African Journal of Environmental Science and Technology Vol. 5(8), pp. 579-588, August, 2011
Available online at http://www.academicjournals.org/AJEST
ISSN 1996-0786 ©2011 Academic Journals

Full Length Research Paper

Effect of biotic and abiotic factors on composition and foraging intensity of subterranean termites

Swidiq Mugerwa[1,2]*, Moses Nyangito[1], Denis Mpairwe[3] and John Nderitu[1]

[1]Department of LARMAT, P. O. Box 30197, University of Nairobi, Kenya.
[2]National Livestock Resources Research Institute, P. O. Box 96, Tororo, Uganda.
[3]Department of Animal Science, Makerere University, P. O. Box 7062, Kampala, Uganda.

Accepted 27 June, 2011

Elucidating the influence of ecological factors on composition and foraging intensity of subterranean termites is critical in development of sustainable termite management strategies. Our aim was therefore to analyze the effect of selected biotic and abiotic factors on composition and foraging intensity of termites. We used principal component and canonical correspondence analysis to select appropriate factors and to model relationships respectively. *Macrotermes* species occurred in sites where the quantity of litter was generally above the mean. However, *Macrotermes herus* (Rambur) and *Macrotermes* spp.4 occurred in sites where the litter quantity was below the mean. *Trinervitermes oeconomous* (Tragardh) and *Odontoremes* spp.1 were noted to occur in the direction of increasing quantity of biomass. Generally, most species occurred in sites where soil pH was above or slightly below the mean (4.8). Majority of the species were also noted to occur in sites where bulk density was below or slightly above the mean (1.55 g/cm^3). Highest bait consumption (95%) occurred within a range of 55 to 60% basal cover beyond which the amount of bait consumed reduced. Litter and biomass quantity, pH and bulk density were noted as the most influential environmental variables determining composition of termites while basal cover was the major determinant of foraging intensity.

Key words: Rangelands, *Macrotermes*, rangelands, vegetation, litter, biomass, basal-cover.

INTRODUCTION

Determinants of the structure and activity of subterranean termites at a large-scale are well known: climate, soil type, land use management practices and landscape structure are among the most influential factors (Dauber et al., 2003, 2005). At smaller scales, however, there is less agreement about the biotic and abiotic factors that drive variability in composition and activity of macro-fauna including subterranean termites (Lavelle and Spain, 2001). Mitchell (2002) reported that the amount of available litter (both leaf and wood) was a major determinant of foraging intensity on vegetation by generalist feeders such as members of the genera *Macrotermes* and *Odontotermes*. He further noted that in sites with limited litter resources, termites resorted to standing biomass and consumed more than 60% of the standing crop. Mathieu et al. (2009) and Attignon et al. (2005) also reported that high encounters of *Macrotermes* species (mainly fungus growers) were associated with sites with high litter biomass and low soil water content. Curry (1994) observed the survival and activity of macro-fauna on various sites to be influenced by the micro-climate and the quality of food in the various sites. Micro-climate is very important since the body temperature of soil macro-fauna varies with external temperature (thermo-conformers) and the range tolerated by many species is narrow (Geiger and Aron, 2003). Geiger and Aron (2003) further noted that soil macro-fauna including subterranean termites need to maintain body water content within fairly narrow limits, which creates a dependence on soil water. This implied that the structure, survival and activity of subterranean termites would be enhanced on sites with acceptable levels of soil water content. Martison et al. (2008) reported that soil

*Corresponding author. E-mail: swidiqk@yahoo.com. Tel: +256782660295.

macro-fauna organisms are also sensitive to the nutrient content of their food because they need to maintain their internal chemical concentrations and the balance between the different nutrients of their body within a strict range. To this effect, elements of food quality such as phosphorus (McGlynn and Salina, 2007), nitrogen (Waren and Zou, 2002) and Ca^{2+} (Reich et al., 2005) content, can become a limiting factor to composition, survival and activity including foraging intensity of subterranean termites. Mathieu et al. (2009) also reported that the composition and activity of subterranean termites was influenced by presence of basal vegetation with more diversity in areas covered with grass tufts than on bare ground.

In the rangelands of Nakasongola District in Uganda, vegetation is typically dominated by large herb turfs of the genera *Hyparrhenia* and *Brachiaria*, which clearly alternate with bare ground and shrubs. The vegetation cover is highly variable, from dense to completely bare ground leading to heterogeneous habitats with varying biotic and abiotic factors. The composition and foraging intensity of subterranean termites seem to be driven by the site-specific biotic and abiotic properties occurring on the different vegetation patches. On some patches, the termite assemblage structure is dominated by *Macrotermes* species while *Cubitermes* species dominate on other patches. Further, the population and foraging intensity of subterranean termites also varies from one site to another with most of the patches experiencing extra-ordinarily high foraging intensity of termites resulting into denudation of basal vegetation, forage scarcity and eventually poor livestock performance. Typical foraging is characterized by subterranean galleries leading to surface foraging holes from which termites emerge to remove dead grass and grass litter under cover of constructed soil sheeting. Termite foraging is particularly obvious during the dry season when bare rangeland can have up to 55 foraging holes per m^2 (Cowie and Wood, 1989). During such times the combined grazing effect of livestock and termites is to virtually denude considerable tracts of grassland, exposing soils to erosion by both wind and water (Mitchell, 2000).

Recognizing the impact of biotic and abiotic factors on composition and foraging intensity of subterranean termites in savanna ecosystems, development of sustainable termite management strategies in the termite infested rangelands of Nakasongola requires adequate knowledge of the site-specific influence of biotic and abiotic factors on the composition and foraging intensity of termites. This will ensure that management of rangeland ecosystems aim at provision of the necessary ecological resources and conditions to overcome the detrimental impact of subterranean termites on rangeland vegetation. However, such information is still poorly documented. In particular, we lack information on the biotic and abiotic factors that enhance foraging intensity of subterranean termites as well as the ecological factors that are responsible for the variation in termite assemblage structure across various rangeland sites.

