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Ecological impact of *Prosopis* species invasion in Turkwel riverine forest, Kenya

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ABSTRACT

The impact of *Prosopis* species invasion in the Turkwel riverine forest in Kenya was investigated under three contrasting: Acacia, Prosopis and Mixed species (Acacia and Prosopis) canopies. Variation amongst canopies was assessed through soil nutrients and physical properties, tree characteristics and canopy closure. Invasion impact was evaluated by comparing herbaceous species cover and diversity, and occurrence of indigenous tree seedlings. Soil characteristics under Prosopis and Mixed species canopies were similar except in pH and calcium content, and had lower silt and carbon contents than soil under Acacia canopy. Tree density was higher under Prosopis intermediate under Mixed and lower under Acacia canopies. *Prosopis* trees had lower diameters than *Acacia tortilis* trees. Diameter classes' distribution in Mixed species canopy revealed invasion of *Prosopis* into mature *A. tortilis* stands. Herbaceous species cover and diversity were negatively correlated to *Prosopis* tree density; thus explaining the lower herbaceous species cover and diversity under Prosopis than under Acacia and Mixed species canopies. The study suggests a gradual conversion of herbaceous rich *A. tortilis* woodland to herbaceous poor *Prosopis* species woodland or thickets, through indiscriminate Prosopis invasion.

1. Introduction

The genus *Prosopis* has 44 tree and shrub species found in the hot dry tropics of Africa, America, Asia and Australia (Burkat, 1976). About 90% of all *Prosopis* species are native to North and South America from which species of commercial value have been extensively introduced in drylands of Asia, Africa and Australia where they have become naturalized (Burkat, 1976; Pasiecznik et al., 2001). *Prosopis chilensis* Stunz, *Prosopis juliflora* (Sw.) D.C. and *Prosopis pallida* Kunth are among the *Prosopis* species introduced in Kenya (Maghembe et al., 1983; Rosenschein et al., 1999; Stave et al., 2003). These species are difficult to differentiate because of their morphological similarities (Pasiecznik et al., 2001). Due to the difficult in differentiating the different Prosopis species in Kenya, the Prosopis species populations are relegated to the genus rather than specific species (Muturi et al., 2010).

In Kenya, Prosopis species have contributed to land rehabilitation, provision of fodder and fuelwood (Maghembe et al., 1983; Mwangi and Swallow, 2008; Rosenschein et al., 1999). However, in some cases the species have spread from their areas of intended introductions and have become invasive as a result of seed dispersal by livestock, wildlife, and water (Mwangi and Swallow, 2008; Mworia et al., 2011). Riverine ecosystems are more prone to invasion than other areas as they are convergent zones for most waterborne and animal dispersed seeds, and are more conducive to plant growth (Richardson et al., 2007; Robinson et al., 2008). Progressive Prosopis invasion in the Turkwel riverine forest in Kenya has led to a decrease in occurrence of the indigenous *Acacia tortilis* Hayne, and a contrasting trend in Prosopis species (Muturi et al., 2010; Stave et al., 2003).

In drylands, *A. tortilis* plays an important ecological function as it co-exists with a diversity of herbs and shrubs in its various habitats (Belsky et al., 1989; Iponga et al., 2009; Ludwig et al., 2004). Although negative effects of *A. tortilis* on herbaceous species occur (Kahii et al., 2009) the contrary is also demonstrated through high herbaceous species biomass production below *A. tortilis* canopies than in the open areas (Belsky et al., 1989, 1993). Species diversity below *A. tortilis* canopy may be higher or lower than in open areas depending on site and prevailing landuse (Belsky et al., 1993; Kahii et al., 2009). The positive interaction between *A. tortilis* and herbaceous species is attributed to hydraulically lifted water (Ludwig et al., 2004) lowering of ambient temperature by shading and concentration of soil nutrients under the canopies as a result of animal droppings, litter fall and nitrogen fixation (Belsky et al., 1989).

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Unlike *A. tortilis* in the native environment, Prosopis species are often associated with low herbaceous species biomass and diversity in introduced areas (El-Keblawy and Al-Rawai, 2007; Kahii et al., 2009; van Klinken et al., 2006). These negative effects are attributed to canopy effects (El-Keblawy and Al-Rawai, 2007; Kahii et al., 2009), allelopathy (El-Keblawy and Al-Rawai, 2007) and competition that emanates from a high tree density (van Klinken et al., 2006). Most studies on impacts of *A. tortilis* and Prosopis species have been conducted on isolated tree canopies independently. To date there are no comparative studies of impacts caused by indigenous trees and invading exotic trees in closed forest canopies such the riverine forests. This therefore means that the relative impacts of *Prosopis* species in the invaded forests have not been ascertained.

In this study we compared the effect of three different riverine forest tree canopies (*A. tortilis*, Mixed *A. tortilis* and Prosopis species, and Prosopis species) on 1) soil characteristics, 2) canopy closure, 3) regeneration of woody species, and 4) productivity, richness and composition of the herbaceous layer. It was hypothesized that: 1) soil conditions were similar amongst canopies; 2) canopy closure was highest under Prosopis canopies due to higher tree densities that characterize invading *Prosopis* species; 3) Prosopis canopies inhibits the regeneration of indigenous trees; 4) Prosopis canopies reduces herbaceous species cover, density and diversity.

