

# Canopy effects of the invasive shrub *Pyracantha angustifolia* on seed bank composition, richness and density in a montane shrubland (Córdoba, Argentina)

ALEJANDRA GIANTOMASTI<sup>†</sup>, PAULA A. TECCO<sup>\*†</sup>, GUILLERMO FUNES,  
DIEGO E. GURVICH AND MARCELO CABIDO

*Instituto Multidisciplinario de Biología Vegetal (CONICET – UNC) and F. C. E. F y N, Universidad Nacional de Córdoba, Casilla de Correo 495, Vélez Sársfield 299, 5000, Córdoba, Argentina*  
(Email: ptecco@efn.uncor.edu)

**Abstract** Invasive woody species frequently change the composition of the established vegetation and the properties of the soil under their canopies. Accordingly, invasion may well affect regenerative phases of the community, especially at the seed bank level, likely influencing community restoration. *Pyracantha angustifolia* (Rosaceae) is an invasive shrub in central Argentina that affects woody recruitment, particularly enhancing the recruitment of other exotic woody species. There is though no information regarding its effect on the soil seed bank within the invaded community. The present study was set up to gain further insight into the canopy effects of *P. angustifolia*. We aimed to assess whether the invasive shrub affects seed bank composition, richness and seed density as compared with the dominant native shrub *Condalia montana* (Rhamnaceae), and to relate the observed seed bank patterns with those of the established vegetation. We evaluated the composition of the germinable seed bank and the established vegetation under the canopy of 16 shrubs of *P. angustifolia*, 16 shrubs of *C. montana*, and in 16 control plots (10 m<sup>2</sup>) without shrub cover. The floristic composition of the seed bank differed among canopy treatments. However, seed bank richness did not differ significantly. There was an overall high seed density of exotic species throughout the study site, though exotic forbs showed significantly lower seed densities under the invasive shrub. *Pyracantha angustifolia* would not promote the incorporation of new species into the seed bank of the invaded community but rather favour the establishment of woody species that do not depend on seed banks. The absence of dominant woody species in the seed bank, the dominance of exotic forbs, and the high similarity between established exotic species and those present in the seed bank may surely affect community restoration following the main disturbances events observed in the region.

**Key words:** biological invasion, *Condalia montana*, established vegetation, invasional meltdown, *Ligustrum lucidum*.

## INTRODUCTION

Many studies have focused upon the effect of invasive plant species on the resident plant community (Williamson 1996; Kwiatkowska *et al.* 1997; Levine *et al.* 2003; Lichstein *et al.* 2004). It is well known that many invasive plants change both the composition of the established community, and the abiotic characteristics of the invaded system, creating different microhabitat conditions under the canopy of the invading species (Mack *et al.* 2000; Belnap & Phillips 2001). Moreover, it has been stated that, through these changes, some established invasive species may even enhance the arrival of new exotic species to the invaded

community (Sallabanks 1993; Simberloff & Von Holle 1999; Richardson *et al.* 2000; Tecco *et al.* 2006), an effect currently named ‘invasional meltdown’ (*sensu* Simberloff & Von Holle 1999). Despite the fact that seed banks play an essential role in community dynamics and regeneration (Bakker *et al.* 1996; Bakker & Berendse 1999; Funes *et al.* 2001), less attention has been addressed to the effects that invasive species exert on seed banks characteristics. There is though evidence that invasion by woody species decreases seed bank diversity, richness and density of the invaded communities (Holmes & Cowling 1997a,b; Holmes 2002). Understanding the impact of a given invader on the seed bank level is therefore a very important aspect in the formulation of effective strategies for addressing invasion and restoration of a given community (Panetta & Sparkes 2001; Vilà & Gimeno 2007). This is particularly evident in systems exposed to frequent disturbance events, such as fire, grazing and logging, where

\*Corresponding author.

<sup>†</sup>Both authors contributed equally to this paper.

Accepted for publication May 2007.

the seed bank may function as a genetic memory of a population (Brown & Venable 1986) and strongly influence community restoration after disturbance (Bakker *et al.* 1996; Bakker & Berendse 1999; Funes *et al.* 2001).

Seed bank composition, richness and density are directly affected by the identity (Harper 1977; Peco *et al.* 1998; Funes *et al.* 2001) and spatial distribution patterns (Aguiar & Sala 1997; Pugnaire & Lázaro 2000) of the species in the established community. Certainly, small scale patterns of distribution of buried seeds are of great importance given the fact that the distribution of seeds affects the probability of a plant of any particular species establishing in a given place (Thompson 1986). For example, in semiarid environments, shrub canopies accumulate large seed banks, and affect temperature, soil moisture, litter accumulation and nutrient distribution (Moro *et al.* 1997a,b), thus influencing both seed bank and understorey species composition in the community (Aguiar & Sala 1997; Pugnaire & Lázaro 2000).

*Pyracantha angustifolia* is a fleshy-fruited shrub native to China naturalized and broadly spread in Central Argentina (Delucchi 1991). In the Córdoba Mountains this shrub invades open shrublands sharing dominance with other native fleshy-fruited shrubs, such as *Condalia montana* (Tecco *et al.* 2006). A previous study reported that *P. angustifolia* generates a differential microenvironment under its canopy, as compared with *C. montana*, and affects woody recruitment, particularly enhancing recruitment of other exotic woody species (Tecco *et al.* 2006). However, there is no information regarding its effect on herbaceous species distribution. Moreover, it is still unknown whether the observed canopy effect leads to seed bank heterogeneity within the invaded community or whether *P. angustifolia* also enhances incorporation of exotic species into the seed bank under their canopy. The present experimental study was set up to gain further insight into the canopy effects of *P. angustifolia* on the regenerative phase of the invaded community. We aimed to assess whether the invasive shrub affects seed bank composition, richness and density heterogeneity within the invaded community. Specifically, we compared native and exotic species composition of the seed bank, seed richness and density under canopies of *P. angustifolia* and *C. montana*, and in patches of herbaceous vegetation without shrub cover. We then related the patterns observed in seed banks with those of the established vegetation.

