academicJournals

Vol. 5(12), pp. 803-809, December 2013
DOI: 10.5897/IJBC2013.0623
ISSN 2141-243X © 2013 Academic Journals
http://www.academicjournals.org/IJBC

International Journal of Biodiversity and Conservation

Full Length Research Paper

Impact of the invasive shrub, *Lantana camara* L. on soil properties in Nairobi National Park, Kenya

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Accepted 10 October, 2013

***Lantana camara* L. (Verbenaceae) is an invasive shrub of global significance in the conservation of biodiversity in terrestrial ecosystems. The invasive species has profound impact on soil ecosystems due to its allelopathic and litter accumulation effect. This study tested for its impact on soil properties in Nairobi National Park (NNP) by randomly sampling soil from the invaded and un-invaded sites in three habitats namely forest, riverine and shrub-grassland using the Modified Whittaker plot design. Six plots were laid in the forest, four in the riverine and eight in the shrub-grassland. Ten samples were collected at invaded and ten at un-invaded sites per habitat totaling to sixty which were obtained and analysed. Two-way analysis of variance (ANOVA) results indicated significant differences in the values of soil pH, the concentrations of magnesium, calcium and potassium between the invaded and un-invaded sites and their levels were higher in invaded sites. Also magnesium, calcium and potassium varied significantly across the forest, riverine and shrub-grassland. These results suggest that *L. camara* can improve the nutrient levels of soil and therefore influence nutrient cycling resulting to making the ground better for its growth and this might explain the capacity of the invasive species to outcompete the native ones.**

Key words: Biodiversity, conservation, impact, soil macronutrients, allelochemicals,

INTRODUCTION

The invasion of Alien Plant Species (APS) in natural and man-made ecosystems is the major threat globally in the conservation of biodiversity. The effects of APS, which are more pronounced in oceanic Islands due to enhancement in species evolution in the absence of competitors and/or predators, have apparently increased in mainland ecosystems mainly due to increased global trade (Hulme, 2009). These plants modify the invaded community in several ways that include alteration of native species diversity, evenness and richness via reduction of light penetration to the ground level where herbs grow and competition for available resources. Furthermore, they can also cause major ecosystem-level changes on nutrient cycling, hydrology and fire regimes and subsequently modify ecosystemic functionality (Gordon, 1998; Ehrenfeld et al., 2003).

Lantana camara is one of the most invasive plants and top 100 highest impacting invasive species globally (GISP, 2003). Like other invasive species, it has profound effects on biodiversity especially in semi-arid areas in Africa, Australia, India and Pacific Islands (Day and Nesser, 2000; Denslow et al., 2009; Dogra et al., 2009). The insidious weed is thought to have been introduced in East Africa in the 1930s (Verdcourt, 1992), and has since naturalized itself in many of the region's semi-arid areas including nature reserves where its negative effects

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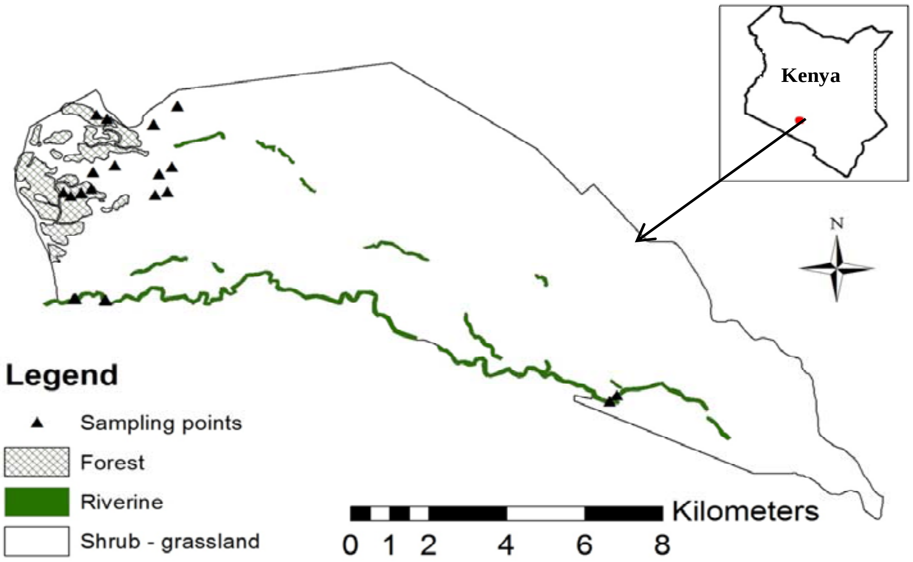

