

# Grazing and landscape controls on nitrogen availability across 330 South African savanna sites

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**Abstract** The availability of nitrogen (N) is an important determinant of ecosystem and community dynamics for grasslands and savannas, influencing factors such as biomass productivity, plant and herbivore composition, and losses of N to waters and the atmosphere. To better understand the controls over N availability at landscape to regional scales, we quantified a range of plant and soil characteristics at each of 330 sites in three regions of South Africa: Kruger National Park (KNP), private game reserves adjacent to KNP (private protected areas – PPAs) and Hluhluwe-iMfolozi Park (HiP). In comparing regions and sites within regions, grazing appeared to have a strong influence on N availability. Sites in the PPAs adjacent to KNP as well as sodic and alluvial sites in general typically had the highest N availability. The high N availability of these sites was not generally associated with greater potential N mineralization, but instead with less grass biomass and more forb biomass that indicated greater grazing pressure. Whereas sodic sites had a long history of high N availability as evidenced by their high soil  $\delta^{15}\text{N}$ , the greater N availability in the PPAs over the two parks appeared to be relatively recent. Grazer biomass, average potential mineralization rates and grass biomass for HiP were greater than KNP, yet there were no differences in N availability as indexed by soil and foliar  $\delta^{15}\text{N}$  between sites in the two parks. Although the short-term increase in N availability in PPAs is not necessarily deleterious, it is uncertain whether current productivity levels in those ecosystems is sustainable. With differences in management causing herbivore biomass to be 150% greater in the PPAs than the adjacent KNP, changes in plant communities and nitrogen cycling might lead to long-term degradation of these ecosystems, their ability to sustain herbivore populations, and also serve as an economic resource for the region.

**Key words:** grazing, isotope, nitrogen, savanna, South Africa.

## INTRODUCTION

The availability of nitrogen (N) is an important determinant of ecosystem and community dynamics for grasslands and savannas, structuring plant and animal assemblages as well as determining transfers of N to aquatic systems and the atmosphere (Jefferies *et al.* 1994; Vitousek *et al.* 1997; Stohlgren *et al.* 1999; Owen-Smith 2004). The controls of N availability are considered to vary on multiple spatial scales, driven by distinct processes at each scale (Smithwick *et al.* 2005). For example, processes such as the accumulation of N by trees and termites are known to drive locally high N availability at scales of a few metres (Gallardo *et al.* 2000; Lopez-Hernandez 2001; Grant

& Scholes 2006), while factors such as fire, climate, geology, and the abundance and movement of animals can structure aspects of the N cycle on regional scales (Anderson *et al.* 2007).

The effects of herbivory on N availability and how landscape properties interact with herbivores in their effects on N availability are likely one of the most complex unanswered questions regarding regional patterns of N availability (Pastor *et al.* 1993; Hobbs 1996; McNaughton *et al.* 1997). For example, Frank and Groffman (1998) found that net N mineralization rates in areas open to large herbivores such as bison (*Bison bison*) and elk (*Cervus elaphus*) in Yellowstone National Park, USA were twice as high as adjacent areas in large-herbivore exclosures that had been erected over three decades previously. There, the average effect of herbivores on N mineralization was greater than the largest differences among landscape

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positions, elevating the effect of grazers on N availability over landscape position. In other ecosystems, herbivory can reduce N availability (Knops *et al.* 2000; Kooijman & Smit 2001), and few rules have been offered to understand the predisposing factors that determine whether herbivores will increase or decrease N availability at a given timescale. For example, even though the Yellowstone exclosures had been in place for decades, it is unknown whether the increases in N availability with grazing in Yellowstone are sustainable at longer time scales.

The importance of questions about the interactions between N cycling and grazers extends beyond our general knowledge of the functioning of ecosystems – processes that regulate large herbivores affect a number of economic and conservation issues (Gordon *et al.* 2004). General questions about the controls over landscape and regional patterns of N availability come into focus for South African savannas (Ellery *et al.* 1995; Schreiner *et al.* 1996; Aranibar *et al.* 2003; Du Toit *et al.* 2003). For example, in many of the private protected areas (PPAs) adjacent to Kruger National Park (KNP), managers have been providing year-round surface water to these previously seasonally waterless areas, resulting in greater grazing pressure than has been historically present. Moreover, fences that were erected in the 1960s to divide KNP from the adjacent PPAs to the west were removed 10–15 years ago, recently increasing herbivore pressure on the areas even more as elephants have migrated into the PPAs. Although it is clear that with a stocking density that is 150% greater than KNP (Palmer *et al.* 2006), herbivory has been greater in the PPAs for a few decades, the consequences for nitrogen cycling are unknown. Another contrast to KNP is Hluhluwe-iMfolozi Park, located 500 km to the south of KNP. Herbivore density in Hluhluwe-iMfolozi Park (HiP) is the highest in all of South African protected areas. Herbivore density in HiP is almost three times greater than in KNP, which is more than can be explained by the 50% greater precipitation at HiP (Palmer *et al.* 2006). N availability could be greater in HiP than KNP because of the greater numbers of herbivores, innate differences in soils, or differences in the prevalence of fire, but it is unknown if any of these factors have even altered N availability.

To compare N availability across the three regions and better understand the landscape-level and regional factors associated with variation in N availability, we sampled 330 sites distributed within KNP, the PPAs adjacent to KNP and HiP. In addition to comparing average differences among regions, we also attempted to standardize for covariates by comparing regions at common catenal positions and standardizing for dominant grass species. At each site, the dominant grass species was identified and above-ground herbaceous biomass and surface soils were collected.