2. Materials and methods

2.1. Study sites description

The fieldwork was done along the Turkwel riverine forest, in Kenya, at sites located near Katilu and Nadapal (Fig. 1). Turkwel riverine forest lies within the dry Turkana District which is characterized by low erratic rainfall, high temperatures and high potential evapotranspiration (Sombroek et al., 1980). Rainfall is bimodal, with peaks around April and November (Stave et al., 2006). Mean annual rainfall along the Turkwel riverine forest ranges from 500 mm upstream to less than 200 mm downstream, with large inter annual variations (Reid and Ellis, 1995; Stave et al., 2006). Mean annual rainfall is higher at Katilu ($\approx$350 mm) than at Nadapal ($\approx$200 mm), as Katilu is near the highlands and Nadapal in the middle of the dry areas. The soil is predominantly developed on

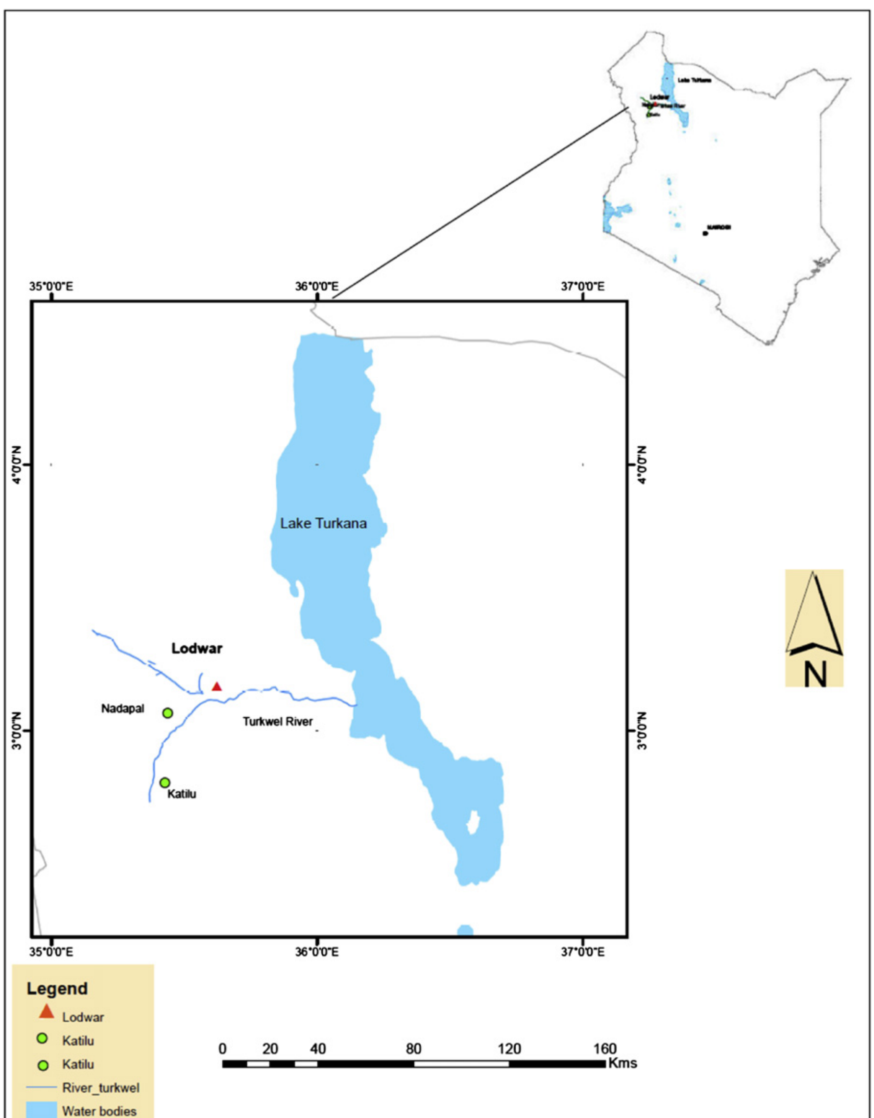

Fig. 1. The geographical location of Turkwel River in Kenya showing the location of Katilu and Nadapal in relation to the Turkwel River.

alluvial deposits and is deep sandy or silty loams classified as calcaric fluvisols (Sombroek et al., 1980; van Bremen and Kinyanjui, 1992).

Turkwel riverine forest is an extensive riparian gallery extending 1–3 km on either side of the riverbank and consists of closed forest and open vegetation patches and (Stave et al., 2003, 2006). Closed canopy riverine forest patches are intercepted by gaps emanating from several factors including shifting cultivation, forest senescence, windfall, floods and change of river course (Muturi et al., 2010; Oba et al., 2002). The forest gaps can be bare, or seasonally covered by grass and bushes before tree colonization occurs. Prior to the 1990s, the canopy of the riverine forest in the study area was dominated by *A. tortilis*, with extensive stands of *Hyphaene compressa* H. Wendl. intercepted by *Acacia elatior* Brenan, *Cordia sinensis* Lam., *Faidherbia albida* (Delile) A.Chev, *Ficus sycomorus* L. and *Tamarindus indica* L. (Adams, 1989; Stave et al., 2003). Abandoned farms and forest gaps in the study area used to be colonized by indigenous trees, mostly by *A. tortilis* and *H. compressa* (Oba et al., 2002; Stave et al., 2006). However, the scenario changed in the 1990s when Prosopis species started to invade abandoned farms, forest gaps and forests indiscriminately (Muturi et al., 2010; Stave et al., 2003). Currently the riverine forest has different canopy patches such as *A. tortilis* canopies, *H. compressa* canopies, Prosopis species canopies, and canopies of 2 or more species.

2.2. Study design

Potential forest patches with distinct canopies of *A. tortilis*, *Prosopis* species and ixed *A. tortilis* and *Prosopis* species (henceforth referred to Acacia, Prosopis and Mixed species canopies respectively) were identified in the study area (Muturi et al., 2010). Subsequently, forest patches with the desired canopies were picked through transect walk based on the methods described by El-Keblawy and Al-Rawai (2007) to minimize site variations among the canopy types. At Katilu, forest patches with the three canopy types were selected. At Nadapal only forest patches with Acacia or Prosopis canopies were available. The distance between canopy types was set at a minimum of 0.3 km in case of adjacent canopies, to avoid the ecotones or a maximum of 9.0 km in one occasion where closer distances were practically unfeasible. These distances were estimated with a global positioning system (GPS) during initial plot establishment.