Figure 1. Map of Nairobi National Park showing locations of the sampling points.

cannot be underestimated. In Kenya, it is widely spread causing considerable damage. It readily invades rangelands outcompeting native species, resulting in reduction of pasture while its impenetrable thickets impede access to desired plant species by herbivores. In addition, the exotic species has been found to drastically reduce above ground biomass by smothering native species thus impacting negatively on the abundance of wildlife forage and consequent loss of biodiversity (Witt, 2010).

The Nairobi National Park (NNP) is the oldest conservation area in Kenya, established in 1947 (Foster and Coe, 1968). It has a natural landscape with a rich biodiversity that require protection from the invasive species for posterity. Despite well knowledge of allelopa-thic and litter accumulation effects of *L. camara* on other species globally (Dobhal et al., 2010), few studies have attempted to quantify its impacts on soil properties. In NNP, equivalent studies were lacking and this study sought to establish if its invasion has effect on soil properties.

MATERIALS AND METHODS

Study area

This study was conducted in the Nairobi National Park (Figure 1) which borders the city of Nairobi. It is located 10 km south of the city centre making it unique in the world as a natural conservation area within a city. It covers 117 km^2 and lies between latitudes 2°18' to 2°20'S and longitudes 36°23' to 36°28'E (Obanda et al., 2007). The area of NNP is gentle undulated from 1800 m above sea level (m.a.s.l.) at the North West to 1500 (m.a.s.l.) at the South East.

The park has mainly three types of vegetation: the forest occurring at the western zones, shrub-grassland found within the central and southern zones and the riverine to the South and central zones (Foster and Coe, 1968). The shrub-grassland formations comprise a substantial part of the plains of NNP, where the animals spend most of their time grazing.

The common animal species in the plains include wildebeest, *Connochaetes taurinus* Burchell; *Zebra*, *Equus burchelli* Gray; Eland, *Taurotragus oryx* Pallas; Thomson's gazelle, *Eudorcas thomsonii* Gunther; Giraffe, *Giraffa camelopardalis* Linn; Granit's gazelle, *Nanger granti* Brooke; Buffalo, *Syncerus caffer* Sparrman; Lion, *Panthera leo* Linn.; Leopard, *Panthera pardus* L.; Black rhinoceros, *Diceros bicornis michaeli* Groves 1967 and Cheetah, *Acinonyx jubatus* Schreber**.**

Most of the park is covered by soils generally described as 'black cotton soils'. The soils crack on drying and become sticky when wet. They are characterized by an impeded drainage with a moderately restricted plant species.

The dominant plant species in the plains are: *Acacia drepanolobium* Sjøstedt, *Themedia triandra* (Forsk), *Pennisetum mezianum* (Leeke), *Digitaria macroblephara,* (Hack*)* and *Panicum maximum* (Jacq.), while the forest is dominated by *Croton megalocarpus* (Hutch.) and *Olea africana* (L.). The invasive species found in the park are *Solanum incanum* (L.), *Lantana camara* (L.), *Parthenium hysterophorus* (L.), *Opuntia valgaris* (L.) Mill and *Opuntia ficus-indica* (L.) Mill. The riverine is dominated by *Acacia xanthophloea* (Benth.) and *Acacia kirkii* (Oliv.), with *Themedia triandra* (Forsk) as the dominant grass.

The park has a modest climate with annual mean minimum and maximum of 13.6 and 25.3°C respectively. The rainfall pattern is bimodal, with long rains (mean per annum: 150 mm) occurring from March to May and the short rains (mean per annum: 90 mm) from November to December (Muya and Oguge, 2000). Therefore, it is dry most of the year and many of the wildlife animals use it as a dry season concentration area. The Park has numerous dams and seasonal rivers which increase the natural supply of drinking water from the perennial Mbagathi River that runs along its southern zones.