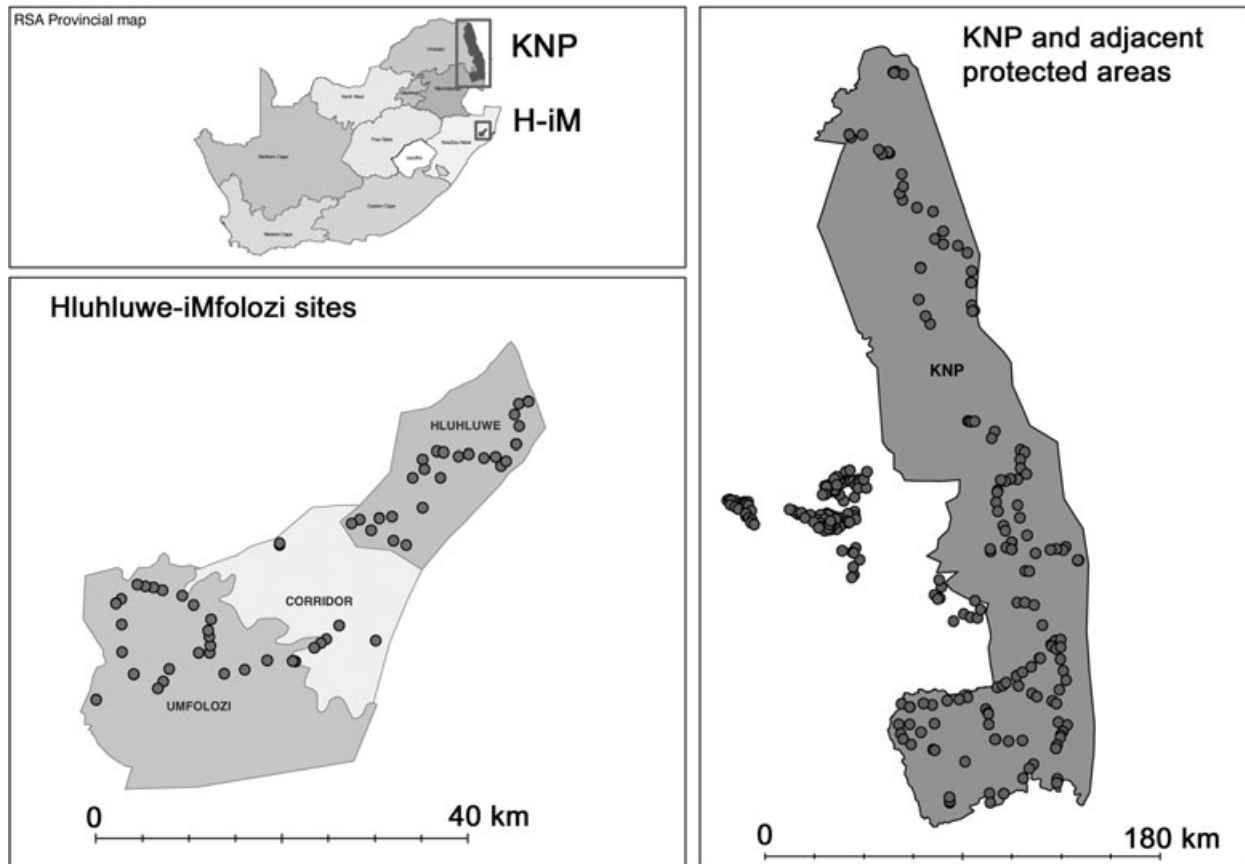
On the green leaf biomass,  $^{15}\text{N}:$  $^{14}\text{N}$  ratios (standardized relative to air,  $\delta^{15}\text{N}$ ) were determined as well as C, N and P concentrations. In addition to soil texture, soil C and N concentrations,  $\delta^{15}\text{N}$ , and potential net N mineralization were determined for each soil sample. We also tested whether high N availability can be explained by there being greater rates of supply or whether biotic uptake of N has likely been reduced by measuring potential N mineralization as an index of soil N supply.

The suite of plant and soil metrics were used to determine which sites might have experienced recent increases in N availability. For example, any sites or regions where recent management changes had increased herbivore biomass would have recently increased N availability to plants as grazers generally reduce plant N demand and increase recycling of N. In contrast, sodic sites or sites on basaltic parent material are defined geologically and are more likely to have experienced high N availability over longer time scales. We predicted that sites that have experienced recent increases in N availability will have high foliar  $\delta^{15}\text{N}$  ( $\delta^{15}\text{N}_L$ ), but not necessarily higher soil  $\delta^{15}\text{N}$  ( $\delta^{15}\text{N}_S$ ), whereas sites that have long experienced high N availability would have high  $\delta^{15}\text{N}_L$  and  $\delta^{15}\text{N}_S$  (Amundson *et al.* 2003). With increasing N availability, mycorrhizal fungi transfer less N to plants and more N is lost via processes, such as denitrification and nitrate leaching from the ecosystem (Hobbie *et al.* 2005; Pardo *et al.* 2006; Craine *et al.*, in press). As the N from mycorrhizal fungi and the N lost from ecosystems are generally depleted in  $^{15}\text{N}$  relative to soil organic N (Hobbie *et al.* 2000; Pardo *et al.* 2002), increasing N availability is associated with greater plant  $\delta^{15}\text{N}$ . As plant material becomes incorporated into soil organic matter,  $^{15}\text{N}$ -enrichment of plant material as a consequence of high N availability becomes reflected in the  $^{15}\text{N}$ -signature of soil organic matter (Amundson *et al.* 2003). In measuring potential N mineralization, we also tested whether high N availability can be explained by greater rates of supply or reduced biotic N uptake.

## MATERIALS AND METHODS

### Plant and soil collection

Plant biomass and soils were collected in 155 sites in KNP, 111 sites in adjacent protected areas to KNP and 64 sites at HiP (Fig. 1). Biomass and soils were collected between 9 February 2005 and 7 April 2005. Sites were selected to vary in catenal position and geology, never located closer than 10 m to a termite mound, and generally not directly under any large trees. Latitude and longitude were established for each



**Fig. 1.** Maps showing location of sampled regions within South Africa (upper left panel), the distribution of sampled points within Hluhluwe-iMfolozi Park (lower left panel) and the distribution of sampled points for KNP and adjacent PPAs (right panel). KNP, Kruger National Park; PPA, private protected area.

site and mean annual precipitation (MAP) for each site was determined from independently compiled databases on climate (Schulze 1997; Zambatis 2003). MAP ranged from 340–690 mm for the PPAs, 260–766 mm for KNP and 523–807 mm for HiP.

At each site, the dominant grass species was identified and then biomass was clipped to 2 cm over a 10 cm × 1 m rectangle using electric shears. When biomass density was low, multiple strips were clipped. Soil for each site was composited from two 5 cm wide × 20 cm diameter cores. All plant biomass was dried and then separated into four fractions: forb, dead grass, live grass stems and live grass leaves. Each fraction was then weighed and ground with a UDY cyclone mill (UDY Corp., Fort Collins, CO, USA). Grass leaves were combusted in a Thermo Finnigan FlashEA 1112 series elemental analyser (Thermo Electron Corp., Waltham, MA, USA) and the C and N isotope values of the resulting gases were determined in a Thermo Finnigan Delta plus XP isotope ratio mass spectrometer. Resultant isotope ratios for C and N were expressed relative to atmospheric N<sub>2</sub> and PDB standards, respectively. For P concentrations, leaf

biomass was first digested in a 10:1:1 mixture of HNO<sub>3</sub>, HClO<sub>4</sub> and H<sub>2</sub>SO<sub>4</sub> for 60 min at 150°C followed by 20 min at 250°C. P concentrations were determined on distilled water extract of the residual with malachite green colorimetry (Diatloff & Rengel 2001) on a Biotek Powerwave XS microplate spectrophotometer (Biotek Instruments, Inc., Winooski, VT, USA).