Our aim was thus to analyze the effect of biotic (tree canopy cover, number of woody species, biomass and basal cover) and abiotic (soil moisture, soil temperature, bulk density, soil pH, litter quantity and soil organic matter) on the composition and foraging intensity of subterranean termites on the grazing lands in semi-arid Nakasongola. We examined two hypotheses: (1) the composition of subterranean termites will not vary among sites with different biotic and abiotic factors and (2) the percentage of baits consumed by subterranean termites (foraging intensity) will not vary among sites with different biotic and abiotic factors.

MATERIALS AND METHODS

Description of the study area

The study was conducted on one savanna site, locally referred to as Kamukama Ranch. The site is located in Nakasongola District (55°140' N, 32° 50' E) of Uganda (Figure 1). The mean daily maximum temperature in the district is 30°C. Rainfall range between 500 to 1000 mm per annum and there are two rain seasons. The main rain season occurs from March-April to June-July while the second rain season follows from August to October-November. A long dry season occurs from December to February while a short spell comes around July-August.

The vegetation on the study site mainly comprised of three vegetation cover types depending on the extent of anthropogenic activities/disturbance on specific ranch sites. The three vegetation cover types included dense vegetation cover (>50% basal cover), sparse vegetation cover (25 to 50% basal cover) and bare ground (<25% basal cover). The vegetation cover types are majorly a product of intricate interactions between climatic conditions and anthropogenic activities such as overgrazing, indiscriminate tree cutting and bush burning among others. The dense vegetation cover category on the study site mainly comprised of *Tarrena graveolens* and *Acacia* species forming 62 and 3% of the total woody canopy cover and woody density of 575, 125 trees ha^{-1} respectively. The herbaceous vegetation was dominated by *Brachiaria* species contributing 88% of the basal cover. The sparse vegetation cover category was dominated by *Cynodon dactylon* and *Loudetia kagerensis* forming 67 and 12% of the species cover. Scattered woody species on the sparse vegetation cover were also dominated by *T. graveolens*, forming 34% of the woody canopy cover. The bare ground category mainly comprised of highly scattered *Harrisonia abyssinica* and *T. graveolens* forming less than 0.5% canopy cover each. The number of mounds ranged from 33 to 525 with an average of 227 mounds ha^{-1}. The soil is generally moderately acidic with the pH ranging between 4 and 5.5. The soil organic matter (%), nitrogen (%), available phosphorus (ppm) and potassium (cmoles/kg) were 1.3, 0.1, 4.2 and 0.23 respectively. The soils generally belonged to the soil textural class of sandy loam.

Sampling and classification of termite species

The standardized sampling protocol developed by Jones and Eggleton (2000) was used to sample termites. The protocol

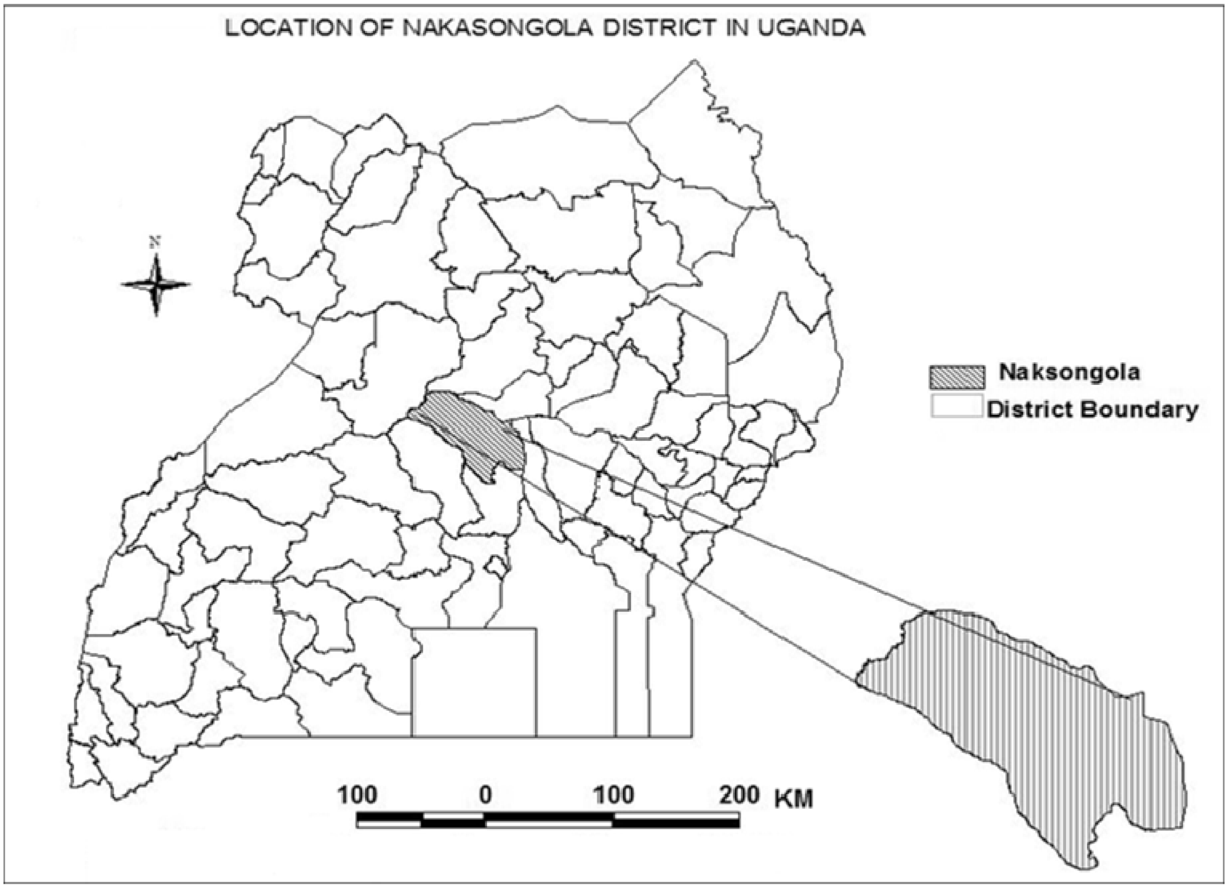

Figure 1. Map of Uganda showing the location of Nakasongola District.

