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Impact of the invader *Ipomoea hildebrandtii* on grass biomass, nitrogen mineralisation and determinants of its seedling establishment in Kajiado, Kenya

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The invasive coloniser *Ipomoea hildebrandtii* aggravates the problem of inadequate grass forage in Kajiado district, Kenya. To test its impact on grass biomass, nitrogen (N) mineralisation and seedling establishment, grazing and coloniser density were controlled using experimental exclosures and weeding treatments separately in a factorial design. Grass biomass increased 47% in weeding treatments and 117% with protection from grazing. *Ipomoea hildebrandtii* removal also led to decline in soil moisture at a depth of 5 cm and an increase at 30 cm, and lower soil compaction. Grazing lowered soil moisture and increased soil compaction. Mineralisation of N was highest under the dominant grass *Chloris roxburghiana* followed by *I. hildebrandtii* and bare ground. Weeding increased N mineralisation whereas grazing lowered it. Multiple regression showed that *I. hildebrandtii* seedling establishment was significantly higher with low grass biomass, high soil moisture at a depth of 30 cm and higher soil N nitrification. Thus weeding, which caused an increase in the latter two factors, led to increased seedling establishment. Grazing, which lowered soil moisture and mineralisation, led to lower seedling establishment despite reduced competition from lowered grass biomass. This shows invasibility by *I. hildebrandtii* in rangelands increases when lowered competition is accompanied by an increase in soil resources such as moisture and nitrogen, thus supporting the resource fluctuation theory.

Keywords: colonisers, grazing, invasive species, semi-arid, weeding

Introduction

The invasion of a community by a new species is thought to be related to the number of propagules of the new species entering the environment, the biological characteristics of the invader, and the susceptibility or invasibility of the environment (Lonsdale 1999). However, inconsistencies in the results from various studies demonstrate that the factors that determine the invasibility of a community by a given species are not yet fully understood (Lavorel *et al.* 1999). In particular, the roles of disturbance, species diversity and productivity are not clear. Some studies have shown invasibility is reduced under grazing, whereas others have shown it to increase (Bellingham and Coomes 2003). This might be expected given that grazing affects a large number of community attributes, including diversity, nutrient availability, living biomass and litter biomass (Kinyamario and Imamba 1992).

Some studies have gone further to identify specific mechanisms that increase invasibility. For example, Davis *et al.* (2000) proposed a quantitative relationship between invasibility and fluctuations in resource availability. For instance, a disturbance that damages the resident vegetation and reduces its competition intensity may free up a flush of resources that an invading species can take

advantage of (Davis and Pelsor 2001). This is relevant to East African savannas where vegetation structure and dynamics are governed by disturbances arising from herbivory, fire and livestock concentration around water sources and settlements (Dougill and Cox 1995). Resource availability can also be influenced by plant species composition, which has been shown to influence mineralisation (Hopper and Vitousek 1998).

In addition to contributing to our understanding of the effects on ecosystems of the interactions between invading species and grazing animals, a number of economic and conservation concerns make the study of invasive plants in African pastoral areas important. Firstly, inadequate grass forage, identified as a major constraint to livestock production in Kajiado (Government of Kenya 2001), is attributed to overgrazing, frequent droughts and invasion by *Ipomoea hildebrandtii* Vatke especially in the Central, Mashuru and Namanga divisions (Government of Kenya 2003). Secondly, any decline in grass biomass production will also negatively impact wildlife numbers and distribution because, even though wildlife are concentrated in conservation areas, the pastoral areas are important seasonal dispersal zones (Ottichilo *et al.* 2000).

This study was conducted on the colonisers *Ipomoea hildebrandtii* and *Astripomoea hyoscyamoides* (Vatke) Verdc., which are classified as an invasive coloniser and a successional coloniser, respectively, according to the classification scheme proposed by Davis and Thompson (2000). Invasive colonisers are not native to the community, whereas successional colonisers are. *Ipomoea hildebrandtii* is perennial whereas *A. hyoscyamoides* is annual; both are unpalatable to livestock and wildlife. The objective of this study was to investigate how grass forage production, nitrogen (N) mineralisation and seedling establishment of the invader *I. hildebrandtii* is influenced by grazing and weeding and to compare these with the local successional coloniser *A. hyoscyamoides*. This study tested the following hypotheses:

- both colonisers and grazing will lower grass forage production, cover and litter;
- both weeding out colonisers and grazing will reduce competition for resources and increase coloniser seedling establishment, which is an indicator of invasibility;
- N mineralisation will be increased by both grazing and weeding of colonisers, and will also be sensitive to plant cover type.