Soils were air-dried within a few days of collection and then sieved through a 2-mm sieve. Soil C and N concentrations, δ<sup>15</sup>N and δ<sup>13</sup>C were determined as with grasses. For grasses, δ<sup>13</sup>C indexes water use efficiency, while soil δ<sup>13</sup>C is more likely to represent the historical abundance of species with the C<sub>4</sub> photosynthetic pathway (here, grasses) and the C<sub>3</sub> photosynthetic pathway (trees and forbs). Soils were fractionated into three texture classes (sand-silt-clay) by the hydrometer method (Elliott *et al.* 1999) and field water capacity determined as gravimetric water content of saturated soils that have drained at 100% humidity for 24 h in a filter funnel (Paul *et al.* 1999). Potential N mineralization was determined by incubating soils at 50% field capacity at 25°C for 30 days

**Table 1.** Large mammalian herbivore biomass densities for Hluhluwe-iMfolozi Park (HiP), Kruger National Park (KNP) and four private protected areas (PPA1–4)

Region	Years	Mass (kg km <sup>-2</sup> )	Range
HiP*	n/a	9272	
KNP	1998–2004 (7)	3525	3015–3908
PPA1 – Balule	1999–2004 (4)	4278	3641–5411
PPA2 – Jejane	1998–2004 (6)	4731	4371–5512
PPA3 – Tshukudu	1991–2003 (12)	5313	3420–7079
PPA4 – Karongwe	1998–2004 (7)	4129	2771–4770

Included are the years for which biomass was assessed with the number of years biomass was sampled in parentheses, the mean biomass and the range of masses over the sampling interval. HiP data from S. van Rensburg (pers. comm. 2006); other data from Palmer *et al.* (2006) and M. Peel (unpublished 2008).

and determining NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> contents with 1 mol L<sup>-1</sup> KCl extracts of each soil before and after the incubation.

### Statistical analysis

All statistical analyses were compiled on JMP statistical software v. 5.1 (SAS Institute, Cary, NC, USA). The relative importance of plant biomass, leaf chemistry and soil chemistry in determining leaf <sup>15</sup>N were determined with backwards elimination regression with variables removed that had *P* > 0.05. Differences among regions and catenal positions were assessed with ANOVA and Tukey's HSD test.

### Herbivore biomass

To better understand some of the differences in vegetation characteristics among regions, for both KNP and HiP, as well as each of the four PPAs in which we sampled, data on mammalian herbivore biomass densities are presented. Biomass densities are presented (Table 1) from annual wildlife census data and include mammalian grazers, mixed-feeders and browse specialists (see Palmer *et al.* (2006) for details).

## RESULTS

### Comparing regions

In interpreting N isotope patterns for the three regions, the PPAs adjacent to KNP stood out as having higher N availability than HiP and KNP. PPAs had plants with leaves that were enriched in <sup>15</sup>N by an average of 0.9‰ compared with HiP and KNP (Table 2), suggesting greater N availability in the private areas. Plants from the PPAs also had higher [N<sub>L</sub>] (20.4 ± 0.5 mg N g<sup>-1</sup>) and foliar N:P

(11.7 ± 0.3) than the two parks, both indicative of greater N availability and/or lower relative N limitation. In contrast to the greater immediate N availability, PPAs did not have higher δ<sup>15</sup>N<sub>S</sub> than other regions (Table 2), suggesting that the causes of the greater δ<sup>15</sup>N<sub>L</sub> are relatively recent and have not affected soil δ<sup>15</sup>N yet.

Grazing is a likely cause of the greater δ<sup>15</sup>N<sub>L</sub> in the PPAs. Among the three regions, PPAs had 53% less herbaceous biomass on average than KNP and HiP (Table 2), which is much less than expected as the PPAs had just 18% lower MAP than the other two parks. In addition, forb biomass was 25% of the total herbaceous biomass in the PPAs, as opposed to 4% in the other two parks (Table 2), again indicative of greater grazing pressure in the PPAs. The greater N availability was likely due to reduced uptake by plants rather than greater rates of supply as the PPAs did not have greater potential N mineralization rates than the two parks (Table 2). Over all samples, potential N mineralization explained little variation in δ<sup>15</sup>N<sub>L</sub> (δ<sup>15</sup>N<sub>L</sub> = 3.53–0.52\*PotNmin, *P* = 0.03, *r*<sup>2</sup> = 0.01; Fig. 2). Soil C:N was lower in PPAs than KNP and HiP (11.3 *vs.* 12.3, 12.5, respectively, Table 2).

When comparing HiP and KNP, although HiP had more above-ground biomass, there were no differences among the two parks in N availability. δ<sup>15</sup>N<sub>L</sub> was similar for HiP and KNP (3.0 ± 0.1, 3.2 ± 0.2), although potential N mineralization rates in HiP were 133% greater than KNP (Table 2). The greater potential N mineralization in HiP was balanced with 47% greater leaf biomass, and 19% greater stem biomass than KNP. [N<sub>L</sub>], soil C:N and δ<sup>15</sup>N<sub>S</sub> did not differ between the two parks, indicating similar quantities and/or qualities of litter inputs relative to decomposition rates and similar long-term N availability.

