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Invasive *Andropogon gayanus* (gamba grass) is an ecosystem transformer of nitrogen relations in Australian savanna

N. A. Rossiter-Rachor,[1,2,3,6] S. A. Setterfield,[1,3] M. M. Douglas,[1,3,4] L. B. Hutley,[1,3] G. D. Cook,[2,3] and S. Schmidt[5]

[1]*School of Environmental and Life Sciences, Charles Darwin University, Darwin, Northern Territory 0909 Australia*
[2]*CSIRO Tropical Ecosystems Research Centre, Darwin, Northern Territory 0822 Australia*
[3]*Tropical Savannas Management Cooperative Research Centre, Charles Darwin University, Darwin, Northern Territory 0909 Australia*
[4]*School for Environmental Research, Tropical Rivers and Coastal Knowledge (TRaCK) Research Hub, Charles Darwin University, Darwin, Northern Territory 0909 Australia*
[5]*School of Integrative Biology, The University of Queensland, Brisbane, Queensland 4072 Australia*

Abstract. Invasion by the African grass *Andropogon gayanus* is drastically altering the understory structure of oligotrophic savannas in tropical Australia. We compared nitrogen (N) relations and phenology of *A. gayanus* and native grasses to examine the impact of invasion on N cycling and to determine possible reasons for invasiveness of *A. gayanus*. *Andropogon gayanus* produced up to 10 and four times more shoot phytomass and root biomass, with up to seven and 2.5 times greater shoot and root N pools than native grass understory. These pronounced differences in phytomass and N pools between *A. gayanus* and native grasses were associated with an altered N cycle. Most growth occurs in the wet season when, compared with native grasses, dominance of *A. gayanus* was associated with significantly lower total soil N pools, lower nitrification rates, up to three times lower soil nitrate availability, and up to three times higher soil ammonium availability. Uptake kinetics for different N sources were studied with excised roots of three grass species ex situ. Excised roots of *A. gayanus* had an over six times higher uptake rate of ammonium than roots of native grasses, while native grass *Eriachne triseta* had a three times higher uptake rate of nitrate than *A. gayanus*. We hypothesize that *A. gayanus* stimulates ammonification but inhibits nitrification, as was shown to occur in its native range in Africa, and that this modification of the soil N cycle is linked to the species' preference for ammonium as an N source. This mechanism could result in altered soil N relations and could enhance the competitive superiority and persistence of *A. gayanus* in Australian savannas.

Key words: ammonium; exotic grasses; invasive alien species; nitrate; nitrification inhibition; nitrogen cycling; nitrogen uptake.

Introduction

It is widely acknowledged that the composition of plant communities is a major determinate of nitrogen (N) cycling, affecting the amount of N stored in various pools in an ecosystem and/or the fluxes of N between these pools (Hooper and Vitousek 1998). In a range of ecosystems, invasive alien plants have altered the composition of resident plant communities, with profound effects on N cycling (see reviews in Ehrenfeld [2003], Levine et al. [2003], Corbin and D'Antonio [2004], D'Antonio and Hobbie [2005], and Liao et al. [2007*b*]). Invasion by alien plants can affect N cycling by altering the rates of N input (Vitousek and Walker 1989, Witkowski 1991, Stock et al. 1995), quality and quantity of litter (Lindsay and French 2004, Rothstein et al. 2004), rates of N uptake by plants (Windham and Ehrenfeld 2003), the soil microbial community associated with soil N transformations (Hawkes et al. 2005, Wolfe and Klironomos 2005), the microclimate in which microbially mediated processes occur (Mack and D'Antonio 2003), the rates of N losses via leaching, denitrification (D'Antonio and Hobbie 2005), and volatilization (Rossiter-Rachor et al. 2008). It is essential to determine the mechanisms underlying the impacts of an invader in order to understand the success of the invader (Levine et al. 2006). This information is also fundamental for identifying the likely short- and long-term impacts of invasion, and for providing a basis for management decisions for invaded ecosystems (Corbin and D'Antonio 2004).

In the tropical savannas of northern Australia, one of the most significant alien plant invaders is the large African grass *Andropogon gayanus* (Kunth) (Whitehead and Wilson 2000) (see Plate 1). *Andropogon gayanus* was introduced into Australia as a pasture species in the 1930s (Oram 1987), but has since invaded beyond

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[6] E-mail: natalie.rossiter@cdu.edu.au

planted areas and into native vegetation (Flores et al. 2005). The rapid spread of *A. gayanus* across northern Australia has raised widespread concern (Whitehead and Wilson 2000, Russell-Smith et al. 2003, Flores et al. 2005) due to its profound impacts on savanna biodiversity (Brooks et al. 2009), fire regimes (Rossiter et al. 2003), and tree survival (Ferdinands et al. 2006).

It has been suggested that the invasive success and persistence of *A. gayanus* in the savannas of tropical Australia may be partly due to ecophysiological and morphological advantages over native savanna grasses (Rossiter 2001, Clifton 2004). Compared with native grasses, *A. gayanus* has (1) higher photosynthetic and transpiration rates (Rossiter 2001); (2) higher soil water use (L. B. Hutley, S. A. Setterfield, M. M. Douglas, and N. A. Rossiter-Rachor, *unpublished data*); (3) longer growth period into the dry season (Rossiter et al. 2003); and (4) earlier onset of growth following early wet season storms (N. A. Rossiter-Rachor, *personal observation*). In Venezuelan savannas, *A. gayanus* also has a higher N uptake and nitrogen use efficiency (NUE) than native savanna grasses (Bilbao and Medina 1990). The remarkable drought resistance and growth properties of *A. gayanus* are well recognized in its native range of Western Africa, and have been attributed to its extensive root system, which accesses water and nutrients at the surface and deeper down the soil profile (Bowden 1964, Groot et al. 1998).

In Australian and African savannas soil N levels are generally low, and N availability has been proposed as one of the major constraints on plant growth (Tothill et al. 1985, Solbrig et al. 1996). The apparent paradox of highly productive grasses thriving in low N ecosystems has been investigated in West African savanna (Abbadie and Lata 2006). *Andropogon gayanus* and several other species in the *Andropogonaceae* supertribe appear to have evolved a successful mechanism for conserving soil N by inhibiting nitrification (Lata et al. 2000, 2004). Roots of these grasses exude allelopathic compounds that inhibit the activity of nitrifying soil microbes by interrupting metabolic pathways (Subbarao et al. 2007), thus reducing the production of the highly mobile nitrate (NO_3^-) (Lata et al. 2004). Suppression of nitrification and maintaining N as relatively immobile ammonium (NH_4^+) in soil therefore reduces the likelihood of N loss via denitrification and leaching (Subbarao et al. 2007) and may be a key mechanism for increasing the residence time of N within the soil–plant system (Abbadie and Lata 2006).

This study compared sites invaded by *A. gayanus* with non-invaded sites to determine if changes in N relations are associated with invasion. Specifically we aimed to (1) quantify the changes in plant phytomass and N pools in savanna following invasion by *A. gayanus*, (2) investigate the impact of changes in grass phytomass on soil N relations by quantifying total and available soil N pools, and net ammonification and nitrification rates, and (3) determine how differences in N cycling relate to N source preferences of *A. gayanus* and native grasses by examining uptake kinetics of different N forms (NH_4^+, NO_3^-, amino acid glycine) in excised roots.