Data collection

Modified Whittaker plot (Stohlgren et al., 1995) was used to sample soil in invaded and un-invaded sites of the park in the three habitats namely forest, riverine and shrub-grassland. The plot is modified to use rectangular subplots dispersed within its main plot. They capture more environmental variation than the original plot, which has ten subplots (1 m^2) placed linearly at the centre of the 100 m^2 plot of the main plot measuring 1000 m^2 (Shimda, 1984).

Six plots were laid in the forest, four in the riverine and eight in the shrub-grassland (Figure 1). Soil was randomly sampled from the centre of the four small (1 m^2) subplots near the centre and at the centre of the middle plot measuring 100 m^2 after litter was removed. A hand held push probe measuring 2.5 cm diameter was used to collect soil from a depth of 15 cm below the ground surface to ensure sufficient quantity of soil was collected for subsequent analysis. Ten samples were collected at invaded and ten at un-invaded sites per habitat totaling to sixty which were obtained and analysed. The soil samples from invaded sites were collected within the *L. camara* thickets for consistency in data capture. Each soil sample was packed in a separate labelled plastic bag and transported to Nairobi national Museums of Kenya soil laboratory for further treatment and analysis

Data analysis

The soil samples were oven dried at 55°C for 24 h to reduce the moisture content and increase the concentration of the nutrients prior to chemical analysis. Then, they were passed through a 2 mm pore sieve for homogenization before they were analyzed for various contents. Potassium and phosphorous were extracted with 0.5 M sodium bicarbonate and their contents were respectively determined by flame photometer (Olsen and Sommer, 1982) and ascorbic acid molybdate (Okalebo et al., 2002). Nitrogen was analyzed using Kjeldahl method (Bremner, 1996) while calcium and magnesium were analysed using potassium chloride (1NKCl) solution and their contents determined by Atomic Absorption Spectrometer (AAS) (Thomas, 1982). Carbon was analysed using wet oxidation method of Walkley-Black procedure and its contents extracted with acidified potassium dichromate (Charles and Simmons, 1986). Measurements of soil pH and electrical conductivity were done with conductivity meter (Seven Multi Mettler Toledo, TDS/SAL/Resitivity. GmbH 8603, Switzerland) in soil to water suspension (Rhoades, 1982) while soil texture was determined using the hydrometer method (Okalebo et al., 2002).

Analysis Of Variance (ANOVA) was carried out to test the effect of invasion at various sampling sites while Principal Component Analysis (PCA) was done to explore the relationship between soil properties and the sites. During the ANOVA test, the soil properties were the dependent variables while the study sites and habitat types were the independent variables. Data were checked for homogeneity of variances as assed by Levine´s test for equality of variances while normality was checked using Shabiro-Wilk test. The ANOVA analysis was performed using GenStat software, 14th edition.

In the PCA analysis, data were standardized by carrying out varimax rotation in order to maximize correlation between soil properties before the analysis was done using R software version 2.15.1. The Principal Components (PCs) were characterized according to the soil properties where soil properties with loading greater than 0.33 in a PC were considered to be related to the PC (Kothari, 2004). In order to explore the spatial patterns of the study sites and distribution of the measured soil properties, an ordination biplot was constructed.

RESULTS

Macronutrients measured in this study (Mg, Ca, K, P and N) showed significant differences between invaded and un-invaded sites (ANOVA, $P < 0.05$), except carbon concentrations which did not differ between both sites (ANOVA, $P = 0.618$) (Table 1).

The macronutrients also strongly differed significantly among the forest, riverine and shrub-grassland habitats (ANOVA, $P < 0.001$) except carbon concentrations which also did not show significant variation a cross habitats (ANOVA, $P = 0.349$). Further, analysis of the possible relationship between the type of habitat and invasion (S × H interaction level), the Ca, K and P concentrations were highly significant (ANOVA, $P < 0.001$) while Mg and N concentrations recorded less significant differences (ANOVA, $P = 0.019$; $P = 0.041$, respectively). Carbon concentration was not significantly different (ANOVA, $P = 0.358$) with regard to site verses habitat (S × H) interaction. Except for silt which was not significantly different between invaded and un-invaded sites (ANOVA, $P = 0.928$), the values of pH, conductivity, sand and clay recorded significant differences (ANOVA, $P < 0.05$) (Table 1).

