



Original article

Soil ecosystem function under native and exotic plant assemblages as alternative states of successional grasslands

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ABSTRACT

Old fields often become dominated by exotic plants establishing persistent community states. Ecosystem functioning may differ widely between such novel communities and the native-dominated counterparts. We evaluated soil ecosystem attributes in native and exotic (synthetic) grass assemblages established on a newly abandoned field, and in remnants of native grassland in the Inland Pampa, Argentina. We asked whether exotic species alter soil functioning through the quality of the litter they shed or by changing the decomposition environment. Litter decomposition of the exotic dominant *Festuca arundinacea* in exotic assemblages was faster than that of the native dominant *Paspalum quadrifarium* in native assemblages and remnant grasslands. Decomposition of a standard litter (*Triticum aestivum*) was also faster in exotic assemblages than in native assemblages and remnant grasslands. In a common garden, *F. arundinacea* showed higher decay rates than *P. quadrifarium*, which reflected the higher N content and lower C:N of the exotic grass litter. Soil respiration rates were higher in the exotic than in the native assemblages and remnant grasslands. Yet there were no significant differences in soil N availability or net N mineralization between exotic and native assemblages. Our results suggest that exotic grass dominance affected ecosystem function by producing a more decomposable leaf litter and by increasing soil decomposer activity. These changes might contribute to the extended dominance of fast-growing exotic grasses during old-field succession. Further, increased organic matter turnover under novel, exotic communities could reduce the carbon storage capacity of the system in the long term.

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1. Introduction

The successional re-assembly of plant communities in abandoned agricultural fields often leads to the establishment of “novel ecosystems” dominated by invasive exotic species (Suding et al., 2004; Hobbs et al., 2006). Exotic plant assemblages may create persistent vegetation states (Seabloom et al., 2003; Kulmatiski, 2006), which are not only resistant to native community restoration (Suding et al., 2004; Cramer et al., 2008), but may also produce fundamental shifts in ecosystem functioning (Ehrenfeld, 2003, 2010; Kardol and Wardle, 2010). While novel plant assemblages are a major feature of modern anthropogenic landscapes (Hobbs et al.,

2006; Ellis et al., 2012), little is known about their functional attributes, compared to the alternative, native plant-dominated counterparts (Wilsey et al., 2009).

The extirpation of native dominant plants by habitat loss and fragmentation (Tilman et al., 1997) creates ‘vacant’ niches, which can be filled by exotic species with various strategies (MacDougall and Turkington, 2005; Tognetti et al., 2010). Invasive exotics may replace functionally equivalent native species or may bring different resource-use attributes (D’Antonio and Hobbie, 2005; MacDougall et al., 2009), with the potential to alter key ecosystem processes like litter decomposition and nutrient cycling (Vitousek et al., 1997; Evans et al., 2001; Ashton et al., 2005; Ehrenfeld, 2003; Liao et al., 2008). Organic matter decomposition returns available nutrients to plants and heterotrophic consumers, thus linking aboveground and belowground ecosystem dynamics (Wardle et al., 2004). Decomposition rates are controlled by the quality and quantity of plant litter inputs (Aerts, 1997; Cornwell et al., 2008; Bontti et al., 2009) and by the soil environment, including soil physico–chemical properties, decomposer communities, and microclimatic conditions created by established plants

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(Chapin et al., 2002; Quested et al., 2007). Exotic plants may influence any of these attributes, initiating positive feedback mechanisms (Wedin and Tilman, 1990; Kardol and Wardle, 2010) that may facilitate the long-term persistence of exotic species mixtures. Furthermore, vegetation–soil interactions under established exotic assemblages could impact on whole-ecosystem processes such as carbon storage and nutrient retention (Ehrenfeld, 2010).

There is increasing empirical evidence that invasive plant species frequently enhance litter decomposition. Ehrenfeld (2003) found that exotic species produced higher quality litter (e.g. low tissue C:N) and had faster decomposition rates than the natives species they replaced. A meta-analysis of 94 invasion studies showed that exotic plants significantly altered C and N fluxes and pools, leading to increases in net primary productivity and litter decomposition (Liao et al., 2008). However, in comparing decay rates for 19 pairs of co-familial native and exotic species, Godoy et al. (2010) observed that exotics decomposed more slowly than natives due to their greater foliar lignin content. Thus, the direction of exotic plant effects on decomposition and nutrient cycling may not be always predictable (Ehrenfeld, 2003; Simberloff, 2011).

Most studies to date have compared patterns of energy flow and nutrient cycling in long-term invaded versus non-invaded sites (Ehrenfeld, 2010; Simberloff, 2011). This approach confounds effects from plant compositional shifts with those associated with site conditions, therefore yielding little insight on the time scales and mechanisms underlying the ecosystem impacts of invaders (Levine et al., 2003). In particular, comparative studies fail to distinguish the direct effects of exotic plants on soil processes induced by changes in litter quality, from the indirect effects mediated by altered biotic or abiotic soil conditions (Belnap et al., 2005; Quested et al., 2007). Understanding ecosystem functioning under alternative, exotic versus native-dominated community states would be essential in setting management priorities for restoration (Heneghan et al., 2008; Seastedt et al., 2009; Kardol and Wardle, 2010).

Land-use changes have caused the pervasive loss of native grasslands throughout North and South America (Samson and Knopf, 1994; Gibson, 2009; Vega et al., 2009). Two major examples are the central prairies of the United States and the pampas of eastern Argentina. In these systems, the once-common, C₄ grass-dominated plant communities have been reduced to small fragments embedded in a landscape matrix of crop fields, pastures and woodlots (Ghersa and León, 1999; Burkart et al., 2011). In the Inland Pampa, native perennial grasses are rarely found in newly abandoned fields, which are swiftly invaded by fast-growing, exotic C₃ grasses with the ability to establish persistent communities' (Omacini et al., 1995; Tognetti et al., 2010). Recent experiments show that, depending on the initial seed bank composition, either exotic or native grass-dominated assemblages may develop during old-field succession (Tognetti and Chaneton, unpublished). This scenario offers an opportunity to examine how dominance by native or exotic grasses might determine contrasting ecosystem attributes during vegetation recovery on a common soil substrate.