involved lying belt transects of 100 m length by 2 m width, divided into 20 contiguous sections of 5 × 2 m. Each section was sampled by two trained people for 30 min (a total of one hour of sampling per section). In each section the following microhabitats were searched: 12 samples of surface soil (each about 12 × 12 cm, to 10 cm depth); accumulations of litter and humus at the base of woody plants, the inside of tree stumps, dead logs, branches and twigs; the soil within and beneath very rotten logs; subterranean nests, mounds, carton sheeting and run ways on vegetation, and arboreal nests up to a height of 2 m above ground level. Workers and soldiers (if present) from every termite population encountered were sampled and the samples were preserved in 80% ethanol. The belt transect provides a measure of relative abundance of termites based on the number of encounters with each species in the transect. An encounter was defined as the presence of a species in one section. The vegetation of the study site was blocked in to three vegetation categories based on the quantity of vegetation covering the ground. The three categories included dense (> 50% basal cover), sparse (25 to 50% basal cover) and bare ground (< 25% basal cover). Two replicate belt transects were run in each of the three vegetation categories between December and January, the period when termite activity and subsequent destruction of vegetation by termites is reported to be severe (Nakasongola District State of Environmental Report, 2004). Sampling for termite species was conducted in 2010 and 2011. Taxonomic identification for collected samples was done at family, sub-family, genus using standard determination keys by Webb (1961) and where possible to species' level using existing records of termite species in Nakasongola rangelands by Sekamatte (2001).

Sampling for biotic and abiotic variables

Several environmental variables were recorded between 2010 and 2011 to assess their influence on termite assemblages. Measurements were made during the main rainy (March-April/June-July) and the dry season (December to February). The soil water content (percent gH_2Og^{-1} oven-dry soil) was measured from four surface soil samples (2 to 10 cm) taken from sections 3, 8, 13 and 18 of every belt transect (Attignon et al., 2005). The same samples were analyzed for bulk density (g/cm^3), soil pH and soil organic matter (%) according to methods described by Anderson and Ingram (1993). Soil temperature (°C) was determined by randomly inserting thermometers in the soil at any two locations in each of the four sections (3, 8, 13 and 18). The same sections were also sampled for herbaceous biomass quantity and litter quantity (both wood and leaf litter). The number of functional/live termite mounds per section was also quantified. Because the size of the sections was no sufficient to quantify canopy cover (Kent and Coker, 1992), three plots of 50 by 50 m were established in every vegetation category to enable estimation of tree/woody species density and woody canopy cover. Herbaceous biomass quantity was estimated by randomly placing two quadrats (1 m^2) in each of the four sections. The above ground herbaceous vegetation within each 1 m^2 quadrat was cut at ground level, put in plastic bags and weighed as described by L.'tMannetje (1978). To quantify the amount of litter

Table 1. Cumulative variability explained by five factors and factor loadings of vegetation variables.

Vegetation variables	F1	F2	F3	F4	F5
Eigenvalue	3.287	0.852	0.457	0.256	0.148
Variability (%)	65.75	17.03	9.14	5.12	2.96
Cummulative (%)	65.75	82.78	91.92	97.04	100
Factor loadings					
Biomass quantity	0.88	-0.35	-0.16	0.04	0.29
Litter quantity	0.84	-0.03	0.47	-0.28	-0.01
No. of woody species	0.61	0.73	-0.28	-0.15	0.03
Woody canopy cover	0.87	0.24	0.2	0.39	-0.06
Basal cover	0.84	-0.38	-0.30	-0.06	-0.25

available, two quadrats (1 m^2) were placed randomly in each of the four sections and all available dead plant material enclosed by the quadrat was collected, oven dried and weighed. The woody canopy cover and the number of woody species for each plot were estimated according to methods described by Kent and Coker (1992).

Estimation of foraging intensity

The effect of biotic and abiotic factors on foraging intensity was estimated using dried *Hyparrhenia rufa* grass baits as described by and Nash et al. (1999) and Pearce (1997). We selected *H. rufa* because the grass is reported to be among the most susceptible grass species in the area and is thus readily consumed by subterranean termites. Four litter bags (18 ×15 cm) of mesh size 4 mm, containing the same quantity of dried *H. rufa* grass were randomly placed on the surface in each of the four sections (3, 8, 13 and 18) of every belt transect. The bags were surrounded by three big stones to hold them in position or to prevent livestock and run-off from displacing them. The bags were removed after two weeks and were replaced twice in every season. After collection of baits, gallery carton and soil were carefully removed from all baits. The cleaned baits were oven dried at 60°C for 72 to 96 h and the dry weight recorded. The percentage of bait consumed (PC) was estimated as PC = $((W_i-W_f)/W_i)*100$ were W_i is initial weight of grass bait before consumption by termites, W_f is final weight after consumption by termites. The percentage of bait consumed by termites was used as a proxy for determination of foraging intensity.

Data analysis

In order to establish the effect of environmental variables on composition of termite species, we subjected the biotic and abiotic factors to principal component analysis (PCA) to obtain non-correlated factors which were linear combinations of the initial variables (Jolliffe, 2002). Based on the eigenvalues and the variability explained by each factor, a few factors were selected. The vegetation and soil variables were analyzed separately in PCA and the selected variables for vegetation and soil were subjected to canonical correspondence analysis (CCA) in XLSTAT (2011). We opted for factors that accounted for at least 90% of the cumulative variability. PCA (Pearson type; correlation biplot) of vegetation variables led to selection of three factors which accounted for 92% of the cumulative variability. PCA (Pearson type; correlation biplot) of soil variables led to selection of four factors that accounted for 98% of the cumulative variability. The selected factors were then used to model relationships in CCA (ter Braak and Verdonschot, 1995) by extracting synthetic environmental gradients from the ecological data set as well as to develop ordination biplots. In order to establish the effect of environmental variables on foraging intensity (percentage of baits consumed), we also subjected the biotic and abiotic factors to (PCA) to obtain non-correlated factors which were linear combinations of the initial variables (Jolliffe, 2002). Based on the eigenvalues and the variability explained by each factor, a few factors were selected. The selected factors were subjected to non-linear regression to clearly model the relationship.