## METHODS

### Study area and species

The study was carried out in a 4-ha site close to Salsipuedes (31°07'18"W; 64°19'13"S), in the

Córdoba mountains, Central Argentina. The altitude is 878 m a.s.l and mean annual temperature is 14°C, with frosts being common from May to October (De Fina 1992). Mean annual rainfall is around 850 mm, mainly concentrated in the warm season (October to April). The natural vegetation of the area is a seasonally dry mountain woodland, known as Mountain Chaco Woodland (Luti *et al.* 1979; Zak & Cabido 2002). Human activities such as livestock grazing, logging and frequent fires have transformed the original woodland into a mosaic of grassland, shrubland and open woodland (Zak & Cabido 2002). In particular, our study site was restricted to an open shrubland, which is now the most widespread community in the Córdoba Mountains.

*Pyracantha angustifolia* (Rosaceae) is an evergreen, thorny and fleshy-fruited shrub, originated in Asia and widely used in gardening and landscaping (Novara 1993). This invader has abundant horizontal branches and twigs, and can attain 3–4 m height and 5–6 m in crown diameter (Novara 1993). As its fruits are bird dispersed, it has escaped from gardens and become naturalized in the study area (Delucchi 1991; Gurvich *et al.* 2005), where it shares dominance with *C. montana* (Rhamnaceae). This native shrub is also evergreen, thorny, with fleshy bird-dispersed fruits, and can attain a similar size to *P. angustifolia* (Escalante *et al.* 1971). Both shrubs have been present and dominating the vegetation cover in the study area for the last 15 years (A. Perez Harguindeguy, pers. comm. 2000). The characteristics of the seed banks are thus stable outcomes of long-term presence of both shrubs in the community. This allows the use of *C. montana* as a native shrub control treatment while examining the effect of the invader (Tecco *et al.* 2006).

### Experimental design

Three canopy treatments were considered: *P. angustifolia* understorey, *C. montana* understorey and no-shrub canopy (patches of herbaceous vegetation). Sixteen mature individuals of *P. angustifolia* and 16 of *C. montana* were used as replicates of canopy treatments. As a control, 16 plots of 10 m<sup>2</sup> of herbaceous vegetation at the same site were randomly chosen as replicates of the no-shrub canopy treatment.

In order to estimate the composition of the germinable seed bank, a compound soil sample (four cores) was collected from each replicate (plot) with a 10-cm diameter bore. Compound soil samples were collected in order to capture the high spatial heterogeneity characteristic of most seed banks (Thompson 1986). Only the first 5 cm soil depth was considered as the majority of viable seeds are located within the first few centimetres (Bakker *et al.* 1996; Hutchings & Booth 1996; Funes *et al.* 2001). Samples were

collected in autumn (May 2001) after the seed rain, in order to capture the highest diversity of species in the seed bank (Bakker *et al.* 1996; Funes *et al.* 2001, 2003). Once collected, soil samples were sieved through 1-cm mesh sieves in order to remove plant fragments and stones (Ter Heerd *et al.* 1996). They were then chilled in a refrigerator at 5°C for 1 month in order to break seed dormancy (McDonald *et al.* 1996; Baskin & Baskin 1998). After that, soil was spread over 2 cm of sterilized sand in 20 × 15 cm plastic trays (Ter Heert *et al.* 1996; Funes *et al.* 2001, 2003), which were placed in a greenhouse at 25°C average temperature. Trays were distributed in the greenhouse at random positions, and watered daily (16 plots per treatment × 3 treatments = 48 trays). Four additional trays containing autoclave-sterilized soil were kept under the same conditions as a control against contamination.

The germinable seed bank in the soil was evaluated in terms of floristic composition and size through the identification and counting of seedlings emerging from the soil samples. Trays were kept in the greenhouse for 12 months until all seedlings were identified.

In order to assess the composition of the established vegetation and compare it with that of the seed bank, species composition and abundance were recorded within each of the experimental plots using the Braun–Blanquet cover-abundance scale (Mueller-Dombois & Ellenberg 1974), without considering the canopies of the individuals used as shrub treatments.

At the same time this experiment was carried out, and considering the same individuals for each canopy treatment, Tecco *et al.* (2006) found that the canopies of *P. angustifolia* and *C. montana*, and the plots with no shrub cover, offered different microhabitat conditions in terms of photosynthetically active radiation and soil temperature and moisture. *Pyracantha angustifolia* offered a significantly shadier microhabitat than *C. montana*, both in summer (2.89  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 6.14  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively) and in winter (12.37  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 20.88  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), cooler environment in the topsoil layer in summer (25.15°C and 30.41°C on soil surface and 19.49°C and 21.43°C at 5 cm soil depth), and moister soil in winter (21.76% and 16.82%). In terms of soil chemical variables there was significantly more organic matter under *P. angustifolia* and *C. montana* (21.99% and 20.40%) than in plots with no shrub cover (13.31%), as well as higher pH under both shrubs (6.37 and 6.62, respectively) than in plots with no shrub cover (6.04).

### Data analysis

Two principal component analyses (PCA; Hill & Gauch 1980) were used to examine the composition of seed bank and established vegetation within the treat-

ments. We then ran ANOVA tests to compare the scores obtained for each treatment along PCA axes 1 and 2 of both ordinations. To evaluate the effect of the three canopy treatments on the richness of the established vegetation and on seed bank richness and density, data were rank-transformed and two-way ANOVAs were run on the ranked data (Zar 1999). This non-parametric analysis yielded the same conclusions as parametric ANOVAs run on the untransformed data, suggesting that it had sufficient power (Zar 1999). Fisher's least-significant differences test was applied as a *post hoc* comparisons test to locate the differences among treatment means. The Sørensen similarity coefficient (Warr *et al.* 1993; Peco *et al.* 1998) was used to compare seed bank and established vegetation compositions within each canopy treatment. ANOVA and Fisher's LSD test were then run to compare means of this similarity index among treatments. We used the InfoStat statistical package to perform the analysis (Di Rienzo *et al.* 2002). Species nomenclature follows Zuloaga *et al.* (1994), Zuloaga and Morrone (1996, 1999) and Boelcke (1992).

## RESULTS

### Soil seed bank

We found a total of 91 species in the germinable soil seed bank of the study area, with 64 species under *P. angustifolia*, 65 under *C. montana*, and 55 in the absence of shrub cover. Soil-stored seed banks were mostly dominated by short-lived species throughout the study site. *Leonurus sibiricus*, *Cyperus* sp., *Solanum chenopodioides*, *Conyza bonariensis* and *Bidens subalternans* were the most abundant taxa in all treatments. Composition of exotic species was also similar among treatments (Table 1).