We studied soil ecosystem functioning under experimentally established (synthetic) plant assemblages of exotic or native perennial grasses and in remnants of native grassland in the Inland Pampa, Argentina. Our main goal was to determine whether dominance by invasive exotic grasses alters carbon and nutrient cycling through the quality of the litter they shed or by changing the soil environment for decomposition. Specifically, we tested the following hypotheses: (1) exotic grass assemblages stimulate ecosystem processes at the plant–soil interface, leading to higher organic matter turnover and nutrient cycling than in native grass assemblages; (2) dominant exotic species accelerate decomposition

by changing both the quality of litter inputs and the soil biotic and physical conditions for decomposition; and (3) prior cultivation history determine persistent differences in soil functional attributes between native assemblages in old fields and remnant grasslands.

To disentangle the short-term effects of grass litter substrate and soil decomposition environment, we assessed litter decomposition for the dominant native and exotic grasses in their own (synthetic) assemblages and in a common garden, and also for a standard litter incubated in the native and exotic assemblages (Fig. 1). Soil functional attributes were also compared between the experimental assemblages and remnants of native grassland, which provided a reference condition for the uncultivated system. Similarity of soil processes under synthetic and remnant grassland patches would imply that recovery of native grass dominance on abandoned land is sufficient to restore some ecosystem functions, at least in the short term.

2. Materials and methods

2.1. Study area

The study was conducted at “Estancia San Claudio”, a farm owned by the University of Buenos Aires, located in the eastern Inland Pampa, Buenos Aires province, Argentina (35° 56' S–61° 12' W). The climate is subhumid, with a mean annual rainfall of 1030 mm, distributed throughout the year. Mean monthly temperatures range from 24 °C in January to 7 °C in July. The dominant soil is a sandy-loam Typic Hapludoll, with a deep and well-drained upper horizon. The original grassland vegetation has been replaced by crop fields and sown pastures (Soriano, 1992). Semi-natural grasslands occur in old fields, where succession gives way to communities dominated by a few exotic grasses (Omacini et al., 1995; Tognetti et al., 2010). Major invasive grasses comprise *Festuca arundinacea*, *Dactylis glomerata*, *Lolium multiflorum*, *Sorghum halepense*, and *Cynodon dactylon*, which may account for over 70% of the plant cover and may establish persistent communities for at least 20 years of succession (Tognetti et al., 2010). Native perennial grasses can be re-introduced by seed addition after removal of the exotic cover (Tognetti and Chaneton, 2012). Remnants of native tussock grassland are presently found in small fragments and corridors along roadsides and abandoned rail lines. These remnants are often dominated by the tall tussock grass *Paspalum quadrifarium*, and comprise a species-rich ensemble of native grasses and forbs (Chaneton et al., 2004; Burkart et al., 2011).

2.2. Experimental design

We assessed several soil functional attributes in exotic- and native-dominated, synthetic assemblages and in remnants of native tussock grassland (Table 1; Fig. 1). The synthetic assemblages were experimentally established from seed during the first year of succession within a 2-ha fallow field. The site had remained under row-crop agriculture for more than 50 years. The remnant grasslands were represented by three corridor fragments (~40-m long × 60-m wide) located within 10 km from the old-field site along a railway track abandoned in the mid 1970s. Since then, they have been only lightly disturbed by sporadic burns. Study remnants were dominated by *P. quadrifarium* with a total aboveground biomass of c.1700 g m⁻² (Table 1; Chaneton et al., 2004).

In May 2005, shortly after the soybean crop harvest, we established six blocks, each containing two 1.5 m × 2.5 m experimental plots, separated by 1-m wide walkways. The plots within a block were randomly assigned to receive a five-species mix of either native or exotic perennial grasses. Plots were sown at a total density