At any given canopy type in a forest patch, assessment was done to pick the general direction in which to maximize the number of plots to be laid on each transect. Thereafter intensive sample plots (Barnett and Stohlgren, 2003) were systematically laid at intervals of about 100 m using GPS, pacing or a tape measure depending on the circumstances. The layout of an intensive sample plot is shown in Fig. 2. The distance of 100 m between plots was deemed appropriate for avoiding spatial autocorrelation (de Knegt et al., 2010; Tiegs et al., 2005), as both soil characteristics and micro-topography which have direct effect on species composition vary within short distances in this area (Patten and Ellis, 1995; Stave et al., 2003). In total, forty intensive sample plots were established in the two sites; 21 in Katilu and 19 in Nadapal. Fifteen plots were under Acacia, 16 under Prosopis and nine under Mixed species. To facilitate subsequent revisits to plots, corner trees were marked with indelible paint, and their GPS locations recorded.

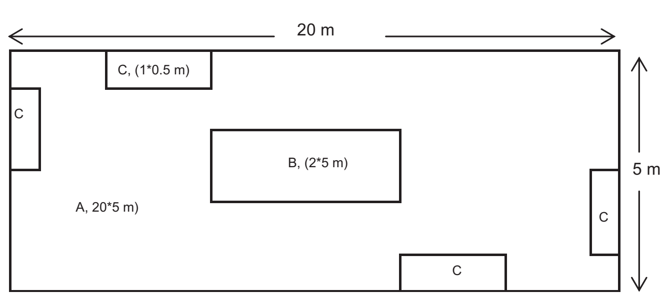

Fig. 2. Intensive plot consisting of the main plot of 20*5 m (A), a mid-plot of 2*0.5 m (B) and four 1*0.5 m sub-plots (C).

2.3. Soil sampling and analysis

In each plot, soil samples were taken from three random sampling points, at depths of 0–10, 10–20 and 20–30 cm. These depths are commonly used because most of the root mass and root activity are concentrated there (Belsky et al., 1989; El-Keblawy and Al-Rawai, 2007). The soil samples were bulked into a single sample per depth, and transferred to soil laboratories at Kenya Forestry Research Institute (KEFRI) and Kenya Agricultural Research Institute (KARI) for analysis following standard analytical procedures (Anderson and Ingram, 1993; Okalebo et al., 2002).

Briefly, soil samples were air-dried at room temperature, sieved with a 2 mm sieve to remove litter and debris, homogenized, and 13 soil variables analyzed. Soil texture was determined with Soil Hydrometer model Number 152 H (152 H: Temperature 68 °F per bouyoucos scale), soil pH using calcium chloride method with Metrohm (type 1.691.0020), and organic carbon determined with Waldey Black method. Dry soil samples were wet digested using Kjeldhal method with Kjeltec system (1028 Distilling unit (serial No. 225012)). The concentration of nitrogen in the digest was calculated, concentration of potassium determined with Flame photometer 410 (Corning M 410, serial No. 52033) and that of calcium and magnesium determined with Unicum Atomic Absorption Spectrophotometer (Unicum 919). Phosphorus concentration was determined with Unicum UV spectrophotometer (Unicum 8625). Micronutrients (copper, manganese and iron) were extracted with ethylenediaminetetraacetic acid (EDTA) and their concentration determined with Unicum Atomic Absorption Spectrophotometer (Unicum 919).

2.4. Determination of canopy closure

Canopy closure was estimated as the proportion of the sky hemisphere obstructed by vegetation when viewed from the middle of the plot (Jennings et al., 1999). Four canopy closure estimates were made per plot during the rainy season in November 2008, October 2009, January 2010 and May 2010, and averaged.

Additional data on canopy closure were collected using two Minolta light meters; with one light meter assigned to take measurement in the forest and the other one to take light measurement outside the forest. Before data collection the two light meters were counterchecked for parity each day, by comparing readings of simultaneous sample measurements in an open area. Thereafter, the two meters were used for collecting data simultaneously within and outside the forest. In each of the forty intensive plots, light data was collected at the center of each of the four 1 m^2 subplots, and at seven points along each of the two diagonals of the main plot. The points on which to take the measurements were predetermined and marked on a sisal twine that was used for data collection in all the plots. All data was collected around noon when the sun's rays were nearly perpendicular to the canopy. After the light measurement, canopy closure was estimated visually, as described above. At the end of each day, parity countercheck was repeated for the two light meters.

All the data collected for parity checks revealed that the reading for the meter designated for use in the forest gave 103.3% of the reading obtained from the meter designated for the open area. Percentage light penetration in the forest canopy was therefore corrected as: (100/103.3)*(Light measured in the forest/light measured in the open)*100. Canopy closure was calculated as 100 minus the canopy light penetration.

2.5. Herbaceous species cover and regeneration

Herbaceous species cover was estimated visually by three persons independently of each other (Murphy and Lodge, 2002) and then averaged. Herbaceous species cover was estimated as the proportion of the ground covered by herbaceous species in the 1 m^2 subplots when viewed from above the subplot. Herbaceous species cover was determined in the rainy season of November 2008, whereas herbaceous species regeneration was determined in January 2010. For herbaceous species regeneration, species were identified; their frequencies determined and recorded per species in each of the 1 m^2 subplots.

2.6. Regeneration and characteristics of woody plants

Data on woody plants was collected on tree seedlings, saplings and trees. In this study tree seedling was any woody plant of $\leq$0.5 m tall, a sapling was any woody plant >0.5 m tall but with a diameter at breast height (DBH) of <2.5 cm and a tree is any wood plant >2.5 cm DBH. In November 2008 (Year 1) and January 2010 (Year 2), tree seedlings were identified; their frequencies determined and recorded per species in each of the 1 m^2 subplots. In both years 1 and 2, saplings were identified per species and recorded from each of the 10 m^2 subplots, while trees DBH were measured and recorded per species from the 100 m^2 plots. For trees with multiple stems below 1.3 m, DBH was measured for each stem. Subsequently, tree and stem data analysis was based on data collected in year 2.

2.7. Species identification and nomenclature

All herbs and woody species were identified by a taxonomist and corroborated with published literature (Beentje, 1994; Dharani, 2006; Morgan, 1981; Timberlake, 1994) and herbaria voucher specimens. The nomenclature of the species list was counterchecked against the international plant names index (www.ipni.org.).