On the other hand, pH, conductivity, sand and silt recorded strong significant variations a cross the forest, riverine and shrub-grassland habitats (ANOVA, $P < 0.001$) while clay recorded less significant difference (ANOVA, $P = 0.023$). At the invasion verses habitat interaction level (S × H level), significant differences were recorded in pH (ANOVA, $P = 0.004$) while conductivity, sand, silt and clay did not vary significantly (ANOVA, $P > 0.05$). The macronutrient concentrations of Mg, Ca and K measured in this study were also found to be higher in invaded sites than un-invaded ones while P and N generally indicated low concentrations in the invaded sites relative to un-invaded ones (Table 1).

In the PCA of soil properties, the first four principal components accounted for 77.13% of the total variance where the first two principal components explained 56.17% of the observed variation in the soil properties. The first principal component was related to K, N, Ca, pH and sand while the second principal component was mainly related to conductivity, silt and soil pH (Table 2). The third principal component which accounted for 67.21% was related to P and Mg and the fourth principal component was mainly related to carbon and clay. The analysis revealed that the first four principal components were sufficient in explaining the variation of the soil properties between the invaded and un-invaded sites in NNP. After correlation, the results were subjected to an ordination biplot, which revealed that the sites separated into clusters based on the sites and their measured properties (Figure 2).

The clusters were identified as follows:

Cluster:	Sites forming the cluster:
A	RB1, RB2, RB3, RB4, RB6, RB7, RB8 RB9, RB10
B	SB2, SB3, SB4, SB5, SB6, SB7, SB8, SB9, SB10, FA6, FB5, FB7, FB8, FB9, FB10 and RA1
C	SB1, SA1, SA2, SA3, SA4, SA5, SA6, SA7, SA8, SA9, SA10, FA2, FA3, FA7, FA8, and FA9

Table 1. Two-way ANOVA summary results of soil properties in *Lantana camara* invaded and un-invaded sites across three habitats in Nairobi National Park, Kenya.

Soil property	Summary ANOVA			Site group mean (± SD)	
	Sites(S)	Habitats (H)	S × H level	Un-invaded (n = 30)	Invaded (n = 30)
Soil pH	***	***	*	6.3 ± 0.5	6.8 ± 0.3
Magnesium (mg/kg)	***	***	*	721.1 ± 126	825.0 ±132
Calcium (mg/kg)	***	***	***	190.5 ± 5.5	235.5 ± 63.8
Potassium (mg/kg)	***	***	***	81.0 ± 15.4	121.5 ± 45.7
Total carbon (%)	ns	ns	ns	3.1 ± 0.5	3.2 ± 0.3
Phosphorous (mg/kg)	***	***	***	9.6 ± 1.2	6.5 ± 2.2
Nitrogen (%)	***	***	*	0.3 ± 0.0	0.2 ± 0.4
Conductivity (µS/cm)	***	***	*	167.4 ± 85.8	228.7 ± 75.5
Sand (%)	***	***	ns	32.6 ± 4.7	29.7 ± 4.2
Silt (%)	ns	***	ns	26.0 ± 3.0	26.1 ± 2.8
Clay (%)	*	*	ns	41.8 ± 3.6	44.2 ± 4.2

*$P \leq 0.05$; ***$P \leq 0.001$; *ns* not significant.

Table 2. Proportions of variations in the soil properties expressed in terms of vector loadings (varimax rotation) for the soil properties measured in all the study sites.