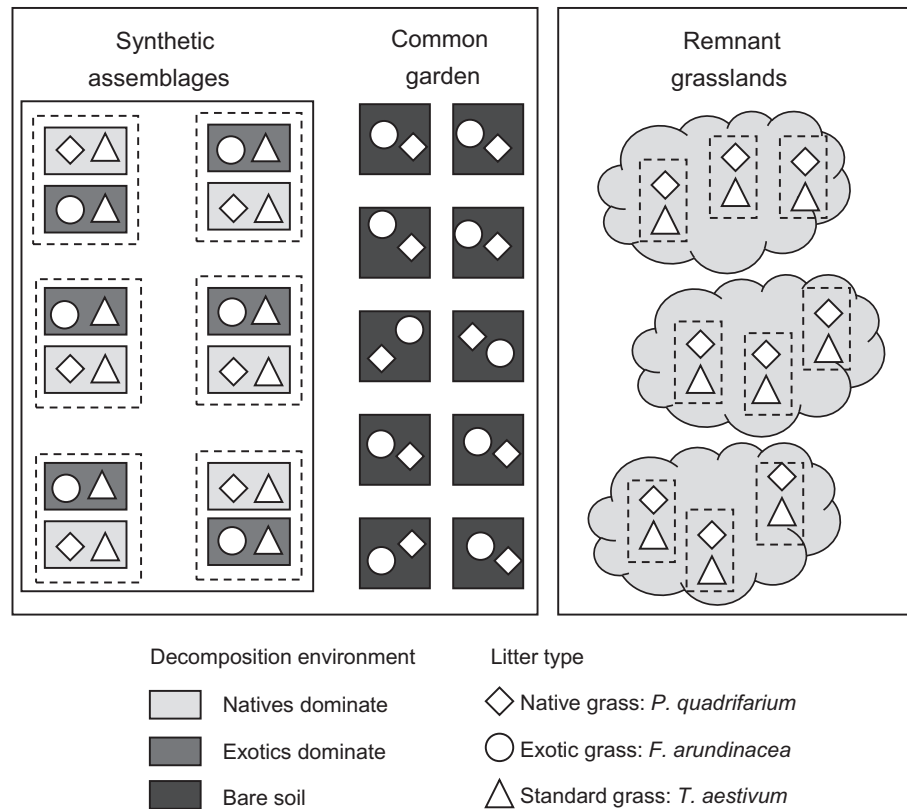


Fig. 1. Schematic diagram of the litterbag experiments. Synthetic assemblages were established from seeds (6 blocks) using a mixture of five exotic or native perennial grasses, but were effectively dominated by *Festuca arundinacea* or *Paspalum quadrifarium*, respectively. The common garden comprised 10 plots, where both grasses decomposed under equal environmental conditions. The remnant grassland fragments involved 3 sites and each contained three sub-replicates of both litter types.

of 2000 viable seeds m^{-2} (400 viable seeds per species; Table 1). This sowing density was sufficient to swamp the local seed bank and homogenize replicate plots within treatments. Selected exotic and native grasses were common constituents of old-field and remnant grasslands, respectively (Tognetti et al., 2010; Burkart

et al., 2011). Seeds were collected from natural populations in the study area. Walkways were maintained by herbicide application and mowing. For two years (2006–2007), we visually estimated plant species cover at the whole-plot scale (Tognetti, 2010). While both the exotic and native assemblages initially comprised C_3 and C_4 species, after three years of succession (2008) they had diverged into well-defined, alternative states dominated by *F. arundinacea* (C_3) or *P. quadrifarium* (C_4) (Table 1). Therefore, we decided to focus on these two species for the decomposition experiments. In spring 2007, synthetic assemblages did not significantly differ in total aboveground biomass (exotic: $1674 \pm 118 \text{ g m}^{-2}$, native: $1823 \pm 119 \text{ g m}^{-2}$; paired $t = 0.71$, $p = 0.51$, $df = 5$). Standing dead and litter material accounted for nearly 70% of the aboveground plant biomass in both assemblage types ($p = 0.30$; Tognetti, 2010).

To study the influence of litter quality and local environment on decomposition, we performed three litterbag experiments (Fig. 1; e.g. Austin and Vitousek, 2000; Quested et al., 2007). (i) In the “home plot” experiment, litter of the dominant grass species was set to decompose under its own synthetic assemblage (exotic or native) or remnant grassland fragment. *F. arundinacea* was used as exotic litter and *P. quadrifarium* as native litter. (ii) In the “standard litter” experiment, a common substrate was incubated in both the exotic and native assemblages, and in the remnant fragments. This allowed us to assess the role of decomposition environment, independent of litter quality. We used wheat straw (*Triticum aestivum*) as standard litter substrate. In both these experiments the vegetation was left intact. (iii) In the “common garden” experiment, litter of *P. quadrifarium* and *F. arundinacea* were incubated in ten $2 \text{ m} \times 2 \text{ m}$ plots established within 50 m of the synthetic assemblages. In each common plot, we removed the aerial vegetation and gently raked the soil to ensure soil contact with the litterbags. Plots

Table 1

Relative abundance of major species in experimentally established (synthetic) exotic and native plant assemblages, and in remnants of native tussock grassland in the Inland Pampa, Argentina. Values show mean relative cover (%), with standard errors in parenthesis ($n = 6$ for synthetic assemblages, and $n = 7$ for remnant grasslands).

Species name	Functional type	Exotic assemblages	Native assemblages	Remnant grasslands
Exotic species				
<i>Festuca arundinacea</i>	C_3	71.4 (2.1)		14.1 (1.7)
<i>Dactylis glomerata</i>	C_3	26.6 (3.5)		
<i>Phalaris aquatica</i>	C_3	1.6 (0.8)		
<i>Sorghum halepense</i>	C_4	0.4 (0.2)	2.1 (0.7)	9.3 (2.9)
<i>Cynodon dactylon</i> ^b	C_4	–		
All exotics		100 (6.6)	2.1 (0.7)	23.4(4.6)
Native species				
<i>Paspalum quadrifarium</i>	C_4		48.3 (10.5)	47.4 (3.9)
<i>Briza subaristata</i>	C_3		41.6 (3.2)	0
<i>Melica brasiliana</i>	C_3		5.6 (1.1)	0
<i>Schizachirium scoparia</i>	C_4		2.9 (0.7)	0
<i>Bothriochloa laguroides</i> ^b	C_4		–	0
<i>Stipa filiculmis</i> ^a	C_3			17.1(5.8)
<i>Eryngium spp</i> ^a	C_3			7.0 (4.8)
<i>Panicum bergii</i> ^a	C_4			5.1 (2.9)
All natives			98.4 (15.4)	76.8 (17.4)

^a Native species not sown in native assemblages.

^b Species sown with the initial mixture that failed to establish in the designated plots. Zero values (0) denote species present in the local community but not in the quadrat samples.

were weeded to prevent plant regrowth. This experiment provided a homogeneous environment to isolate the effect of litter type on decomposition (Quested et al., 2007).

The three experiments were conducted simultaneously between April 2008 and November 2009. Litter decomposition rates were estimated allowing for sequential litterbag harvests after 1, 3, 6 and 12 months of field incubation. For the home plot and standard litterbag experiments, in each synthetic assemblage we placed four litterbags of the dominant species (*P. quadrifarium* or *F. arundinacea*) and four wheat litterbags (Fig. 1). The full design comprised 2 litter types \times 4 harvest dates \times 2 assemblages \times 6 blocks = 96 litterbags. In each grassland fragment, we incubated *P. quadrifarium* and wheat litterbags, for a total of 2 litter types \times 3 subsamples \times 4 harvest dates \times 3 fragments = 72 litterbags. We included three subsamples of each litter type per harvest date to increase the level of replication, because native remnants were uncommon in the study area. The full design of the common garden experiment included 2 litter types \times 4 harvest dates \times 10 blocks = 80 litterbags. Litterbags were anchored to the soil using wire pins, and were randomly placed in a grid pattern within each experimental plot, leaving 5–10 cm between adjacent bags.