2.8. Data analysis

Variation of soil and plant variables between Katilu and Nadapal was tested using *t*-test. Herbaceous species diversity was calculated for each plots with Shannon–Wiener; diversity index (H') as $\Sigma(p_i)/\ln(p_i)$ where p_i is the proportion of each species in a sample (Krebs, 1999). Tree and stem densities were derived from plots data and expressed in terms of trees or stems per hectare. Light penetration data was transformed into canopy closure. All data on canopy closure from the different assessment methods was then averaged per plot.

One-way analysis of variance (ANOVA) was used to determine whether the three canopy types differed in soil characteristics, canopy closure, vegetation characteristics and Shannon–Wiener diversity index. Prior to statistical analyses, variables were tested for normality using Levene's normality test in order to decide on the appropriate post hoc tests. Means for variables with equal variance were separated by Tukey post hoc test and those with unequal variance separated with Tamhane post hoc test. Chi-square test was used to evaluate tree seedling frequencies amongst canopies.

A forward multiple regression was undertaken to evaluate how soil characteristics under Prosopis species, and Prosopis stem density affect the regeneration of woody and herbaceous species. The dependent variables were number of tree seedlings, number of herbaceous species, herbaceous species cover and density, whereas independent variables were density of stems, % sand, % silt, % carbon, pH, and dummies for Prosopis canopies and Mixed species canopies. The variables for Acacia canopies were used as the reference. Acacia canopy was assigned a dummy value of 0 and Mixed species and Prosopis canopies assigned a dummy value of 1 using separate columns for each dummy variable. With the exception of the dummy variables, all other variables were selected from ANOVA results based on their significant differences amongst canopies. Tree density was excluded from the regression variables adopted as it was a sub component of the stem density. All statistical analyses were performed with Predictive Analysis Software (PASW) for Windows version 18, (formerly SPSS).

3. Results

3.1. Soil characteristics amongst the three canopy types

The *t*-test comparing soils between Katilu and Nadapal revealed similarity of soil properties in the two sites (data not shown). Therefore soil properties were evaluated for variation among the canopy types which was also the focus for plant variables. Sand, silt, pH, carbon and calcium under Acacia, Prosopis and Mixed species canopies differed significantly (Table 1). Soil under Acacia had higher concentration of silt, carbon and calcium than soil in the other two canopies. Soil under Prosopis and Mixed canopies were similar in sand, silt and carbon concentration but differed in calcium concentration and pH.

3.2. Canopy closure among the canopy types

Mean canopy closure were similar amongst canopy types. However, the range of canopy closure was low under Acacia

Table 1
Soil characteristics under three tree canopy types (*Acacia*, Mixed *Acacia* and *Prosopis* species and *Prosopis* species). Analysis of variance results are shown by *F* and corresponding *P* values if significantly different amongst canopies or Ns if not significant. Means and standard errors are shown; values in the same row followed by a different letter are significantly different at $P < 0.05$ (Tukey post-hoc test).

Soil variable	*F*	*P*	*Acacia*	Mixed	*Prosopis*
Sand (%)	4.9	0.013	47.6 ± 5.19 b	72.6 ± 4.94 a	64.4 ± 5.74 a
Silt (%)	9.5	0.000	27.2 ± 3.30 a	11.1 ± 2.11 b	14.1 ± 2.19 b
Clay (%)	Ns		25.2 ± 4.14	16.3 ± 3.54	21.6 ± 3.98
pH	15.3	0.000	7.4 ± 0.05 a	7.1 ± 0.08 b	7.5 ± 0.03 a
Carbon (%)	6.0	0.006	0.68 ± 0.058 a	0.49 ± 0.059 b	0.39 ± 0.068 b
Calcium (meq)	4.9	0.013	10.5 ± 0.70 a	6.3 ± 1.40 b	8.3 ± 0.78a b
Nitrogen (%)	Ns	–	0.10 ± 0.007	0.09 ± 0.008	0.08 ± 0.008
Phosphorus (meq)	Ns	–	1.2 ± 0.06	1.0 ± 0.10	1.1 ± 0.08
Potassium (meq)	Ns	–	1.9 ± 0.20	1.5 ± 0.28	1.5 ± 0.26
Magnesium (meq)	Ns	–	2.1 ± 0.28	1.7 ± 0.51	1.6 ± 0.28
Manganese (meq)	Ns	–	0.85 ± 0.118	0.69 ± 0.216	0.62 ± 0.120
Iron (meq)	Ns	–	0.37 ± 0.040	0.41 ± 0.062	0.35 ± 0.029
Copper (meq)	Ns	–	0.009 ± 0.001	0.007 ± 0.001	0.006 ± 0.001

canopies (72–83%), intermediate under Mixed species canopies (60–82%) and high under Prosopis canopies (58–88%).

3.3. Herbaceous species cover and regeneration

Forty-six herbaceous species were recorded under the three canopy types in 2008, compared with fifty in 2010. Sixty herbaceous species were found in the three canopy types over the two years; 51 under Acacia, 34 under Prosopis and 33 under Mixed species canopies (Appendix I). *Achyranthes aspera* L., was the most abundant herbaceous species (83% occurrence), followed by *Crotalaria deflersii* Schweinf. (78%), *Corchorus olitorius* L. (60%), *Commelina benghalensis* Forssk. (58%), *Setaria verticillata* (L.) P. Beauv. (55%), *Chenopodium pumilio* R.Br. (53%) and *Justicia caerulea* Blume (53%).

Herbaceous species cover, density and number were significantly higher under Acacia and Mixed species canopies than under Prosopis canopy (Table 2). Shannon–Wiener diversity index (H') was higher under Acacia canopies, intermediate under Mixed species canopies and low under Prosopis canopies (Table 2).