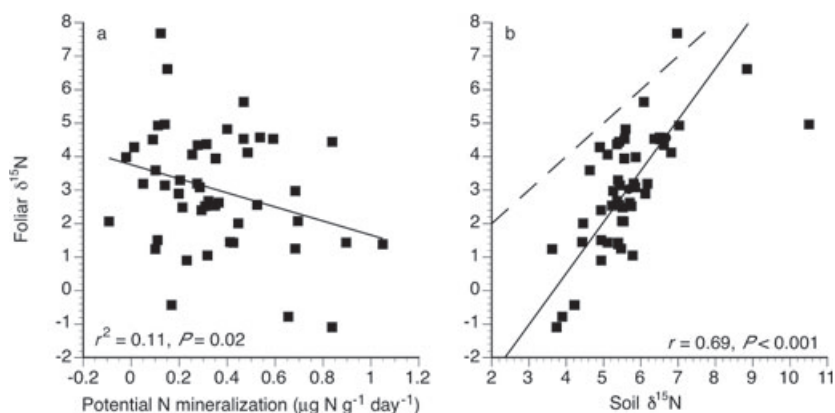
### Catenal positions

Among all sites of the three regions, N availability varied among catenal positions with habitats that were

**Table 2.** Means of metrics for each region, averaged across all sites

<i>n</i>	PPA 111	HiP 72	KNP 184
<b>Plant biomass</b>			
Live grass leaf (g m <sup>-2</sup> )	17.8 (2.1) <sup>a</sup>	60.5 (4.9) <sup>b</sup>	41.1 (2.3) <sup>c</sup>
Dead grass (g m <sup>-2</sup> )	17.3 (2.1) <sup>a</sup>	55.4 (5.2) <sup>b</sup>	38.8 (2.0) <sup>c</sup>
Live grass stem (g m <sup>-2</sup> )	27.3 (3.0) <sup>a</sup>	78.0 (7.8) <sup>b</sup>	65.4 (3.4) <sup>b</sup>
Forb (g m <sup>-2</sup> )	20.3 (3.7) <sup>a</sup>	8.8 (1.9) <sup>b</sup>	6.4 (1.1) <sup>b</sup>
Total (g m <sup>-2</sup> )	81 (8.3) <sup>a</sup>	202.6 (10.4) <sup>b</sup>	152.4 (6.5) <sup>c</sup>
<b>Plant nutrients and isotopes</b>			
[N <sub>L</sub> ] (mg g <sup>-1</sup> )	20.4 (0.5) <sup>a</sup>	15.6 (0.5) <sup>b</sup>	16.5 (0.4) <sup>b</sup>
[P <sub>L</sub> ] (mg g <sup>-1</sup> )	1.86 (0.06) <sup>a</sup>	1.58 (0.09) <sup>a</sup>	2.73 (0.10) <sup>b</sup>
[C <sub>L</sub> ] (mg g <sup>-1</sup> )	418.7 (1.2) <sup>a</sup>	416.1 (1.9) <sup>a</sup>	418.7 (1.0) <sup>a</sup>
[N <sub>L</sub> :P <sub>L</sub> ]	11.7 (0.3) <sup>a</sup>	10.9 (0.4) <sup>a</sup>	7.2 (0.2) <sup>b</sup>
δ <sup>15</sup> N <sub>L</sub> (‰)	4.0 (0.1) <sup>a</sup>	3.2 (0.2) <sup>b</sup>	3.0 (0.1) <sup>b</sup>
δ <sup>15</sup> N <sub>L</sub> -δ <sup>15</sup> N <sub>S</sub>	-1.4 (0.1) <sup>a</sup>	-2.4 (0.2) <sup>b</sup>	-2.7 (0.1) <sup>b</sup>
<b>Soil nutrients and isotopes</b>			
δ <sup>15</sup> N <sub>S</sub> (‰)	5.4 (0.1) <sup>a</sup>	5.7 (0.1) <sup>a</sup>	5.7 (0.1) <sup>a</sup>
[N <sub>S</sub> ] (mg g <sup>-1</sup> )	0.9 (0.0) <sup>a</sup>	1.7 (0.1) <sup>b</sup>	1.0 (0.0) <sup>a</sup>
[C <sub>S</sub> ] (mg g <sup>-1</sup> )	10.5 (0.6) <sup>a</sup>	21.7 (1.5) <sup>b</sup>	12.8 (0.5) <sup>c</sup>
[C <sub>S</sub> :N <sub>S</sub> ]	11.3 (0.1) <sup>a</sup>	12.5 (0.2) <sup>b</sup>	12.3 (0.1) <sup>b</sup>
NH <sub>4</sub> <sup>+</sup> Min (μg N g <sup>-1</sup> d <sup>-1</sup> )	-0.063 (0.006) <sup>a</sup>	-0.084 (0.009) <sup>b</sup>	-0.058 (0.003) <sup>a</sup>
NO <sub>3</sub> <sup>-</sup> Min (μg N g <sup>-1</sup> d <sup>-1</sup> )	0.42 (0.04) <sup>a</sup>	0.71 (0.07) <sup>b</sup>	0.33 (0.03) <sup>c</sup>
N Min (μg N g <sup>-1</sup> d <sup>-1</sup> )	0.35 (0.04) <sup>a</sup>	0.63 (0.05) <sup>b</sup>	0.27 (0.03) <sup>c</sup>

Standard errors presented in parentheses. Superscript letters designate significant differences in means compared across regions with Tukey's HSD ( $P < 0.05$ ). Sites include ones located in the private protected areas (PPAs) adjacent to Kruger National Park (KNP), Hluhluwe-iMfolozi Park (HiP) and KNP.



**Fig. 2.** Relationships between foliar δ<sup>15</sup>N and potential N mineralization (a) and soil δ<sup>15</sup>N (b) after averaging metrics for each species ( $n = 48$ ) across all three regions. Dashed line is 1:1 line.

considered to have higher grazing intensity having higher N availability. Sodic sites and alluvial sites had higher δ<sup>15</sup>N<sub>L</sub> than other catenal positions (Table 3), but only sodic sites had greater δ<sup>15</sup>N<sub>S</sub>, indicating greater long-term N availability on those sites. None of the differences in δ<sup>15</sup>N<sub>L</sub> among catenal positions were associated with greater potential N mineralization (data not shown). Among the three regions, only crests, midslopes and footslopes were sampled at high enough frequency ( $n \geq 5$  for each region) to allow

comparisons of the same catenal position among regions. Comparing across a common catenal position among regions, PPAs still had greater short-term N availability without differences in long-term N availability. δ<sup>15</sup>N<sub>L</sub> was greater on crests and midslopes in PPAs than the other two regions (average of 2.2‰ and 0.9‰, respectively), while there was no significant difference among regions in δ<sup>15</sup>N<sub>L</sub> for footslopes. There were no significant differences among regions in δ<sup>15</sup>N<sub>S</sub> for each catenal position ( $P > 0.1$ ).