Litterbags were made of 10 cm \times 20 cm fiberglass screen (2 mm mesh) and contained 2 g of air-dried leaf litter. The litter material was collected in August 2007 from old-field and remnant grasslands within the study area. Only recently senesced leaf material was used in the experiments. Subsamples of each litter type ($n = 5$) were used to calculate initial moisture and ash contents after ignition at 500 °C for 4 h. Initial carbon (C) and nitrogen (N) content in the litter were measured ($n = 6$) using a TrueSpec elemental analyzer (LECO®, St. Joseph, Mich., United States). Specific C fractions (sugar, hemicellulose and lignin) were determined by successive extractions with neutral and acid detergent reactions (Van Soest, 1963). These data were used to calculate various standard predictors of litter decomposability, including C:N and lignin:N ratios (e.g., Dorrepaal et al., 2005). The litter remaining in each harvest date was gently brushed to remove soil particles and oven-dried (70 °C, 48 h) for dry mass determination. Percent ash content was determined for each litter sample and harvest, and the litter mass loss was then expressed on an ash-free basis (Harmon et al., 1999). For each field plot and litter type, the decomposition rate (k) was determined by fitting the litter mass data to a single exponential decay model of the form, $\ln(M_t/M_0) = -kt$, where M_0 is the initial dry mass, M_t is the dry mass remaining at time t , and k is the decomposition constant (Swift et al., 1979; Wieder and Lang, 1982). Overall, the negative exponential decay model adequately described litter mass loss dynamics in the experiments (mean $r^2 = 0.70$; $p < 0.05$).

Soil respiration was measured in the synthetic grass assemblages and remnant grasslands in October and November 2008 (spring) and March and April 2009 (autumn) using a portable closed-flow gas exchange system (EGM-4, PP Systems, Hitchin, United Kingdom) equipped with a 850 cm³ cylindrical chamber (area: 40.7 cm²). Measurements were taken by first sampling for ambient CO₂ concentrations and then pushing the chamber on a bare soil spot in-between plants to ~1 cm depth. Where necessary, the surface soil litter was pushed aside. Care was taken not to disturb the soil to prevent artificially rising the soil CO₂ flux. We took three subsamples within each plot and then averaged these values to obtain one value per plot and sampling date.

Soil mineral nitrogen content (NH₄⁺-N and NO₃⁻-N) was measured in the synthetic assemblages and remnant grasslands in May and October 2008 and in April 2009. Soil samples were extracted using a 2 N KCl solution within one day of collection; extracts were assessed colorimetrically in an AlpKem® autoanalyser (O-I Analytical, Corvallis, Oregon, United States). A subsample was

oven-dried at 105 °C (48 h) to determine the soil gravimetric water content; soil N concentrations were expressed on a soil dry mass basis. Net nitrogen mineralization was measured during October–November (spring) 2009 using the *in situ* soil core incubation method (Robertson et al., 1999). A 5 cm-diameter PVC tube was buried to 10 cm depth at the center of each plot and sealed with a plastic top. Pre- and post-incubation soil samples were taken from outside and inside the tube, respectively, using a 2.5 cm-diameter soil corer. Samples were extracted with a KCl solution to calculate net ammonification, nitrification and total N mineralization rates, as the difference in content of each N fraction between the initial and the 30-day incubated soil samples.

Lastly, soil temperature was measured in the synthetic assemblages between April 2008 and October 2009. Temperature was recorded to 5 cm-depth at hourly intervals using TC 1047A thermocouples (Microchip Inc) placed at the center of each plot and connected to a datalogger (Cavadevices, Buenos Aires, Argentina). Data were used to calculate soil mean daily temperature and thermal amplitude throughout the experiment. Logistics preclude us from simultaneously measuring soil temperatures in the remnant grassland fragments.

2.3. Data analysis

Differences in initial litter chemistry between the native and exotic grass species were examined through analysis of variance (ANOVA). Decomposition constants (k) and the mean litter mass remaining for *F. arundinacea* and *P. quadrifarium* after 12 months of incubation in the “home plot” and “common garden” experiment were compared using one-way, blocked ANOVA, followed by Bonferroni adjusted pairwise tests. Patterns in decomposition of *T. aestivum* litter across environments (native and exotic assemblages, and remnant fragments) were evaluated separately using one-way, blocked ANOVA followed by Bonferroni tests.

Soil respiration rates, gravimetric water contents, and mineral N levels were analyzed using repeated-measures ANOVA with blocks, including the plant community as between-subjects factor and the sampling date as repeated measure. When the assumption of sphericity was not met, separate one-way, blocked ANOVAs were performed for each sampling date. Data were transformed as necessary to meet assumptions of ANOVA. All analyses were implemented in InfoStat 2004 (InfoStat Group, Universidad Nacional de Córdoba, Argentina).

3. Results

3.1. Litter decomposition

In the home plot experiment, litter decomposition of the exotic *F. arundinacea* was faster than that of the native *P. quadrifarium* in the native assemblages and remnant grasslands (Fig. 2a). Decomposition rate (k) of the dominant grass species was nearly one order of magnitude higher in the exotic assemblage ($1.24 \pm 0.35 \text{ year}^{-1}$) than in the native assemblage ($0.35 \pm 0.12 \text{ year}^{-1}$) ($F_{1, 11} = 5.08$, $p = 0.04$). There was no significant difference in decomposition rates of *P. quadrifarium* between synthetic assemblages and remnant grasslands ($k_{\text{remnant}} = 0.44 \pm 0.07 \text{ year}^{-1}$; $F_{1, 12} = 0.32$, $p = 0.58$). As a result, the litter mass remaining after one year was significantly lower for *F. arundinacea* in its home plot than for *P. quadrifarium* in either the native assemblages or remnant grasslands ($F_{2, 18} = 22.27$, $p < 0.0001$; Fig. 2a).