3.4. Indigenous tree regeneration

Seedlings density was significantly different among the three canopy types (Table 2). The density was highest under Prosopis canopies, intermediate under Mixed species canopies and lowest under Acacia canopy. Seedlings (up to 0.5 m height) of six woody species (*A. tortilis*, *Ficus sycomorous*, *Grewia bicolor*, *Prosopis* spp., *Recinnus communis* and *Zizyphus Mauritania*) and one palm (*H. compressa*) were found in the sampled plots (Table 3). *A. tortilis*, *F. sycomorous* and *Prosopis* had a sufficient number of seedlings to be statistically tested, and their frequencies varied significantly amongst canopy types (Table 3). *F. sycomorous* and *Prosopis* species seedlings were found in the three canopy types but *A. tortilis* seedlings were found only under *Acacia* canopy. Seedlings of the three species accounted for 98.4% of the total seedlings: the vast majority (83.4%) was *Prosopis*, followed by *F. sycomorous* (7.3%) and *A. tortilis* (6.7%). Only *Prosopis* saplings (>0.5 m tall but <2.5 cm DBH) were found, mainly under the Prosopis canopy, hence comparison of saplings among the canopy types was not feasible.

3.5. Characteristics of woody plants

Tree and stem densities were significantly higher under Prosopis canopies than in the other two canopies (Table 2). Diameter structure among the three canopies revealed; a near-normal DBH distribution curve for *A. tortilis* trees under Acacia canopy (Fig. 3a), skewed DBH distribution for *A. tortilis* and *Prosopis* species trees in Mixed species canopy (Fig. 3b) and negative exponential structure of *Prosopis* species trees under Prosopis canopy (Fig. 3c).

3.6. Effects of soil and trees on herbaceous layer species and tree seedlings

All soil variables except calcium had a positive effect on herbaceous species characteristics (Table 4a). Carbon had a significant positive effect on herb density and diversity; silt had a positive effect on herbaceous species cover, while sand and pH had positive effect on herb density. The forward multiple regression analysis revealed that the dummy variable for Prosopis canopy had significant negative effect on all herbaceous characteristics and a positive significant effect on seedlings (Table 4a). The effect of Prosopis on herbaceous species was further clarified by the negative correlations between *Prosopis* tree stem density and herbaceous species cover and species diversity (Table 4b).

4. Discussion

4.1. Soil characteristics amongst the three canopy types

Although soil characteristics vary over short distances in the study area (Patten and Ellis, 1995; Stave et al., 2003), equal concentration in seven soils nutrients (nitrogen, potassium, phosphorous, magnesium, manganese, iron, and copper) under Acacia, Mixed species and Prosopis canopies suggests a certain level of soil homogeneity in the three canopy types. However, the soil differed in pH, and concentration of calcium, carbon and silt, among the canopy types. We opined that the variation of soil pH, and concentration of calcium, carbon and silt, among the canopy types, was caused by direct and indirect effects of the trees found in each canopy type. For example, high carbon content, and high herbaceous species density under *A. tortilis*, and the positive regression coefficient between Carbon content and herbaceous species density is cause–effect indicator for high carbon content arising from herbaceous species decay under *A. tortilis*. Our findings are consistent with high calcium and carbon contents found under *A. tortilis* tree canopies than in open areas (Belsky et al., 1989); high calcium and carbon contents found under *P. juliflora* (Bhojvaid and Timmer, 1998; Mishra and Sharma, 2010) and variation of soil pH depending on *P. juliflora* density (El-Keblawy and Al-Rawai, 2007).

Alluvial riverine soil in the study area has low clay content and high sand content (Oba et al., 2001; Patten and Ellis, 1995) as found in our study. Nevertheless, sand and silt content may vary with topography or herbaceous species cover. Topography has direct influence on alluvial deposition whereas vegetation traps the alluvial soil. Thus, it is conceivable that the high silt content under Acacia canopy was due to the trapping of alluvial soil by the high herbaceous species cover found under Acacia canopy; as alluvial

Table 2
Characteristics of trees and herbaceous plants in three canopy types (*Acacia*, Mixed *Acacia* and *Prosopis* species and *Prosopis*). Analysis of variance results are shown by F and corresponding P values. Means and standard errors are shown; values in the same row followed by a different letter are significantly different at $P < 0.05$ (Tamhane or Tukey post-hoc tests).

Plant variable	F	P	*Acacia*	Mixed	*Prosopis*
Tree density (#/ha)	9.9	0.000	333 ± 61 b	756 ± 138 b	1225 ± 198 a
Stem density (#/ha)	57.2	0.000	387 ± 60 b	889 ± 190 b	3031 ± 254 a
Seedling density (#/ha)	8.6	0.001	9464 ± 3024 b	19,722 ± 3760 ab	71,093 ± 16,294 a
Herb cover (%)	24.9	0.000	33.5 ± 3.90 a	29.3 ± 3.93 a	5.3 ± 1.84 b
Herb density (#/m^2)	6.3	0.004	41 ± 7.8 a	38 ± 13.2 a	7 ± 4.6 b
Species number (#/4 m^2)	20.5	0.000	15 ± 1 a	14 ± 3 a	6 ± 1 b
Herb diversity (H')	3.6	0.042	1.75 ± 0.11 a	1.40 ± 0.20 ab	1.18 ± 0.13 b

Table 3
Mean density of tree seedlings (No./ha) found under each canopy type (*Acacia*, Mixed *Acacia* and *Prosopis* species and *Prosopis*). The mean is based on the two years but Chi^2 test was based on mean for plot counts. Chi^2 and *P*-values are shown for the three species with a sufficient number of individuals.