Methods

Site description

The study site was at Wildman Reserve, Northern Territory, Australia (12°43′ S, 131°49′ E). Air temperature is high throughout the year (mean 27°C), while rainfall is highly seasonal (mean 1434 mm) and concentrated in the wet season (October–April). Soils are Kandosols, with a low N concentration (0.01–0.11% N; Day et al. 1979). This savanna is dominated by *Eucalyptus miniata* (Cunn. Ex Schauer) and *E. tetrodonta* (F. Muell), with a grass understory dominated by native perennial grasses *Alloteropsis semialata* (R. Br.) Hitchc. and *Eriachne triseta* Nees ex Steud. with patches of annual grasses, such as *Pseudopogonatherum irritans* (Br.) A. Camus. *Andropogon gayanus* has invaded extensive areas of the reserve over the last 20 years, forming dense, tall, almost monospecific swards up to 4 m high, and replacing the much shorter (~0.5 m) native grass communities (Fig. 1). *Andropogon gayanus* infestations on the reserve generally range from single plants to patches of 500 m^2, within a matrix of uninvaded savanna (Rossiter et al. 2003). The savanna communities of Wildman Reserve are burned frequently (typically annually or biennially) as part of the Reserve's fire management strategy. During this study, a controlled fuel-reduction burn was carried out by the Park Rangers, at the end of May 2003, after the plant and soil sampling had been carried out for that month (Table 1). This fire frequency is typical for this region, with up to 50% of the northern Australian savannas burnt annually (Russell-Smith et al. 2003).

Experimental design

Nitrogen relations in native grass savanna were compared with those occurring in *A. gayanus* invaded savanna using a randomized block design. Five paired plots (blocks) were studied, with each plot pair consisting of an area dominated by native grass (hereafter referred to as "native grass" plots), and a nearby (approximately 50 m distance) *A. gayanus*-dominated area (hereafter referred to as "*A. gayanus* plots"). Plot pairs were located up to 600 m apart, and each plot was 50 × 50 m in size, with a canopy dominated by *E. miniata* and *E. tetrodonta*. In native grass plots, the grass component included several native grass species, while in *A. gayanus* plots only *A. gayanus* was present. The study was conducted over two wet-dry season cycles: October 2002–September 2003 (1614 mm) and October 2003–June 2004 (1785 mm) (Table 1). Average gravimetric soil moisture (0–30 cm) ranged from 13.3% (wet season) to 5% (dry season), average soil pH was 5.2 ± 0.1 (mean ± SE), and bulk density ranged from 1.46 g/cm^3 at the soil surface, to 1.55 g/cm^3 at 30 cm depth. These results were similar to those of Day et al. (1979) and there were no

FIG. 1. Changes to vegetation structure due to *Andropogon gayanus* (gamba grass) invasion. Photos of (a) native grass savanna (dominated by *Alloteropsis semialata* and *Eriachne triseta*) at Wildman Reserve, in the early dry season (June) and (b) *A. gayanus*-invaded savanna in the early dry season (June) [photo (b) was taken 100 m to the northwest of the location of photo (a)].

significant differences in these soil characteristics between the two grass plot types.

Grass phytomass and nitrogen pools

To determine the above ground N pool of *A. gayanus* and native grasses, the mass and tissue N concentration (%N) of the grass phytomass were quantified. Leaf litter derived from woody savanna plant species was also collected at each sampling time. Samples were collected at key times over two years: (1) dry–wet season transition (October–November); (2) early wet season (December–January); (3) late wet season (February–March); (4) early dry season (May–June); and (5) late dry season (August–September) (Table 1); with the exception of January 2003, when logistics prevented phytomass sampling. Samples were collected from three random replicate quadrats, within each of the five paired native grass and *A. gayanus* plots (n = total of 15 quadrats per grass plot type per sampling time). Aboveground grass phytomass was quantified by harvesting all aboveground grass material within three randomly placed 2×2 m quadrats per plot. This grass phytomass included all dead standing material and also grass material that had fallen to the ground and was disconnected from the plant. Leaf litter from woody plants was also collected from each quadrat. Grass

TABLE 1. Summary of plant and soil sampling times throughout this study.

Measurement	2002		2003											
	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Plant														
Aboveground phytomass	x				x		x				x		x	
Belowground biomass														
Soil														
Total N			x				x							
Inorganic N availability														
Resin bags	x		x		x		x				x		x	
Soil incubation														
Fire														
Fuel reduction burn							x†							

Notes: The study was conducted over two wet–dry season cycles (October 2002–September 2003; October 2003–June 2004). Samples were collected at five key times of the wet–dry cycle: (1) dry–wet season transition (October–November); (2) early wet season (December–January); (3) late wet season (February–March); (4) early dry season (May–June); and (5) late dry season (August–September).

† The fuel reduction burn was carried out at the end of May 2003, after the plant and soil sampling had been completed.

samples were returned to the lab and sorted into green leaves and stems (live biomass) and dead standing grass (necromass). All grass and leaf litter samples were dried for 48 h at 60°C, weighed, ground, and analyzed for percentage of N on a Carlo Erba analyzer (Thermo Electron, Thermo Fisher Scientific, Waltham, Massachusetts, USA). Due to budgetary constraints, only samples from three of the five plot pairs, from the first year of sampling, were analyzed. Nitrogen pools in native grass and *A. gayanus* plots were calculated on a quadrat basis (product of plant mass and tissue N concentration). For each quadrat, four N pools were calculated: (1) live biomass, (2) necromass, (3) phytomass (sum of live biomass and necromass), and (4) woody leaf litter.

Differences between grass and woody litter mass and grass and woody litter N pools between grass types were compared using a three-factor analysis of variance (ANOVA) with factors grass type (fixed), sampling time (fixed), and plot pair (random). Before statistical analyses were undertaken, assumptions of ANOVA were checked using Cochran's test, and where necessary data were transformed prior to analyses to improve normality and homogeneity. All analyses were done using Statistica 5.5 (StatSoft, Tulsa, Oklahoma, USA).

Root nitrogen pools

Root biomass was sampled in March 2004 from three of the five plot pairs previously described, using a fixed volume PVC core-sampling device (7.65 × 30 cm; Table 1). In native grass plots, five cores were taken within each of three randomly located quadrats (n = total of 15 cores per native grass plot, and a total of 45 for the study). In *A. gayanus* plots stratified sampling was undertaken, due to the clumped distribution of *A. gayanus*. Three cores were collected from the "tussock region" (through the centre of a plant) and three from the "inter-tussock region" (>30 cm from a plant center)

TABLE 1. Extended.

2004					
Jan	Feb	Mar	Apr	May	Jun
x		x			x
		x			
x					x
x		x			
		x			

within each of the three randomly located quadrats (n = total of 18 cores for each *A. gayanus* plot, and a total of 54 for the study). Basal area of *A. gayanus* at ground level was measured and the location of each plant in the quadrat was drawn on a location map to determine the area of tussock and inter-tussock regions in each quadrat. The average tussock area was 63% of the 1-m^2 quadrat. To determine root mass in each core, soil was air dried in aluminum trays, then sieved to 0.2 mm following Cornelissen et al. (2003). Dead roots, defined as darkened, limp, or deflated (Cornelissen et al. 2003), and roots that clearly belonged to trees or shrubs, were discarded. Root samples were dried at 40°C for 48 h, weighed, ground, and analyzed for percentage of N on a Carlo Erba analyzer. In native grass plots, the dry mass of roots per quadrat was calculated using the average mass of roots from the five cores from the quadrat (over the 30 cm corer depth) and expressed as g/m^2. In *A. gayanus* plots, root mass per quadrat was calculated using the average root mass from "tussock" and "inter-tussock" cores scaled by the proportional area occupied by each region within each quadrat. The root N pool in each quadrat (g N/m^2) was calculated as the product of root biomass and root N concentration. Differences between root biomass and N pools between grass types were compared using a two-factor ANOVA with factors grass type (fixed) and plot pair (random).

