are found to be among the least invasive species in the Pampean region, despite being among the earliest introduced and most widely planted tree species. All this, once again, demonstrates the value of analyzing the previous performance of a species as an invader as a powerful tool in evaluating its potential success in a given ecosystem (Williamson 1996), and adds to the idea of developing measures to prevent the introduction of potentially dangerous species (Daehler and Carino 2000; Reichard and Hamilton 1997).

It is of primary importance to recognize that the invasion process is dynamic, and that some species that at one time may be classified as casual and non-invasive could become aggressive invaders due to small increases in propagule pressure (for example, by an increase in the area planted) (Richardson 1998), changes in the disturbance regime (Hobbs 1991; Richardson and Bond 1991) or the introduction of other species that might facilitate their expansion (Simberloff and Von Holle 1999). The present tendencies of environmental alteration seem to point to an intensification of the processes already mentioned and so it is logical to forsee an increase in the invasion pressure of woody exotic species on the last remaining natural grasslands. This emphasizes the need to develop diagnostic methods directed towards preventing the introduction of potentially dangerous species and establishing objective priorities for controlling invasive plants that have already become established (Rejmánek and Richardson 1996; Rejmánek et al. 2001).

The setting of priorities devised in the second part of this study offers a management approach that allows priorities to be established for control, based on objective documented criteria. An order of priorities allows

Table 5. Overlap between the studied stands and habitats that are typical for nine plant species endemic to the area.

Stand	Species	*Grindelia ventanensis*	*Senecio ventanensis*	*Rorippa ventanensis*	*Poa iridifolia*	*Festuca pampeana*	*Festuca ventanicola*	*Lupinus aureonitens*	*Plantago bismarkii*	*Polygala ventanensis*	OI
1	*Acacia dealbata*	—	—	—	—	—	—	+	+	+	0.33
2	*Cedrus deodara*	—	+	—	—	—	—	+	+	+	0.44
3	*Cedrus deodara*	—	—	—	—	—	—	+	+	+	0.33
4	*Cupressus sempervirens*	—	—	—	—	—	—	+	+	+	0.33
5	*Eucalyptus viminalis*	+	+	—	—	—	+	+	+	+	0.66
6	*Eucalyptus viminalis*	+	+	—	—	—	+	+	+	+	0.66
7	*Eucalyptus viminalis – E. camaldulensis*	—	—	—	—	—	—	+	—	—	0.11
8	*Pinus halepensis*	—	—	—	—	—	—	+	+	+	0.33
9	*Pinus halepensis – P. radiata*	+	+	—	+	+	+	+	+	+	0.90
10	*Pinus halepensis – P. radiata*	—	—	—	—	—	—	+	—	—	0.11
11	*Populus alba*	—	—	+	—	—	—	+	—	—	0.22
12	*Populus alba*	—	—	+	—	—	—	+	—	—	0.22
13	*Robinia pseudoacacia*	—	+	—	—	+	+	+	+	+	0.66
14	*Robinia pseudoacacia*	—	—	—	—	—	—	+	—	—	0.11
15	*Ulmus pumila*	—	—	—	—	—	—	—	—	—	0.00

+ Represents overlap between the exotic stand and the habitat of the corresponding endemic species. OI is the index of overlap with endemic species.

Table 6. Alien woody plant stands growing in Ernesto Tornquist Provincial Park, ordered by their index of IS.