Methods

Study area

The study was conducted in the semi-arid Kajiado district of Kenya. Within the study area two sites were used: Lonsugurai where the invasive coloniser *Ipomoea hildebrandtii* was common; and Lumuruti where the successional coloniser *Astripomoea hyoscyamoides* was common. Lonsugurai and Lumuruti are hereafter referred to as site A and site B, respectively. The vegetation of the study area is generally dominated by trees of the genera *Acacia*, *Commiphora* and *Balanites* in thickets and scattered in open grass expanses. In this semi-arid savanna soil moisture and soil nutrients are the key environmental variables as they regulate productivity and relative abundance of vegetation (Huntley 1982).

Experimental layout and data collection

In each site six replicate plots measuring 6 m × 6 m were demarcated. Three were fenced to exclude livestock and wildlife. The other three plots remained accessible to herbivores. In half the area of all plots the coloniser plants were manually removed by monthly weeding during the rainy season. Data collection was carried out at the start of the short rainy season in October 2002 and after the long dry season in September 2003; thus the data was collected after a period of two rainy and two dry seasons. Two data sets, namely on the herbaceous layer and soil attributes, were collected.

Herbaceous layer data collected included the number of seedlings of the two coloniser species, above-ground grass biomass, percentage grass cover and litter dry weight. Grass biomass was determined by clipping to 2 cm stubble height inside a 0.5 m² quadrat. After clipping, the litter within the quadrat was collected separately.

Grass and litter samples were oven-dried at 60 °C for 48 h and then weighed. Herbaceous cover was determined using the line intercept method (Clarke, 1986). To assess herbaceous cover a 5 m line transect was allocated to each sub-plot to make three line transects per treatment or 15 m per treatment per site. Seedling establishment of the coloniser species was determined by counting the number of seedlings within 1 m × 1 m quadrats at the end of the second rainy season.

Soil attributes data recorded included soil moisture, which was measured at two depth levels (5 cm and 30 cm) and was assessed using the gravimetric method (Black 1986). Soil bulk density was determined to a depth of 5 cm using the core method (Black 1986), for which core rings of 5 cm diameter were used. Soil bulk density was measured because it influences root growth, aeration and water infiltration. Soil moisture was measured because it influences the structure and function of semi-arid communities. Soil N mineralisation was determined at site A only. Mineralisation was not determined for site B because *A. hyoscyamoides* is a smaller, erect annual and mineralisation variation adjacent to it may not be fully attributable to its influence, whereas *I. hildebrandtii* is a larger perennial and mineralisation can be measured under its canopy. Mineralisation was determined by *in situ* incubation using the paired core samples method as described by Raison *et al.* (1987). Mineralisation was determined under the canopy of the two main ground-cover types, namely the dominant grass *Chloris roxburghiana* and *I. hildebrandtii*, and on bare-ground patches in all plots and treatments. Nitrate concentration was determined using the colorimetric method as described by Anderson and Ingram (1993). Net nitrification was calculated as the increase in nitrate in the incubated sample relative to the paired sample.

Six replicate herbaceous and soil samples were collected per sub-plot, making a total of 18 samples per treatment per site, to determine grass biomass soil moisture and soil bulk density. A similar number of quadrats were assessed to determine seedling establishment. To estimate N mineralisation eight pairs of samples per treatment were assessed.

Data analysis

Data for sites A and B were analysed together to allow comparison of the effects of the invasive species and locally dominant successional coloniser. Data on grass biomass, grass cover, litter amount and soil bulk density was subjected to three-way fixed effects analysis of variance (ANOVA) in a nested design using the software Statistica. The factors were site, weeding and grazing. Each of the factors was at two levels, i.e. site (sites A and B), grazing (grazed and non-grazed) and weeding (weeded and non-weeded). The experimental manipulations (weeding and grazing) were nested in site and analysed as fixed effects ANOVA. Where the analysis of variance was significant Tukey's test was used to separate the means. Multiple regression was used to relate seedling establishment to the factors grass biomass, grass cover, soil moisture at 5 cm and 30 cm depths, soil compaction and N mineralisation. Regression analysis was conducted using a generalised linear model in Statistica applying a Poisson distribution for seedling counts.

