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RESEARCH ARTICLE

Austroeupatorium inulifolium invasion alters litter dynamics in *Cymbopogon nardus*-dominated man-made grasslands

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Abstract: *Austroeupatorium inulifolium* has become a noxious invader, expanding its populations in a variety of habitats in the mid-country of Sri Lanka. Highly degraded man-made grasslands dominated by *Cymbopogon nardus* in the Knuckles Conservation Area (KCA) have shown a high vulnerability for *A. inulifolium* spread. The present study was aimed at assessing the ability of *A. inulifolium* to alter soil nutrient turnover through changes in quality and quantity of litter inputs, and decomposition rates. Two grassland communities were selected based on the extent of *A. inulifolium* invasion *viz.,* less-invaded (LIG) and highly-invaded (HIG). The surface litter and standing litter biomass was quantified using randomly placed 1 m^2 and 0.25 m^2 quadrats, respectively. An *in situ* litterbag experiment was conducted using air-dried *A. inulifolium* and *C. nardus* litter separately and as a mixture to estimate decomposition rates and nutrient release patterns. The surface and standing litter biomass were significantly higher (at $p \leq 0.001$ and ≤ 0.05, respectively) in HIG than in LIG, with *A. inulifolium* contributing significantly (at $p \leq 0.001$) to the standing litter biomass in both communities. *A. inulifolium* litter decayed and released nutrients rapidly than that of *C. nardus*. The findings of the study suggest that *A. inulifolium* invasion has the potential to increase the soil nutrient status through its high-nutrient litter inputs, rapid decomposition and nutrient release patterns. The results demonstrated the positive impact of *A. inulifolium* invasion on these nutrient-starved grasslands, while highlighting the potential role of invasive species in altering ecosystem functions, especially when they colonise degraded habitats.

Keywords: Decomposition, degraded grasslands, litter inputs, litter quality, nutrient release patterns, Sri Lanka.

INTRODUCTION

Inputs of plant litter and their quantity, quality and decomposition rates play key roles in maintaining soil fertility status and nutrient cycling processes in natural ecosystems (Berg *et al*., 2000; Wieder *et al*., 2009). Invasive plants generally produce more litter due to their rapid growth and release nutrients more quickly compared to native plants (Zhang *et al*., 2014), influencing not only the soil nutrients but also other properties such as soil moisture, microbiota and soil structure (Malinich *et al*., 2017). The mixing of litter of invasive plant species with that of native species may also modify litter dynamics in soil (Zhang *et al*., 2014).

Any change to plant communities that would occur following a single species becoming dominant alters the litter decomposition rates. Litter of different species belonging to different functional groups exert varying effects on soil properties (Zhang *et al*., 2014) through their ability to change the microenvironment including soil temperature (Parton *et al*., 2007), the decomposer community (Zhang *et al*., 2008), decomposition rates (Zhang *et al*., 2008; Shi *et al*., 2015) and competition for resources (Adair *et al*., 2008). The spread of invaders has the potential to alter soil moisture, temperature and niche availability over time, eventually influencing the decomposer communities (Bassett *et al*., 2010; Madawala, 2014). Some plant-specific factors such as high specific

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leaf area, rapid growth rate, high productivity and elevated leaf nutrient concentrations are also considered as crucial factors in increasing the rate of decomposition and nutrient release pattern (Allison & Vitousek, 2004). In addition, lignin content of plant litter, lignin:nitrogen ratio, carbon:nitrogen ratio, physical toughness and polyphenol content are also known contributing factors (Pe´rez-Harguindeguy *et al*., 2000; Coq *et al.,* 2010). High quality litter (nutrient-rich litter) inputs together with rapid decomposition rates could affect the nutrient cycling process in an ecosystem (Kueffer *et al.,* 2008; Chau *et al.,* 2013). Since last decade, *Austroeupatorium inulifolium* (Kunth) R.M. King & H. Rob. has been invading *Cymbopogon nardus* (L.) Rendle. dominated grasslands in the Central Highlands of Sri Lanka.

The *Cymbopogon*-dominated grasslands seem to show the highest vulnerability for this invasion compared to other land use types in the region. The present study quantified and compared the litter inputs, decomposition rates and nutrient-release patterns following invasion of *Cymbopogon*-dominated grasslands. The study hypothesised that *A. inulifolium* invasion shows the potential to alter the litter dynamics of *Cymbopogon*-dominated grasslands through increases in nutrient-rich litter inputs that decay and release nutrients faster than that of nutrient-poor *Cymbopogon* litter.