Soil seed bank composition tended to differ among treatments, particularly between plots with (*P. angustifolia* and *C. montana*) and without shrub cover. The PCA ordination considering seed bank composition tended to differentiate plots without shrub cover from those under either shrub treatment along axis 1, whereas along axis 2 plots under *P. angustifolia* tended to be differentiated from those under *C. montana* (Fig. 1a). Means of total native and exotic species richness in the soil seed bank did not differ among treatments (Table 2). Accordingly, there were no general differences in seed bank richness among treatments when considering main growth forms (Table 2), with the exceptions of native forbs (higher richness under both shrub treatments) and the exotic woody species (higher richness under *P. angustifolia*).

**Table 1.** Mean cover of exotic species in the established vegetation (EV) and percentages of exotic species ((number of seed of each species/total number of seeds) × 100) in the seed bank (SB) in the three treatments

	<i>Pyracantha angustifolia</i>		<i>Condalia montana</i>		No shrub cover	
	EV	SB	EV	SB	EV	SB
<b>Woody species</b>						
<i>Acer negundo</i>	0.2500	–	0.0625	–	–	–
<i>Cotoneaster</i> sp.	1.1875	–	0.9375	–	–	–
<i>Gleditsia triacanthos</i>	0.3125	–	–	–	2.1250	–
<i>Ligustrum lucidum</i>	26.1875	0.0018	6.9375	–	0.1875	–
<i>Ligustrum sinense</i>	2.4375	–	2.0625	–	–	–
<i>Melia azederach</i>	0.0625	–	–	–	–	–
<i>Morus alba</i>	2.5000	0.0035	0.9375	–	–	–
<i>Ulmus pumila</i>	0.0625	–	–	–	–	–
<i>Pyracantha angustifolia</i>	1.3750	1.3392	0.0625	0.0040	–	–
<b>Vines</b>						
<i>Hedera helix</i>	1.1250	–	–	–	–	–
<b>Graminoids</b>						
<i>Sorghum halepense</i>	–	0.0018	–	–	–	–
<i>Tragopogon pratensis</i>	–	–	–	–	0.1875	–
<b>Forbs</b>						
<i>Ammi majus</i>	–	0.0018	–	–	–	–
<i>Ammi visnaga</i>	–	0.0070	0.9375	0.0053	32.5000	0.0084
<i>Carduus acanthoides</i>	0.3750	0.0634	5.5000	0.0916	24.6875	0.0928
<i>Cirsium vulgare</i>	–	0.0088	–	0.0040	1.1250	–
<i>Chenopodium album</i>	–	0.0106	0.0625	0.0106	–	0.0028
<i>Duchesnea indica</i>	5.2500	0.0441	4.0625	0.0146	0.7500	0.0056
<i>Geranium rotundifolium</i>	–	–	–	–	0.0625	–
<i>Lactuca serriola</i>	–	–	0.2500	0.0013	0.3750	–
<i>Leonurus sibiricus</i>	0.4375	1.9929	23.1250	3.3295	24.5000	3.8248
<i>Oenothera rosea</i>	–	–	–	–	0.0625	–
<i>Polycarpon tetraphyllum</i>	–	–	–	0.0013	–	–
<i>Rapistrum rugosum</i>	–	0.0053	–	0.0013	–	–
<i>Silene antirrhina</i>	–	–	–	–	0.0625	0.0014
<i>Sonchus asper</i>	–	0.0018	0.0625	–	0.2500	0.0056
<i>Stellaria media</i>	–	0.0035	–	0.0080	–	0.0098
<i>Stellaria pallida</i>	–	0.0018	–	–	–	–
<i>Taraxacum officinale</i>	0.1250	–	0.2500	–	0.2500	–
<i>Torilis nodosa</i>	–	–	–	0.0053	–	0.0253
<i>Trifolium repens</i>	–	–	–	–	0.1875	–
<i>Veronica arvensis</i>	–	0.0053	–	0.0027	–	0.3348
<i>Viola odourata</i>	–	–	–	0.0053	0.9375	–

Some significant differences were observed among canopy treatments in terms of seed density (Fig. 2). Seed density of native species was significantly higher under *C. montana*, intermediate under *P. angustifolia* and lowest in the absence of shrub cover whereas seed density of exotic species did not differ among canopy treatments (Fig. 2a). Accordingly, seed density of native forbs was significantly higher under both shrub treatments as compared with the no-shrub treatment, whereas exotic forbs had a significantly lower seed density under *P. angustifolia* (Fig. 2b).