Total soil nitrogen pools

Total soil N profile analyses were carried out at four sampling times: (1) wet season, January 2003; (2) dry season, May 2003; (3) wet season, January 2004; and (4) dry season, June 2004 (Table 1). Samples were taken from the top 30 cm of the soil profile, as this is where the majority of soil N is in savanna systems, and the N pool drops off sharply in the lower soil depths (Scholes and Walker 1993). Samples were collected from three random replicate quadrats, within each of the five native grass and *A. gayanus* plot pairs (n = total of 15 quadrats per grass plot type, per sampling time). A pit was dug (~30 × 30 cm wide × 40 cm deep) and soil cores were collected from three different depths (0–5 cm, 5–10 cm, 20–30 cm) by inserting a 2 × 10 cm soil corer horizontally into the wall of the pit. Approximately 200 g of soil was taken at each depth (n = 3 soil cores for each depth, per native grass and *A. gayanus* plot). The sample was placed in a snap-lock polyethylene bag and stored on ice until return to the lab, where the soil was sieved, and approximately 100 g of soil was taken for determination of gravimetric moisture determination (weighed, dried at 105°C for 48, and reweighed; results not presented). The remainder of the soil sample was dried at 40°C for 48 h, ground, and then analyzed for total N (% N) on a Carlo Erba analyzer. Total soil N pools for each depth (0–5 cm, 5–10 cm, 20–30 cm) were calculated as the product of soil N concentration and soil bulk density of soil for that depth, and were expressed as g/m^2. Differences between total soil N

PLATE 1. (Top) Dense infestation of *Andropogon gayanus* (gamba grass) near Adelaide River, Northern Territory, Australia. *A. gayanus* invasion leads to a near monoculture of the understorey at this site. (Bottom) Savanna tree death due to repeated high-intensity *Andropogon gayanus* (gamba grass) wildfires (Northern Territory, Australia). *A. gayanus* fires led to a 53% reduction in tree cover in just 12 years (Ferdinands et al. 2006) at this site. Photo credits: S. A. Setterfield.

pools, between grass types were compared for (1) January 2003, (2) May 2003, (3) January 2004, and (4) June 2004, using a four-factor ANOVA with factors grass type (fixed), plot pair (random), depth (fixed), and core (nested in grass type, plot pair, time, and depth).

Soil inorganic N availability

Two in situ techniques were used to examine the effect of *A. gayanus* on soil inorganic N (NH_4^+ and NO_3^-) relations: (1) ion-exchange resin bags and (2) whole-soil incubations, which measure the availability of soluble N ions in the presence and absence of live roots, respectively. Ion exchange resin bags provide an index of plant N availability, as ion accumulation on the resin bags depends on the rates of mineralization, the ion form, water movement in the soil, and plant and microbial uptake; the same factors that determine N availability for plants (Binkley 1984). Alternatively, the whole soil incubation also allows for inorganic N availability and net ammonification and nitrification rates to be quantified in root zone soil (Hart and Firestone 1989).

Soil inorganic N availability in the presence of roots was measured using mixed ion-exchange resin bags (Dowex-MR3; Sigma, St. Louis, Missouri, USA) following Schmidt et al. (1998). Measurements were taken over two years at the same five seasons and plot pairs, previously described for the grass phytomass sampling (Table 1). Resin bags were buried at a 45°C angle, 5 cm below the soil surface and incubated in situ for 7–14 days. After incubation, the resin was extracted with 1 mol/L KCl, the extract was analyzed NH_4^+ and NO_3^- using a Lachat flow injection autoanalyzer (Lachat Instruments, Loveland, Colorado, USA). Inorganic N availability (NH_4^+ and NO_3^-) over the incubation period (ng $N \cdot g^{-1}$ resin$\cdot d^{-1}$) was calculated. Differences between inorganic N availability between grass types were compared using a three-factor ANOVA with factors grass type (fixed), sampling time (fixed), and plot pair (random). Post-hoc Tukey's tests were used to make comparisons between treatment means.

Soil inorganic N availability in the absence of roots was determined in the wet season (March 2004) using buried-bag in situ incubations (following Hart and Firestone 1989) (Table 1). This method involved incubating soil inside a gas-permeable, water impermeable polyethylene bag (Hart and Firestone 1989). Measurements were taken within three random replicate quadrats, at three of the five native grass and *A. gayanus* plot pairs (n = total of 9 quadrats for each grass plot type). At $t = 0$, two intact 10×7.5 cm soil cores were taken from each quadrat. One core was sealed in a polyethylene bag, placed on ice, and returned to the laboratory, where it was sieved to 2 mm to remove large roots. A subsample of the soil was dried to determine gravimetric water content, and the remainder was analyzed for NH_4^+ and NO_3^- after extraction with 2 mol/L KCl. The second core taken from each quadrat was carefully removed from the soil with minimal disturbance, tightly sealed in a thick (1.5 mm) polyethylene bag, and immediately returned to the same hole from which the soil core was removed. After a 28-day incubation period in the field, the incubated core was removed and processed as per the initial core. The results were used to calculate the rates of net ammonification and nitrification over the incubation period (calculated as the difference between the pool size in the initial and incubated soil cores). Differences between net ammonification and nitrification rates between grass types were compared using a two-factor ANOVA with factors grass type (fixed) and plot pair (random).

Root ^{15}N uptake

^{15}N uptake by excised roots was measured in two native grasses (*A. semialata* and *E. triseta*) and *A. gayanus*. Fine roots were sampled by carefully excavating three grass tussocks of each grass species with a shovel and transferring tussocks with attached roots and

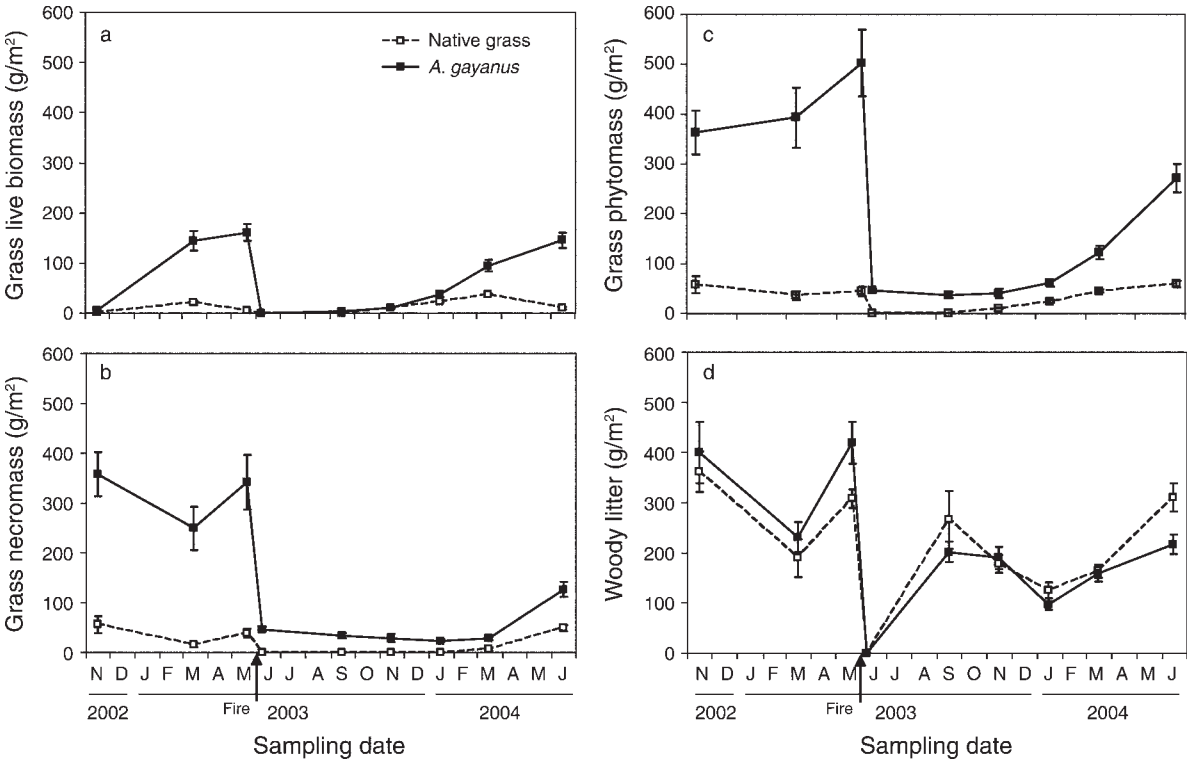

FIG. 2. Grass (a) live biomass (green leaves and stems), (b) standing necromass (dead leaves and stems), and (c) phytomass (live biomass + necromass); and (d) woody litter, in native grass and *A. gayanus* plots at Wildman Reserve (Northern Territory, Australia) from November 2002 to June 2004. Values are means ± SE. A controlled fuel-reduction burn was carried out at the study site in late May 2003, after that month's sampling had been completed.