Soil property	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
pH	0.36[a]	0.03	-0.31	-0.01	-0.24	-0.45[a]	-0.16	-0.6[a]	0.26	0.16	-0.04
N	-0.40[a]	0.22	0.08	-0.02	-0.08	0.21	0.02	0.02	0.78[a]	0.28	-0.04
P	-0.17	0.44[a]	0.53[a]	-0.02	0.07	-0.14	0.44[a]	-0.48[a]	-0.23	0.01	0.00
K	0.42[a]	-0.01	0.05	0.12	0.32	0.38	0.07	-0.05	-0.1	0.73[a]	0.08
Mg	0.22	-0.19	0.56[a]	0.11	0.28	-0.55[a]	-0.14	0.30	0.30	0.04	0.01
Ca	0.40[a]	-0.02	0.12	0.14	0.28	0.44	0.05	-0.27	0.36[a]	-0.58[a]	-0.09
C	0.10	0.06	0.27	0.64[a]	-0.68[a]	0.17	-0.06	0.09	0.03	0.05	-0.03
EC	-0.10	-0.60[a]	-0.13	0.17	-0.05	-0.10	0.74[a]	-0.05	0.15	0.05	0.01
Clay	0.32	-0.11	0.23	-0.55[a]	0.40[a]	0.11	0.10	0.06	0.01	-0.06	0.59[a]
Sand	-0.39[a]	-0.25	-0.05	0.31	0.20	0.05	-0.32	-0.33	0.00	-0.02	0.65[a]
Silt	0.15	-0.54[a]	-0.36	0.28	0.14	-0.20	0.30	-0.62[a]	0.26	0.16	0.45[a]

[a] Soil property is related to the corresponding principal component.

D RA2, RA3, RA4, RA5, RA6, RA7, RA8, RA9 and RA10 The separation of cluster A was influenced by P and silt while sand and N played a significant role in the separation of cluster B (Figure 2). Electrical conductivity was influential in the separation of cluster C while K, Ca, pH, clay and Mg were important in the separation of cluster D. Cluster D mainly comprised of soils collected from the invaded riverine while cluster A comprised of soils collected from the un-invaded riverine. Clusters B and C mainly comprised of soils collected from un-invaded and invaded shrub-grassland respectively. While major variations were revealed between invaded and un-invaded sites of the riverine and shrub-grassland habitats, there were minor variations in the soils obtained from invaded and un-invaded sites of the forest habitat (Figure 2).

DISCUSSION

Variation of macronutrients

Soil macronutrients form a substantial proportion of soil quality indicators and thus their measurements are essential in biodiversity conservation (Li, 2013). In the present study, differences were found in the concentrations of Mg, Ca and K between invaded and un-invaded sites of the park (Table 1). Though the differences may not be completely ascribed to *L. camara* invasion *per se* due to the complexities in invasion.

Increasing evidence suggests that the increase in nutrient levels in sites invaded by exotic plants is a consequence of litter accumulation (Ehrenfeld, 2010). *L.*