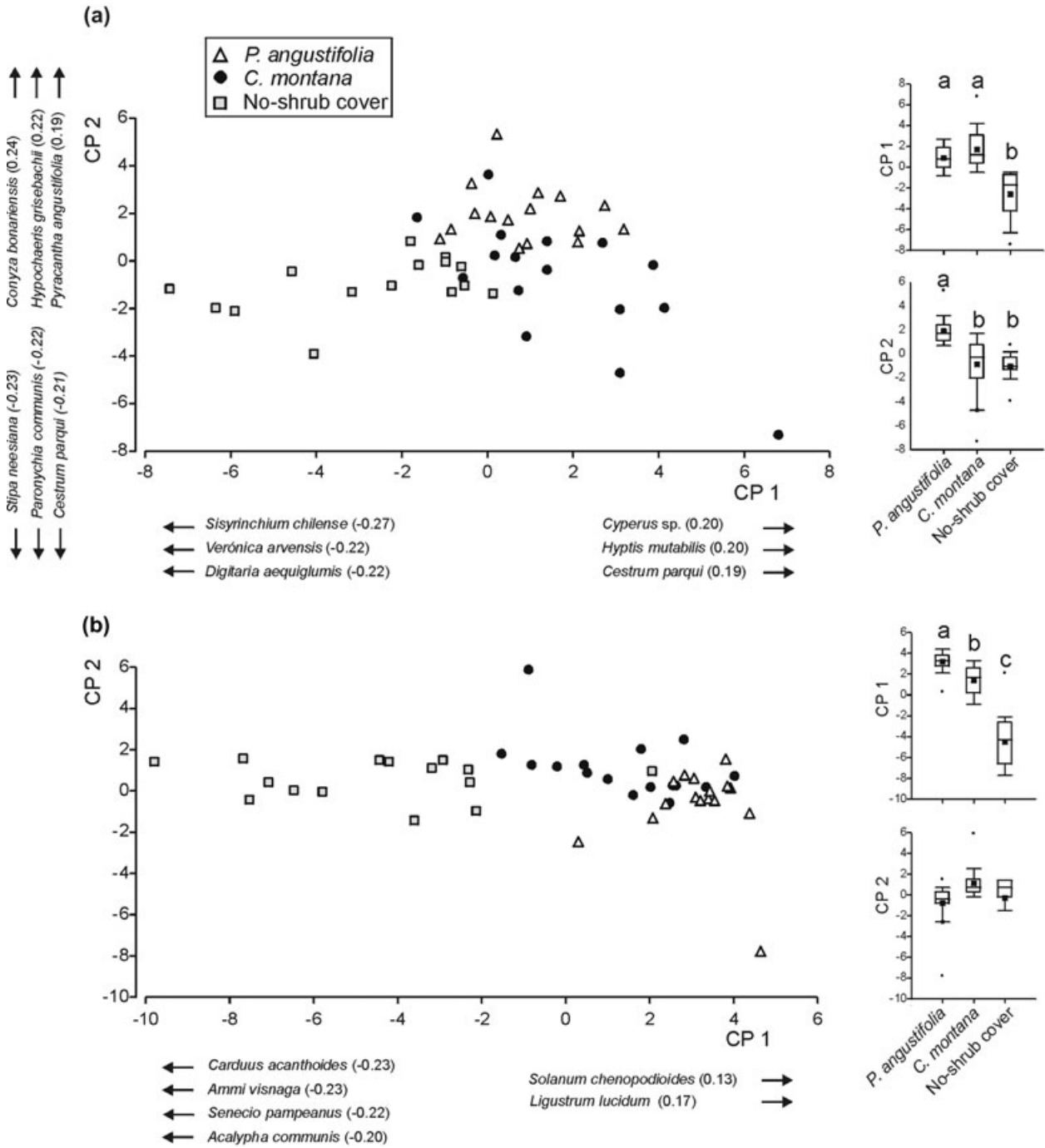
Exotic species dominated the seed banks in terms of seed density within the no-shrub treatment (Fig. 1a). Native and exotic species had similar seed densities within the seed banks of both shrub treatments (Fig. 1a). Dominance of exotic species in the seed bank

was particularly related to the high seed density of exotic forbs (Fig. 2b). Exotic forbs had significantly higher seed density than native forbs under *C. montana* and the no-shrub treatment ( $T = 3.93$ ,  $P = 0.01$  and  $T = 6.25$ ,  $P = 0.001$ , respectively) and did not differ under *P. angustifolia* ( $T = 0.69$ ,  $P = 0.497$ ).

### Established vegetation

We found a total of 128 species in the established vegetation of the study area. Seventy species were found in the *P. angustifolia* treatment, with *Ligustrum lucidum*, *L. sinense*, *Hyptis mutabilis* and *Acacia caven* being the most abundant. Eighty-two species were identified in the *C. montana* treatment, where *L. sibiricus*, *H.*





**Fig. 1.** PCA ordination of the plots of all three treatments taking into account (a) germinable soil seed bank composition, and (b) composition of the established vegetation. Distribution of the plot scores corresponding to each canopy treatment along both PCA axes (1 and 2) is illustrated on the right of each ordination. Box = interquartile range, containing 50% of values; square inside box = mean; line across box = median; whiskers = highest and lowest values, excluding outliers (i.e. cases with values >1.5 box lengths from the upper or lower edge of the box). Letters indicate significant differences between canopy treatments ( $P < 0.05$ , ANOVA and Fisher's LSD test). Labels display species with the highest eigenvector scores on PCA axes. The corresponding eigenvector values are indicated for each species in parenthesis. *C. Montana*, *Condalia montana*; PCA, principal component analysis.

**Table 2.** Native and exotic species richness (mean  $\pm$  standard errors) in the established vegetation and seed banks of the three canopy treatments

	<i>Pyracantha angustifolia</i>	<i>Condalia montana</i>	No shrub cover	$F_{2,47}$
<b>Seed bank</b>				
Native richness				
Total	17.25 $\pm$ 0.70	17.31 $\pm$ 0.99	16.06 $\pm$ 1.06	0.80
Woody	0.19 $\pm$ 0.14	0.38 $\pm$ 0.16	0	(§)
Vines	0.25 $\pm$ 0.14	0.75 $\pm$ 0.21	0.50 $\pm$ 0.16	2.04
Graminoids	4.06 $\pm$ 0.34	4.00 $\pm$ 0.37	5.31 $\pm$ 0.64	1.29
Forbs	12.75 $\pm$ 0.54 <sup>a</sup>	12.19 $\pm$ 0.79 <sup>a</sup>	10.25 $\pm$ 0.58 <sup>b</sup>	3.84 <sup>*</sup>
Exotic richness				
Total	4.63 $\pm$ 0.44	3.69 $\pm$ 0.40	3.50 $\pm$ 0.24	2.41
Woody	1.13 $\pm$ 0.09 <sup>a</sup>	0.06 $\pm$ 0.06 <sup>b</sup>	0	(§)**
Vines	0	0	0	–
Graminoids	0.06 $\pm$ 0.06	0	0	–
Forbs	3.44 $\pm$ 0.39	3.63 $\pm$ 0.40	3.50 $\pm$ 0.24	0.03
<b>Established vegetation</b>				
Native richness				
Total	14.75 $\pm$ 1.54 <sup>b</sup>	16.50 $\pm$ 0.77 <sup>b</sup>	21.5 $\pm$ 1.04 <sup>a</sup>	9.63**
Woody	4.00 $\pm$ 0.40 <sup>a</sup>	2.50 $\pm$ 0.30 <sup>b</sup>	2.56 $\pm$ 0.24 <sup>b</sup>	5.93**
Vines	1.31 $\pm$ 0.24	1.56 $\pm$ 0.33	1.25 $\pm$ 0.21	0.08
Graminoids	2.06 $\pm$ 0.47 <sup>b</sup>	2.56 $\pm$ 0.26 <sup>b</sup>	4.81 $\pm$ 0.43 <sup>a</sup>	13.99**
Forbs	7.38 $\pm$ 0.80 <sup>c</sup>	9.88 $\pm$ 1.01 <sup>b</sup>	12.88 $\pm$ 0.74 <sup>a</sup>	11.07
Exotic richness				
Total	4.06 $\pm$ 0.42	4.56 $\pm$ 0.41	4.94 $\pm$ 0.34	1.66
Woody	2.38 $\pm$ 0.32 <sup>a</sup>	1.125 $\pm$ 0.239 <sup>b</sup>	0.56 $\pm$ 0.13 <sup>b</sup>	13.76**
Vines	0.13 $\pm$ 0.09	0	0	–
Graminoids	0	0	0	–
Forbs	1.56 $\pm$ 0.24 <sup>c</sup>	3.44 $\pm$ 0.26 <sup>b</sup>	4.38 $\pm$ 0.29 <sup>a</sup>	27.54**