METHODOLOGY

Study sites

The study was carried out in *C. nardus*-dominated grasslands in the Knuckles Conservation Area (KCA) in the Wet Zone of Central Sri Lanka. The mean annual precipitation and temperature of the KCA were 2,725–4,470 mm and 21–25 ºC, respectively. The grasslands were once tea plantations and later abandoned due to low productivity, approximately 30 years ago. With time, the abandoned tea plantations have been converted into highly degraded *C. naruds*-dominated grasslands. However, despite the ready availability of a rich seed source from nearby lower montane forest remnants, the grasslands remained as it is for the last few decades with no signs of natural regeneration. The lack of soil nutrients, high competition from the grass matrix and frequent fire incidences could have arrested its natural succession (Gunaratne *et al*., 2010).

Six representative sites (three from each) were randomly selected from two grassland communities; highly-invaded (HIG) and less-invaded (LIG) grasslands. LIG were dominated by *C. nardus* while the HIG were dominated by the invasive shrub, *A. inulifolium*. The HIG and LIG were categorised based on the stem density and plant cover (%) values of *A. inulifolium* in respective sites. In HIG, the stem density was approximately 20 per m^2 with a plant cover value of > 80 %, while in LIG the stem density was 7 per m^2 with a plant cover value of < 30 %. The slope of the study sites varied from 20–40 %.

Quantification of surface litter and standing litter

Six plots representing two different habitat categories (HIG and LIG) were selected within an area of 6 km^2. The surface litter was collected down to the mineral soil interface from two randomly placed 0.0625 m^2 wooden quadrats per plot totaling 6 litter samples per habitat category. The litter samples were weighed after oven-dried at 65 ˚ C to a constant weight. Standing litter was quantified using two randomly placed 0.25 m^2 quadrats in each LIG and HIG plots. The vegetation was clipped to the ground level, and the clippings were dried at 65 ºC to a constant weight and weighed. The litter samples were sorted into *Austroeupatorium* and *Cymbopogon* to estimate their relative contributions towards the total standing litter biomass.

In situ litter decomposition experiment

An *in situ* litterbag experiment was conducted using recently senesced foliage of *A. inulifolium* and *C. nardus* to measure their decomposition rates and nutrient release patterns separately as well as in mixtures. Litterbags (625 cm^2) were made out of 2 mm black nylon mesh material. Recently senesced foliage was collected from the field, air-dried, cut into 2.5 cm pieces and homogenised before adding 10 g into each litter bag (in litter mixtures, 5 g litter from each species). A total of 168 litterbags (56 each for *A. inulifolium* and *C. nardus* separately and 56 as a mixture of both species) were randomly distributed in LIG and HIG. The litter bags were placed in a manner that they had direct contact with the soil surface. From each habitat category (LIG and HIG), twelve litter bags (4 from each species and 4 from the mixture) were retrieved at regular time intervals, *viz.,* 0, 7, 14, 28, 42, 56, 84, 112, 178 days. The collected litter bags were weighed after oven-drying at 65 ºC (for about 48 h). Before oven-drying, the litter samples were cleaned manually to remove sand particles and other debris as much as possible. The litter samples at 178 days were not included in the analysis due to the lack of litter material. The litter samples were analysed for total carbon (C), nitrogen (N) and phosphorus (P). Total carbon was measured using the wet oxidation method with potassium dichromate and total nitrogen using

Kjeldahl technique. Total phosphorus was measured by a colourimetric method after the samples were digested in Kjeldahl oxidation (Anderson & Ingram, 1993).

The mass loss of litter samples was estimated in terms of mass remaining (%) with the help of equation (1).

$$\text{Mass remaining (\%)} = M_t / M_0 \times 100 \quad ...(01)$$

where M_0 = initial mass (g) and M_t = mass (g) at time t.

The decomposition rate constant (k) was calculated from the decay curve using equation (2).

$$ln\,[M_0 / M_t] = k \times t \quad ...(02)$$

where M_0= mass (g) of litter at time 0 and M_t = mass (g) of litter at time t.

The percentage of nutrients remaining in decomposing litter (E) at different times of retrieval was also determined using equation (3).

$$E = [M_t \times C_t / M_0 \times C_0] \times 100 \quad ...(03)$$

where, M_0 is the initial mass (g), C_0 is the initial nutrient concentration (mg g^{-1}), M_t is the oven-dry mass at time t and C_t is the nutrient concentration at time t (Zhao *et al*., 2013).

Descriptive statistics were carried out using Microsoft Excel version 10.1. All statistical analyses were performed using Minitab® 17.1.0 statistical package. The level of significance for statistical tests was $p < 0.05$. Initial litter chemistry data (carbon, nitrogen, phosphorus and their respective ratios) were statistically analysed using one way ANOVA and mean separations were done using Tukey's family error rate. Repeated measures ANOVA was used to test the significant differences in litter mass remaining (%) values in the litter bag experiment between different treatments (LIG/HIG and Aus/Cym/Mix), where time is treated as a factor. Repeated measures ANOVA was also used to test the differences in mass loss and nutrient concentrations during the course of the incubation period. Species (*Austroeupatorium/Cymbopogon*), habitat (HIG and LIG) and time (incubation period) were considered as fixed factors. A test (Grubb's test at 5 % level of significance) was performed to locate any outliers in the dataset. The outliers were removed before carrying out the statistical analyses. Mean separations for repeated measures ANOVA were also carried out using Tukey's family error rate.