**Table 3.** Means and SE for different catenal positions

	<i>n</i>	[N <sub>L</sub> ] (mg N g <sup>-1</sup> )	δ <sup>15</sup> N <sub>L</sub> (‰)	Residual δ <sup>15</sup> N <sub>L</sub> (‰)	δ <sup>15</sup> N <sub>S</sub> (‰)
Crest	28	17.8 ± 1 <sup>bc</sup>	3.40 ± 0.34 <sup>bc</sup>	-0.01 ± 0.28 <sup>b</sup>	5.88 ± 0.22 <sup>b</sup>
PPA	15	21.5 ± 1.5 <sup>x</sup>	4.41 ± 0.47 <sup>x</sup>	0.28 ± 0.26 <sup>x</sup>	6.08 ± 0.18 <sup>x</sup>
KNP	8	15.1 ± 1.6 <sup>y</sup>	2.62 ± 0.63 <sup>xy</sup>	-0.24 ± 0.51 <sup>x</sup>	5.98 ± 0.49 <sup>x</sup>
HiP	5	11.7 ± 0.5 <sup>y</sup>	1.82 ± 0.14 <sup>y</sup>	-0.36 ± 0.08 <sup>x</sup>	4.93 ± 0.28 <sup>x</sup>
Midslope	105	17.8 ± 0.5 <sup>bc</sup>	3.48 ± 0.17 <sup>c</sup>	0.10 ± 0.14 <sup>b</sup>	5.43 ± 0.11 <sup>b</sup>
PPA	67	19.9 ± 0.6 <sup>x</sup>	3.84 ± 0.14 <sup>x</sup>	0.03 ± 0.13 <sup>x</sup>	5.36 ± 0.12 <sup>x</sup>
KNP	18	14.4 ± 0.8 <sup>y</sup>	3.13 ± 0.46 <sup>xy</sup>	0.41 ± 0.34 <sup>x</sup>	5.83 ± 0.29 <sup>x</sup>
HiP	20	13.7 ± 1.0 <sup>y</sup>	2.62 ± 0.43 <sup>y</sup>	0.05 ± 0.3 <sup>x</sup>	5.31 ± 0.15 <sup>x</sup>
Footslope	54	16.1 ± 0.7 <sup>c</sup>	2.95 ± 0.24 <sup>c</sup>	-0.11 ± 0.20 <sup>b</sup>	5.66 ± 0.15 <sup>b</sup>
PPA	6	21.1 ± 1.3 <sup>x</sup>	3.67 ± 0.57 <sup>x</sup>	-0.38 ± 0.51 <sup>x</sup>	4.71 ± 0.38 <sup>x</sup>
KNP	26	15.9 ± 1.1 <sup>xy</sup>	2.79 ± 0.31 <sup>x</sup>	-0.23 ± 0.3	5.67 ± 0.28 <sup>x</sup>
HiP	22	15.2 ± 0.8 <sup>y</sup>	2.97 ± 0.38 <sup>x</sup>	0.09 ± 0.31 <sup>x</sup>	5.89 ± 0.18 <sup>x</sup>
Sodic	12	21.9 ± 1.6 <sup>ab</sup>	5.84 ± 0.51 <sup>a</sup>	1.92 ± 0.42 <sup>a</sup>	7.18 ± 0.32 <sup>a</sup>
Alluvial	23	20.4 ± 1.5 <sup>a</sup>	4.82 ± 0.37 <sup>ab</sup>	0.20 ± 0.31 <sup>b</sup>	5.84 ± 0.23 <sup>b</sup>
Plain	97	15.5 ± 0.5 <sup>c</sup>	2.90 ± 0.19 <sup>c</sup>	-0.07 ± 0.15 <sup>b</sup>	5.56 ± 0.11 <sup>b</sup>

Metrics include foliar N concentrations ([N<sub>L</sub>]), foliar δ<sup>15</sup>N (δ<sup>15</sup>N<sub>L</sub>), the differences in residual δ<sup>15</sup>N<sub>L</sub> from the relationship between δ<sup>15</sup>N<sub>L</sub> and [N<sub>L</sub>], and soil δ<sup>15</sup>N (δ<sup>15</sup>N<sub>S</sub>) for each catenal position averaged across all regions. Among the 330 sites in this study, no catenal position was identified for 12 sites, and two sites in KNP were identified as seep lines and not included here. Superscript letters (a–c) refer to Tukey's HSD comparisons (*P* < 0.05) among catenal positions for a metric, while superscript letters (x,y) refer to comparisons among regions for a given catenal position. HiP, Hluhluwe-iMfolozi Park; KNP, Kruger National Park; PPA, private protected area.

### Plant species differences

Differences among regions could be due to differences in grass species as the <sup>15</sup>N signatures of the leaves differed consistently across species with species associated with grazing and/or disturbance indicating greater N availability. Forty-eight species were identified as dominant on at least one site with some species dominant at only one site, e.g. *Chloris mossambicensis*, and others at over 50 – *Panicum maximum* dominated 60 sites (Table 4). Plots that were dominated with species that had high leaf δ<sup>15</sup>N had species that were associated with disturbance, high grazing and/or low incidence of fire, for example, *Dactyloctenium aegyptium* (7.7‰), *Sporobolus nitens* (6.4‰) and *Dactyloctenium australe* (5.6‰). Plots with species whose leaves were relatively depleted in <sup>15</sup>N were associated with low grazing palatability, indicative of low physical disturbance and/or associated with high incidence of fire, for example *Hyperthelia dissoluta* (-1.1‰), *Setaria sphacelata* var. *sericea* (-0.8‰) and *Aristida stipitata* (-0.4‰). Species-averaged δ<sup>15</sup>N<sub>L</sub> was not associated with greater potential N mineralization of the sites they occupied, as there was no positive relationship between species-averaged δ<sup>15</sup>N<sub>L</sub> and potential N mineralization, but instead a weak, but negative relationship (Fig. 2). Species-averaged δ<sup>15</sup>N<sub>L</sub> was positively correlated with δ<sup>15</sup>N<sub>S</sub> (Fig. 2). Although species with high δ<sup>15</sup>N<sub>L</sub> occupied sites with high long-term soil N availability, the slope between δ<sup>15</sup>N<sub>L</sub> and δ<sup>15</sup>N<sub>S</sub> was greater than 1 (-5.77 + 1.56\*δ<sup>15</sup>N<sub>S</sub>, 95% CI = 1.13–2.16; Fig. 2), implying that the difference between leaf and soil narrows with increasing δ<sup>15</sup>N<sub>S</sub>.