Different superscript letters represent significant differences among treatments ( $P < 0.05$ ; ANOVA and Fisher's LSD test in all cases except for woody species (§) where  $t$ -test was used). Degrees of freedom are indicated in parentheses for the source of variance and significant differences are indicated as \* $P < 0.05$  and \*\* $P < 0.01$ .

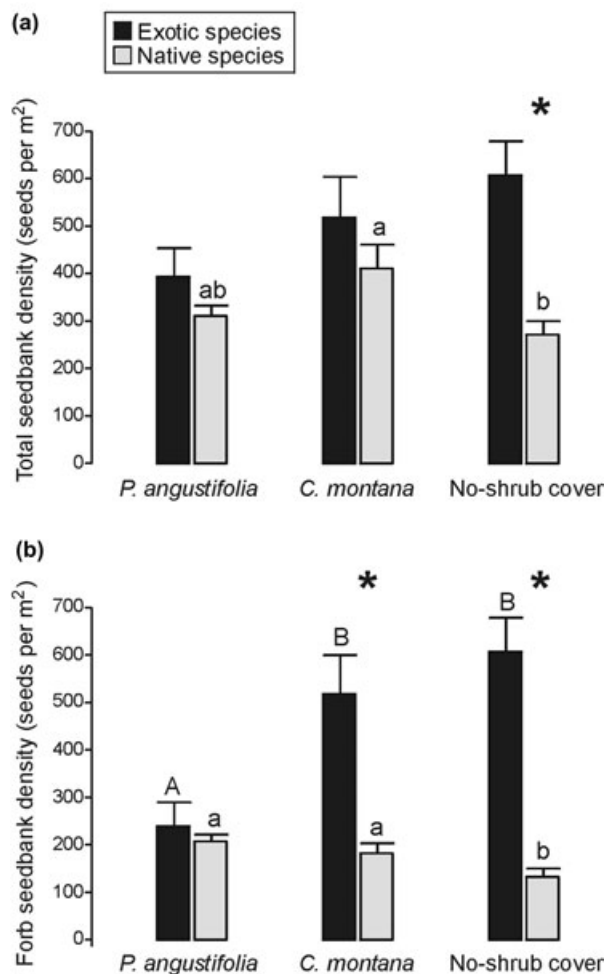
*mutabilis*, *L. lucidum* and *Carduus acanthoides* were the most abundant. Finally, 89 species were recorded in the plots without shrub cover. *Leonurus sibiricus*, *Ammi visnaga*, *C. acanthoides*, *H. mutabilis*, *Senecio pampeanus* and *A. caven* were the most abundant species in this treatment. Among all species recorded within the established vegetation on the study site, the exotic tree *L. lucidum* was the most abundant. Its cover was highest under *P. angustifolia*, intermediate under *C. montana* and lowest in the absence of shrub cover (Table 1).

The floristic composition of the established vegetation tended to differ among treatments (Fig. 1b). All three canopy treatments were differentiated by PCA ordination with plots under *P. angustifolia* occupying the positive extreme of PCA axis 1, plots with no shrub cover the opposite extreme and plots under *C. montana* intermediate positions (Fig. 1b). Mean total native species richness was significantly higher in the absence of shrub cover than in either shrub treatment (Table 2). Considering main growth forms, there was a higher richness of native forbs and graminoids within the no-shrub treatment, whereas native woody richness was higher under *P. angustifolia* (Table 2). The total exotic species richness did not vary among

canopy treatments though it differed when considering main growth forms (Table 2). As observed for the native forbs and woody species, the established vegetation under *P. angustifolia* canopy showed the lowest numbers of exotic forb species and the highest number of exotic woody species (Table 2).

### Relationship between seed bank and established vegetation

Both the composition of the seed bank and that of the established vegetation seemed to differ among canopy treatments (Fig. 1). However, species determining those apparently similar floristic trends were not the same. Accordingly, low similarity indexes were found between established vegetation and soil seed bank under all three treatments. The mean Sørensen coefficients were  $29 \pm 2.5\%$  under the *P. angustifolia* treatment,  $35 \pm 1.3\%$  under *C. montana* and  $31 \pm 2\%$  in the absence of shrub cover and did not differ significantly among treatments ( $P = 0.098$ ). *Acacia caven*, *C. montana*, *Ligustrum sinense*, *Mandevilla pentlandiana* and *M. laxa*, all woody species, two of them vines,



**Fig. 2.** Seed bank density of exotic and native species (number of seeds per m<sup>2</sup>) within all three treatments ( $n = 16$ ) considering (a) all species and (b) only forbs species. Letters indicate differences in seed density of exotic (capital letters) and native species (small letters) between treatments ( $P < 0.05$ , ANOVA and Fisher's LSD test). Asterisks (\*) indicate significant differences between seed densities of natives and exotics within each canopy treatment ( $t$ -test,  $P < 0.05$ ). *C. Montana*, *Condalia montana*; *P. angustifolia*, *Pyracantha angustifolia*.

were only found in the established vegetation. *Stipa trichotoma*, *Sisyrinchium chilense*, *Gamochaeta americana*, *G. filaginea* and *G. simplicicaulis*, all herbaceous species, did occur in the seed bank but were absent from the established vegetation.