soil into plastic bags, ensuring that roots from individual plants were kept separate. Samples were stored on ice, transported to the laboratory within 2 hours, and processed immediately. Fine roots were washed, cut into 2-cm lengths, and transferred into 25 mL of ^{15}N-labelled (98–99 atom% excess) solution. Roots were incubated in one of three different N sources (NH_4^+, NO_3^-, or glycine [GLY]) at one of five N concentrations (1, 10, 100, 300, and 1000 μmol/L N; each with 100 μmol/L $CaSO_4$ added to maintain membrane integrity). Root samples were incubated for 30 minutes at 30°C in an agitating (100 rpm) water bath. After the ^{15}N incubation, roots were shaken for 10 minutes in 10 mmol/L KCl to remove ^{15}N from the apoplast, rinsed with deionized water, and dried at 50°C for 24 h. Samples were subsequently ground to a fine powder and analyzed for ^{15}N using a continuous flow isotope mass spectrometer (CFIRMS, Micromass Isochrom, Manchester, UK). Differences in N uptake kinetics between the three grass species were compared by determining V_{max} (maximum uptake rate over 30 minutes) and K_m (substrate concentration at 50% maximum uptake rate). V_{max} and K_m values were calculated by nonlinear curve fitting of the experimental data to the Michaelis-Menten equation: $V = V_{max}(S/[K_m + S])$, where V_{max} is the maximum uptake rate (μmol·g^{-1}·30 min^{-1}); K_m is the Michaelis-Menten affinity constant describing the substrate concentration when 50% of maximum uptake occurs (μmol/L); and S is the substrate concentration (μmol/L).

RESULTS

Aboveground plant material

Grass live biomass, necromass, and overall grass phytomass, were significantly higher in *A. gayanus* plots than in native grass plots (Fig. 2, Table 2a). Mean grass phytomass in *A. gayanus* plots were more than 10 times greater than that in native grass plots (May 2003; means 502 vs. 44.4 g/m^2, respectively, Fig. 2c). *Andropogon gayanus* and native grasses had significantly different live biomass, necromass and phytomass over time (Fig. 2, Table 2a) and these temporal patterns differed between grass types (Table 2a), particularly for live biomass. Live biomass of *A. gayanus* and native grasses increased significantly as the wet season progressed. However, native grasses generally reached peak live biomass in the late wet season (March), while *A. gayanus* reached peak live biomass several months later in the early dry season (May/June) at a time when the native grasses had already senesced, demonstrating that *A. gayanus* has a much longer growing season than the native grasses (Fig. 2a). The patterns in live biomass production showed small scale spatial variation, as

TABLE 2. Summary of significant results from a three-factor ANOVA on grass and woody litter mass (g) and N pools (g N/m^2), a four-factor ANOVA on total soil N pools (g N/m^2), and a three-factor ANOVA on inorganic soil N (NH_4^+ and NO_3^-) availability (ng N·[g resin]$^{-1}$·d^{-1}).

Factor	df	Live biomass	Necromass	Phytomass	Woody litter	Total N	NH_4^+	NO_3^-
a) Mass								
Grass type	1, 4	47.06**	38.83***	42.18**				
Time	8, 32	30.03***	17.13***	17.91***	39.07***			
Plot pair	4, 180				3.64**			
Grass type × time	8, 32	19.60***	8.30***	10.18***	3.44**			
Grass type × plot pair	4, 180	7.67***	2.58***	8.11***				
Time × plot pair	32, 180	2.48***	2.58***	2.79***				
Grass type × time × plot pair	32, 180	2.92***	3.16***	3.38***				
b) N pools								
Grass type	1, 2	22.52*	28.06*	68.19*				
Time	4, 8	32.21***	19.89	28.02***	61.13***			
Grass type × time	4, 8	4.94*						
Grass type × plot pair	2, 60	5.89**	3.27*					
Time × plot pair	8, 60	2.98**						
Grass type × time × plot pair	8, 60	7.41***	3.58**	4.46***				
c) Total soil N pools								
January 2003								
Grass type	1, 4					7.87*		
June 2003								
Grass type	1, 4					22.46***		
Depth	2, 8					10.81**		
January 2004								
Grass type	1, 4					45.48**		
Depth	2, 8					56.74***		
Grass type × depth	2, 8					6.69*		
June 2004								
Depth	2, 8					33.85***		
d) Inorganic soil N availability								
Grass type	1, 4							46.07**
Time	7, 28						7.15***	9.91***
Grass type × time	7, 28						3.15*	9.37***
Time × plot pair	28, 160						1.96**	1.66*

Note: Values in the table are *F* values, and significant results are indicated by asterisks.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

indicated by the significant interactions between plot pair and all other factors (Table 2a). However, there was no overall effect of plot pair for any of the grass mass components and the mean squares for their interaction terms were smaller than for all other main effects and the species by time interaction. Trends were the same at all plot pairs, but on a few occasions the difference between native grass and *A. gayanus* plots were more pronounced at one plot pair than at another.

Leaf litter from woody plant species did not vary significantly between grass type but varied significantly over time, with more woody litter in both grass communities at the start of the wet season, decreasing over the wet season, and then increasing again in the dry season (Fig. 2d, Table 2a). In addition to the significant differences between grass type and time, there was significant spatial variation in woody litter at the scale of plot pairs (Table 2a).

Aboveground plant N pools

The significantly higher grass live biomass, necromass, and total phytomass, in combination with higher tissue N concentrations of *A. gayanus* (Appendix A), resulted in significantly higher N pools in *A. gayanus* plots compared with native grass plots (Fig. 3, Table 2b). N pools of *A. gayanus* phytomass were up to seven times greater than native grass phytomass N pools (March 2003, 1.61 vs. 0.23 g N/m^2 for *A. gayanus* and native grass plots respectively, Fig. 3c). As expected, all grass N pools (live biomass, necromass and phytomass) varied significantly with time (Fig. 3, Table 2b). However the effect of grass type on live biomass N pools differed between sampling times (Table 2b) because the grass N pool for both grass types was zero for several months after fire. Patterns in grass N pools showed small scale spatial variation, as indicated by the significant interactions between plot pair and all other factors and the significant three-way interaction with grass type, plot pair, and time (Table 2b). Trends were the same at all plot pairs, although in some instances the difference between native grass and *A. gayanus* plots were more pronounced at one plot pair than at another.