Results

Seedling establishment

There were significantly more seedlings of the annual *A. hyoscyamoides* at site B ($F_{1,111} = 55.3$; $p < 0.001$) than there were seedlings of the perennial *I. hildebrandtii* at site A (Figure 1). Disturbance (weeding) led to a significant increase ($F_{2,111} = 3.4$; $p < 0.05$) in seedlings of both colonisers. However, there was no significant effect of grazing on seedling establishment ($F_{2,111} = 0.18$; $p > 0.05$) for either species. A multiple regression analysis, carried out separately for *I. hildebrandtii* and *A. hyoscyamoides*, showed that weeding and grazing influenced several site and herbaceous attributes (Table 1). Grass biomass was the most important variable influencing seedling establishment of *I. hildebrandtii*, together with grass cover and litter biomass. It was also positively related to soil moisture at 30 cm, but not soil moisture at 5 cm. Soil N mineralisation, which influences nitrogen levels, was also positively related to *I. hildebrandtii* seedling establishment. The most important factors influencing seedling establishment for the annual *A. hyoscyamoides* were soil compaction and ground cover.

Grass biomass, cover and litter amount

At the onset of the study mean grass biomass did not differ between treatments; it was, however, significantly higher ($F_{1,89} = 59.0$, $p < 0.001$) at site A (70.2 g m^{-2}) than at site B (51.8 g m^{-2}). In comparison, mean biomass of *I. hildebrandtii* at site A was 71.6 g m^{-2} , while *A. hyoscyamoides* at site B was 26.4 g m^{-2} . Grazing had a highly significant ($F_{2,128} = 28.3$, $p < 0.001$) effect on grass biomass with more biomass in non-grazed treatments than grazed plots (Figure 2a).

Weeding colonisers had no significant impact on grass biomass when averaged across grazed and non-grazed treatments; however, its interaction with grazing was highly significant ($F_{2,128} = 5.1$, $p < 0.01$). Thus removal of colonisers in the absence of grazing led to a 47% increase in grass biomass, whereas in the presence of grazing it led to a decline of 28% (Figure 2a).

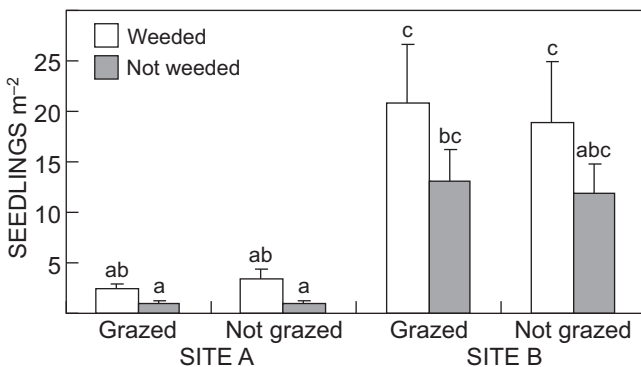


Figure 1: Mean seedling establishment (number m^{-2}) of the colonisers *Ipomoea hildebrandtii* at site A and *Astripomoea hyoscyamoides* at site B. Values are means and vertical lines on each bar indicate the standard error (total $n = 119$). Bars sharing the same letter do not differ significantly (Tukey test, $p < 0.05$)

Although strongly correlated with biomass, ground cover is an important determinant of potential erosion of a site and grass contributes to the highest cover class of all plant groups in the area. The trend in grass cover variation was similar to that of grass biomass (Figure 2b). Mean grass cover across all plots at site A and site B was 22.7% and 20.2%, respectively. Grazing had a highly significant ($F_{2,128} = 26.9$, $p < 0.001$) effect on grass cover with means of 11.5% and 32% for grazed and non-grazed treatments, respectively. Although weeding alone did not have an effect on grass cover, its interaction with grazing did ($F_{2,128} = 3.49$, $p < 0.05$). Thus, weeding colonisers in non-grazed treatments led to a mean increase in ground cover of 10.2%, whereas weeding in grazed treatments led to a mean decrease of 5%.