Species	*Acacia*	Mixed	*Prosopis*	X^2	*P*
Acacia tortilis	6167	0	0	61.7	<0.001
Prosopis spp.	4500	14,444	58,594	351.1	<0.001
Ficus sycomorus	833	4167	1719	13.2	<0.01
Grewia bicolor	167	0	0	–	–
Hyphaene compressa	167	0	313	–	–
Ricinus communis	0	0	156	–	–
Ziziphus mauritiana	333	278	0	–	–

soil is rich in silt contents (Jacobson et al., 2000). Although our hypothesis is not fully sustained, similarity of all soil variables (except pH and calcium content) under Prosopis canopy and Mixed species canopy provides the basis for evaluating the effect of

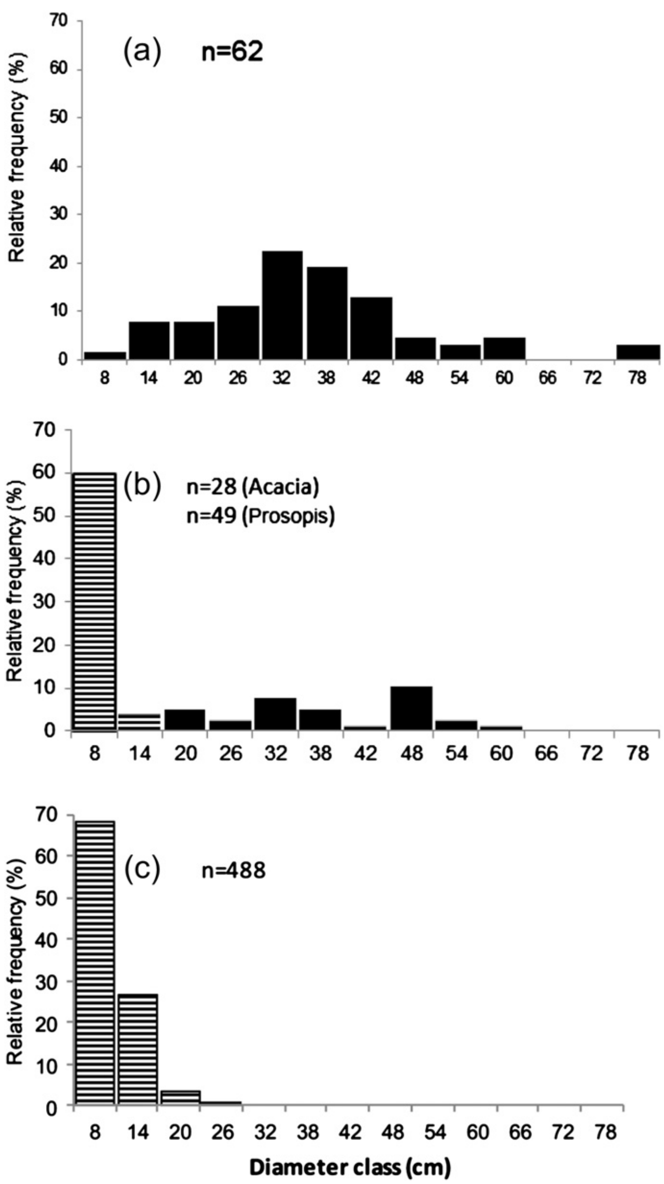

Fig. 3. Relative frequency of diameter at breast height (DBH) for trees found under *Acacia* (a), Mixed *Acacia* and *Prosopis* species (b) and *Prosopis* (c) canopies. Diameter classes have a width of 6 cm, starting from 2.5 (2) cm onward. For each class the upper limit is shown. All trees per canopy type were pooled and their total number is shown in each graph. *Acacia tortilis* is shown by dark bars and *Prosopis* spp. shown by lined bars.

Table 4a
Results of multiple regression of tree seedlings and herbaceous characteristics against biotic stand characteristics. Only those characteristics that differed significantly amongst canopies were included (see Tables 1 and 2). *Prosopis* canopy and Mixed *Acacia* and *Prosopis* species canopy were included as dummy variables. Standardized regression coefficients (β), significance levels (*P*), *F* value and coefficient of determination (R^2) are shown.

Variable	Seedlings		Herbaceous species cover		Herb density		Herb diversity	
	β	*P*	β	*P*	β	*P*	β	*P*
Calcium (meq)	–		–		–		–	
Sand (%)	–		–		0.65	0.003	–	
Silt (%)	–		0.28	0.010	–		–	
Carbon (%)	–		–		0.87	0.000	0.40	0.001
pH	–		–		0.36	0.016		
Stems density (#/ha)	–		–		–		–	
Dummy Mixed	–		–		–		–	
Dummy *Prosopis*	0.57	0.000	−0.67	0.000	−0.45	0.005	−0.55	0.000
R^2	0.33		0.64		0.53		0.65	

A. tortilis and *Prosopis* species trees on the herbaceous species and tree regeneration.

4.2. Canopy closure among the canopy types

Our hypothesis that canopy closure is highest under Prosopis canopies due to higher tree densities that characterize invading *Prosopis* species is not sustained. This is because mean canopy closure was similar under the three canopy types. *A. tortilis* has been the dominant canopy species (Adams, 1989) but canopies associated with the invading *Prosopis* species in this forest are reported for the first time. Thus, our study provides a baseline against which canopy dynamics and resultant impacts under the indigenous *A. tortilis* and the invading *Prosopis* species can be periodically evaluated.

4.3. Herbaceous species cover and regeneration

In our study we found higher herbaceous species cover and species diversity under Mixed species canopy than under Prosopis canopy and a contrast in tree density, as hypothesized. Since both mean canopy closure and soil characteristics were similar under the two canopy types, we attribute the contrast of herbaceous species under Mixed species and Prosopis canopies to the differences in their tree densities. High *Prosopis* species tree density is associated with low herbaceous species productivity and species diversity (El-Keblawy and Al-Rawai, 2007; van Klinken et al., 2006), as found in this study. This may be attributed to competition for water and nutrients between herbaceous species and trees

Table 4b
Results of a repeat of multiple regression of [4a], but with substitution of dummy variables with *Acacia tortilis* and *Prosopis* species stem densities.

Test variable	Seedlings		Herbaceous species cover		Herbs density		Species diversity	
	β	*P*	β	*P*	β	*P*	β	*P*
Calcium (meq)			–		0.41	0.028	–	
Sand (%)	–		–		0.88	0.000	–	
Silt (%)	–		0.70	0.000	–		–	
Carbon (%)	−0.31	0.020	−0.32	0.047	0.86	0.000	0.43	0.000
pH			−0.57	0.000			−0.25	0.026
Acacia stems density (#/ha)	–		–		–		–	
Prosopis stems density (#/ha)	0.40	0.003	−0.35	0.003	–		−0.35	0.004
R^2	0.34		0.61		0.44		0.57	

(Simmons et al., 2008; van Klinken et al., 2006), or Prosopis litter allelopathy (Nakano et al., 2002).