The N pool of leaf litter from woody species did not vary significantly between plots for the two grass types

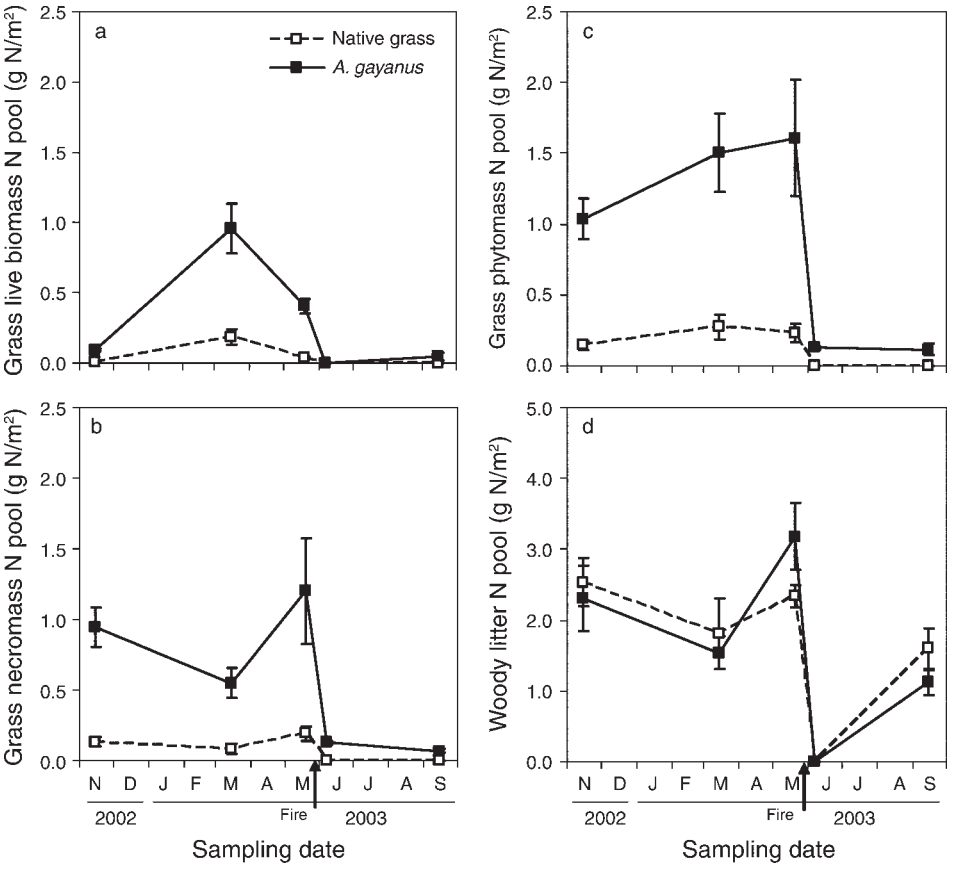

FIG. 3. Grass (a) live biomass (green leaves and stems) N pool, (b) standing necromass (dead leaves and stems) N pool, and (c) phytomass (live biomass + necromass) N pool; and (d) woody litter N pool, in native grass and *A. gayanus* plots at Wildman Reserve (Northern Territory, Australia) from November 2002 to September 2003. Values are means ± SE. A controlled fuel-reduction burn was carried out at the study site in late May 2003, after that month's sampling had been completed.

(Fig. 3d), but varied significantly over time (Table 2b). There was a higher N pool in both grass types at the start of the wet season, which decreased over the wet season, and increased again in the following dry season (Fig. 3d). Although all woody leaf litter was consumed in the fire (May 2003), the woody litter N pool quickly returned to almost pre-fire levels four months after the fire in September 2003 (Fig. 3d).

Belowground root biomass and N pool

Root biomass (0–30 cm) was four times greater in *A. gayanus* plots, compared to the native grass plots (267.3 ± 36.0 vs. 64.9 ± 9.0 g/m^2 [mean ± SE], respectively; $F_{1,2} = 44.77$, $P < 0.05$). However, root N concentrations (% N) did not differ significantly between native grass and *A. gayanus* plot pairs (data not presented), ranging from 0.16% to 0.34% N in the native grass and 0.01% to 0.20% N in *A. gayanus*. Due to biomass differences, the root N pool was significantly higher in *A. gayanus* plots (0.41 ± 0.05 g root N/m^2) compared to the native grass plots (0.16 ± 0.03 root N/m^2), a difference of 2.5 times ($F_{1,2} = 28.37$, $P < 0.05$).

Total soil N pools

Total soil N pools in *A. gayanus* plots were significantly lower than those in native grass plots in the wet season (Fig. 4, Table 2c), and this difference was more pronounced with increasing soil depth. Over two wet seasons (January 2003, January 2004) the total soil N pools in *A. gayanus* plots were 13–28% lower (0–5 cm depth), 18–51% lower (5–10 cm depth), and 25–78% lower (20–30 cm depth) than in the native grass plots (Fig. 4, Table 2c). For example, in January 2004, the mean total soil N at 20–30 cm depth was 93.4 ± 4.2 vs. 20.9 ± 2.2 g N/m^2 in native grass and *A. gayanus* plots, respectively. However in the dry season, the total soil N pool of *A. gayanus* plots was either significantly higher (May 2004) or similar (June 2004) to the total N pool of the native grass plots (Fig. 4, Table 2c). Total soil N pools also varied significantly with depth in both grass types (Fig. 4, Table 2c). However, in January 2004 the effect of depth was not the same in both grass types, resulting in a significant interaction between grass type and depth, with a much larger change in total soil N pools at 20–30 cm depth for the native grass plots (Fig. 4, Table 2c).

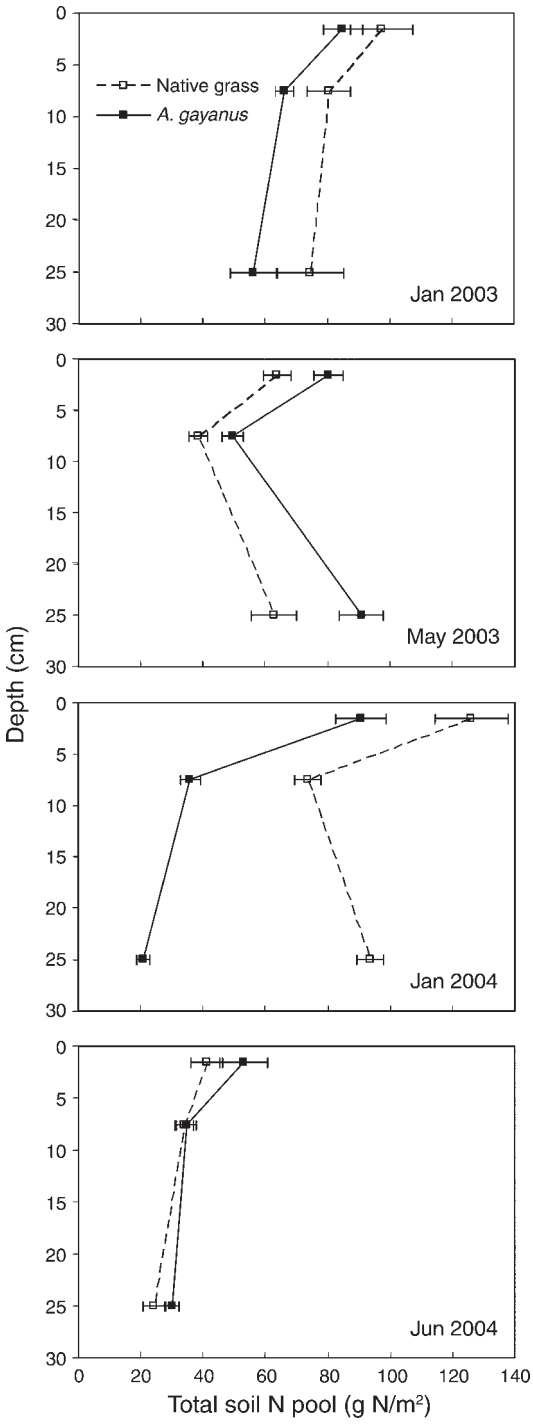

FIG. 4. Mean total soil N in native grass and *A. gayanus* plots at Wildman Reserve (Northern Territory, Australia) over two wet–dry season cycles (January 2003 and May 2003; January 2004 and June 2004). Data are means ± SE. A controlled fuel-reduction burn was carried out at the study site in late May 2003, after that month's sampling had been completed.