When comparing the same grass species across the three regions, the greater N availability of the PPAs over the other two regions was maintained. Only *Panicum maximum* was sampled frequently enough in each region for robust comparisons of the same species in all three regions. The δ<sup>15</sup>N<sub>L</sub> of *Panicum maximum* in the PPAs was not greater than in the other two regions. In KNP, δ<sup>15</sup>N<sub>L</sub> of *Panicum maximum* was lower than in PPAs or HiP (3.17 ± 0.33 vs. 4.13 ± 0.30, 4.84 ± 0.53; *P* = 0.02). Yet, of the 13 species that were present in the PPAs and KNP, 12 of the 13 species had higher δ<sup>15</sup>N<sub>L</sub> in the PPAs than KNP. This led to a greater average δ<sup>15</sup>N<sub>L</sub> in the PPAs than KNP (1.06 ± 0.47, *P* = 0.04, paired *t*-test), but there was no significant difference in δ<sup>15</sup>N<sub>S</sub> for species in PPAs and KNP (*P* = 0.45). Only three species were sampled in common between the PPAs and HiP, which were not enough for meaningful comparison. Of the 10 species that were sampled in common between KNP and HiP, there was no significant difference in δ<sup>15</sup>N<sub>L</sub> between the two regions (*P* = 0.46, paired *t*-test).

### Explaining variation in δ<sup>15</sup>N<sub>L</sub>

The differences in δ<sup>15</sup>N<sub>L</sub> among regional contrasts were no longer significant when compared at a common [N<sub>L</sub>], implying that the factors that were enriching plants in <sup>15</sup>N were generally also causing higher leaf N concentrations. For the entire dataset, the strongest relationship with δ<sup>15</sup>N<sub>L</sub> was with [N<sub>L</sub>] (*r* = 0.53, *P* < 0.001; Fig. 3) with similar explanatory power for leaf C:N and log-transformed [N<sub>L</sub>] (data not shown).

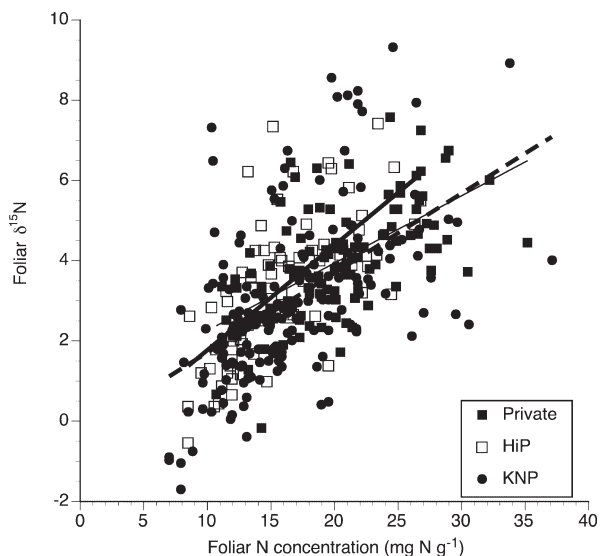
**Table 4.** Dominant grass species, number of plots observed (*n*), total above-ground biomass (AG), leaf nitrogen concentrations ([N<sub>L</sub>]), leaf δ<sup>15</sup>N and soil δ<sup>15</sup>N