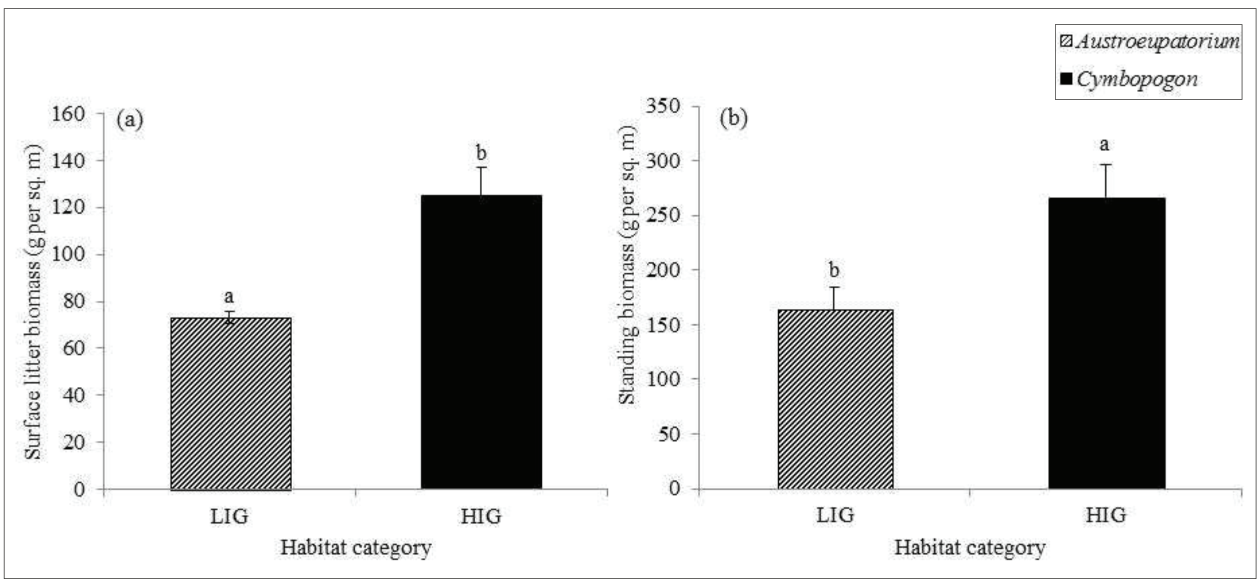

Figure 1: a) Surface litter biomass (g per sq. m) and b) above ground total biomass (g per sq. m) in less-invaded grassland (LIG) and highly-invaded grassland (HIG) habitats. Different letters indicate significant differences (surface litter biomass: ANOVA; F = 13.29, p = 0.000; above-ground total biomass: ANOVA; F = 4.71, p = 0.037). Vertical bars represent standard error of the mean (SEM).

RESULTS AND DISCUSSION

Litter loading

The surface and standing litter biomass were significantly higher in HIG than in LIG (surface litter biomass: ANOVA; F = 13.29, p = 0.000; total above ground biomass: ANOVA; F = 4.71, p = 0.037; Figure 1). *A. inulifolium* contributed significantly to the standing biomass in both habitats (75 % - HIG; 73 % - LIG) compared to that of *C. nardus* (25 % - HIG; 26 % - LIG) (Figure 2). Different plant traits show varying effects on their respective ecosystems (Hobbie *et al*., 2006; Knapp *et al*., 2008). The present findings show that *A. inulifolium* invasion contributed significantly to the litter loading in these grasslands, further proving the positive role of the invasive shrub. Litter accumulation in grasslands is more noticeable in areas with higher standing aboveground biomass (Wang & Xu, 2012). *A. inulifolium* contributed significantly to the standing biomass and surface litter in both less- and highly-invaded areas of the grasslands. The rapid growth of *A. inulifolium* has significantly increased the litter inputs even in LIG where *C. nardus* dominates the vegetation. Higher litter inputs mean higher addition of nutrients to the soil. A recent study also reported a higher accumulation of litter in Californian grasslands invaded by *Avena fatua* and *Elymus caput-medusae*, suggesting long-term changes in litter dynamics (Mariotte *et al*., 2017). Not only the soil chemistry, but other microclimatic parameters including the reduction of sunlight reaching the ground level, increase in soil moisture and decrease in soil temperature fluctuations can be affected by the increase of high quality litter inputs following invasions (Wang & Ruan, 2011; Montane *et al*., 2013; Warren *et al*., 2013; Medina-Villar *et al*., 2015). Such changes in the micro-habitat may sometimes affect the co-occurring native species negatively (Warren *et al*., 2013; Mariotte *et al*., 2017).