4.4. Indigenous tree regeneration

We hypothesized that Prosopis canopy would hinder the regeneration of indigenous species. Although the regeneration of indigenous species was low, effect of Prosopis species on indigenous species was species-dependent. The lack of *A. tortilis* regeneration under canopies with *Prosopis* trees supports our hypothesis, whereas occurrence of *F. sycomorus* under all the three canopy types contradicts that hypothesis.

A. tortilis seed trees were present in Acacia and Mixed species canopies; *A. tortilis* seeds are randomly dispersed by livestock (Reid and Ellis, 1995); and they germinate shortly after rains (Stave et al., 2006). Moreover, *A. tortilis* establishes in a wide variety of soil (Loth et al., 2005; Ludwig et al., 2004; Reid and Ellis, 1995). Therefore, the notable absence of *A. tortilis* seedlings in Mixed species and Prosopis canopies cannot be attributed to lack of seeds or unfavorable soil but probably due to *Prosopis* somehow inhibiting its seed germination. The finding that unlike *A. tortilis*, seeds of *F. sycomorus* germinated under all the canopies is consistent with other studies in which establishment and growth of *Schinus molle* L. in the field did not vary between *A. tortilis* and *Prosopis* species canopies (Iponga et al., 2009).

The high number of Prosopis seedlings found under Prosopis canopy and Mixed species canopy is consistent with other studies (El-Keblawy and Al-Rawai, 2007; van Klinken et al., 2006). This may be attributed to prolific seeding of *Prosopis* species (Zimmermann, 1991). Occurrence of Prosopis seedlings under Acacia canopy found in this study is not surprising as Prosopis seeds are randomly dispersed by livestock (Mwangi and Swallow, 2008; Mworia et al., 2011). The fact that *Prosopis* species seedlings occurred in all three canopy types whereas *A. tortilis* seedlings were found only under the *Acacia* canopy indicates that *A. tortilis* is losing out in areas that until now were available for its establishment.

4.5. Characteristics of woody plants

For the Mixed species canopy, the DBH distribution of *Prosopis* species and *A. tortilis* trees revealed an encroachment of *Prosopis* species into mature *A. tortilis* stands, as *Prosopis* species trees were found in lower diameter classes and *A. tortilis* trees found in upper diameter classes. *Prosopis* species encroachment into the riverine forest point to *Prosopis* species gaining a canopy tree status similar to that exhibited by *A. tortilis* in this ecosystem.

The density of *A. tortilis* trees found in this study is common for mature stands in the region (Oba, 1998), but young stands can have a higher density that decreases with stand age (Reid and Ellis, 1995). The high *Prosopis* species tree density in this study is consistent with the high densities of invasive *Prosopis* species (van Klinken et al., 2006). Such high tree densities are uncharacteristic for this riverine ecosystem (Oba, 1998). Since the negative exponential diameter structure of *Prosopis* trees in Prosopis canopy is typical for a regenerating forest, it remains to be seen if self-thinning of the dense *Prosopis* stands will occur and result to a stand structure similar to that of the indigenous *A. tortilis* stands.

4.6. Effects of soil and trees on herbaceous layer species and tree seedlings

Regression analysis revealed that herbaceous species were affected by soil conditions or the vice versa; as evident from the positive correlations between herbaceous species cover with silt, and between herbaceous species density with carbon. The study findings suggests that the relationships between herbaceous species and both soil silt and carbon can be attributed to cyclic processes in which silt is trapped by the herbaceous layer and soil carbon content enhanced by the decaying herbs. Subsequently, carbon and silt content ameliorates the site (Gicheru et al., 2004) to stimulate herbaceous layer species growth and diversity; and the cycle continues.

Whereas some past studies have attributed the negative impacts of *Prosopis* species on herbaceous layer to their canopies (El-Keblawy and Al-Rawai, 2007; Kahii et al., 2009; Schade et al., 2003) the current study did not reveal a direct effect of canopy on the herbaceous species characteristics measured. Instead, reduction of productivity and biodiversity of herbs under Prosopis canopy can be attributed to the high stem density in Prosopis canopy, as reported previously in Australia (van Klinken et al., 2006). The positive correlation found between Prosopis stems with tree seedlings can be attributed to the large number of seeds emanating from Prosopis trees, which is previous studies (El-Keblawy and Al-Rawai, 2007; van Klinken et al., 2006). We infer the variation of soil properties and herbaceous species variables among the canopy types to the conceivable positive cyclic processes between soil and herbaceous species variable and the gradual negative effects of Prosopis trees on herbaceous species.

5. Conclusions

We predicted that Prosopis canopy closure has negative effect on herbaceous species cover, herbaceous species diversity and regeneration of indigenous trees. As the mean canopy closures were similar under Acacia, Prosopis and Mixed species canopies, we could not attribute the variation in the herbaceous layer variables to canopy closure directly. Nevertheless, the study found that herbaceous species cover and diversity were lower under Prosopis canopy than under Mixed species canopy. Soil characteristics (except pH and calcium content) were similar under Prosopis and Mixed species canopies. Therefore we attribute low herbaceous species cover to *Prosopis* trees. This is evident from negative correlation between Prosopis canopy dummy with herbaceous species cover, density and diversity; in contrast to lack of such correlations between Mixed species canopy dummy and herbaceous species cover, density and diversity when Acacia canopy is used as a reference. The absence of *A. tortilis* seedlings under Mixed species canopy suggests negative effect of *Prosopis* trees on the regeneration of this important tree, since *A. tortilis* seeding trees were present in that canopy and *A. tortilis* seeds are also randomly dispersed by livestock in this ecosystem. However, the occurrences of *F. sycomorus* seedlings under all the three canopy types suggest that the effect of *Prosopis* trees on regeneration of indigenous tree species is species-dependent.

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Appendix I

Checklist of herbaceous species found under each canopy type and the cumulative number of species under each canopy. Most species are used as fodder (✓) or have fodder potential (*) or their fodder potential is unknown (–). Occurrence of a species under each canopy is denoted by X and the absence shown by –.