The similarity between established vegetation and seed bank was higher when considering only the exotic species, particularly under *C. montana* ( $49 \pm 2.9\%$ ) and in the absence of shrub cover ( $49 \pm 5.7\%$ ). The mean Sørensen coefficient was significantly higher under both these treatments as compared with *P. angustifolia* ( $27 \pm 4.2\%$ ) where similarity remained low ( $F = 8.11$ ;  $P = 0.001$ ).

## DISCUSSION

This study aimed to evaluate whether *P. angustifolia* affects small scale distribution and characteristics of the seed bank within an invaded community. Our results suggest that, in addition to quite large impacts on the established vegetation underneath the invading shrub, *P. angustifolia* has also some discernable impacts on seed bank composition, seed richness and density, as compared with the dominant native shrub *C. montana* and the herbaceous patches.

There is growing evidence suggesting that some established invaders enhance the arrival of other exotic species into the invaded community (Sallabanks 1993; Simberloff & Von Holle 1999; Richardson *et al.* 2000; O'Down *et al.* 2003). In this study, as observed previously (Tecco *et al.* 2006), richness of established woody species (either native or exotic) was positively associated with the canopies of *P. angustifolia*. The exotic tree *L. lucidum*, though abundant throughout the study area, was particularly dominant under the canopies of *P. angustifolia*. However, this likely 'invasional meltdown' between *P. angustifolia* and other exotic woody species within the established vegetation seemed not to be present at the seed bank level. With the exception of some woody species, most of the exotic species present in the soil seed bank were not particularly associated with the invasive shrub but consistently distributed across all treatments. Moreover, seed density of exotic forbs was significantly lower under *P. angustifolia* as compared with the native shrub and the plots without shrub cover. As a result, *P. angustifolia* appears not to be promoting or favouring the dispersal of new species into the seed bank of the community. The invasive shrub would rather be favouring the dispersal and establishment of woody species that do not form a seed bank, such as *L. lucidum*, probably by enhancing seed rain and certainly by providing differential microenvironmental conditions (Tecco *et al.* 2006) and favouring *Ligustrum* sapling survival (Tecco *et al.* 2007).

Contrary to the woody species distribution patterns within the established vegetation, herbaceous species tend to be negatively associated with shrub cover. Mean richness of both native and exotic forbs was higher in the absence of shrub cover than in either shrub treatment, suggesting that there is no 'invasional meltdown' between *P. angustifolia* and the established exotic herbaceous species. Conversely, seed density and richness of native forbs in the seed bank was higher under both shrub treatments than in the absence of shrub cover. This may be related to the fact that patches under shrubs accumulate large and rich seed banks (Aguiar & Sala 1997) because of the high seed output of clumped vegetation, the trapping of wind-dispersed seeds, the protection from predators and deposition by birds using the shrubs as

perches (Keeley 1987; Mull & MacMahon 1996). However, despite this accumulation of large seed banks, as shrubs also modify microenvironmental conditions (Moro *et al.* 1997a) they may restrict the actual number of species able to establish within these conditions. In effect, within-patch gradients of radiation and temperature interact with gradients of litter accumulation and nutrient distribution (Moro *et al.* 1997b) creating a varied environment where different species may find their optimum, be tolerant or be restricted. Accordingly, in our study, most herbaceous species were established in the absence of shrub cover and to a lesser degree under *C. montana*, both treatments with significantly more photosynthetic active radiation and higher soil temperature as compared with microenvironmental conditions under *P. angustifolia* canopies (Tecco *et al.* 2006). This suggests that the established vegetation, rather than the seed bank, would be affected by microenvironmental differences among treatments (i.e. dominance of the shade-tolerant *L. lucidum*). Whether these differences are related to effects on the *in situ* germination and establishment phase clearly deserves investigation.

The presence or absence of species in the seed bank of the study site appears to be consistent with their growth form. It is broadly accepted that a high number of woody species (i.e. trees and shrubs) do not form a seed bank (Ogden 1985; Demel & Granström 1995; Sem & Enright 1995). This could explain the low richness and seed density of woody species observed within the seed bank. The presence, though scarce, of *P. angustifolia* and *L. lucidum* in the seed banks under shrub canopies may be more related to the fact that the soil samples were collected at the time those species were dispersing (Tecco *et al.* 2006). On the other hand, most herbaceous species produce large number of small seeds, which tend to form persistent seed banks (Funes *et al.* 1999). This would in turn explain the dominance of forbs within the seed banks throughout the study site.

As previously observed on grasslands (Thompson & Grime 1979; Bigwood & Inouye 1988; D'Angela *et al.* 1988; Kitajima & Tilman 1996; Luzuriaga *et al.* 2005) and temperate forests (Nakagoshi 1985; Pickett & McDonnell 1989; Schiffman & Johnson 1992; Sem & Enright 1996) species composition of the established vegetation had very low similarity with that of the seed bank. In the present study, this low similarity may be attributable to the absence of the dominant established woody species in the seed bank (i.e. *A. caven*, *C. montana*, *L. lucidum*) and suggests that seed banks are poor predictors of mature vegetation composition and structure in the invaded community. Moreover, it would also suggest that whereas *P. angustifolia* affects both the richness and composition of the established vegetation under its canopy, this effect seems not to be

driven by its additional alteration of the seed bank, but rather related to microenvironmental differences and/or to differential recruitment of species that do not form seed banks.

The overall absence of the dominant woody species in the seed bank together with the dominance of exotic forbs and the high similarity indexes between established exotic species and those present in the seed bank under *C. montana* and in the absence of shrub cover may surely affect community restoration following disturbance. Through a high probability of establishing and dominating in the community, exotic forbs (such as *L. sibiricus*) may well preclude native community restoration following major disturbances such as livestock grazing, logging and fire, frequently observed in the region (Zak & Cabido 2002).

Finally, this study suggests that, although *P. angustifolia* does not exert an invasional meltdown effect at the seed bank level, the soil-stored seed bank would have a limited potential in the restoration of the original vegetation of the area owing to the absence of the dominant species from the mature community and to the dominance of exotic forbs. As a result, any attempt to eradicate *P. angustifolia* should be accompanied with reintroduction of native woody species such as *C. montana*, *Lithrea molleoides*, *Fagara coco*, *Schinus fasciculata*, *Acacia praecox* in order to prevent dominance of exotic herbaceous species within the established vegetation.