Stand	Species	AI	AC	PS	DS	RV	FC	OI	IS
9	*Pinus halepensis – P. radiata*	1	1.00	1	0.5	0.82	0.62	0.9	0.88
1	*Acacia dealbata*	0.003	0.08	1	0.35	0.97	0.79	0.33	0.55
12	*Populus alba*	0.02	0.19	1	0.15	0.71	0.72	0.22	0.51
11	*Populus alba*	0.006	0.12	1	0.15	0.73	0.76	0.22	0.50
13	*Robinia pseudoacacia*	0.027	0.06	0.5	0.5	0.9	0.86	0.66	0.43
7	*Eucalyptus viminalis – E. camaldulensis*	0.032	0.11	0.5	0.3	0.85	0.86	0.11	0.39
4	*Cupressus sempervirens*	0.028	−0.01[a]	0.5	0.3	0.95	0.81	0.33	0.38
5	*Eucalyptus viminalis*	0.023	0.00	0.5	0.3	0.86	0.68	0.66	0.38
6	*Eucalyptus viminalis*	0.004	0.01	0.5	0.3	0.68	0.63	0.66	0.37
14	*Robinia pseudoacacia*	0.018	[b]	0.5	0.5	0.93	0.95	0.11	0.37
10	*Pinus halepensis – P. radiata*	0.202	0.00	0.5	0.5	0.69	0.7	0.11	0.34
15	*Ulmus pumila*	0.001	0.01	0.5	0.5	0.85	0.68	0	0.34
2	*Cedrus deodara*	0.024	0.00	0	0.5	0.94	0.7	0.44	0.03
3	*Cedrus deodara*	0.016	−0.01[a]	0	0.5	0.95	0.78	0.33	0.00
8	*Pinus halepensis*	0.013	[b]	0	0.5	0.98	0.83	0.33	0.00

[a] Computed as zeros in the IS formula; [b] no data available.

AI is the area index for each stand; AC, the index of change in the area covered by each stand; PS, the population structure index; DS, the dispersal strategy index; RV, the index of change in native *versus* exotic species ratio; FC, the proportion of species showing significant changes in their frequency or being exclusive of grasslands or stands; OI, the index of overlap with endemic species and IS, the index of invasion severity.

control methods to be used more effectively in terms of biodiversity conservation and avoids the tendency, noted by Westman (1990), of starting with the more conspicuous invaders. Moreover, an objective hierarchy provides a strong backing for fund raising and support for unpopular control methods, especially in the case of a group of charismatic species such as trees in a pasture ecosystem (Zalba 2000).

Our proposal is based on other systems of ranking and basically includes the same categories of information: the current and the potential extent of invasion, the rate of spread and the ecological impact on the area invaded (Hiebert and Stubbendieck 1993; MacDonald and Jarman 1985; Macdonald et al. 1991). The difference in the ranking system used in this study is that tree stands, rather than exotic species, are used as the management units since we consider them to be more appropriate for controlling invasive tree species in a nature reserve. Even on a local scale, different stands of the same species can pose significantly different threats to biodiversity (depending, for instance, on their location in the reserve) and they can also have different control feasibilities. Moreover, the index was constructed taking into account the specific objectives of the protected area included in our case study: the conservation of the natural communities of the Pampean grasslands and, especially, the protection of the endemic species of the area. Finally, some improvements have been made to the setting of priorities previously cited with respect to quantifying the impact of the invasive species by incorporating the analysis of vegetation associated with each stand.

Among the selected variables that make up our index of IS, the information about the area covered by each stand tries to reflect the size of the problem that each one represents and it has been included in most systems that evaluate the seriousness of invasions. It is necessary to include a variable of this nature since we can assume that, all other things being equal, an invasion will be more serious the larger the area of the reserve that is affected. However, to concentrate the priorities of control on species that are widely distributed would be to contradict one of the basic principles of management of biological invasions: early intervention (Cronk and Fuller 1995: 43; Macdonald and Frame 1988). If we are only guided by the area covered by each stand, we will lose the opportunity of acting on the species most recently established, which are also the cases in which there is a greater chance to carry out effective control (Macdonald 1990; Moody and Mack 1988). Our proposed ranking system attempts to compensate for this problem with the variables related to the size of expansion of each wood (AC) and population structure (PS). The first of these indexes is corrected for the initial size of each stand and therefore it is expected to underestimate the growth rate of the smaller stands, to which the addition of only a few trees might represent significant increases in the area. The index of population structure also assigns larger values to a stand with proportionately more young trees, as occurs in the case of recent invasions.