The standard litter material (*T. aestivum*) decomposed faster ($F_{1, 9} = 5.69$, $p = 0.04$) in the exotic than in the native synthetic assemblages ($k = 1.14 \pm 0.12 \text{ year}^{-1}$ vs. $0.64 \pm 0.16 \text{ year}^{-1}$, respectively). This resulted in wheat litter mass loss after one year

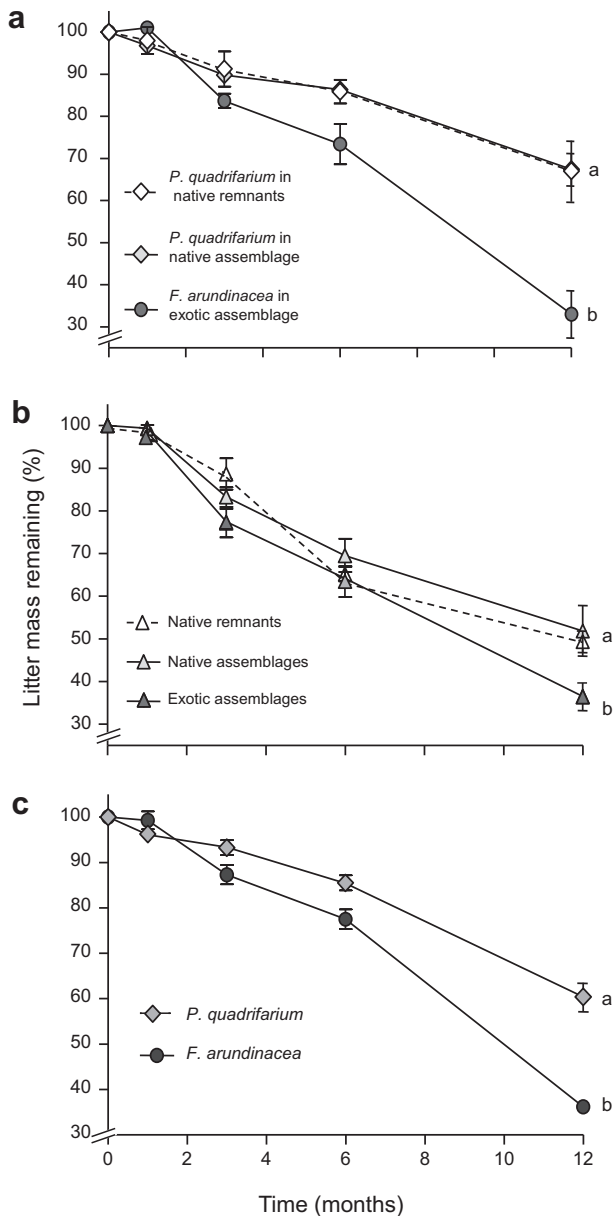


Fig. 2. (a) Litter mass loss for the dominant grasses *Festuca arundinacea* (exotic) and *Paspalum quadrifarium* (native) when incubated separately under exotic and native plant assemblages, respectively (means \pm 1 SE, $n = 6$), and for *P. quadrifarium* in remnant grassland fragments ($n = 3$). (b) Litter mass loss for *Triticum aestivum* incubated in native and exotic assemblages (mean \pm 1 SE, $n = 5$) and in remnant grassland fragments ($n = 3$). (c) Litter mass loss for the exotic *F. arundinacea* and the native *P. quadrifarium* in the common garden experiment (means \pm 1 SE, $n = 10$). Significant differences ($p < 0.05$) at the final harvest are denoted by different letters.

being greater in the exotic (62%) than in the native (48%) assemblages (Fig. 2b). In contrast, *T. aestivum* decomposition rate did not differ between native-dominated synthetic assemblages and remnant grasslands ($k_{\text{remnant}} = 0.74 \pm 0.04 \text{ year}^{-1}$; $F_{1, 11} = 0.66$, $p = 0.43$; Fig. 2b).

Table 2
Initial leaf litter chemistry for *Festuca arundinacea* (exotic) and *Paspalum quadrifarium* (native). Values are means with standard errors in parenthesis ($n = 5$). Different superscript letters indicate significant differences ($p < 0.05$) between species.

Species	% N	% C	% sugar	% hemicell	% lignin	Lignin:N	C:N
<i>Festuca arundinacea</i>	0.80 ^a (0.02)	42.92 ^a (0.35)	54.48 ^a (0.03)	39.92 ^a (0.02)	5.13 ^a (0.30)	6.44 ^a (0.33)	53.97 ^a (1.09)
<i>Paspalum quadrifarium</i>	0.63 ^b (0.03)	47.27 ^b (0.20)	36.39 ^b (0.09)	25.06 ^b (0.07)	4.82 ^a (0.08)	7.81 ^a (0.50)	77.83 ^b (4.26)

In the common garden experiment, the decomposition rate of *F. arundinacea* litter was significantly higher than that of *P. quadrifarium* litter ($k = 1.01 \pm 0.02 \text{ year}^{-1}$ vs. $0.54 \pm 0.05 \text{ year}^{-1}$, respectively; $F_{1, 19} = 53.34$, $p < 0.001$). Litter mass loss after one year of incubation in the common garden was nearly 60% for *F. arundinacea*, but only 30% for *P. quadrifarium* ($F_{1, 19} = 59.1$, $p = 0.001$; Fig. 2c).