RESULTS

Effect of environmental variables on composition of subterranean termites

Principal component analysis on vegetation variables indicated that the first three factors explained 92% of the cumulative variability (Table 1). Biomass quantity (BQ), number of wood species (NWS) and litter quantity (LQ) were strongly correlated with factors one (r = 0.88), two (r = 0.73) and three (r = 0.5) respectively. Biomass quantity, number of wood species and litter quantity also loaded highest on F1, F2 and F3 respectively. The factor loading for BQ, LQ and NWS was 0.88, 0.73 and 0.47 on F1, F2 and F3 respectively. The three vegetation variables were thus selected for inclusion in canonical correspondence analysis to establish the effect of the factors on composition of termite species. On the other hand, principal component analysis on soil variables showed that the first four factors explained 98% of the cumulative variability (Table 2). Soil water content (SWC), pH, bulk density (BD) and soil organic matter (SOM) were highly correlated with factors one (r = 0.86), two (r = 0.69), three (r = 0.69) and four (0.38) respectively. SWC, pH, BD and SOM also loaded highest on F1, F2, F3 and F4 respectively. The factor loading for SWC, pH, BD and SOM was 0.86, 0.69, 0.69 and 0.38 on F1, F2, F3 and F4

Table 2. Cumulative variability explained by five factors and factor loadings of soil variables.

Soil variables	F1	F2	F3	F4	F5
Eigenvalue	2.692	1.001	0.763	0.443	0.100
Variability (%)	53.85	20.029	15.255	8.861	2.005
Cummulative (%)	53.85	73.879	89.134	97.995	100.00
Factor loadings					
Soil temperature	-0.78	0.31	0.39	0.34	0.15
Soil water content	0.86	-0.25	-0.30	0.25	0.20
pH	0.63	0.69	0.13	-0.33	0.10
Soil organic matter	0.83	0.35	0.16	0.38	-0.16
Bulk density	0.51	-0.5	0.69	-0.11	0.02

respectively. Four soil variables were selected for inclusion in canonical correspondence analysis to establish the effect of the variables on composition of termite species.

Since the origin (0, 0) of any environmental variable on the ordination biplot represents the mean of that particular variable, *Macrotermes* species are generally considered to have occurred in sites where the quantity of litter was above the mean (Figure 2). However, *Macrotermes herus* and *Macrotermes* spp.4 occurred in sites where litter quantity was below the mean (778 $kgha^{-1}$). *Pseudocanthotermes* species, *Cubitermes* spp.3 and 1 also occurred in sites where the amount of litter was lower than the average litter quantity. By projecting species points on the line of litter quantity, it was indicated that *Macrotermes* spp.2 had the highest weighted average for litter quantity while *Pseudocanthotermes* species seemed to occur in sites where the litter quantity was extremely below the average. It was further noted that although *Macrotermes* species occurred in sites where amount of litter was above the mean, the species disappeared in sites where litter quantity was greatly above the mean. *Trinervitermes oeconomous* and *Odontoremes* species were noted to occur in the direction of increasing quantity of biomass and once the line of biomass quantity is extended beyond the displayed maximum point, *T. oeconomous* and *Odontoremes* spp.1 would have the highest weighted average than all the displayed species. The point for number of woody species (NWS) occurred at the origin of both litter quantity and biomass quantity and was associated with species which occurred in sites where the quantity of litter and biomass was around the mean.

Projection of soil variables on the axes showed that pH was more correlated with axis 1 while BD was more correlated with axis 2 than other variables (Figure 3). Generally, most species occurred in sites where soil pH was above or slightly below the mean (4.8). It was noted that the majority of *Macrotermes* species and *Odontotermes* species occurred in sites where the pH was slightly above or below the mean. The species (*Macrotermes* and *Odontotermes*) were noted to disappear in the direction of increasing pH. Most of the species occurred in sites where bulk density was below and slightly above the mean (1.55 g/cm^3). The diversity of species was noted to decline in the direction of increasing bulk density. It was also noted that *Macrotermes* spp.1, *Odontotermes* spp.1, *Microtermes* species and *Pseudocanthotermes* species were the only members of the sub-family *Macrotermitinae* that occurred in sites were bulk density was below average. Most members of the sub-family *Macrotermitinae* occurred in sites where bulk density was slightly above the mean and finally disappeared in sites with high bulk density. Only *Ancistrotermes* species and *Cubitermes* spp.3 were noted to occur in sites with high values of bulk density.

Effect of environmental variables on foraging intensity of subterranean termites

Principal component analysis on environmental variables led to selection of four principal components (factors) that contributed 96% of the cumulative variability (Table 3). Based on the loading of various environmental variables on the selected factors, four variables were selected to explain the effect of the variables on foraging intensity of subterranean termites. The selected variables included basal cover (BC), number of mounds (NM), litter quantity (LQ) and woody canopy cover (WCC). BC and NM loaded highest on F1 (0.99) and F2 (0.799) while WCC and LQ loaded highest on F3 (0.641) and F4 (0.45) respectively. Pearson correlation tests showed significant ($p>0.05$) correlations between BC and the other three selected variables. BC was positively correlated with NM ($r=0.65$, $p=0.001$), WWC ($r=0.7$, $p<0.0001$) and LQ ($r=0.83$, $p<0.0001$). Based on results from principal component analysis and Pearson correlation tests, only one variable (BC) was selected to explain the variability in foraging intensity since the remaining variables were