Soil inorganic N availability

Availability of NH_4^+ and NO_3^-, as measured with in situ ion exchange resin bags, varied significantly over time in native grass and *A. gayanus* plots (Fig. 5, Table 2d). Although the general pattern of variation of NH_4^+ and NO_3^- availability was similar in both grass types, dissimilarity at some sampling times resulted in a grass type × time interaction (Fig. 5, Table 2d). Post-hoc tests revealed that NH_4^+ availability was significantly (up to three times) higher in *A. gayanus* plots at several times in the wet season (January, March, and November 2003; March 2004; Fig. 5b). For example, in March 2003, the mean NH_4^+ availability was 1643 ± 444 vs. 500 ± 109 ng $NH_4^+ \cdot [\text{g resin}]^{-1} \cdot d^{-1}$ in *A. gayanus* and native grass plots respectively. In contrast, NO_3^- availability was significantly (up to three times) lower in *A. gayanus* plots compared to native grass plots at several times in the wet season (November 2002, January and March 2003, November 2003; Fig. 5c). For example, in November 2002, the mean NO_3^- availability was 226 ± 69 vs. 727 ± 155 ng $NO_3^- \cdot [\text{g resin}]^{-1} \cdot d^{-1}$, in *A. gayanus* and native grass plots, respectively. Although all plot pairs exhibited the same general trend of NH_4^+ and NO_3^- availability, some had a greater magnitude of difference than others at some times, resulting in a plot pair × time interaction (Table 2d).

Net ammonification rates as measured with in situ soil incubations did not vary significantly with grass type or plot pair (means 0.67 vs. 0.73 mg $NH_4^+ \cdot [\text{kg soil}]^{-1} \cdot [28\ d]^{-1}$ in *A. gayanus* and native grass, respectively). In contrast, net nitrification rates were significantly (53%) lower in *A. gayanus* plots, compared to those in native grass plots (means 0.23 vs. 0.50 mg $NO_3^- \cdot [\text{kg soil}]^{-1} \cdot [28\ d]^{-1}$, respectively; $F_{1,2} = 50.70$, $P < 0.05$.

N uptake by excised roots

At concentrations ranging from 1 to 1000 μmol/L N, excised roots of *A. gayanus* and native grass *A. semialata* exhibited a similar order of preference for uptake of the three N sources with $NH_4^+ > \text{GLY} > NO_3^-$, whereas native grass *E. triseta* incorporated N sources in the order of preference $NH_4^+ > NO_3^- > \text{GLY}$ (Fig. 6). Compared with the native grasses, *A. gayanus* had greater incorporation rates of each of the three N sources, but this was most pronounced with NH_4^+ (Fig. 6). The calculated maximum uptake rate (V_{max}) for NH_4^+ of *A. gayanus* was six and 7.5 times higher than V_{max} of *E. triseta* and *A. semialata*, respectively (Fig. 6). In contrast to NH_4^+, *E. triseta* had the highest V_{max} for NO_3^-, with approximately three times higher V_{max} than *A. gayanus* and *A. semialata* (Fig. 6). Uptake of GLY by *A. gayanus* did not follow Michaelis-Menten kinetics, but was linear in the experimental conditions, while the native grasses did exhibit Michaelis-Menten kinetics for GLY uptake (Fig. 6). Substrate affinity (K_m value, substrate concentration at which 50% of the maximum uptake rate is reached) for NH_4^+ was three and ten times

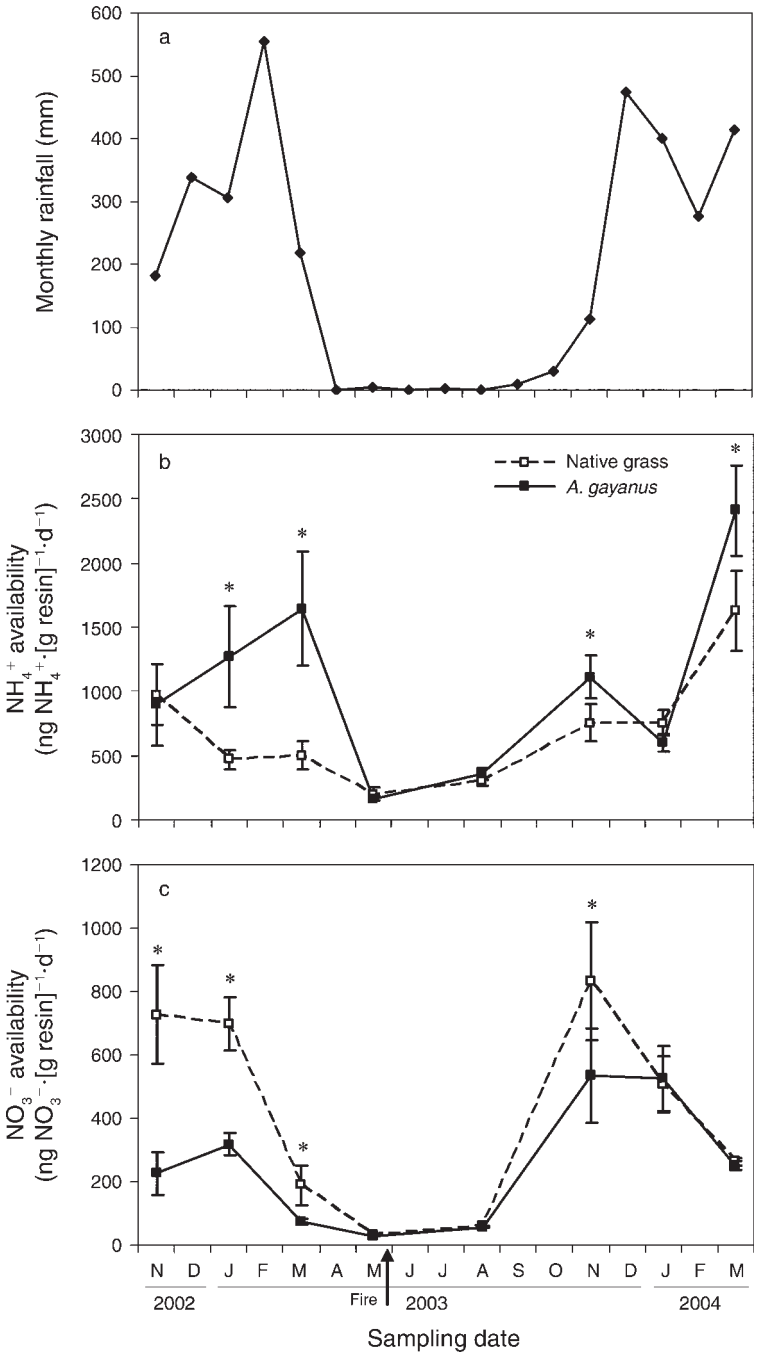

FIG. 5. (a) Monthly rainfall (mm) over the study period, and availability of (b) NH_4^+ and (c) NO_3^- (as determined with in situ ion exchange resin bags) in native grass and *A. gayanus* plots, at Wildman Reserve (Northern Territory, Australia) from November 2002 to March 2004. Values are means ± SE. Asterisks indicate significant differences among grass types ($P < 0.05$). See Table 2d for statistics. A controlled fuel-reduction burn was carried out at the study site in late May 2003, after that month's sampling had been completed.

greater in *A. gayanus* than in *A. semialata* and *E. triseta*, respectively (Fig. 6). *Alloteropsis semialata* had a greater affinity for NO_3^-, with over five times higher K_m values than *A. gayanus* and *E. triseta*, and both the native grasses had a similar affinity for GLY.