3.2. Litter chemistry

Litter chemistry differed widely between species (Table 2). Litter of *P. quadrifarium* had a lower sugar content ($F_{1, 11} = 16.18$, $p = 0.002$) and N content ($F_{1, 11} = 20.57$, $p = 0.001$), and a higher C content ($F_{1, 11} = 84.91$, $p < 0.0001$) than litter of *F. arundinacea*. Consequently, the C:N ratio of the native grass litter was substantially higher than that of the exotic grass ($F_{1, 11} = 22.04$, $p = 0.001$; Table 2). Lignin content and lignin:N ratio did not differ between the two grass species (both $p > 0.05$; see Table 2).

3.3. Soil attributes

Soil respiration increased from mid spring to late summer (October to March), before declining again in mid autumn (April) in all three communities (Fig. 3). Soil respiration rates in the exotic assemblage were significantly higher than in the native assemblage throughout the study ($F_{1, 11} = 18.9$, $p = 0.001$). Soil respiration did not generally differ between the native assemblages and remnant grasslands ($p > 0.05$), except for a small difference in early spring ($F_{1, 8} = 6.99$, $p = 0.03$; Fig. 3).

Patterns in standing soil mineral N depended on the ion form. Soil available N was mostly found as $\text{NH}_4^+ - \text{N}$, which occurred at significantly higher concentrations in synthetic assemblages than in remnant grasslands (May $F_{2, 15} = 5.55$, $p = 0.01$; October $F_{2, 15} = 6.9$, $p = 0.009$), except in autumn (April $p = 0.76$; Fig. 4a). On average, $\text{NO}_3^- - \text{N}$ accounted for 0.4–1.8% (synthetic assemblages) and 4.5–20.2% (remnant grasslands) of the soil mineral N, but $\text{NO}_3^- - \text{N}$ levels were too variable and showed no significant pattern ($p > 0.10$). As a result, total available N did not differ across communities in May and April, but was higher under synthetic assemblages than in remnant grasslands in spring (October $F_{2, 15} = 6.18$, $p = 0.01$; Fig. 4a). Soil gravimetric water content was lower in the exotic assemblages than in the native assemblages and remnant fragments throughout the study (May $F_{2, 16} = 5.35$, $p = 0.02$; October $F_{2, 16} = 2.25$, $p = 0.01$; April $F_{2, 16} = 1.11$, $p = 0.03$; Fig. 4b).

Mean soil temperature did not differ between synthetic grass assemblages ($p > 0.05$), but soil thermal amplitude was significantly reduced in the exotic assemblages, compared to the native ones (Table 3). Net N mineralization and net ammonification rates were similar under the exotic and native assemblages and, on average, tended to be higher in synthetic grass assemblages than in remnant grasslands (Table 3). Still, these differences were not statistically significant (p values > 0.05).

4. Discussion

The emergence of anthropogenic ecosystems based on novel mixtures of exotic species is one of the major consequences of land-

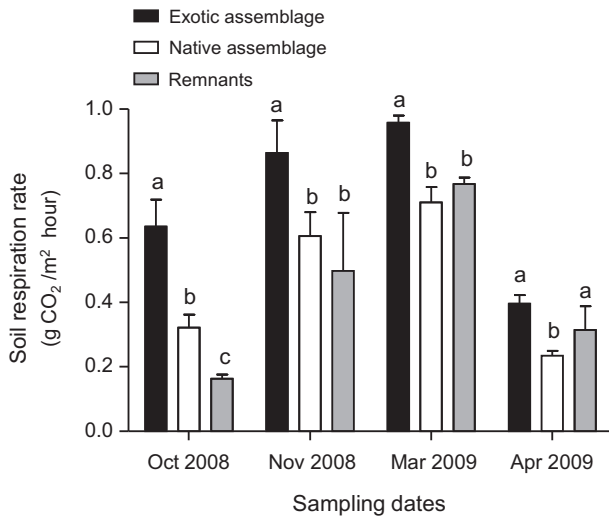


Fig. 3. Soil respiration rates ($\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) measured under native and exotic grass assemblages (means \pm 1 SE, $n = 6$) and in remnant grassland fragments ($n = 3$). Different letters show significant differences ($p < 0.05$) within sampling dates.

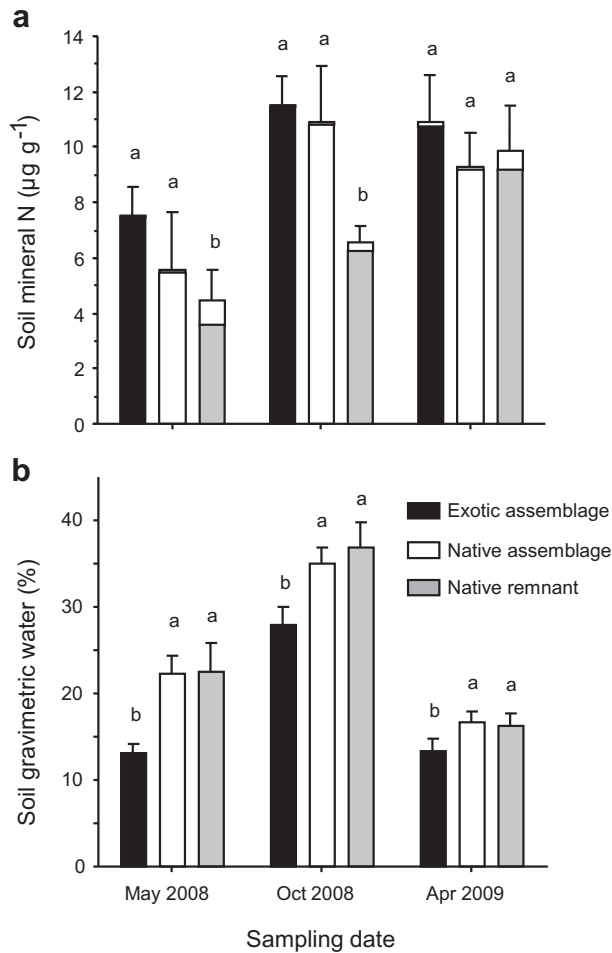


Fig. 4. Soil mineral nitrogen (a) and gravimetric water content (b) under native and exotic grass assemblages (mean \pm SE, $n = 6$) and in remnant grassland fragments ($n = 3$). In panel (a), split bars denote $\text{NH}_4^+ \text{-N}$ (bottom) and $\text{NO}_3^- \text{-N}$ (top) fractions. Different letters show significant differences ($p < 0.05$) within sampling dates; only for $\text{NH}_4^+ \text{-N}$ in panel (a).