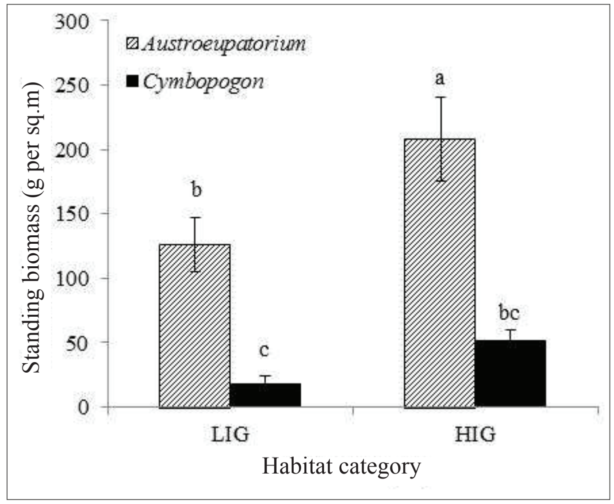

Figure 2: Average contribution of *A. inulifolium* and *C. nardus* plants (g per sq. m) in less-invaded grassland (LIG) and highly-invaded grassland (HIG) habitats. Different letters indicate significant differences (GLM; F = 41.38, p = 0.000). Vertical bars indicate standard error of mean (SEM) values.

Litter quality

The litter quality varied significantly between species and their mixtures (Table 1). Nitrogen was significantly higher in *A. inulifolium* and in litter mixtures (*Austroeupatorium* + *Cymbopogon*) compared to *C. nardus* only. *C. nardus* litter showed significantly higher C:N and C:N:P ratios compared to other two litter types (*A. inulifolium* only and *Austroeupatorium* + *Cymbopogon*), with the lowest C:N recorded in *Austroeupatorium*. Invasive plants are known to produce high quality litter than that of native species due to their rapid growth rates (Orwin *et al*., 2010). Previous studies have shown evidences to support that shrub invasions alter not only the existing

Table 1: The chemical composition (± standard error of mean) and their respective ratios of *A. inulifolium* (*Austro*.), *C. nardus* (*Cymbo*.) and mixed litter (*Austro* + *Cymbo*) samples used in the *in situ* litter decomposition experiment. Different superscript letters indicate significant differences between species for each chemical parameter.

Species	Total C (%)	Total N (%)	Total P (μg/g)	C:N	C:P	C:N:P
A. inulifolium	35 ± 0.29^{b}	1.27 ± 0.05^{a}	0.08 ± 0.03^{a}	27 ± 0.89^{c}	968 ± 644^{a}	740 ± 477^{b}
C. nardus	40 ± 1.5^{ab}	0.33 ± 0.07^{b}	0.05 ± 0.01^{a}	141 ± 40.8^{a}	864 ± 34.3^{a}	3003 ± 869^{a}
Mixed litter	45 ± 3.32^{a}	1.14 ± 0.06^{a}	0.09 ± 0.00^{a}	39.3 ± 1.08^{b}	497 ± 32.6^{a}	436 ± 13.9^{a}
Level of significance	**	**	ns	***	ns	**

Significant differences are indicated as p ≤ 0.001***, p ≤ 0.01 **, p ≤ 0.05 * and not significant, ns.

vegetation in grasslands but also the edaphic properties and ecosystem functions (McLaren & Turkington, 2011). The present study suggested that high inputs of quality litter following *A. inulifolium* invasion seems to alter the nutrient turnover rates in these highly-invaded grasslands. Montane *et al.* (2013) also noted that a shrub invasion has increased litter inputs in grasslands with the potential of altering the decomposition patterns through litter mixing.