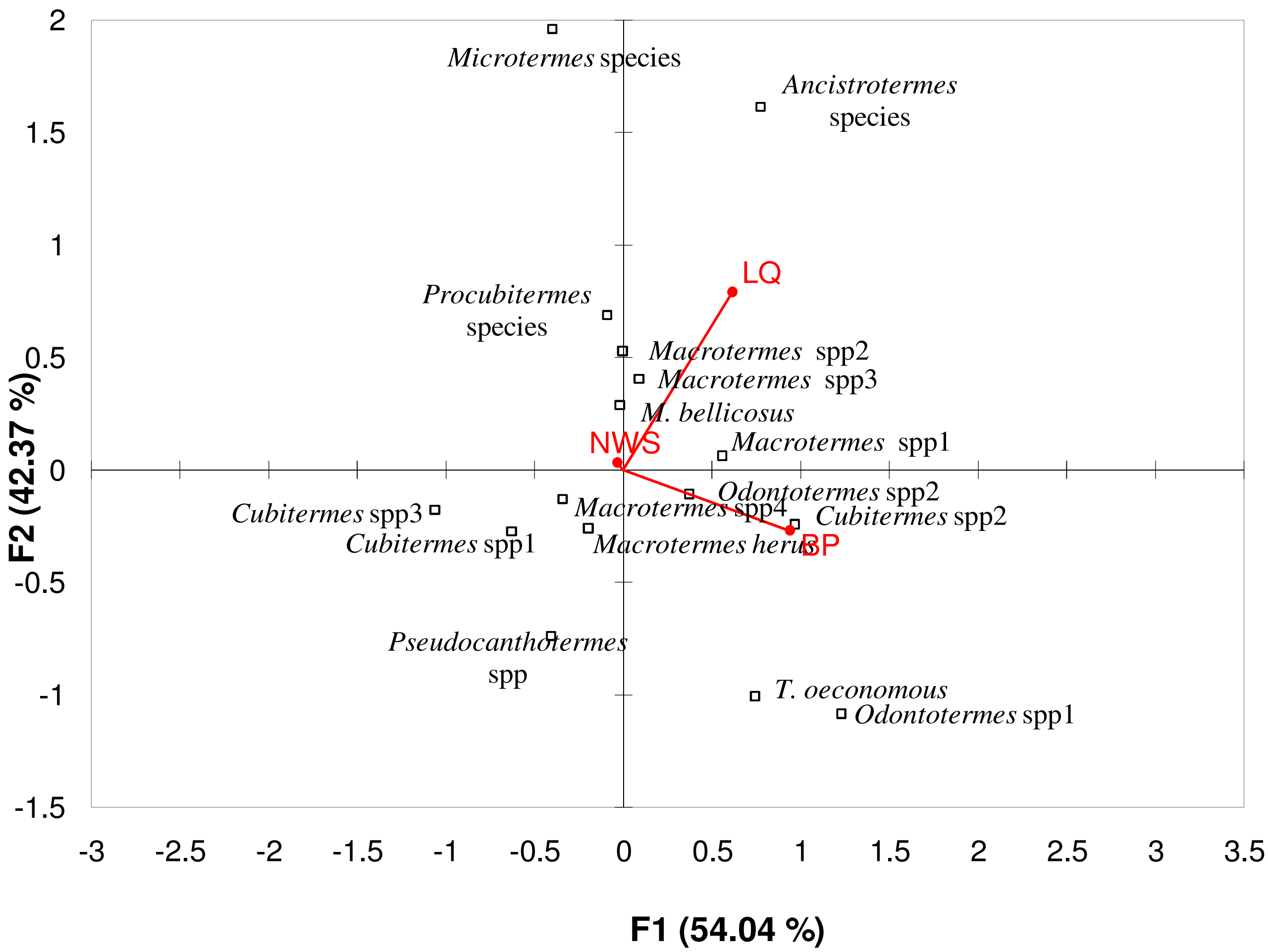

Figure 2. Ordination biplot based on canonical correspondence analysis of species/vegetation matrixes displaying 17.6% the inertia (= weighted variance) in species' abundances and 96% of variance in weighted averages with respect to the vegetation variables. The eigenvalues of axis 1 (horizontally) and axis 2 (vertically) are 0.29 and 0.23 respectively. The eigenvalue of axis 3 (not displayed) is 0.019.

positively correlated with the selected variable.

Results from nonlinear regression of percentage of bait consumed with basal cover indicated that highest consumption of baits (95%) occurred within a range of 55 to 60% basal cover (Figure 4). Below this range, bait consumption was noted to decrease up to 0%. Beyond the same range, bait consumption was observed to decline but did not reach 0%. Reduction in basal cover from 100 to 80% was noted to double bait consumption from 38 to 76% while basal cover reduction from 80 to 60% caused 24% increase in bait consumption.

DISCUSSION

Effect of environmental variables on composition of subterranean termites

Although *Macrotermes* species are regarded as generalist feeders (Donovan et al., 2001; Wood, 1991) that forage on various organic resources such as grass, wood, dung and plant debris, Mitcheal (2002) noted that the species are predominantly litter feeders and their diversity and density would increase in areas with adequate availability of food (litter) resources. Okwakol and Sekamatte (2007) also noted that increased availability of litter due to clearance of trees led to an increase in density and diversity of litter feeding species, particularly *Macrotermes* species in forest ecosystems in Uganda. These observations agree with the observed trend in the current study where more species occurred in sites where litter quantity was above the mean. The occurrence of more *Macrotermes* species in areas with adequate litter resources implied that availability of food resources was one of the key factors influencing the spatial variability in diversity and density of the species. However, the absence of the same species in sites where the LQ was highest (greatly above the mean) could be