Species	<i>n</i>	Total AG (g m <sup>-2</sup> )	[N <sub>L</sub> ] (mg g <sup>-1</sup> )	Leaf δ <sup>15</sup> N	Soil δ <sup>15</sup> N
<i>Aristida adscensionis</i>	6	21.33 ± 5.78	17.98 ± 1.68	3.08 ± 0.52	5.85 ± 0.29
<i>Aristida congesta barbicollis</i>	4	128.97 ± 39.44	12.1 ± 0.8	2.89 ± 0.36	6.12 ± 0.43
<i>Aristida congesta congesta</i>	2	81.25 ± 15.25	12.6 ± 0.3	1.51 ± 0.59	4.94 ± 0.29
<i>Aristida stipitata</i>	1	166.1	13.1	-0.43	4.22
<i>Bothriochloa insculpta</i>	8	77.41 ± 12.77	19.84 ± 1.01	4.77 ± 0.63	5.4 ± 0.39
<i>Bothriochloa radicans</i>	7	75.83 ± 21.45	17.97 ± 1.36	2.71 ± 0.38	5.27 ± 0.28
<i>Brachiaria deflexa</i>	25	32.74 ± 6.66	23.84 ± 1.15	4.52 ± 0.3	5.56 ± 0.17
<i>Cenchrus ciliaris</i>	17	108.67 ± 14.36	18.5 ± 1.29	2.58 ± 0.3	5.24 ± 0.19
<i>Chloris gayana</i>	2	225.95 ± 4.45	11.75 ± 1.15	1.39 ± 1.04	5.39 ± 0.13
<i>Chloris mossambicensis</i>	1	35.3	16.7	4.96	10.51
<i>Chloris virgata</i>	3	138.4 ± 67.2	18.1 ± 3.19	4.34 ± 1.61	6.62 ± 0.91
<i>Cymbopogon plurinodis</i>	1	168.3	13.2	1.24	3.62
<i>Cymbopogon</i> spp.	3	112.07 ± 37.92	12.13 ± 0.32	1.44 ± 0.27	5.11 ± 0.65
<i>Dactyloctenium aegyptium</i>	2	72.08 ± 34.03	20.75 ± 3.85	7.68 ± 1.61	6.97 ± 0.53
<i>Dactyloctenium australe</i>	4	81.4 ± 13.68	20.48 ± 2.16	5.63 ± 1.05	6.08 ± 0.67
<i>Digitaria eriantha</i>	17	79.29 ± 12.54	16.89 ± 1.48	3.38 ± 0.36	5.42 ± 0.27
<i>Digitaria longiflora</i>	5	75.62 ± 13	17.76 ± 1.59	4.57 ± 0.8	6.51 ± 0.25
<i>Digitaria sanguinalis</i>	1	294.7	12.6	2.01	4.45
<i>Digitaria</i> spp.	1	42.7	20.5	4.12	6.81
<i>Digitaria velutina</i>	1	237.1	12.4	2.52	5.75
<i>Enneapogon cenchroides</i>	16	80.89 ± 10.4	14.13 ± 0.67	2.63 ± 0.15	5.71 ± 0.31
<i>Eragrostis curvula</i>	4	142.3 ± 29.21	12.45 ± 0.93	4.53 ± 0.96	6.36 ± 1.19
<i>Eragrostis lehmanniana</i>	6	110.02 ± 21.48	18 ± 2.07	4.51 ± 0.9	6.53 ± 0.62
<i>Eragrostis racemosa</i>	2	108.5 ± 8.6	12.15 ± 2.45	1.45 ± 1.18	4.43 ± 1.67
<i>Eragrostis rigidior</i>	7	52.68 ± 9.37	18.17 ± 1.61	3.59 ± 0.66	4.63 ± 0.44
<i>Eragrostis</i> spp.	2	108.5 ± 72.6	14.15 ± 3.85	2.98 ± 0.15	5.26 ± 0.85
<i>Eragrostis superba</i>	7	113.24 ± 21.63	15.64 ± 1.38	4 ± 0.55	5.93 ± 0.32
<i>Heteropogon contortus</i>	6	111.81 ± 26.79	15.68 ± 2.98	1.57 ± 0.67	5.5 ± 0.26
<i>Hypparrhenia tamba</i>	4	186.45 ± 19.13	8.78 ± 0.24	0.9 ± 0.67	4.94 ± 0.28
<i>Hyperthelia dissoluta</i>	1	51.9	7.9	-1.09	3.74
<i>Melinis repens</i>	10	72.3 ± 19.35	21.81 ± 2.05	4.37 ± 0.64	5.36 ± 0.5
<i>Microchloa caffra</i>	1	94.1	26.8	5.49	8.07
<i>Panicum coloratum</i>	4	178.5 ± 13.46	16.1 ± 1.87	3.35 ± 0.67	5.97 ± 0.33
<i>Panicum deustum</i>	4	81.23 ± 20.56	17.53 ± 2.23	2.97 ± 0.63	5.24 ± 0.27
<i>Panicum maximum</i>	61	120 ± 10	18.87 ± 0.53	3.88 ± 0.21	5.5 ± 0.13
<i>Pogonarthria squarrosa</i>	8	102.48 ± 25.23	13.13 ± 0.75	3.14 ± 0.33	5.44 ± 0.37
<i>Schmidtia pappophoroides</i>	5	74.6 ± 53.1	19.55 ± 1.7	4.06 ± 0.72	5.11 ± 0.26
<i>Setaria sphacelata sericea</i>	3	124.53 ± 35.41	8.73 ± 1.31	-0.78 ± 0.63	3.89 ± 0.45
<i>Setaria sphacelata torta</i>	5	173.24 ± 13	10.82 ± 0.54	1.25 ± 0.75	5.47 ± 0.66
<i>Setaria</i> spp.	1	101.4	13.2	1.05	5.78
<i>Sporobolus africanus</i>	1	169.3	14.9	2.4	4.93
<i>Sporobolus fimbriatus</i>	1	89.2	15.8	4.28	4.9
<i>Sporobolus ioclados</i>	6	45.06 ± 15.15	17.45 ± 2.28	4.93 ± 0.75	7.03 ± 0.5
<i>Sporobolus nitens</i>	5	66.64 ± 13.72	24.26 ± 2.74	6.42 ± 0.99	7.75 ± 1.11
<i>Sporobolus panicoides</i>	1	183.6	14.6	2.48	5.51
<i>Sporobolus pyramidalis</i>	4	73.25 ± 16.1	18.1 ± 2.64	4.9 ± 0.81	5.8 ± 0.46
<i>Themeda triandra</i>	28	191.3 ± 19.92	13.64 ± 0.52	2.07 ± 0.22	5.49 ± 0.11
<i>Tricholaena monachne</i>	1	138.6	8.2	1.43	5.39
<i>Urochloa mosambicensis</i>	55	101.41 ± 8	19.28 ± 0.76	3.21 ± 0.21	5.72 ± 0.15

Means and standard errors are presented.

Using the linear relationship between [N<sub>L</sub>] and δ<sup>15</sup>N<sub>L</sub>, with each 10 mg N g<sup>-1</sup> increase in [N<sub>L</sub>], δ<sup>15</sup>N<sub>L</sub> increased by 2.9‰. There were no differences among the three regions in δ<sup>15</sup>N<sub>L</sub> when compared at the mean [N<sub>L</sub>] for all samples (*P* = 0.12), but sodic sites remained elevated in <sup>15</sup>N when compared at a common [N<sub>L</sub>] (Table 3).

In a multiple regression model of δ<sup>15</sup>N<sub>L</sub> (Table 5), beyond the 34% of the total variation explained by [N<sub>L</sub>], δ<sup>15</sup>N<sub>s</sub> explained an additional 14%. δ<sup>15</sup>N<sub>L</sub> declined with both increasing soil δ<sup>13</sup>C and [N<sub>s</sub>], but these two factors explained a small amount of additional variation over [N<sub>L</sub>] and δ<sup>15</sup>N<sub>s</sub> (partial *r*<sup>2</sup> = 0.02



**Fig. 3.** Standardized major axis relationships between foliar  $\delta^{15}\text{N}$  and N concentrations for sites from private reserves adjacent to KNP (thin line), sites from KNP (dashed line) and sites from HiP (thick line). The slope of the relationship for HiP sites was greater than those of the other two sites at  $P = 0.06$ . HiP, Hluhluwe-iMfolozi Park; KNP, Kruger National Park.

**Table 5.** Regression model results explaining foliar  $\delta^{15}\text{N}$  ( $\delta^{15}\text{N}_L$ ) for all sites

	Estimate	SS	<i>P</i>
Intercept	$-4.47 \pm 0.59$		<0.001
$[\text{N}_L]$	$1.58 \pm 0.13$	232.9	<0.001
Soil $\delta^{15}\text{N}$	$0.64 \pm 0.06$	188.5	<0.001
Soil $\delta^{13}\text{C}$	$-0.12 \pm 0.03$	26.2	<0.001
$[\text{C}_S]$	$-4.62 \pm 1.18$	24.8	<0.001

Estimates represent slopes between metrics and  $\delta^{15}\text{N}_L$ . Units for  $[\text{N}_L]$  and  $[\text{C}_S]$  are  $\text{mg g}^{-1}$ , while soil  $^{15}\text{N}$  and  $^{13}\text{C}$  in ‰. Model  $r^2 = 0.53$ .

and 0.03, respectively,  $P < 0.001$  for each). There was no consistent pattern in  $\delta^{15}\text{N}_L$  with increasing grass or forb biomass,  $[\text{P}_L]$ ,  $[\text{C}_S]$ ,  $^{13}\text{C}_L$  or any texture class after controlling for the four significant variables in the model ( $P > 0.05$ ).