Litter decomposition rates

In all litter types, litter decomposition was rapid initially and then followed by a much slower pace. However, *A. inulifolium* litter decomposed more rapidly throughout the incubation period than that of *C. nardus*, where the latter showed comparatively slow decay rates in both habitats with a 50 % mass loss recorded after approximately 14 days (Figure 3). The present study has supported the fact that *A. inulifolium* invasion has the potential to influence the litter dynamics, thus the soil nutrient status may alter due to the increase in litter inputs and rapid decay in grasslands once dominated by *C. nardus*. However, the litter decomposition rates did not vary much between the two habitat categories. Litter decomposition is an important process in nutrient cycles that controls soil fertility, thus affecting the community composition and net primary production (Throop & Archer, 2007). The results showed that *A. inulifolium* litter decomposed and released nutrients relatively faster than that of *C. nardus*. In support, previous studies have also shown that litter of invasive species decomposes faster than the native counterparts (Allison & Vitousek, 2004; Blair & Stowasser, 2009). Litter mixing events following invasions seem to alter the decay and nutrient release rates in ecosystems. The study also indicated that decay followed by nutrient release could be somewhat rapid in HIG than in LIG, suggesting perhaps a change of decomposer communities following shrub invasion. Previous studies have demonstrated that litter mixing may alter the microbial community, thus contributing positively in litter decomposition (Allison & Vitousek, 2004; Ashton *et al*., 2005; Blair & Stowasser, 2009; Chapman *et al*., 2013). The invasive species, *Berberis thunbergii* and *Microstegium vimineum* show the potential to alter soil microbial communities in forest soils (Kourtev *et al*., 1999). The leaf-related traits of invasive plants can play a major role in deciding the structure and functions of invaded communities (Goya *et al*., 2008; Godoy *et al*., 2010). A previous study carried out in the same grasslands at KCA noted an increase in the population of arbuscular mycorrhizal fungi (AMF) following the invasion of *A. inulifolium* (Madawala, 2014). Alteration of the soil microbial population and their functions may facilitate the growth of the invader over other co-occurring native species (Freschet *et al*., 2012; Karunaratne & Madawala, 2016). Hence, invasive litter and their mixing ability seem to show the potential to alter the microbial composition and increase their functions, eventually contributing to high nutrient turnover in these highly invaded grasslands.

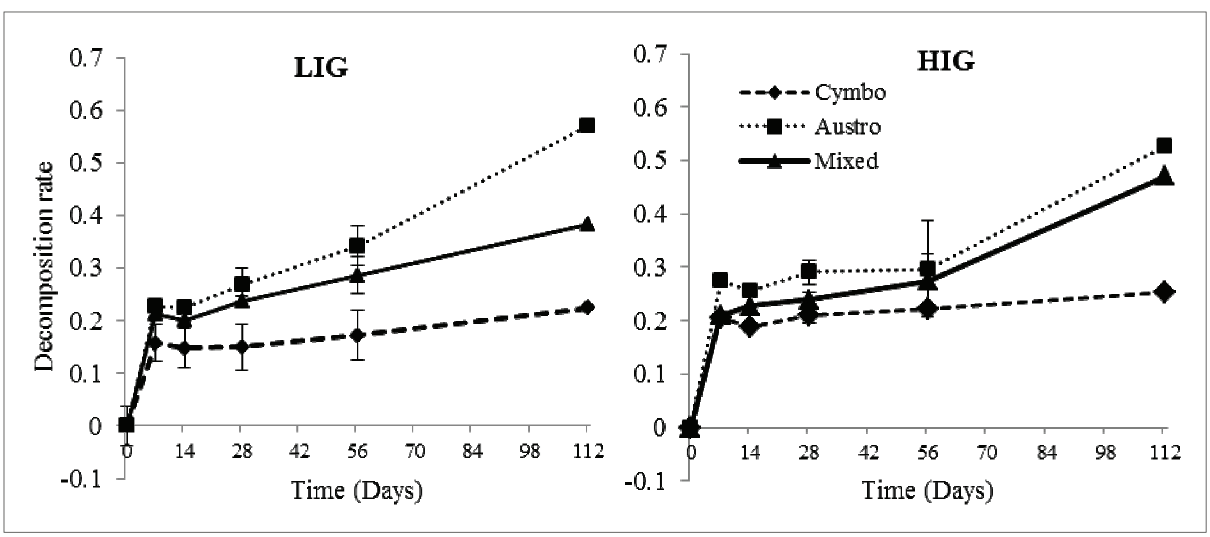

Figure 3: Decomposition rate (k) of *A. inulifolium* and *C. nardus* in a litter decomposition experiment under less-invaded grassland (LIG) and highly-invaded grassland (HIG) habitats. Vertical bars represent standard error of the mean (SEM).

Nutrient release patterns

Repeated measures ANOVA indicated a significant interaction effect between the time and species (once nested within habitats) in litter samples and their mixtures (Table 2). When species nested in habitats, the remaining mass, N and P significantly differed among species. The results also showed that *A. inulifolium* litter released nutrients more rapidly compared to that of *C. nardus*. This rapid decay and subsequent release of nutrients can make a significant impact on these otherwise nutrient-starved grasslands (Gunaratne *et al*., 2010). Higher N content in litter may promote decomposition (Cornwell *et al*., 2008). Edaphic properties in invaded habitats including higher levels of inorganic N (Kourtev *et al*., 1999; Mack *et al*., 2001) and higher rates of N mineralisation and nitrification (Evans *et al*., 2001; Mack *et al*., 2001) may involve in facilitating decomposition rates. The present study indicated that the release of N and P in *A. inulifolium* accelerates at the latter stage of the decaying process. Nitrogen and phosphorus in litter can accumulate during decomposition, hence providing nutrients for the decomposer communities. *A. inulifolium* leaf litter may consist of easily degradable organic compounds thereby releasing nutrients relatively rapidly than its co-occurring *C. nardus*.