## ACKNOWLEDGEMENTS

We thank C. Urcelay, A. Cingolani, N. Perez-Harguindeguy, M Bull and one anonymous reviewer for valuable comments on the manuscript and N. Horak for English review. We are grateful to the Pérez-Harguindeguy family for kindly providing access to the study site. This research was supported by Universidad Nacional de Córdoba, CONICET (research grant to GF and MC and scholarships to PAT and DEG), SECyT-UNC, IAI, Agencia Córdoba Ambiente S.E., CYTED Project XII.5 (Spain) and FONCyT Project 8148.

## REFERENCES

- Aguiar M. R. & Sala O. E. (1997) Seed distribution constrains the dynamics of the Patagonian steppe. *Ecology* **78**, 93–100.
- Bakker J. P., Bakker E. S., Rosén E., Verweil G. L. & Bekker R. M. (1996) Soil seed bank composition along a gradient dry alvar grassland to Juniperus shrubland. *J. Veg. Sci.* **7**, 165–76.
- Bakker J. P. & Berendse F. (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends Ecol. Evol.* **14**, 63–8.



- Baskin C. C. & Baskin J. M. (1998) *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego.
- Belnap J. & Phillips S. L. (2001) Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. *Ecol. Appl.* **11**, 1261–72.
- Bigwood D. W. & Inouye D. W. (1988) Spatial pattern analysis of seed banks: an improved method and optimized sampling. *Ecology* **69**, 497–507.
- Boelcke O. (1992) *Plantas Vasculares de la Argentina: Nativas y Exóticas*. Editorial Hemisferio Sur, Buenos Aires.
- Brown J. S. & Venable D. L. (1986) Evolutionary ecology of seedbank annuals in temporally varying environments. *Am. Nat.* **127**, 31–47.
- D'Angela E., Facelli J. M. & Jacobo E. (1988) The role of the permanent soil seed bank in early stages of a post-agricultural succession in the Inland Pampa, Argentina. *Vegetatio* **74**, 39–45.
- De Fina A. L. (1992) *Aptitud Agroclimática de la República Argentina*. Academia Nacional de Agronomía y Veterinaria, Buenos Aires.
- Delucchi G. (1991) Especies adventicias y naturalizadas nuevas o críticas para la Argentina. *Bolet. Soc. Argent. Bot.* **27**, 179–81.
- Demel T. & Granström A. (1995) Soil seed banks in dry Afromontane forests of Ethiopia. *J. Veg. Sci.* **6**, 777–86.
- Di Rienzo J. C., Robledo W., Casanoves F., Balzarini M. G., González L. A., Guzmán A. W. & Tablada E. M. (2002) *Infostat. Versión Beta. Estadística y Biometría*. Facultad de Ciencias Agropecuarias, Universidad Nacional de Córdoba, Córdoba.
- Escalante M. G., Nájera M. & Galdeano H. L. (1971) Las Especies argentinas del Género *Condalia* (Rhamnaceae). *Revista Museo la Plata, Sección Bot.* **11**, 153–84.
- Funes G., Basconcelo S., Diaz. S. & Cabido M. (1999) Seed size and shape are good predictors of seed persistence in soil in temperate mountain grasslands of Argentina. *Seed Sci. Res.* **9**, 341–5.
- Funes G., Basconcelo S., Díaz. S. & Cabido M. (2001) Edaphic patchiness influences grassland regeneration from the soil seed-bank in mountain grassland of central Argentina. *Austral. Ecol.* **26**, 205–12.
- Funes G., Basconcelo S., Diaz. S. & Cabido M. (2003) Seed bank dynamics in tall-tussock grasslands along an altitudinal gradient. *J. Veg. Sci.* **14**, 253–8.
- Gurvich D. E., Tecco P. A. & Díaz. S. (2005) Plant invasions in undisturbed ecosystems: the triggering attribute approach. *J. Veg. Sci.* **16**, 723–8.
- Harper J. L. (1977) *The Population Biology of Plants*. Academic Press, London.
- Hill M. O. & Gauch H. G. (1980) Detrended correspondence analysis: an improved ordination technique. *Vegetatio* **42**, 47–58.
- Holmes P. (2002) Depth distribution and composition of seed banks in alien-invaded and uninvaded fynbos vegetation. *Austral. Ecol.* **27**, 110–20.
- Holmes P. M. & Cowling R. M. (1997a) The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrublands. *J. Appl. Ecol.* **34**, 317–32.
- Holmes P. M. & Cowling R. M. (1997b) Diversity, composition and guild structure relationships between soil-stored seed banks in mature vegetation in alien plant-invaded South African fynbos shrublands. *Plant Ecol.* **133**, 107–22.
- Hutchings M. J. & Booth K. D. (1996) Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. I. The potential roles of the seed bank and the seed rain. *J. Appl. Ecol.* **33**, 1171–81.
- Keeley J. E. (1987) Role of fire on seed germination on woody taxa in California chaparral. *Ecology* **68**, 434–43.
- Kitajima K. & Tilman D. (1996) Seed banks and seedling establishment on an experimental productivity gradient. *Oikos* **76**, 381–91.
- Kwiatkowska A. J., Spalik E., Michalak A., Palinska K. & Panufnik D. (1997) Influence of the size and density of *Carpinus betulus* on the spatial distribution and rate of deletion of forest-floor species in thermophilous oak forest. *Plant Ecol.* **129**, 1–10.
- Levine J. M., Vilà M., D'Antonio C. M., Dukes J. S., Grigulis K. & Lavorel S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proc. R. Soc.* **270**, 775–81.
- Lichstein J. W., Grau H. R. & Aragón R. (2004) Recruitment limitation in secondary forests dominated by an exotic tree. *J. Veg. Sci.* **15**, 721–8.
- Luti R., Bertrán de Solís M. A., Galera F. M. et al. (1979) Vegetación. In: *Geografía Física de la Provincia de Córdoba* (eds J. Vasquez, R. Miatelo & M. Roqué) pp. 328–34. Boldt, Buenos Aires.
- Luzuriaga A. L., Escudero A., Olano J. M. & Loidi J. (2005) Regenerative role of seed banks following an intense soil disturbance. *Acta Oecologica* **27**, 57–66.
- Mack R. N., Simberloff D., Lonsdale W. M., Evans H., Clout M. & Basal Z. F. A. (2000) Biotic Invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* **10**, 689–710.
- McDonald A. W., Bakker J. P. & Vegelin K. (1996) Seed Bank classification and its importance for the restoration of species-rich flood-meadows. *J. Veg. Sci.* **7**, 157–64.
- Moro M. J., Pugnaire F. I., Haase P. & Puigdefábregas J. (1997a) Effect of the canopy of *Retama sphaerocarpa* on its understorey in a semiarid environment. *Funct. Ecol.* **11**, 425–31.
- Moro M. J., Pugnaire F. I., Haase P. & Puigdefábregas J. (1997b) Mechanisms of interaction between a leguminous shrub and its understorey in a semi-arid environment. *Ecography* **20**, 175–84.
- Mueller-Dombois D. & Ellenberg H. (1974) *Aims and Methods of Vegetation Ecology*. Wiley Intern., New York.
- Mull J. F. & MacMahon J. A. (1996) Factors determining the spatial variability of seed densities in a shrub-steppe ecosystem: the role of harvester ants. *J. Arid Environ.* **32**, 181–92.
- Nakagoshi N. (1985) Buried viable seeds in temperate forests. In: *The Population Structure of Vegetation* (ed. J. White) pp. 551–70. Junk, Dordrecht.
- Novara L. (1993) Rosaceae. Flora del Valle de Lerma. *Aportes Botánico Salta, Flora* **2**, 1–44.
- O'Down D. J., Green P. T. & Lake P. S. (2003) Invasional 'meltdown' on an oceanic island. *Ecol. Lett.* **6**, 812.
- Ogden J. (1985) An introduction to plant demography with special reference to New Zealand tress. *NZ. J. Bot.* **23**, 751–72.
- Panetta F. D. & Sparkes E. C. (2001) Reinvasion of a riparian forest community by an animal-dispersed tree weed following control measures. *Biol. Invasions* **14**, 75–88.
- Peco B., Ortega M. & Levassor C. (1998) Similarity between seed bank and vegetation in Mediterranean grassland: a predictive model. *J. Veg. Sci.* **9**, 815–28.
- Pickett S. T. A. & McDonnell M. J. (1989) Seed Bank Dynamics in Temperate Deciduous Forest. In: *Ecology of Soil Seed*