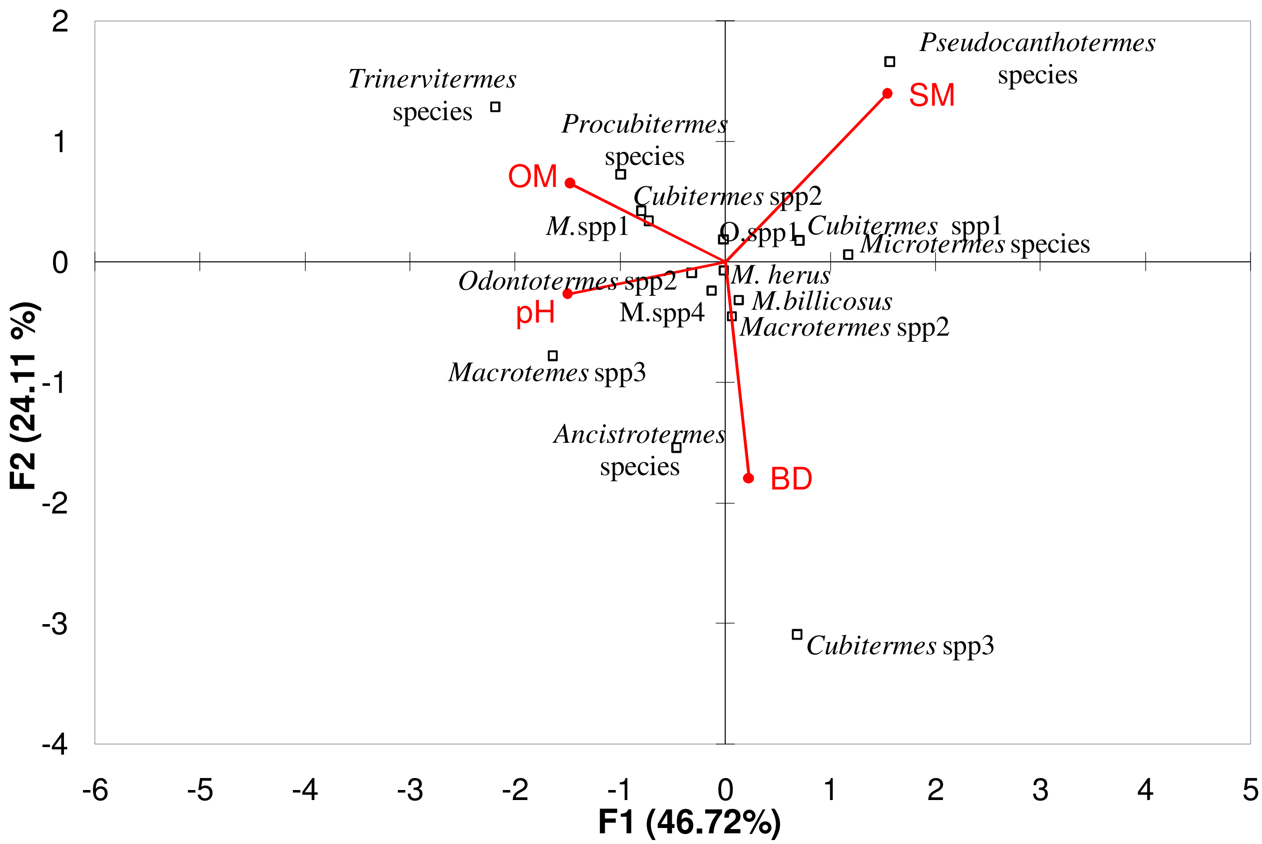

Figure 3. Ordination biplot based on canonical correspondence analysis of species/soil matrixes displaying 24% the inertia (= weighted variance) in species' abundances and 71% of variance in weighted averages with respect to the soil variables. The eigenvalues of axis 1 (horizontally) and axis 2 (vertically) are 0.34 and 0.18 respectively. The eigenvalue of axis 3 and 4 (not displayed) are 0.12 and 0.09 respectively.

Table 3. Cumulative variability explained by ten factors and factor loadings of environmental variables.

Environmental variables	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10
Eigenvalue	7.42	1.23	0.67	0.31	0.21	0.13	0.03	0.01	0.002	0.001
Variability (%)	74.2	12.3	6.6	3.1	2.1	1.3	0.3	0.1	0.02	0.01
Cummulative (%)	74.2	86.5	93.1	96.2	98.3	99.6	99.86	99.97	99.99	100.0
Factor loadings										
BQ	0.941	0.061	-0.04	-0.11	0.109	0.286	0.053	0.016	0.002	-0.002
LQ	0.85	-0.10	-0.23	0.45	0.055	-0.04	0.054	-0.003	0.000	-0.003
BC	0.992	0.091	-0.013	-0.002	-0.009	-0.032	-0.071	0.027	0.034	-0.010
NWS	0.692	-0.607	0.243	-0.163	0.221	-0.123	0.039	-0.016	0.001	-0.005
WCC	0.723	-0.048	0.641	0.123	-0.219	0.029	0.017	0.010	-0.002	0.002
NM	0.583	0.791	0.031	-0.124	-0.015	-0.113	0.071	-0.030	0.005	-0.003
ST	-0.991	0.004	0.011	-0.028	-0.008	-0.068	0.075	0.081	0.005	-0.004
SM	0.986	0.090	-0.059	-0.034	0.093	-0.073	-0.015	0.035	-0.001	0.025
SOM	0.980	0.167	-0.060	-0.050	0.005	-0.048	-0.045	0.032	-0.033	-0.013
BD	-0.754	0.414	0.354	0.169	0.306	0.029	-0.036	0.005	-0.001	-0.0

BQ: Biomass quantity, LQ: litter quantity, BC: basal cover, NWS number of woody species, WCC: woody canopy cover, NM: number of mounds, ST: soil temperature, SM: soil moisture, SOM: soil organic matter, BD: bulk density.