Table 2: Repeated measures ANOVA results for *A. inulifolium*, *C. nardus* and their mixtures in two habitats [less-invaded (LIG) and highly-invaded grasslands (HIG)] after 112 days of *in situ* incubation period

	Mass remaining			Remaining N			Remaining P		
	df	F	p	df	F	p	df	F	p
Habitat	1	1.27	0.262^{ns}	1	3.71	0.057^{ns}	1	17.73	0.000***
Species (Sp)	2	8.28	0.000***	2	0.94	0.391^{ns}	2	0.46	0.635^{ns}
Time (T)	5	268	0.000***	5	7.18	0.000***	5	12.20	0.000***
Sp (Habitat)	4	57.82	0.000***	4	23.44	0.000***	4	13.9	0.000***
Sp (Habitat)*T	20	5.62	0.000***	20	2.98	0.000***	20	2.23	0.005**

Significant differences are indicated as $p \leq 0.001^{***}$, $p \leq 0.01^{**}$ and $p \leq 0.05^{*}$

Table 3: Decay rate (per days), mass and nutrients (nitrogen and phosphorus) remaining (as a percentage ± standard error of mean) in leaf litter of *A. inulifolium (Aus)*, *C. nardus* (*Cym*) and their mixture (Mix) in less-invaded grassland (LIG) and highly-invaded grassland (HIG) habitats after 112 days of *in situ* incubation period

		Decay rate (per days)	Mass remaining	% N	% P	C:N	C:P	N:P
Aus	HIG	0.27 ± 0.03^{a}	54.2 ± 4^{c}	90.1 ± 10^{ab}	62.3 ± 7^{a}	29.4 ± 7^{bc}	36.3 ± 6^{cd}	75.7 ± 8^{bc}
	LIG	0.27 ± 0.04^{a}	53.2 ± 6^{c}	83.6 ± 14^{b}	49.3 ± 8^{c}	24.1 ± 7^{c}	28.5 ± 7^{d}	57.2 ± 12^{c}
Cym	HIG	0.18 ± 0.02^{c}	71.5 ± 3^{a}	55.5 ± 6^{b}	69.5 ± 7^{a}	60.9 ± 8^{a}	52.8 ± 6^{ab}	64.5 ± 12^{c}
	LIG	0.14 ± 0.02^{d}	73.8 ± 6^{a}	96.6 ± 14^{a}	49.3 ± 7^{ab}	35.3 ± 6^{bc}	64.6 ± 6^{a}	139 ± 21^{a}
Mix	HIG	0.24 ± 0.03^{b}	61.2 ± 4^{b}	78.9 ± 9^{ab}	61.4 ± 8^{a}	39.7 ± 6^{b}	47.5 ± 7^{bc}	75.8 ± 12^{bc}
	LIG	0.22 ± 0.02^{b}	63.2 ± 4^{b}	64.5 ± 11^{b}	43.0 ± 7^{bc}	54.3 ± 7^{a}	65.7 ± 9^{a}	95.4 ± 14^{ab}

Different superscript letters indicate significant differences between habitats. Values are given as mean percentage of dry weight (n = 4).

The nutrient release patterns of single-species litter samples (*A. inulifolium* and *C. nardus)* and their mixtures did not vary significantly among the habitats, LIG and HIG (Table 3; Figure 4). The elemental ratios of C:N and C:P in *A. inulifolium* litter have also shown a rapid decline over time than that of *C. nardus* and mixed litter with no differences between LIG and HIG (Figure 5). The C:P ratio in *C. nardus* litter demonstrated a slower decline over time in both habitats compared to *A. inulifolium* and mixed-leaf litter. A relatively higher C content in *C. nardus* litter indicated a slower decay compared to other litter types. *C. nardus* also showed a relatively slow release of nutrients during decomposition compared to *A. inulifolium*. The nutrient release patterns of litter samples showed somewhat different trends between habitat types, but not significantly (Figure 4; Table 3). *A. inulifolium* showed a comparatively faster release of C compared to *C. nardus* and mixed litter, while *A. inulifolium* showed a rapid immobilisation of nutrients (P and N) with no noticeable differences