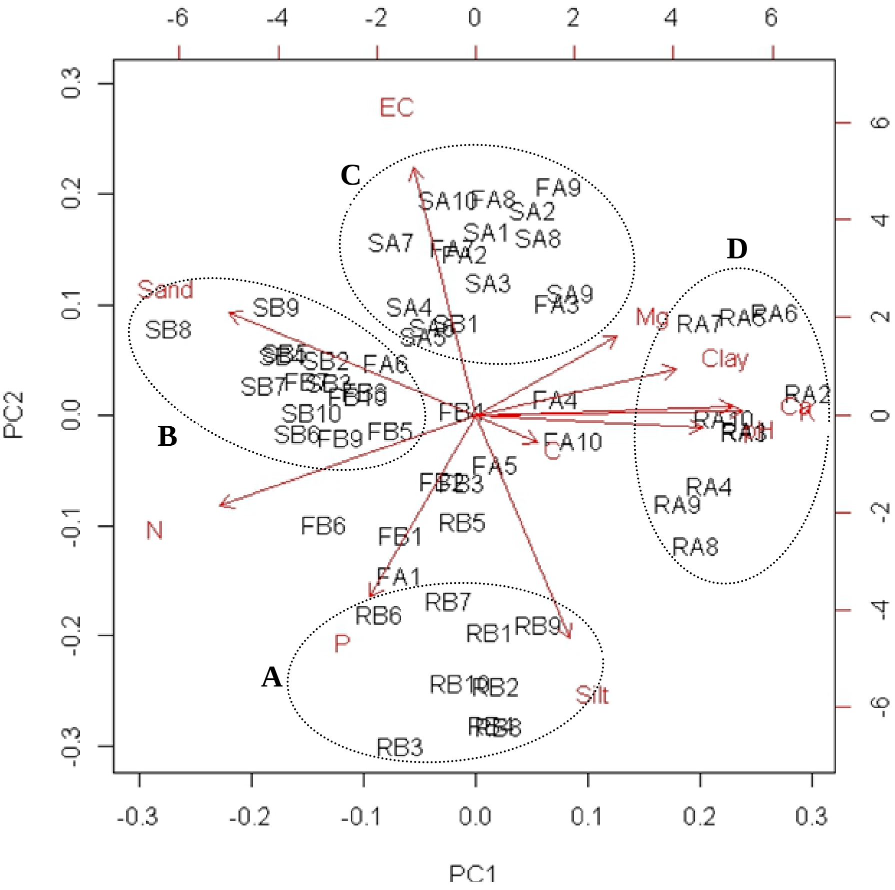

Figure 2. Ordination plot showing separation of the sites into clusters: A, B, C and D. Sites are identified as: RA, Invaded riverine; RB, Un-invaded riverine; SA, Invaded shrub-grassland; SB, Un-invaded shrub-grassland; FA, Invaded forest; FB, Un-invaded forest. EC, Electrical conductivity. (n = 10 soil samples per site).

camara being a highly branched species with a lot of leaf biomass released its leaf tissues with time and accumulated a lot of litter within its understory. On decomposition, cations were released into the soil within its root rhizosphere and subsequently increased the concentrations of Mg, Ca and K. The accumulated organic matter also mulches the soil surface under the invasive species thereby inhibiting the leaching of these nutrients from the soil surface. This might be the possible explanation for the higher concentrations of these nutrients in the invaded sites than the un-invaded ones. The findings of the present study agree with those of Fan et al. (2010) and Sharma and Raghubanshi (2011) who recorded higher concentrations of Mg, Ca and K following *L. camara* invasion in Southern China and India respectively. In addition, though not for *L. camara,* recent studies carried out on different invasive plant species; European forb, *Alliara petiolata* (Rodgers et al., 2008) and *Fallopia javanica* (Dassonville et al., 2007) recorded higher concentrations of Mg, Ca and K in invaded plots than in un-invaded ones following the invasions of these plants in northern hard-wood conifer forests of North America and Belgium respectively, which is consistent to the findings of the current study and general trends in exotic plant invasions.

The higher soil pH found in the sites invaded by *L. camara* is consistent with the results reported by Osunkonya and Perret (2011) following *L. camara* invasion in south eastern Queensland, Australia. However, both increases and decreases in soil pH have also been reported following plant invasions (Koutika et al., 2011). It is not clear if the increase in the present study was due to *L. camara* invasion or it favours the site with high soil pH. Thus, the exact pathway causing the increase in the invaded sites demands for an extensive study on its root chemistry and the overall litter biomass. However, the effect of high pH on soil nutrients within *L. camara* root rhizosphere is underscored. High soil pH is known to accelerate litter decomposition and thus plays a crucial role in regulating nutrient availability. Under high soil pH in the invaded sites, the soil cation exchange process was probably enhanced resulting in more cations being available in the root rhizo sphere of the invasive species compared to the native ones. This might have contributed to the accumulation of Mg, Ca and K in the invaded soils thus increasing their levels.

However, the findings from the present study indicated low concentrations of N and P in the invaded sites than the sites lacking *L. camara* and the differences were also significantly different (*P* < 0.001) (Table 1). These results contradict the findings of Sharma and Raghubanshi (2011). However, the results are in line with the reviews of Ehrenfeld (2003) that both decreases and increases of N and P concentrations in the invaded sites have occurred roughly on equal measures following plant invasions. The low concentrations of N and P recorded in the current study as well as for other invasive plants (*Hieracium* spp. - Scott et al., 2001; *forb, Centaurea maculosa* - Thorpe et al., 2006; *Heracleum mantegazzianum* - Koutika et al., 2011) suggested that organic matter dynamics slow in the sites invaded by the exotic plants and/or the plants enhance the competition for the uptake of these nutrients. The latter suggestion is mostly associated with the decreases because it offers a better mechanism believed to underlie the decreases in the N and P.