Weeding of both colonisers led to a significant ($F_{2,105} = 2.5$, $p < 0.05$) decrease in litter dry weight with a mean of 37 g m^{-2} and 28.2 g m^{-2} for non-weeded and weeded treatments, respectively. The interaction of grazing and weeding on litter was significant ($F_{2,105} = 2.7$, $p < 0.05$), indicating that the response of litter dry weight to removal of colonisers varied with grazing treatment (Figure 2c). Thus the combination of grazing and weeding (24 g m^{-2}) produced the least litter, while the presence of colonisers and grazing produced the highest litter (42 g m^{-2}).

Soil moisture and bulk density

Soil moisture increased significantly ($F_{2,121} = 111.6$, $p < 0.001$) as depth increased (Figure 3a, b). Weeding at site A led to a decrease in soil moisture at a depth of 5 cm but an increase at 30 cm. Weeding the perennial invasive *I. hildebrandtii* had a greater impact on soil moisture at the 30 cm depth than at 5 cm, whereas weeding the annual coloniser *A. hyoscyamoides* caused greater depletion of soil moisture at 5 cm than at 30 cm. Grazing had a significant effect ($F_{2,121} = 3.37$, $p < 0.05$) on soil moisture with 8.6% and 8.0% for non-grazed and grazed plots, respectively, when averaged across depths and weeding treatments. Grazing had a greater effect on soil

Table 1: Results of multiple regression analysis of coloniser seedling establishment with a range of soil and herbaceous layer attributes at site A (*Ipomoea hildebrandtii*) and site B (*Astripomoea hyoscyamoides*). The number of samples (n) in site B is smaller because mineralisation data was not collected this site

	Site A ¹		Site B ²	
	β	F	β	F
Intercept		25.9***		7.1*
Grass biomass	-1.86	42.4***	-4.26	3.6ns
Grass cover	0.90	9.2**	5.42	6.1*
Soil moisture (5 cm)	-0.81	3.7ns	-0.38	2.7ns
Soil moisture (30 cm)	0.49	7.7**	-0.22	1.2ns
Soil compaction	-0.20	0.3ns	3.08	16.1***
Litter biomass	0.92	8.2**	-0.27	0.1ns
N mineralisation	0.35	9.0**	NA	NA

¹ $n = 72$, $R^2 = 0.761$, $p < 0.00$

² $n = 47$, $R^2 = 0.519$, $p < 0.00$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns = non-significant, NA = not available

moisture at 5 cm depth than at 30 cm resulting in a difference of 0.8% and 0.3%, respectively.

Weeded plots had significantly ($F_{2,62} = 4.6, p < 0.05$) lower soil bulk density.

Soil N mineralisation

Mineralisation of N was significantly higher ($F_{2,24} = 7.0, p < 0.05$) under the canopy of *Chloris roxburghiana* and *I. hildebrandtii* than bare ground (Figure 4a). Mean mineralisation under different cover types in each treatment showed grazed plots had a significantly ($F_{1,23} = 10.4, p < 0.01$) lower nitrification than ungrazed plots (Figure 4b). Grazed plots also had lower grass biomass and cover, lower soil moisture at 5 cm depth and higher bulk density.

The treatment with the highest nitrification had the highest soil moisture at 30 cm depth, lowest soil compaction and highest grass biomass, whereas the treatment with lowest nitrification had the lowest soil moisture at 30 cm, highest soil compaction and low grass biomass. Thus the presence of grazing and *I. hildebrandtii* produced the lowest

mineralisation, whereas the absence of the two factors produced the highest mineralisation.