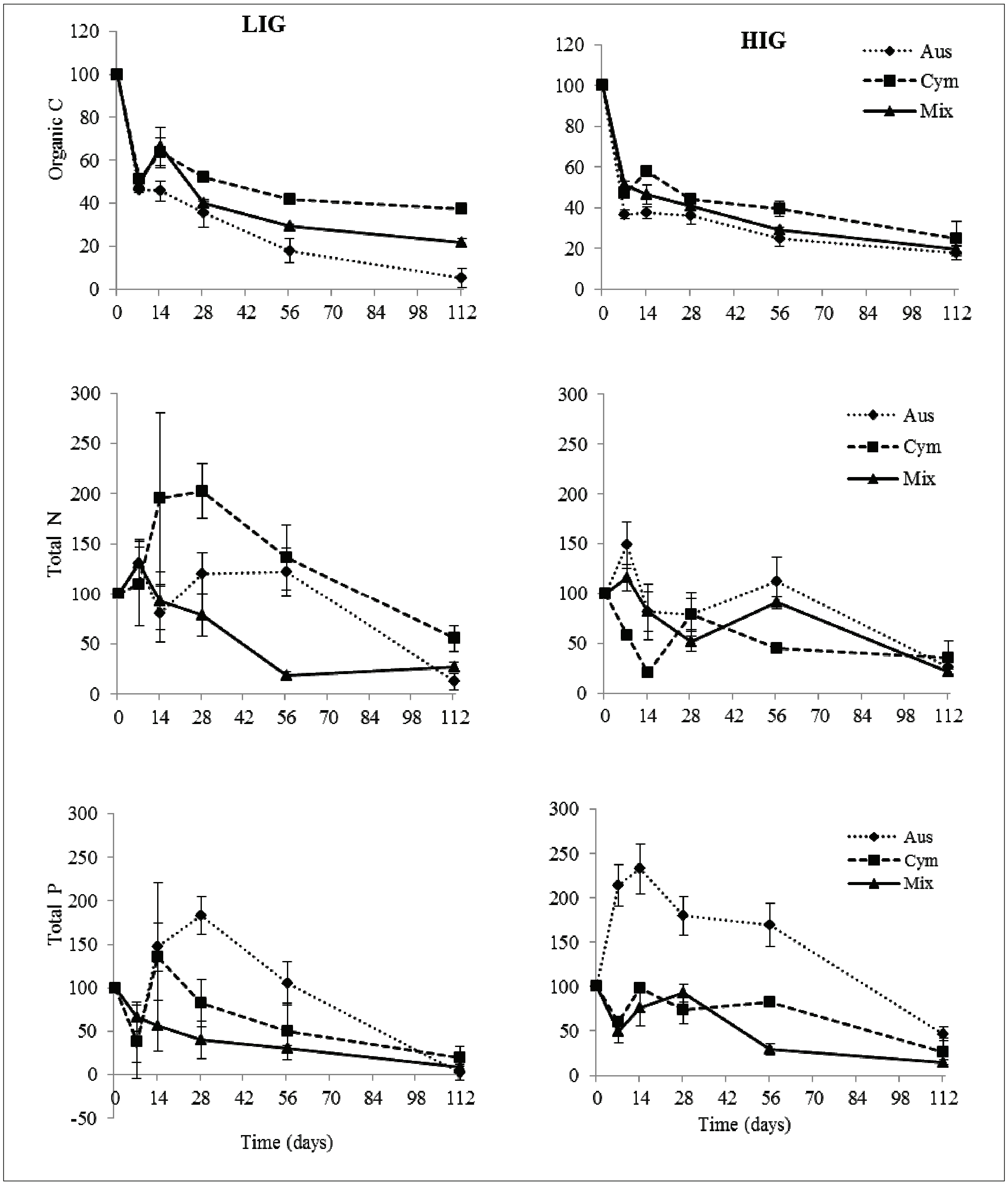

Figure 4: Remaining organic carbon (%), nitrogen (%) and phosphorus (%) during the incubation period of litter decomposition study of *A. inulifolium* and *C. nardus* litter in less-invaded grassland (LIG) and highly-invaded grassland (HIG) habitats. Vertical bars represent standard error of the mean (SEM).

between habitat categories (Figure 4). The decomposition rates of leaf litter are largely influenced by litter nutrient levels and their ratios (Karberg, 2008). The present study observed a rapid decline of nutrients and their ratios in *A. inulifolium* during the incubation period. The litter decomposition rates are positively correlated with the initial N concentrations of litter, and negatively with the initial C:N and C:P ratios (Karberg *et al*., 2008). During early stages of decomposition, the C:N ratio can be the best predictor of mass loss and N release, while lignin