- Banks* (eds M. A. Leck, V. Thomas Parker & R. L. Simpson) pp. 123–47. Academic Press, Inc., San Diego.
- Pugnaire F. & Lázaro R. (2000) Seed bank and understory species composition in a semi-arid environment: the effects of shrub age and rainfall. *Ann. Bot.* **80**, 807–13.
- Richardson D. M., Allsopp N., D'Antonio C., Milton S. J. & Rejmánek M. (2000) Plant invasions—the role of mutualism. *Biol. Rev.* **75**, 65–93.
- Sallabanks R. (1993) Fruiting plant attractiveness to avian seed dispersers: native vs. invasive *Crataegus* in western Oregon. *Madroño* **40**, 108–16.
- Schiffman P. M. & Johnson W. C. (1992) Sparse buried seed bank in a southern Appalachian Oak forest: implications for succession. *Am. Midl. Nat.* **127**, 258–67.
- Sem G. & Enright N. J. (1995) Soil seed bank in *Agathis australis* (D. Don) Lindl. (kauri) forests of northern New Zealand. *N.Z. J. Bot.* **33**, 221–35.
- Sem G. & Enright N. J. (1996) The relationship between seed rain and the soil seed bank in a temperate rainforest stand near Auckland, New Zealand. *N.Z. J. Bot.* **24**, 215–126.
- Simberloff D. & Von Holle B. (1999) Positive interactions of nonindigenous species: invasional meltdown?. *Biol. Invasions* **1**, 21–32.
- Tecco P. A., Díaz. S., Gurvich D. E., Perez-Harguindeguy N., Cabido M. & Bertone G. A. (2007) Experimental evidence of facilitation and interference underlying the positive association between two woody invaders. *Pyracantha angustifolia* and *Ligustrum lucidum*. *Appl. Veg. Sci.* **10**, 211–18.
- Tecco P. A., Gurvich D. E., Díaz. S., Perez-Harguindeguy N. & Cabido M. (2006) Positive interaction between invasive plants: the influence of *Pyracantha angustifolia* on the recruitment of native and exotic woody species. *Austral. Ecol.* **31**, 293–300.
- Ter Heerdt G. N. J. T., Verweis G. L., Bekker R. M. & Bakker J. P. (1996) An improved method for seed banks analysis: seedlings emergence after removing the soil by sieving. *Funct. Ecol.* **10**, 144–51.
- Thompson K. (1986) Small-scale heterogeneity in the seed bank of an acidic grassland. *J. Ecol.* **74**, 733–8.
- Thompson K. & Grime J. P. (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *J. Ecol.* **67**, 893–921.
- Vilà M. & Gimeno I. (2007) Does invasion by an alien plant species affect the soil seed bank? *J. Veg. Sci.* **18**, 423–30.
- Warr S. J., Thompson K. & Kent M. (1993) Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. *Prog. Phys. Geogr.* **17**, 329–47.
- Williamson M. (1996) *Biological Invasions*. Chapman & Hall, London.
- Zak M. R. & Cabido M. (2002) Spatial patterns of the Chaco vegetation of central Argentina: integration of remote sensing and phytosociology. *Appl. Veg. Sci.* **5**, 213–26.
- Zar J. H. (1999) *Biostatistical Analysis*, 4th edn. Prentice Hall, Upper Saddle.
- Zuloaga F. O. & Morrone O. (1996) Catálogo de las Plantas Vasculares de la República Argentina. *Monogr. Syst. Bot. Missouri Botanical Garden* **60**, 1–323.
- Zuloaga F. O. & Morrone O. (1999) Catálogo de las Plantas Vasculares de la República Argentina. *Monogr. Syst. Bot. Missouri Botanical Garden* **74**, 1–1269.
- Zuloaga F. O., Nicora E. G., Rúgolo de Agrasar Z. E., Morrone O., Pensiero J. & Cialdella A. M. (1994) Catálogo de la Familia Poaceae en la República Argentina. *Monogr. Syst. Bot. Missouri Botanical Garden* **47**, 1–178.