The concept of the population structure index may be understood more clearly when the life histories of the tree species are examined. For instance, the three stands of pines included in this study showed the three alternative population profiles (stable or growing with a high proportion of young individuals, multi-modal and in apparent decline with very low representation of young trees). Pine trees have heliophilous saplings and recruitment depends to a large extent on the occurrence of disturbances, mainly fires, creating open spaces within the shady wooded areas (Daskalakou and Thanos 1996; Thanos and Daskalakou 2000). Fire also enhances seed germination and seedling establishment (Thanos 2000). The variety of population profiles observed in pines in Tornquist Park corresponds to the history of occurrence of natural fires in the sectors of the reserve where each stand grows (Zalba et al. 2000). This shows that in the presence of an adequate supply of propagules, even disturbances considered to be natural, such as fires in temperate grasslands, might result in increased abundance of exotic species. On the other hand, fire could also be a useful tool to control pines in this reserve, provided that burning was repeated within a shorter period than that required for species to reach a reproductive stage, and as long as the arrival of propagules from surrounding areas can be kept under control.

The index of population structure is actually one of the components of our system of priorities that presents the most uncertainty as a measure for the prioritization of control actions. This is due to the population profiles that have been constructed from size data rather than from the age of the trees, and we know that it is very risky to assume a relationship between size and age since differences in size are often found in specimens of the same age (Harper 1977, pp. 601, 634). On the other hand, the values of the population structure index were assigned quite arbitrarily, according to the proportion of individuals in each age class and only for comparison between the different alternatives of the population structure. A more biologically sound alternative could be to use some demographic parameter (like population growth rate), but the precision of this measurement would also be conditioned by not taking into account age estimations. Unfortunately, the estimation of the age of individuals in the stands under study is incompatible with the time and resources available for establishing priorities of control. In spite of this uncertainty, it was decided to keep this index for the reasons already given in a preceding paragraph and for its usefulness as an indicator of the invasion potential of each stand.

Another important source of uncertainty is related to the dispersal strategy index. In general terms, we know that the success of an invader relies upon its dispersal efficiency and colonizing ability, and requires the ability to self-propagate or the action of co-evolved or generalist dispersal agents (e.g., mammals, birds and insects). In an environment distant from the area of the species' natural distribution, an abiotic dispersal strategy should be advantageous (Richardson et al. 1990). However, it has been demonstrated that vertebrate-dispersed plants are generally not reproductively limited by the lack of dispersers and that many species have invaded with the aid of generalized local frugivores (Richardson et al. 2000a). If the invasive species succeeds in establishing this interaction with animal agents, a new and highly efficient alternative dispersal opportunity will be gained for its expansion. In our study area, strong winds appear to facilitate seed dispersal of the anemophilous species over long distances from the mother plant and, as a matter of fact, wind dispersal is the most common mechanism among the studied species and is associated with the stand that showed the highest expansion rate. Notwithstanding, some animal-dispersed species, such as *G. triacanthos*, also showed an important increase in the area occupied within the reserve. The dispersal strategy index proposed in this study is only a first approximation to the evaluation of the function of propagation mechanisms of exotic trees in terms of their potential invasion; for that reason, we decided *a priori* that species with abiotic dispersal methods were potentially more invasive than animal-dispersed species. Increased knowledge about the availability of generalist dispersal agents and the characteristics of fruits and seeds of the invasive plants would allow increased precision of this index.

Regarding the impact of invasive species on biodiversity, most discussions on this subject are based on descriptive data (Parker et al. 1999) or on qualitative indexes (Hiebert and Stubbendieck 1993; Macdonald 1988; Macdonald et al. 1991), often in function of the lack of available scientific information for the protected areas. The impact associated with biological invasions is frequently measured in terms of changes in the richness or diversity of associated species