Discussion

Resource fluctuation and seedling establishment

The mechanisms governing invasibility and impacts of invaders in semi-arid ecosystems are poorly understood. We investigated the applicability of the resource fluctuation theory by relating coloniser seedling establishment to soil nitrogen variation and soil moisture. Seedling establishment of *Ipomoea hildebrandtii* was significantly related to soil N nitrification, which was higher in weeded than control plots. These results tend to support the resource fluctuation theory whereby increase in the soil resources as a result of weeding increases the invasibility of the community (Davis and Pelsor 2001). This has important implications for the invasibility of semi-arid pastoral areas where the concentration of soil

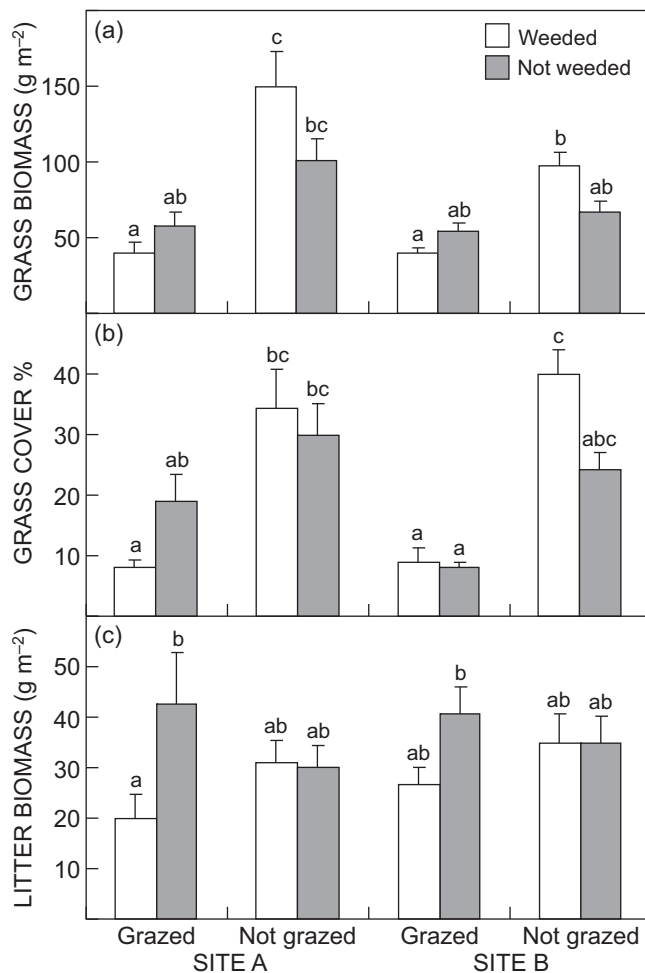


Figure 2: Mean grass biomass (a), percentage grass cover (b) and litter biomass (c) in each treatment and site. Error bars are the standard error of the mean (total n = 119). Bars sharing the same letter do not differ significantly (Tukey test, $p < 0.05$)