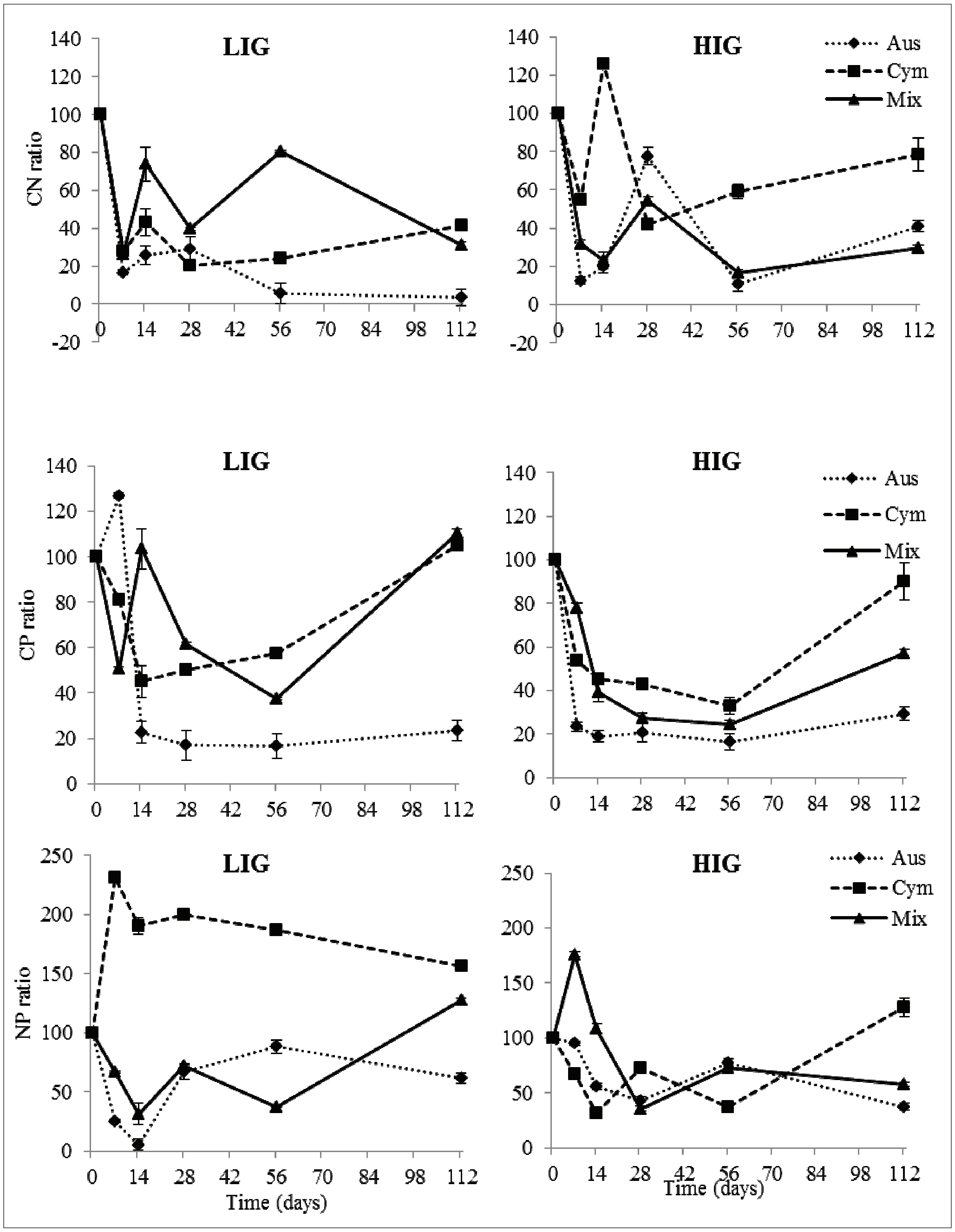

Figure 5: Remaining carbon:nitrogen (C:N), carbon:phosphorus (C:P) and nitrogen:phosphorus (N:P) ratios of *A. inulifolium* and *C. nardus* in litter decomposition experiment under less-invaded grassland (LIG) and highly-invaded grassland (HIG) habitats. Vertical bars represent standard error of the mean (SEM).

becoming increasingly significant during the latter stages (Heal *et al*., 1997). In approval, the decomposition rate of *A. inulifolium* increased with the decreasing C:N ratio. The reduction of C:N ratios over time in both *A. inulifolium* and *C. nardus* suggested relatively rapid respiration and immobilisation of N. Litter with low C:N ratio, but relatively rich in N, is readily degraded by fungi and bacteria than litter having higher C:N ratios (Mack *et al*., 2001; Blair *et al*., 2009). The increases in nutrient contents observed during the initial stages of decomposition are possibly due to the immobilisation of nutrients by the microbes (Kourtev *et al*., 1998). Similar observations were also noted in the present study.

CONCLUSIONS

Austroeupatorium inulifolium invasion of grasslands previously dominated by *Cymbopogon nardus* has shown the potential to alter nutrient dynamics in these nutrient-starved man-made ecosystems. *A. inulifolium* litter has shown the ability to decompose and release nutrients faster than that of *C. nardus*. The invasion has also increased the nutrient-rich litter inputs significantly. Litter mixing following the invasion has also accelerated the decomposition rates and nutrient release patterns. The study concludes that *A. inulifolium* invasion has the potential to increase the soil fertility status in these degraded grassland communities over time. Enhanced edaphic properties together with improved micro-habitat conditions may eventually trigger the arrested natural succession in these grasslands. The present study further supports the general notion that invasions can be productive when it occurs in nutrient-starved habitats.

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