Table 3

Soil temperature regime (yearly) and net nitrogen mineralization rates (spring) in the synthetic, native and exotic grass assemblages, and in the remnant grassland fragments. Values are means with standard errors in parenthesis. Different superscript letters indicate significant differences ($p < 0.05$) between sampling sites. n/d: no data.

Soil attribute	Exotic assemblages ($n = 6$)	Native assemblages ($n = 6$)	Remnant grasslands ($n = 3$)
Mean daily temperature ($^{\circ}\text{C}$)	14.6 (2.3)	14.7 (2.5)	n/d
Thermal amplitude ($^{\circ}\text{C}$)	3.8 (0.6) ^a	7.1 (1.3) ^b	n/d
Net nitrification ($\mu\text{g NO}_3^- \text{ g}^{-1} \text{ mo}^{-1}$)	0.005 (0.007)	-0.001 (0.004)	-0.011 (0.011)
Net ammonification ($\mu\text{g NH}_4^+ \text{ g}^{-1} \text{ mo}^{-1}$)	0.104 (0.094)	0.192 (0.138)	0.016 (0.073)
Net N mineralization ($\mu\text{g N g}^{-1} \text{ mo}^{-1}$)	0.109 (0.100)	0.190 (0.142)	0.005 (0.078)

use changes worldwide (Vitousek et al., 1997; Hobbs et al., 2006; Ellis et al., 2012). These novel plant assemblages are common in abandoned fields, especially where recovery of native vegetation is limited by dispersal and propagule availability (MacDougall and Turkington, 2005; Cramer et al., 2008). In the Inland Pampa, old-field communities typically become dominated by fast-growing exotic grasses within a few years of succession (Omaccini et al., 1995; Tognetti et al., 2010). We found that ecosystem function diverged between exotic and native grass-dominated assemblages established from seed on the same soil substrate. Exotic grass assemblages accelerated litter decomposition by producing a more decomposable leaf litter and through increased soil decomposer activity, relative to their native-dominated counterparts. These patterns are consistent with previous analyses evaluating the ecosystem-level impacts of invasive exotic plants (Ehrenfeld, 2003, 2010; Liao et al., 2008). The focal exotic grasses in this study are also problematic invaders in other grassland regions (e.g., Cully et al., 2003; Gibson, 2009; Wilsey et al., 2009), which increases the scope of our findings for understanding the functional consequences of invasions. Observed differences in vegetation–soil interactions may have implications for the extended dominance of exotic grasses in successional fields, and the ecosystem services provided by semi-natural grasslands (see Kardol and Wardle, 2010).

Consistent with our first hypothesis, *in situ* decomposition of dominant species' litter was higher in exotic than in native assemblages. This result adds to previous work showing that invaded systems generally support faster decomposition rates than non-invaded, native-dominated communities (e.g. Allison and Vitousek, 2004; Rothstein et al., 2004; Liao et al., 2008). Frequently, however, studies examined litter mass loss for either whole-community mixtures or individual species selected to represent contrasting land-use situations (Cortez et al., 2007; Quedstedt et al., 2007). Here, we chose to focus on the functional attributes of the dominant grass species in each community type. Both the structure and composition of our exotic and native synthetic assemblages were representative of old-fields and remnant grasslands within the study region (Chaneton et al., 2004; Tognetti et al., 2010). Moreover, these communities are usually dominated by *F. arundinacea* and *P. quadrifarium*, respectively, which contribute most of the aboveground litter produced annually (Tognetti, 2010). Thus, we expect our results being broadly applicable to Inland Pampa grasslands alternatively dominated by exotic or native perennial grasses.

Our results show that exotic grass dominance enhanced decomposition rates by changing both the quality of litter substrate for decomposers and the soil environment for decomposition (Fig. 2). In the common garden, the exotic *F. arundinacea* decomposed much faster than the native *P. quadrifarium*, reflecting the

higher N concentration and lower C:N ratio of the exotic grass litter (Table 2). Craine et al. (2005) found similar results when comparing C₄ native vs. C₃ exotic species in US midwest grasslands. These patterns support previous ideas regarding the greater litter quality of exotic C₃ species compared to co-occurring native C₄ species (Ehrenfeld, 2003; Dijkstra et al., 2006; Mahaney et al., 2008). Lignin content had little influence on litter decay patterns (Chapin et al., 2002; Bontti et al., 2009), perhaps because lignin concentrations for both study grasses were relatively low (less than 10% of dry mass; Aerts, 1997). The striking similarity between decomposition rates of *F. arundinacea* and *P. quadrifarium* in the common garden and home-plot experiments (cf. Fig. 2a, c) suggests that initial litter chemistry played a prominent role in driving decomposition patterns (Bontti et al., 2009). Shifts in functional trait values, like those associated with replacing C₃ by C₄ grasses, represent a fundamental mechanism whereby exotic species may alter soil ecosystem processes (D'Antonio and Hobbie, 2005; Quested et al., 2007).