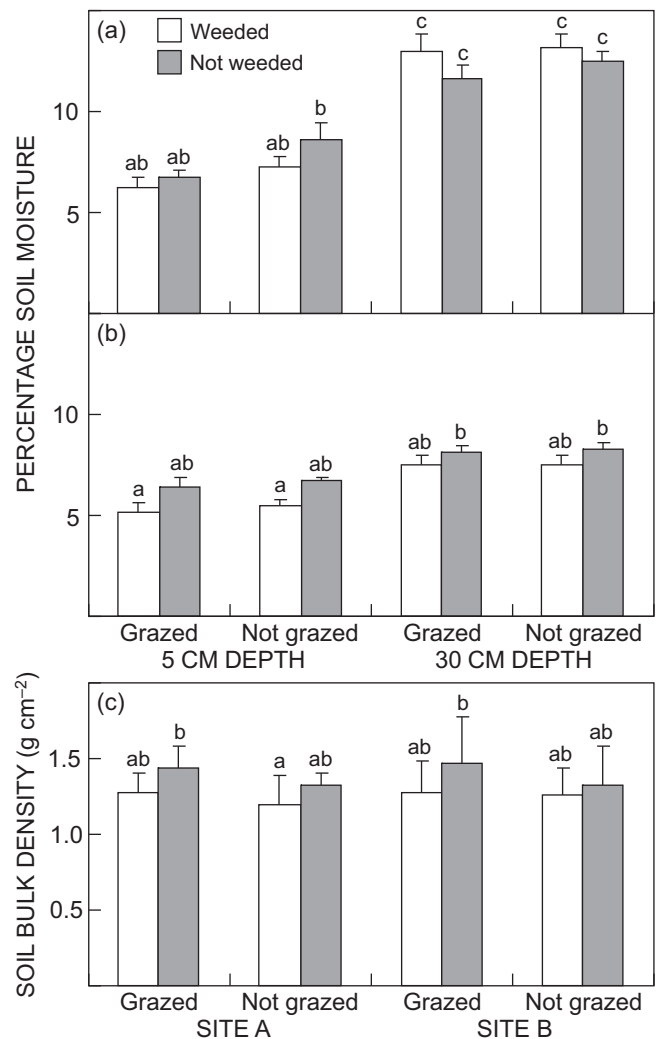


Figure 3: Mean soil moisture in each treatment at two depths at site A (a) and site B (b), and mean soil bulk density (c). Error bars are the standard error of the mean (total n = 119). Bars sharing the same letter do not differ significantly (Tukey test, $p < 0.05$)

nutrients increases with decreasing distance to boreholes and settlements as a result of increasing livestock concentration (Moleele and Perkins 1998).

There was no difference in seedling establishment between the grazed and non-grazed plots for both colonisers. The observation that the two colonisers are found frequently in areas of livestock concentration led to the study hypothesis that invasibility will increase with grazing. Literature shows contradicting effects of grazing on invasibility (Bellingham and Coomes 2003). In this study, grazing, unlike weeding, lowered soil N nitrification and did not have a significant influence on soil moisture at a depth of 30 cm, a factor that was related to *I. hildebrandtii* seedling establishment. Thus, even though competition was reduced in grazed plots due to significantly lower grass biomass, soil resources were also reduced due to lower soil moisture and lower N nitrification, hence seedling establishment was not enhanced by the grazing treatment. These results suggest that reduced competition alone is not sufficient to enhance the invasibility by *I. hildebrandtii* but that increased soil resource availability is also necessary. This is important in African semi-arid grazing areas where livestock play a critical role in nutrient redistribution.

Soil compaction was lower in weeded plots, which had higher seedling establishment. The lowered soil compaction could be due to soil loosening during weeding and hence increased microsite availability resulting in increased water infiltration and soil aeration favouring seedling establishment (Hillel 1982). This may also explain why *I. hildebrandtii* is frequently observed in recently abandoned cultivation fields (JKM, JIK and EAJ unpubl. data).

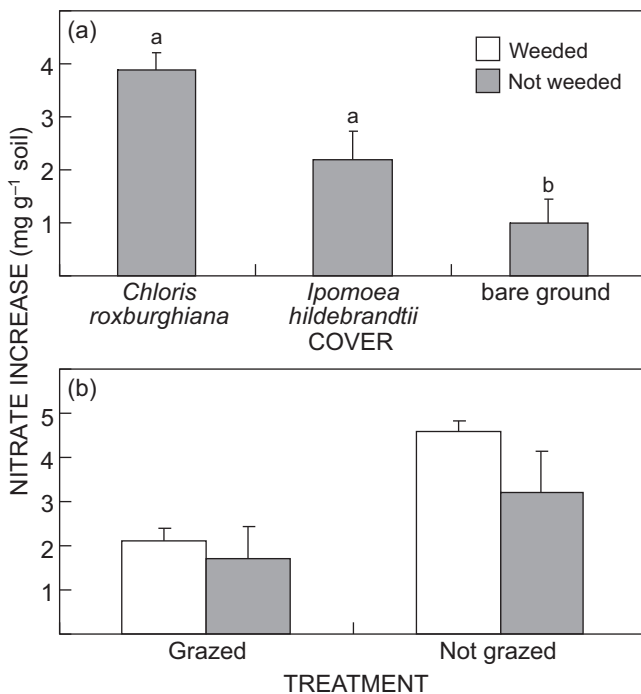


Figure 4: Mean nitrate increase due to nitrification under three cover classes (a) and in each treatment regime (b). Error bars are the standard error of the mean (total n = 119). Bars sharing the same letter do not differ significantly (Tukey test, $p < 0.05$)

Coloniser species and grazing effects on grass biomass, cover and litter

Inadequate grass forage has been identified as a major constraint to livestock production by pastoralists in Kajiado (Government of Kenya 2001). Colonisers contribute to this problem, as shown by *I. hildebrandtii* constituting 50% of the herbaceous biomass and *A. hyoscyamoides* contributing 34% at the onset of the study. This study established that in the absence of grazing, both *I. hildebrandtii* and *A. hyoscyamoides* had a large and significant negative impact on grass biomass. The results therefore not only confirm the hypothesis that the invasive coloniser *I. hildebrandtii* lowers grass forage production but also showed that successional colonisers indigenous in the area, such as *A. hyoscyamoides*, have a similar effect. Lowered grass forage production can have a negative herbivore-carrying capacity in the region with consequent economic and conservation implications.