DISCUSSION

This study demonstrates that invasion of low-nutrient Australian savanna by *Andropogon gayanus* alters the composition of the community understory and the above- and belowground N pools (Fig. 7). Associated

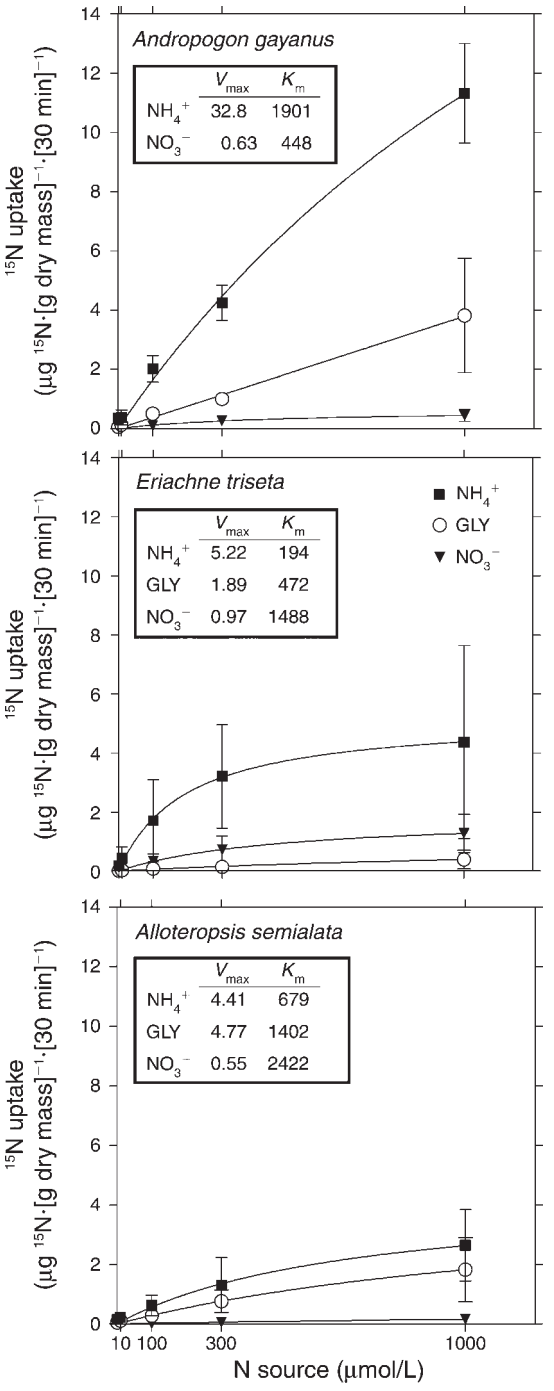

FIG. 6. Uptake of different N forms by excised roots of *A. gayanus* and native grass species *E. triseta* and *A. semialata*. Roots were incubated for 30 minutes in 1, 10, 100, 300, and 1000 μmol/L ^{15}N-labeled (98–99 atom% enriched) ammonium, glycine, and nitrate. Data are averages of three replicates (±SD). V_{max} (maximum uptake rate over 30 minutes) and K_m (substrate concentration at 50% maximum uptake rate) were calculated from uptake curves. Uptake of glycine by *A. gayanus* did not follow Michaelis-Menten kinetics but was instead linear in the studied concentration range.

with the large N pools in the phytomass of *A. gayanus*-dominated understory were marked changes in soil N relations. In a growing season, *A. gayanus* produced an order of magnitude more phytomass than native grasses, resulting in seven and 2.5 times greater shoot and root N pools. The higher growth rate and live biomass accumulation of *A. gayanus* is supported by up to four times greater root biomass per volume of soil, greater rooting depth, and more efficient uptake of N from soil compared with native grasses. Roots of *A. gayanus* had a 52 times higher maximum uptake rate (V_{max}) for ammonium than for nitrate, and six to 7.5 times greater V_{max} for ammonium than native grasses. The kinetics suggest that *A. gayanus* possesses a low affinity/high capacity uptake system for ammonium which would allow efficient uptake from mmol/L concentrations, although a high affinity/low capacity uptake system for μmol/L concentrations may also be present, since plants generally have high and low affinity transport systems (Loqué and von Wirén 2004). Of the studied grasses, *A. gayanus* had the most pronounced difference in ammonium and nitrate uptake, with only high affinity/low capacity uptake of nitrate. *Andropogon gayanus* also had lower nitrification rates in its root zone compared to native grasses. Taken together, these findings indicate that *A. gayanus* has a superior ability to acquire ammonium from high concentrations, a low preference for nitrate, and may inhibit nitrification in its root zone. Nitrification inhibition has been demonstrated for *A. gayanus* and other African grasses (Subbarao et al. 2007).

Savanna trees have a similar order of preference for N sources as *A. gayanus* (NH_4^+ > glycine > NO_3^-) (Schmidt and Stewart 1999) suggesting that ammonium is the main N source for savanna plants, followed by organic N (amino acid-N). Ammonium was taken up preferentially by the native grasses, but nitrate was preferred over organic N (glycine) by *E. triseta*, while nitrate uptake was lower than organic N in *A. semialata* but higher than in *A. gayanus*. The greater capacity for ammonium uptake of *A. gayanus* could affect native savanna plant species via direct competition for ammonium and/or reduced availability of nitrate. Wedin and Tilman (1990) showed that individual grass species can influence soil N availability within just a few years, and they suggested that competition for N may lead to positive feedbacks between the processes controlling species composition.

The significantly greater ammonium availability in *A. gayanus* plots indicates that savanna N relations were altered by the presence of the invasive grass. In the presence of grass roots, soil ammonium availability was three times higher in soil associated with *A. gayanus* invasion compared to soil associated with native grasses. In support of the notion that the presence of *A. gayanus* changes soil N relations, similar ammonium availability was detected in soil of all grasses in the absence of roots. One possible explanation for the discrepancy between

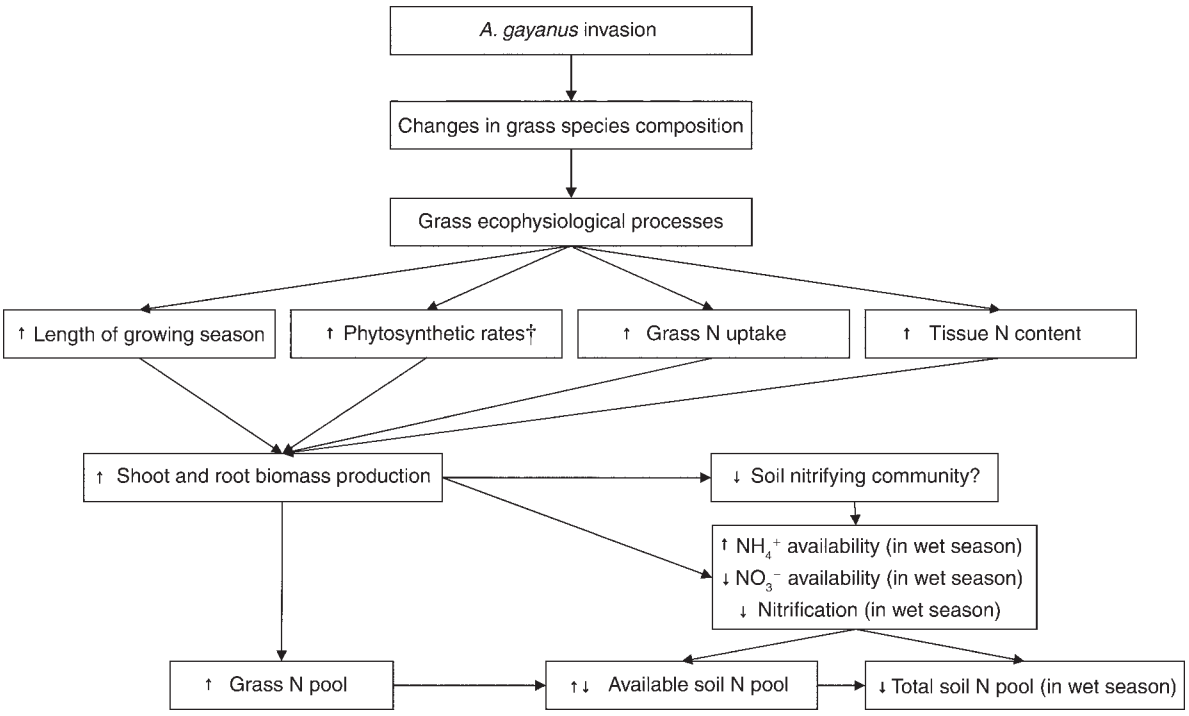

FIG. 7. Model of the effect of *A. gayanus* invasion on ecosystem nitrogen cycling in a savanna woodland (after Liao et al. 2007*a*). Symbols denote an decrease in response to *A. gayanus* invasion (↓), an increase in response to *A. gayanus* invasion (↑), or no change in response to *A. gayanus* invasion (=).Question marks ("?") denote processes that were not directly measured here.
† Data are from Rossiter (2001).