The results of the present study show evidence in support of ''novel weapons hypothesis''. The hypothe-sis proposes that some exotic plant species gain advantage by releasing secondary compounds (through leaf leachates and root exudates) that are novel to the native species and provide them with a head start advantage in the competition for resources (Callaway and Ridenour, 2004; Weidenhamer and Callaway, 2010).

These secondary allelochemicals potentially alter the basic nature of substrates in which plants grow and in turn increases the competitive ability of the invasive species for certain nutrients uptake. This could be the possible force behind the declines of N and P in the invaded sites in NNP. Like other invasive species, *L. camara* in the presence of low levels of N and P nutrients availability might have exuded novel allelochemicals from its roots which changed the soil chemistry and inhibited the native species in invaded sites.

As a result, during the trade-offs for resource acquisition, *L. camara* utilized the novel nutrient uptake strategy as a defence mechanism hence lowering the levels of N and P in the soil within its environment (Asner and Vitousek, 2005). The phenol-menon has also been noted where *Centaurea maculosa* at very low levels of P in the soil increased its uptake in six times more than the native *Lupinus argenteus* in Montana grasslands (Thorpe et al., 2006). Given that the present study recorded 0.18 and 0.3% of nitrogen in the invaded and un-invaded sites of the park respectively, these levels were found to be lower than the ranges recommended by Landon (1991) who classified nitrogen percentages of 0.1 to 0.47% ranges as low to medium. The present study suggested that the nutrients (N and P) were probably deficient in the park indicating a possible likelihood that its uptake by *L. camara* increased hence lowering their concentrations in the invaded sites.

This study did not find major variations in soil texture between invaded and un-invaded sites of the park. Generally, the soils consisted of more clay than silt and sand particles (Table 1). Clay tightly binds soil water than sand and silt and has more sites for cations hence more rich in nutrients than sand. This study therefore suggests that the changes between the invaded and un-invaded sites did not result from soil texture but as a result of L. *camara* invasion.

Implications of results for wildlife conservation

The high concentrations of Mg, Ca and K in *L. camara* rhizosphere mainly benefit the invasive plant since most herbivores avoid it as a food plant due to its toxicity and unpleasant aroma when its stem and leaves are crushed (Hakim et al., 2005; Lui, 2011). Equally, the lower concentrations of N and P in the invaded sites (Table 1) as established in this study show the ability of the weed to cause imbalances in the normal distribution of these nutrients. These changes impact negatively on the habitat viability to support wildlife. Kamau (1986) established that herbivores feed on most nutritious plant species with nitrogen content greater than the average concen-tration in a given habitat while the findings of Boutton et al. (1988), indicated that food quality lower than 0.8% nitrogen content decreases the food intake by ruminants and eventually inhibits microbes making the animal to excrete more nitrogen than the intake.

Equally, the large quantity of litter accumulation associated with *L. camara* invasion in Nairobi National Park consists of poor quality wildlife forage which is only consumed by herbivores in the absence of more nutritious live herbage (McNaugton, 1985). The dead litter has a half-live of more than two years (Deshmukh, 1985) and this may cause prolonged shortage of forage which impacts negatively on herbivore forage, grazing patterns and biomass.

Conclusion

The results obtained in this study suggest that the invasion of *L. camara* in NNP alters the concen-trations of the soil nutrients within its rhizosphere and probably maximises their uptake and subsequent utilization relative to the native species. This may possibly be the possible cause for its successful proliferation. Soil being the main source of nutrients for plant species, the current research is crucial and its findings are imperative for the Park management in the effective conservation of the habitat and its biodiversity. In view of this study, conservation planners need to give a special consideration to the conservation of soil ecosystems in the face of growing threats from *L. camara* and make it a priority in the conservation of biodiversity in protected areas.

ACKNOWLEDGEMENT

Many thanks go to Dr. Samwel M. Kasiki of Kenya Wildlife Service for allowing the research to be carried out in NNP and the technical staff of National Museums of Kenya where the physical and chemical analysis of soil samples were done. The zoology department, Jomo Kenyatta University of Agriculture and Technology is highly appreciated for its co-operation throughout the process of preparing this paper.

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