There were differing responses of grass biomass and cover to weeding under grazing and non-grazing. This led to an apparent contradiction in that in the presence of grazing, it was expected that grazed + weeded plots would have a higher grass cover and biomass than grazed + non-weeded, but in fact the reverse was found. We speculate that this was due to livestock foraging selectivity with livestock preferring to graze in the weeded areas. The relative and absolute abundance of plant species are known to have an important influence on foraging selectivity and the degree of consumption of a given plant population (Mnene and Kibet 1995, Mnene *et al.* 1996, Augustine and McNaughton 1998). It follows that the absence of both *I. hildebrandtii* and *A. hyoscyamoides* encouraged grazing by livestock, hence the greater reduction in grass biomass in those plots.

In this study non-weeded plots had more litter than weeded plots, which could be due to either significant contribution of litter amount by both colonisers or livestock avoidance of non-weeded areas leading to a build up of litter. The quantity of litter is an important determinant of mineralisation, but its quality is critical (Hobbie 1992). Studies have shown that unpalatable species have high levels of secondary compounds, which reduce decomposition rates (Bryant *et al.* 1992). In this study grazing did not have a significant effect on litter biomass. Other studies have shown litter to increase with grazing, while others have found that it decreases (van Wijnen and van der Wal 1999). The trend under intensive grazing is, however, an initial increase in litter followed by decline as grass forage declines (Mworia *et al.* 1997).

Invasive species and grazing effects on N mineralisation

This study assessed N nitrification as an indicator of net N over three land cover categories selected to reflect the main cover types in the area. This is because overgrazing leading to large areas of bare ground is common in pastoral areas, while moderately grazed sites in the study area are dominated by *Chloris roxburghiana*. Nitrification was highest under the canopy of *C. roxburghiana*, followed by *I. hildebrandtii* and lowest on bare ground, thus supporting the theory that species can influence nutrient mineralisation (van der Krift and Berendse 2001). Generally, compounds

that reduce plant palatability also reduce litter decomposition rate (Augustine and McNaughton 1998). This may explain the reduced nitrification measured under *I. hildebrandtii*, which is unpalatable. The dominant species is an important factor governing mineralisation and hence fertility of an ecosystem, so an expansion in dominance of the invader *I. hildebrandtii* and bare ground would seriously depress nutrient cycling and productivity.

The study supported the hypothesis that grazing influences nutrient cycling due to the observation of less nitrification in grazed plots. Important soil factors that affect the rate of nitrification are temperature, soil moisture, pH and the availability of the substrate NH_4 , O_2 and CO_2 (Stevenson 1986). In this study it seems that nitrification was lower in grazed plots due to decreased soil moisture, which has been shown to be an important modifier of N mineralisation in other studies (Holland and Detling 1990). Grazing also increased soil compaction, which influences the balance at liquid, solid and air phases of the soil (Hillel 1982) and therefore modifies N mineralisation.

The increase in nitrification in weeded plots may be attributed to changes in soil and herbaceous layer conditions brought about by removal of *I. hildebrandtii*, which include lower soil compaction, higher soil moisture and higher herbaceous biomass. Higher nitrification was associated with the dominant grass *C. roxburghiana*.