soil ammonium relations measured in the presence or absence of roots is differences in microbial activity. Microbial activity may be stimulated in the presence of *A. gayanus* roots and result in increased rates of mineralization and ammonification. Further research has to substantiate this hypothesis, as little is known about soil microbial communities in Australian savanna soils, or the potential impact of *A. gayanus* invasion on microbial communities. However, both techniques, in situ resin and whole soil incubations, detected lower nitrification rates in soil associated with *A. gayanus* when compared to rates from native grass soils. The lower nitrification rates in soil associated with *A. gayanus,* in combination with the greater availability of ammonium, supports the notion that the presence of *A. gayanus* inhibits nitrification in soil. This concurs with observations from Columbian savanna (Sylvester-Bradley et al. 1988) where after six weeks incubation soil nitrate levels had increased 6.5 times in control plots but only 1.2-times in *A. gayanus* plots. Furthermore, recent research by J. C. Lata, P. Jouquet, X. Raynaud, R. Lensi, L. Abbadie, and S. Barot (*unpublished manuscript*) has documented that in its native range in Western Africa *A. gayanus* reduces the nitrification potential of soil by 78%. This is also consistent with previous studies (Lensi et al. 1992, Lata et al. 2004) demonstrating that the African grass *Hyparrhenia diplandra* decreased the nitrification potential of African savanna soils. A transplant experiment by Lata et al. (2000) showed that the presence of *H. diplandra* altered nitrification by inhibiting the activity of nitrifying bacteria in the soil, and we propose a similar mechanism for *A. gayanus* in Australian savannas. Allelochemicals inhibiting nitrification have been studied intensively (reviewed by Subbarao et al. 2006, 2007) and numerous compounds inhibit growth of nitrifying bacteria, although few studies have investigated these compounds *in situ* and associated with plant roots. It was recently shown that African grass *Brachiaria humidicola* exudes as yet unidentified compounds which inhibit function of nitrifying microbe *Nitrosomonas europea* by blocking the enzymes converting ammonium to nitrite (Subbarao et al. 2007). While it has long been hypothesized that grasses have mechanisms for inhibiting nitrification (Theron 1951, Munro 1966, Meiklejohn 1968), it was only recently demonstrated that grasses, including *Melinis minutiflora*, *Megathyrus maximus* (formerly *Pannicum maximum*), *Brachiaria decumbens* and *A. gayanus* exude compounds that inhibit biological nitrification (Subbarao et al. 2007). The effect of these so-called "biological nitrification inhibition (BNI) compounds" released from *A. gayanus* roots was considerable when compared with artificial nitrification inhibitor allylthiourea (AT), since *A. gayanus* roots produced 7.7 AT units/g root dry mass (Subbarao et al. 2007).

In the current study, the potential advantage for *A. gayanus* provided by suppressed nitrification is that N loss from an invaded site could be markedly reduced. Soil moisture dynamics at our study site suggest that given high intensity rainfall associated with the north Australian monsoon, drainage from the root zone in the top 1 m of soil is significant and in the order of 200–300 mm per annum (L. B. Hutley, S. A. Setterfield, M. M. Douglas, and N. A. Rossiter-Rachor, *unpublished data*). Given that nitrate availability in these savannas is up to 16-fold greater than ammonium (Schmidt et al. 1998), it is likely that nitrate leaches from soil in the wet season. Consequently, inhibition of nitrification and rapid uptake of ammonium would provide an important competitive advantage to *A. gayanus* in this ecosystem, complementing previously documented traits relating to higher photosynthetic and transpiration rates, higher soil water use, and longer growing period, by maximizing N retention and minimizing N loss in this low N system.

In addition to the pronounced changes in available N pools, *A. gayanus* invasion led to significant decreases in total soil N pools in the wet season (the growing season). Decreases in total soil N have been reported for a range of alien grass invasions (Johnson and Wedin 1997, Christian and Wilson 1999, Ibarra-Flores et al. 1999, Kourtev et al. 1999, Reed et al. 2005, Sperry et al. 2006, Drenovsky and Batten 2007). For example, total soil N pools were 40% lower in *Bromus tectorum* invaded communities in southeastern Utah, USA (Sperry et al. 2006). However in some studies the reduction in total soil N due to alien grass invasion varied spatially (Ibarra-Flores et al. 1999, Kourtev et al. 1999), seasonally (Mack and D'Antonio 2003, this study), or following disturbance events such as fire (Reed et al. 2005). The reduction in total soil N following alien plant invasion can be due to their effects on N uptake and N transformation rates, or alterations in disturbance regimes (Corbin and D'Antonio 2004). In the current study the large decreases in total soil N in the wet season are most likely to be caused by increases in N uptake due to *A. gayanus*' higher root and shoot production, deeper rooting depth and longer growing season. Burning of *A. gayanus* phytomass in the frequent savanna fires could also lead to increases in N uptake by *A. gayanus* to support its rapid post-fire growth and reestablishment. In this study, the high levels of *A. gayanus* live biomass had almost completely regrown just one year after complete combustion, and this was accompanied by large reductions in total soil N throughout the entire soil profile. Regular burning of grass phytomass would also result in significant increases in N losses from the ecosystem via volatilization of the large pool of N stored in the aboveground biomass (Rossiter-Rachor et al. 2008), with possible implications for total soil N pools. In the longer term, *A. gayanus* fires could have further effects on the total soil N pool by decreasing tree density, due to increases in fire intensity (Rossiter et al. 2003). Although it was originally thought that it may take several decades for significant decreases in savanna tree cover to occur, a recent study showed that repeated high intensity *A. gayanus* wildfires led to a 53% reduction in tree cover in just 12 years (Ferdinands et al. 2006). High-intensity *A. gayanus* fires and the subsequent reduction in tree cover could lead to further reductions in total soil N, due to the loss of "islands of fertility" associated with trees (reviewed by Schmidt and Lamble 2002). One study, in the Australian savannas, estimated that a 20% reduction in tree density could result in a loss of up to 21 000 kg of N (21 metric tons) from a 10-km^2 area (Ludwig et al. 2000). This could be an important additional effect of *A. gayanus* on savanna N cycling, and should be examined in future studies.

In summary, we have demonstrated that *A. gayanus* significantly alters plant and soil N relations in the mesic savannas of Northern Australia, providing a clear example of how a single species may alter ecosystem N dynamics. We hypothesize that *A. gayanus* inhibits nitrification, as it does in its native range in Africa. This mechanism could play a role in the invasive success and persistence of *A. gayanus* in the low N savannas, in addition to the previously described ecophysiological and morphological traits, as it could allow *A. gayanus* to regulate soil N relations in the invaded system and outcompete native species for N. These changes in N relations, combined with the 8-times higher fire intensities following *A. gayanus* invasion (Rossiter et al. 2003) and the resultant loss of woody cover (Ferdinands et al. 2006), clearly make *A. gayanus* an ecosystem transformer of the mesic savannas of northern Australia.

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APPENDIX

Grass and woody litter tissue nitrogen concentrations in native grass and *Andropogon gayanus* plots (*Ecological Archives* A019-061-A1).