No.	Species	% Occurrence	Family	Fodder use	Occurrence of under canopies of		
					A. tortilis	Prosopis	Mixed species
1	*Abution hirtum* (Lam.) Sweet	10	Malvaceae	✓	X	X	X
2	*Abutilon mauritianum* (Jacq.) Medik.	22.5	Malvaceae	✓	X	X	X
3	*Acalypha fruticosa* Forssk.	27.5	Euphorbiaceae	✓	X	X	X
4	*Achyranthes aspera* L.	82.5	Amaranthaceae	*	X	X	X
5	*Aerva lanata* (L.) Schult	15	Amaranthaceae	*	X	X	–
6	*Amaranthus graecizens* Desf.	15	Amaranthaceae	✓	X	–	–
7	*Amaranthus hybridus* L.	35	Amaranthaceae	✓	X	X	X
8	*Aristida mutabilis* Trin. & Rupr.	10	Poaceae	✓	X	–	X
9	*Asparagus falcatus* L.	2.5	Asparagaceae	–	–	X	–
10	*Barleria acanthoides* Vahl	10	Acanthaceae	✓	X	–	–
11	*Bidens hildebrandtii* O. Hoffm	2.5	Asteraceae	*	–	–	X
12	*Bidens pilosa* L.	10	Asteraceae	*	X	X	X
13	*Brachiaria deflexa* (Schumach.) Robyns	27.5	Poaceae	✓	X	X	X
14	*Calotropis procera* (Ait.) Ait. f.	2.5	Asclepiadaceae	✓	X	–	–
15	*Cenchrus cilliaris* L.	40	Poaceae	✓	X	X	X
16	*Chenopodium pumilio* R.Br.	52.5	Chenopodiaceae	–	X	X	X
17	*Chloris virgata* Sw.	2.5	Gramineae	✓	X	–	–
18	*Coccinia grandis* (L.) Voigt	32.5	Cucurbitaceae	✓	X	X	X
19	*Combretum aculeatum* Vent.	10	Combretaceae	✓	X	X	X
20	*Commelina benghalensis* Forssk.	57.5	Commelinaceae	✓	X	X	X
21	*Corchorus olitorius* L.	60	Tiliaceae	–	X	X	X
22	*Crotalaria deflersii* Schweinf.	77.5	Papilionaceae		X	X	X
23	*Cucumis dipsaceus* Spach	15	Cucurbitaceae	✓	X	X	–
24	*Cucumis prophetarum* L.	20	Cucurbitaceae	✓	X	X	X
25	*Cynodon dactylon* (L.) Pers.	2.5	Poaceae	✓	X	–	–
26	*Cyphostemma manieriense* (Th. Fr. jr) Desc	5	Vitaceae	✓	X	–	–
27	*Cyperus articulatus* L.	2.5	Cyperaceae	–	–	X	–
28	*Digitaria gayana* (Kunth) A. Chev	45	Poaceae	*	X	X	X
29	*Digitaria horizontalis* Willd.	2.5	Poaceae	*	X	–	–
30	*Euphorbia granulata* Forssk.	5	Euphorbiaceae	✓	X	–	–
31	*Evolvulus alsinoides* (l.) L. Plate	25	Convolvulaceae	✓	X	X	X
32	*Geigeria acaulis* Oliv. & Hiern	2.5	Compositae	✓	X	–	–
33	*Glycine wightii* (Wight & Arn.) Verdc	17.5	Fabaceae	✓	X	X	X
34	*Gynandropsis gynandra* Briq.	2.5	Capparaceae	✓	X	–	–
35	*Hibiscus fuscus* Garcke	7.5	Malvaceae	–	X	–	–
36	*Hibiscus ovalifolius* Forssk.	2.5	Malvaceae	✓	X	–	–
37	*Indigofera errecta* Thunb.	5	Leguminosae	–	X	–	–
38	*Ipomoea wightii* Choisy	47.5	Convolvulaceae	–	X	X	X
39	*Justicia caerulea* Blume	52.5	Acanthaceae	✓	X	X	X
40	*Justicia odora* Vahl	2.5	Acanthaceae	✓	X	–	–
41	*Leucas glabrata* (Vahr) R. Br	12.5	Labiatae	✓	X	X	X
42	*Maerua subcordata* (Gilg) DeWolf	2.5	Capparaceae	✓	X	–	–
43	*Maerua triphylla* T. Durand & Schinz	7.5	Capparaceae	✓	X	X	X
44	*Momordica trifoliolata* Hook. f. Mathew	7.5	Cucurbitaceae	✓	X	–	X
45	*Ocimum staminosum* Baker	20	Lamiaceae	✓	X	–	X
46	*Plectranthus ignarius* (Schweinf.) Agnew	2.5	Labiatae	✓	–	–	X
47	*Portulaca oleracea* L.	15	Portulacaceae	✓	X	X	–
48	*Portulaca quadrifida* L.	17.5	Portulacaceae	✓	X	X	–
49	*Seddera hirsuta* Damm. ex Hallier f.	5	Convolvulaceae	✓	X	–	–
50	Senna spp.	2.5	Caesalpiniaceae	–	–	X	–
51	*Setaria verticillata* (L.) P. Beauv.	55	Gramineae	✓	X	X	X
52	*Sida ovata* Forssk.	45	Malvaceae	✓	X	X	X
53	*Solanum coagulans* Forsk	5	Solanaceae	✓	X	–	–
54	*Solanum incanum* L.	10	Solanaceae	✓	X	X	–
55	*Solanum nigrum* L.	2.5	Solanaceae	✓	–	–	X
56	*Sorghum bicolor* (L.) Moench	2.5	Poaceae	✓	X	–	–
57	*Sonchus oleraceus* L.	2.5	Asteraceae	*	–	–	X
58	*Tephrosia uniflora* Pers.	20	Leguminosae	✓	X	X	X
59	*Withania sommifera* (L.) Dunal	2.5	Solanaceae	✓	–	X	–
60	*Zehneria scabra* Sond.	2.5	Cucurbitaceae		–	–	X
Total number of species					**51**	**34**	**33**

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