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References

- Augustine DJ and McNaughton SJ 1998. Ungulate effects on the functional species composition of plant communities — herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 67: 165–183.
- Anderson JM and Ingram JSI 1993. *Tropical Soil Biology and Fertility: A Handbook of Methods*. CAB International, Wallingford, UK.
- Bellingham PJ and Coomes DA 2003. Grazing and community structure as determinants of invasion success by Scotch broom in a New Zealand montane shrubland. *Diversity and Distributions* 9: 19–28.
- Black CA (ed) 1986. *Methods of Soil Analysis, 2nd edn*. American Society of Agronomy, Madison, Wisconsin, USA.
- Bryant JP, Reichardt PB and Claussen TP 1992. Chemically mediated interactions between woody plants and browsing mammals. *Journal of Range Management* 45: 18–24.
- Clarke R (ed) 1986. *The Handbook of Ecological Monitoring*. Clarendon Press, Oxford, UK.
- Davis MA, Grime JP and Thompson K 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88: 528–534.
- Davis MA and Pelsor M 2001. Experimental support for a resource-based mechanistic model on invasibility. *Ecology Letters* 4: 421–428.
- Davis MA and Thompson K 2000. Eight ways to be a colonizer; two ways to be an invader: a proposed nomenclature scheme for invasion ecology. *Bulletin of the Ecological Society of America* 81: 226–230.
- Dougill A and Cox J 1995. *Land Degradation and Grazing in the Kalahari: New Analysis and Alternative Perspectives*. Pastoral Development Network Paper 38c. Overseas Development Institute, London, UK.
- Government of Kenya 2001. *Poverty Reduction Strategy Paper for the Period 2001–2004*. Ministry of Finance and Planning. Government Printer, Nairobi, Kenya.
- Government of Kenya 2003. *State of Environment Report for Kajjado District*. National Environmental Management Authority. Government Printer, Nairobi, Kenya.
- Hillel HF 1982. *Introduction to Soil Physics*. Academic Press, San Diego, California, USA.
- Hobbie SE 1992. Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution* 7: 336–339.
- Hopper DU and Vitousek PM 1998. Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs* 68: 121–149.
- Holland EA and Detling JK 1990. Plant response to herbivory and below ground nitrogen cycling. *Ecology* 71: 1040–1049.
- Huntley BJ 1982. *Southern African savannas*. In: Huntley BJ and Walker BH (eds) *Ecology of Tropical Savannas*. Springer-Verlag, Berlin, Germany. pp 101–119.
- Kinyamario JI and Imamba SK 1992. *Savanna at Nairobi National Park*. In: Long SP, Jones MB and Roberts MJ (eds) *Primary Productivity of Grass Ecosystems of the Tropics and Sub-tropics*. Chapman and Hall, London, UK. pp 25–69.
- Lavorel S, Prieur-Richard AH and Grigulis K 1999. Invasibility and diversity of plant communities: from patterns to processes. *Diversity and Distributions* 5: 41–49.
- Lonsdale WM 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80: 1522–1536.
- Moleele NM and Perkins JS 1998. Encroaching woody plant species and boreholes: is cattle density the main driving factor in the Olifants Drift communal grazing lands, south-eastern Botswana? *Journal of Arid Environments* 40: 245–253.
- Mnene WN and Kibet PFK 1995. Effects of plant community types on botanical composition and nutritive value of cattle diets. *East Africa Agriculture and Forestry Journal* 60: 247–253.
- Mnene WN, Stuth JW and Lyons RK 1996. Effects of herbage and bush level on diet selection and nutrient intake of cattle in a *Commiphora* savanna. *Tropical Grasslands* 30: 378–388.
- Mworia JK, Mnene WN, Musembi DK and Reid RS 1997. Resilience of soils and vegetation subjected to different grazing intensities in semi-arid rangeland of Kenya. *African Journal of Range and Forage Science* 14: 25–30.
- Ottichilo WK, Leeuw JD, Skidmore AK, Prins HHT and Said MY 2000. Population trends of large non-migratory wild herbivores and livestock in the Masai Mara ecosystem, Kenya, between 1977 and 1997. *African Journal of Ecology* 18: 202–216.
- Raison RJ, Connell MH and Khanna PK 1987. Methodology for studying fluxes of soil mineral-N *in situ*. *Soil Biology and Biochemistry* 19: 521–530.
- Stevenson FJ 1986. *Cycles of Soil: Carbon, Nitrogen, Phosphorus, Sulfur, Micronutrients*. John Wiley and Sons, New York, USA.
- van der Krift TAJ and Berendse F 2001. The effect of plant species on soil nitrogen mineralization. *Journal of Ecology* 89: 555–561.
- van Wijnen HJ and van der Wal R 1999. The impact of herbivores on nitrogen mineralization rate: consequences for salt-marsh succession. *Oecologia* 118: 225–231.