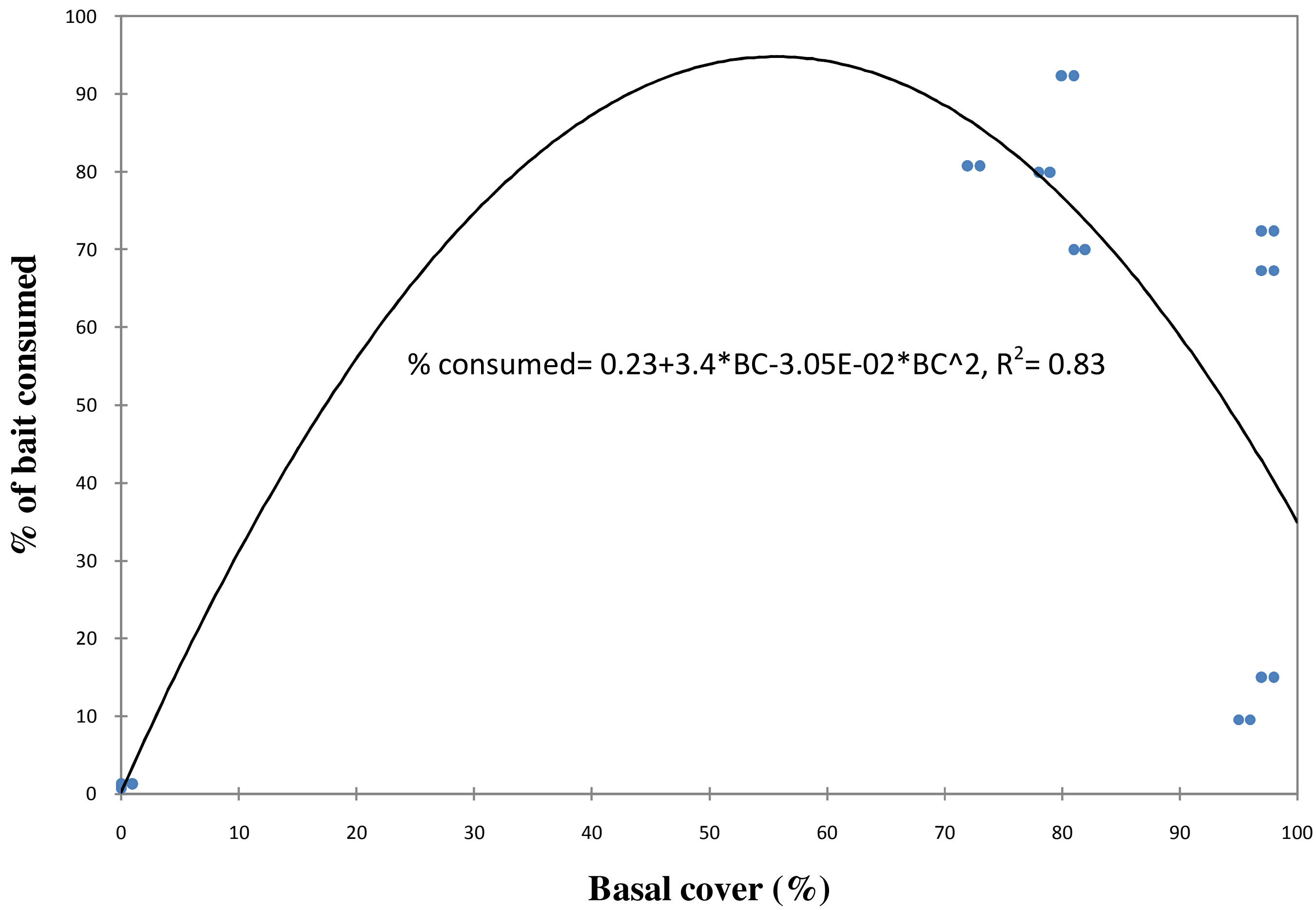

Figure 4. Nonlinear regression curve of basal cover and percentage of bait consumed.

partly attributed to presence high densities of predators particularly predator ants that nest in litter. *Cubitermes* species were noted to occur in sites where litter quantity was below the mean and this was partly attributed to the fact that the species are generally soil feeders (Donovan et al., 2001) and can survive in areas with limited litter resources. *Trinervitermes oeconomous* is a specialized grass feeder while *Odontotermes* species have also been reported to consume significant amounts of herbaceous vegetation. This could be a possible explanation of the occurrence of the species in sites with high biomass production as the sites could avail the species with adequate feed resources.

The significant positive correlation between pH and soil organic matter meant that sites with low soil pH had low soil organic matter which limited availability of nutrients for plant establishment and this could have limited availability of adequate food resources for survival and activity of most termite species. Further, limited availability of soil organic matter meant that termites lacked the necessary nutrients to sustain their nutrition requirements. In this regard, Martison et al. (2008) also reported that soil macro-fauna organisms are sensitive to the nutrient content of their food because they need to maintain their internal chemical concentrations and the balance between the different nutrients of their body within a strict range. To this effect, elements of food quality such as phosphorus (McGlynn and Salina, 2007), nitrogen (Waren and Zou, 2002) and Ca^{2+} (Reich et al., 2005) content, can become a limiting factor to composition, survival and activity including foraging intensity of subterranean termites.

Trampling by grazing animals causes soil compaction, reduction of permeability, organic carbon, and nutrients, and restrict plant growth (Yates et al., 2000), reducing the input of organic matter into the soil and resources available to decomposers (Chapin et al.,2002). Eventually, the soil faunal diversity and density is likely to decrease in highly compacted areas. This explains the limited occurrence of termites in sites where the bulk density was greatly above the mean. The results have also indicated that members of the sub-family *Macrotermitinae*, the dominant sub-family on grazing lands in semi-arid Nakasongola, are sensitive to changes in bulk density and their activity and survival could be influenced by interventions that alter soil bulk density. Since the species are associated with destruction of herbaceous vegetation in termite infested rangelands, management decisions aimed at reducing bulk density below the average value reported in the current study would possibly check their activity and eventually reduce their destructive effect on herbaceous vegetation. However, more scientific investigations are necessary to determine the most appropriate level of bulk density that ensures optimum biomass production for livestock nutrition but also mitigating the destructive effect of subterranean termites on vegetation.

Effect of environmental variables on foraging intensity of subterranean termite

The significant positive correlation between basal cover and litter quantity meant that sites with high proportion of basal cover also had high quantities of litter. This implied that such sites had adequate food resources for both generalist termite feeders (members of sub-family *Macrotermitinae*) and the specialized grass feeders (*Trinervitermes* species). This could have resulted to the low response of termites to supplementary food sources in form of baits. The observed increase in bait consumption due to a decline in basal cover from 100% implied that feed availability was limiting and hence termites responded greatly to provision of additional/alternative food resources in form of baits. However, this trend occurred up to a certain point (55 to 60%) beyond which the proportion of bait consumed started to decline. As basal cover continues to decline, the land becomes bare leading to high rates of run-off, erosion, and eventually loss of soil organic matter. The bare surfaces are also associated with low soil water content due to reduced water infiltration and high soil temperature which limit the survival and populations of termites. Eventually, the consumption of baits decreased as the land became bare not because the termites had plenty of food resources to forage on but because there were limited populations of termites to feed on the baits. The findings of the study suggested that availability of adequate food resources (litter and standing biomass) is critical in determining the foraging intensity of subterranean termites on organic resources. This implied that the foraging intensity of subterranean termites on alternative food resources would be high in sites with inadequate conventional food resources. No wonder, foraging intensity of termite on rangeland vegetation was reported to be highest on degraded patches with sparse vegetation cover and limited availability plant biomass and litter. The results of the study are consistent with findings of Wood (1991) who noted that destructive effect of termites on rangeland vegetation was more severe on overgrazed land with limited net primary productivity and litter availability.