In addition, we found that exotic grass assemblages modified the local environment in ways that enhanced litter breakdown. This was shown by the increased decomposition rates of the standard litter when incubated in the exotic grass plots (Fig. 2b). It thus appears that three years of establishment allowed exotic grasses to create a more active soil biotic environment, relative to that developed under native grasses. We measured soil respiration rates that were consistently higher under the exotic assemblages. Soil CO₂ production is strongly affected by heterotrophic respiration, and may be taken as an indicator of total soil microbial biomass (Chapin et al., 2002; Hernández and García, 2003). This finding suggests that observed differences in decomposition rates were mediated by a change in total activity of soil decomposer communities (Belnap et al., 2005; Ehrenfeld, 2010). Shifts in microbial biomass or composition between plant communities may be induced by changes in the quality of litter inputs to soil (Wardle et al., 2004), which in this study were associated with dominance by exotic or native grasses. However, it should be also recognized that soil CO₂ production under field conditions partly reflects root respiration from established plants (Arrigo et al., 2002).

In contrast to our initial hypothesis, effects of grass assemblage composition on litter decomposition did not correspond with significant changes in mineral N pools or N cycling rates (Table 3, Fig. 4). Similarly, Funk (2005) were unable to find differences in nutrient cycling between invaded and non-invaded plots, despite the higher litter quality and decomposition rates of exotic species. These results contradict meta-analyses showing that soil N availability and net mineralization rates were generally higher in invaded systems than in native counterparts (Ehrenfeld, 2003; Liao et al., 2008). There are several plausible explanations for this result. First, we assessed net (rather than gross) mineralization rates, which reflect the balance between production of mineral N during decomposition and consumption of soluble N forms by soil microbes and plants. It is therefore possible that N cycling was indeed faster under exotic assemblages, but the surplus N was rapidly taken up by grass roots or microbial immobilization. Second, soil mineralization rates may respond more slowly than decomposition to changes in plant composition. This is because microbial mineralization largely depends on soil organic matter pools, not freshly produced plant litter (Knops et al., 2002). Lastly, we only measured N mineralization in spring, which may have failed to capture dynamic differences in N cycling rates between native and exotic grass assemblages.

We did not detect differences in mean soil temperature between native and exotic dominated assemblages. However, the soil daily thermal amplitude was higher beneath native grass assemblages (Table 3). Topsoil temperature is primarily controlled by plant

cover, and our synthetic assemblages did not differ in terms of aboveground biomass (see Methods). It is possible that native assemblages underwent greater seasonal fluctuations in ground cover, and thus periods of wider thermal amplitudes, as they contained an even mix of short C₃ and tall C₄ tussock grasses, whereas the exotic assemblages were dominated by tall-tussock pasture grasses (see Table 1). A buffered thermal environment may have stimulated soil microbial activity beneath exotic grass patches (Gonzalez-Polo and Austin, 2009).

We also found differences in soil water content, with exotic grass assemblages having lower levels of gravimetric water in the rooting zone than the native assemblages (Fig. 4b). It thus seems unlikely that differences in litter decomposition between synthetic assemblages were driven by soil moisture. These results suggest that exotic communities dominated by fast-growing C₃ pasture grasses (Table 1) may exploit available water more intensively, for instance, by having higher transpiration rates than C₄ native grasses (Ehrenfeld, 2003). In contrast, C₄ grass-dominated native communities may help to retain soil water through lower consumption and higher water-use efficiency (Chapin et al., 2002). Overall, we posit that shifts in the quality of grass litter entering the soil and resulting differences in soil decomposer communities, rather than microclimatic conditions (as measured in this study), exerted an overriding influence on decomposition rates in exotic vs. native assemblages (Cornwell et al., 2008).

Interestingly, measured soil attributes did not generally differ between native synthetic assemblages and remnant grasslands (see Fig. 2a, b, Table 3), thus rejecting our third hypothesis. There appeared to be no 'legacy' effect on litter decomposition, N mineralization and soil microclimate, despite obvious differences in land-use history (see Cortez et al., 2007; Cramer et al., 2008). Native grass assemblages were grown from seed in an old field abandoned after several decades of agriculture. Remnant grasslands were located in landscape corridors that were never ploughed, and have remained dominated by native tussock grasses. It seems that 3–5 years of succession might be sufficient to reverse certain functional soil properties presumably altered by prior cultivation (Ghera et al., 2002). Hence, recovery of native perennial grasses on set-aside farmland would help to restore at least some ecosystem functions over a short time scale (Suding et al., 2004; Seastedt et al., 2009). We still found that soil available N and especially the NH₄⁺-N pool were lower in the remnant grasslands than in both types of synthetic assemblages (Fig. 4a). We speculate that this could reflect differences in the quality of soil organic matter (Knops et al., 2002), and perhaps microbial community structure (Wardle et al., 2004), which may be expected to change over longer time scales.

5. Conclusions

Invasion of abandoned land by exotic plant species is emerging as a worldwide trend, with pervasive consequences for restoring native communities and ecosystem services (Suding et al., 2004; Cramer et al., 2008; Seastedt et al., 2009). We have shown here that several aspects of soil ecosystem function differed between exotic and native grass assemblages representative of alternative community states during old-field succession. Exotic grass dominance accelerated organic matter turnover through surface litter decomposition, and also increased soil CO₂ emissions while reducing topsoil water retention. One major implication of these functional changes may be the development of positive feedback mechanisms (Suding et al., 2004; Kardol and Wardle, 2010) allowing the persistence of fast-growing exotic grasses in invaded fields. Yet the extent to which competition between native and exotic grasses in pampean old fields is dependent on soil attributes is not known (e.g., Baer and Blair, 2008).

Exotic plant impacts on soil processes may not only interfere with the recovery of native vegetation, but may also alter whole-ecosystem functions (Levine et al., 2003; Ehrenfeld, 2010). Our results suggest for the Inland Pampas that exotic grass-dominated communities may reduce the carbon storage capacity of the system in the long term. This is a major problem given that the few remaining native grasslands are increasingly converted into crop fields or grazed pastures under current intensification trends (Lattera et al., 2009). Management actions emphasizing early recovery of a few dominant (seed-limited) native grasses in abandoned fields may preclude establishment of exotic grass communities that erode key ecosystem functions.

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