## DISCUSSION

### Grazing in private protected areas

In comparing soil and vegetation characteristics among regions, there was strong evidence that N availability has increased relatively recently in the PPAs adjacent to KNP. In the PPAs compared with the other two parks, foliar N concentrations, plant N:P and

plant  $\delta^{15}\text{N}$  were higher. The greater plant  $\delta^{15}\text{N}$  was still evident when compared at common catenal positions and when comparing sites dominated by the same grass species. The lack of difference in  $\delta^{15}\text{N}_S$  implies that this increase is relatively recent and the low above-ground biomass coupled with high forb biomass suggested it is the recent increase in the density of herbivores in the PPAs adjacent to KNP that is increasing N availability. The lack of differences in potential mineralization rate suggested that it is reduced uptake rather than greater supply rates that lead to the greater N availability in the PPAs.

From long-term monitoring efforts, herbivore abundance has been high in the PPAs for at least 15 years. For example, herbaceous plant composition and mammalian herbivore biomass density has been monitored in many of the PPAs since 1992 (M. Peel, unpublished). Both stocking density and forb density in some PPAs have been high since monitoring began over a decade ago (M. Peel, unpublished). For example, across multiple years, herbivore biomass density was 31% greater in the PPAs than KNP (Table 1). Quite likely, the herbivore density (and therefore N availability) has been high for longer, likely since surface water availability in the PPAs was increased in the 1960s. The lack of change in soil  $^{15}\text{N}$  values for the PPA relative to foliar  $^{15}\text{N}$  only suggests that N availability in the PPAs has not been high at the century scale. With the plant N pool being small relative to the soil N pool, and the enrichment of plant material in the PPAs relatively low compared with the other two regions, mass-balance calculations suggest that soil  $\delta^{15}\text{N}$  is relatively unresponsive at decadal scales (data not shown), even with the potentially rapid incorporation of mineralized N into SOM (Kaye *et al.* 2002).

### Patterns of $\delta^{15}\text{N}$

It should also be noted that the consistently greater  $\delta^{15}\text{N}$  of soil compared with leaves is the general rule at the global scale (Craine *et al.*, in press), most likely as a result of fractionation by mycorrhizal fungi that depletes plants in  $^{15}\text{N}$ . There is evidence that arbuscular mycorrhizal fungi fractionate against heavy N in transfers to plants (Spriggs *et al.* 2003; Craine *et al.*, in press), but the degree of fractionation associated with plants that utilize arbuscular mycorrhizal fungi relative to non-mycorrhizal plants ( $\sim 1\%$ ) would make it unlikely that enrichment in some sites, where foliar  $^{15}\text{N}$  is much greater than soils, could be explained solely by reduction in mycorrhizal dependence with increasing N availability. As foliar  $\delta^{15}\text{N}$  was assessed at the stand level (all biomass in a given area was sampled), the relative enrichment of foliar N in grasses from the PPAs is unlikely to be due to differential acquisition of ammonium by some plants over nitrate by others.

Instead of these mechanisms explaining the isotopic enrichment of foliar N, depleted N can be lost during volatilization of ammonium, gaseous N loss during nitrification, denitrification and loss of  $\text{NO}_3^-$  via leaching if nitrification is present, but not complete (Högberg 1997; Houlton *et al.* 2006; Craine *et al.*, in press). In Yellowstone, Frank and Evans (1997) had found that plants in grazed sites had vegetation with lower  $\delta^{15}\text{N}$  than ungrazed sites, which they postulated was associated with uptake of  $^{15}\text{N}$ -depleted ammonia that had volatilized. If this is a general feature of sites dominated by ammonia losses, then ammonia losses are unlikely to explain the enrichment in the three regions investigated here. Most likely,  $^{15}\text{N}$  enrichment of plants occurs as a result of N lost during or after nitrification. As increased grazing reduces N uptake by plants, more ammonium is available for nitrification and more nitrate is denitrified. Rates of  $\text{NO}_x$  losses at KNP are greatest in sites that have the highest N availability (Parsons *et al.* 1996), but more *in situ* measurements and modelling would be required to confirm that these gaseous losses would be sufficient to explain patterns of foliar  $^{15}\text{N}$  enrichment. Even though the differences among regions held when holding the dominant species constant, part of the pattern of grazing-induced increases in N availability could be in the changes in species abundance that accompany grazing, but we know little at this time about these indirect feedbacks to N availability.

### Management considerations

As mentioned earlier, in many other grasslands, the presence of grazers increases N availability (Detling 1998; Frank & Groffman 1998; Johnson & Matchett 2001; Augustine & McNaughton 2004). As such, the recent increase in N availability in PPAs does not necessarily require prescriptive remedial action. Yet, the sustainability of the recent increases in N availability and the ability to maintain higher herbivore densities are an open question. Already the increased fraction of forbs could indicate a decreased ability to support herbivores as palatable grasses decrease in relative abundance. It is possible that the greater N availability caused by grazing in the PPAs could be a relatively temporary phenomenon. Although pre-existing conditions cannot be ruled out, soil C:N is also lower in the PPAs than the two parks, most likely as a result of decreased inputs of C and reducing the ability of the soil to immobilize N. With the greater plant  $\delta^{15}\text{N}$  likely indicating greater rates of N losses, if these losses are not offset with increased inputs of N, mineralization might decline causing long-term degradation of the soil.

An open question that would help contextualize the greater N availability in the PPAs is how sodic sites

have maintained their productivity despite a long history of grazing and elevated N availability. If nitrogen lost from sodic sites is replaced by within-site fixation and/or deposition, then it is possible that the same mechanisms could replace lost N in parts of the PPAs. Yet, if the sodic sites are reliant on inputs of N from other parts of the landscape, then what maintains long-term productivity for sodic sites is unlikely to be transferable to the regional scale.

Although the increased N availability in the PPAs attracts the most attention, the lack of difference in N availability as indexed by foliar  $^{15}\text{N}$  between KNP and HiP deserves as much consideration. Compared with KNP, HiP has higher herbivore density (163% more, Table 1) and greater potential rates of N mineralization. Yet, there is little evidence that the losses of N would be greater in HiP as there were no differences in foliar  $^{15}\text{N}$  between the two regions. If we could better understand the mechanisms that apparently lead to N cycling to be as tight in HiP as KNP, there is the potential for adjusting the management of private areas, if not KNP itself, to sustainably maintain higher herbivore numbers.

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