(Lonsdale and Braithwaite 1988). This alternative has great restrictions because the presence of certain exotic species may increase total richness (Parker et al. 1999), as happened with the plants associated with one of our cedar stands. In the case of the Pampean grasslands, the availability of numerous plant surveys allows a more precise evaluation of the impact of the introduced trees on the native flora, including variables related to changes in the structure and composition of communities. The index of invasion severity formulated in our study values the components of biodiversity of particular interest for conservation in the area, such as the endemic plant species. In actual fact, the analysis of the overlap between stands of exotic and endemic species contains another source of uncertainty because it is assumed that the threat to the biodiversity of the reserve is greater in the case of a tree whose distribution coincides with the habitat of a large number of endemic species, even though practically nothing is known about the interaction between each species of exotic trees and the selected endemic species, and that the coexistence or not is not in itself a test of niche overlapping. Notwithstanding, this variable is included because it allows the differential evaluation of stands which, though they belong to the same species, have different impacts on the conservation objectives of the protected area, as happened with the two stands of *Robinia pseudoacacia* that were investigated.

An interesting aspect related to the results obtained in our case study is the increase of the proportion of exotic species in the understorey of introduced woody stands, indicating that this environment could be better tolerated by other invasive plants such as *Carduus tenuiflorus*, *Conium maculatum*, *Echium plantagineum*, *Geranium molle*, *Hedera helix*, *Hordeum murinum* subsp. *leporinum*, *Prunus mahaleb* and *Taraxacum officinale.* Some of these species, such as *Hedera helix*, are restricted to shade inside the stands, whereas most of them are able to grow outside as well. This observation reinforces the concept developed by Simberloff and Von Holle (1999) concerning the facilitating effect of certain exotic species on the establishment of other species, known as 'invasion meltdown', in opposition to the concept of 'biotic resistance', according to which the probabilities of the success of new invasions are reduced with the arrival of each new species (Simberloff 1986). From a practical point of view for management, it is important to know which of the two concepts dominate the relationships between the species that invade the conservation area (Simberloff and Von Holle 1999). In the particular case of exotic trees advancing on relicts of Pampean grasslands, this would mean whether, in general, the trees that are already naturalized prevent or facilitate the arrival of new invaders. According to our results, the 'invasion meltdown' seems to be the rule more than the exception in the area of study. This situation shows the risk of the presence of woody species in relicts of grassland, because, although they may not cause a significant impact themselves, they might encourage the arrival of other more aggressive invaders.

It is important to emphasize that the ranking developed in this study must be complemented by an analysis of feasibility of the control measures to be initiated. It must be taken into account that the control of biological invaders is 'the art of the possible' (Cronk and Fuller 1995) and that information about the technical, economic, social and legal feasibility of any control measure is just as important as the values of invasion severity in terms of the success of the management strategy to be carried out (Parker et al. 1999; Zalba et al. 1999). It is also fundamental to understand that the results of this study, as with any other priority setting, must be taken as a hypothesis, and that any control measures should be aimed at testing not only their own effectiveness but also the precision of the initial diagnosis of invasion severity.

The problem of alien woody plants invading relict native grasslands is a serious and fast-growing threat to the conservation of a component of the global biodiversity that has historically suffered other intense transformations originating from human activities, like agriculture and cattle ranching. Invasive trees deeply transform the structure and composition of native grasslands and can also enhance the invasion by other exotic species. The chances to efficiently control their advancement are challenged by the increase in the land devoted to forestry and the aging of the plantations. The problem needs an active management strategy including prevention of new invasions and control or eradication of existing ones.

Acknowledgements

We wish to thank those who helped with information about alien species, including Facundo Casale Pintos, Carlos D'Alfonso, Rolf Delhey, Eduardo Haene, Pedro Laterra, Rolando León, Flavio Moschione and Darién Prado. We are also grateful to J.T. Carlton, Roxana Aragón, Diego Vázquez and the anonymous referees who revised preliminary versions of the manuscript and to Rosemary Scoffield who kindly helped us with the language. This project was funded by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). The exotic species control strategy is included in an agreement between the Universidad Nacional del Sur, the Ministerio de Agricultura, Ganadería y Alimentación de Buenos Aires and the Municipalidad de Tornquist, which is funded by the Asociación Cooperadora Parque Tornquist.

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