Conclusion

In sum, the composition and foraging intensity of subterranean termites on grazing lands in semi-arid Nakasongola was influenced by certain biotic and abiotic factors. Litter and biomass quantity were noted as the most influential vegetation variables while soil pH and bulk density were noted as the most influential soil variables driving the variability in composition of subterranean termites. Increasing litter quantity was noted to favor occurrence of *Macrotermes* species to a certain level beyond which the species disappear. Recognizing the fact that *Macrotermes* species are reported as the major pests to vegetation on grazing lands in Nakasongola, interventions that enhance accumulation of litter beyond the level for their optimum occurrence would reduce their destructive effect on vegetation. It was further observed that basal cover was the main determinant of foraging intensity of termites on dried *H. rufa* grass. The foraging intensity was noted to decrease with increase in basal cover suggesting that management decisions for rangeland vegetation need to focus on maintaining adequate basal cover if termite damage on vegetation is to be reduced.

The termite species in the Nakasongola ecosystem are predominantly litter feeders but can forage on herbaceous biomass in absence of adequate litter sources to cause significant denudation of rangeland vegetation. Ecologically sustainable management of these species requires rangeland managers to sustain the ecological integrity of termite infested ecosystems through undertaking appropriate ecosystem management techniques that maintain an ecological equilibrium between termites and other ecosystem components to prevent competition for ecological resources. Anthropogenic activities that degrade ecosystems such as overgrazing and indiscriminate tree cutting need to be checked. It is also important to sustain adequate availability of organic materials (such as litter) and herbaceous vegetation cover to avail termites with adequate food resources to prevent them from damaging vegetation. However, further research in the field need to focus on development of thresholds for litter (both quantity and quality) and amount of vegetation cover beyond which termites become destructive.

ACKNOWLEDGEMENT

The study was partially funded by the Regional Universities Forum for Capacity building in Agriculture (RUFORUM) and the National Livestock Resources

Research Institute (NaLIRRI) in Uganda.

REFERENCES

Anderson JM, Ingram JSI (1993). TSBF: A Handbook of Methods of Analysis. CAB Int., p. 39.

Attignon SE, Lachat T, Sinsin B, Nagel P, Peveling R (2005). Termite assemblages in West-African semi-deciduous forest and teak plantations. Agric. Ecosyst. Environ., 110: 318-326.

Chapin FSIII, Matson PA, Mooney H (2002). Principals of Terrestrial Ecosystem Ecology. Springer-Verlag, New York.

Cowie RH, Wood TG (1989). Termite damage to crops, forestry and rangeland in Ethiopia. Sociobiol., 15: 139-153.

Curry JP (1994). Glassland Invertebrates, Ecology, influence of soil fertility and effects on plant growth. Chapman and Hall, London, UK, pp. 437-146.

Dauber J, Hirsch M, Simmering D, Waldhardt R, Otte A, Wolters V (2003). Landscape structure as an indicator of biodiversity: Matrix effects on species richness. Agric. Ecosys. Environ., 98: 321-329.

Dauber J, Purtauf T, Allspach A, Frisch J, Voigtlander K, Wolters V (2005). Local vs landscape controls on diversity: A test using surface-dwelling soil macro-invertebrates of different mobility. Global Ecol. Biogeogr., 14: 213-221.

Donovan SE, Eggleton NP, Bignell DE (2001). Gut content analysis and a new feeding group classification of termites. Ecol. Entomol., 26: 356-366.

Geiger R, Aron RH (2003). The climate near the ground. Rowman & Litlefield Publishers, Lanham, USA, 600 p.

Jolliffe IT (2002). Principal Component Analysis, Second Edition. Springer, New York.

Jones DJ, Eggleton P (2000). Sampling termite assemblages in tropical forests: testing a rapid biodiversity assessment protocol. J. Appl. Ecol., 37: 191-203.

Kent M, Coker P (1992). Vegetation description and analysis. A practical approach. Elhaven Press, London, UK.

Lavelle P, Spain AV (2001). Soil ecology. Kluwer Scientific Publications, Amsterdam, 654 p.

L.'t Mannetje (1978). Measurement of Grassland Vegetation and Animal Production. CSIRO Division of Tropical Agronomy. Cunningham Laboratory. Brisbane, Queensland, Australia.

Martinson HM, Schneider K, Gilbert J, Hines JE, Hamback RA, Fagan WF (2008). Detritivory: Stoichiometry of a neglected trophic level. Ecol. Res., 23: 487-491.

Mathieu J, Grimaldi M, Jouquet P, Rouland C, Lavelle P, Desjardins T, Rosi J-P (2009). Spatial patterns of grasses influence soil macrofauna biodiversity in Amonia pastures. Soil Biol. Biochem., 41: 586-593.

McGlynn TP, Salinas DJ (2007). Phosphorus limits tropical rain forest fauna. Biotrop., 39: 50-53.

Mitchell JD (2002). Termites as pests of crops, forestry, rangeland and structures in southern Africa and their control. Sociobiol., 40: 47–69.

Nakasongola District State of Environment Report (2004). Nakasongola District Council,http://www.nemaug.org.

Nash SM, Anderson PJ, Whitford GW (1999). Spatial and temporal variability in relative abundance and foraging behavior of subterranean termites in desertified and relatively intact Chicuahuan Desert ecosystems. Appl. Soil Ecol., 12: 149-157.

Okwakol MJN, Sekamatte MB (2007). Soil macrofauna research in ecosystems in Uganda. Afr. J. Ecol., 45(Suppl. 2): 2–8.

Pearce MJ (1997). Termites: Biology and pest management. University press, Cambridge, UK, 172 p.

Reich PB, Oleksyn J, Modrzynski J, Mrozinski P, Hobbie SE, Eissenstat DM, Chorover J, Chadwick OA, Hale CM, Tjoelker MG (2005). Linking litter calicium, earthworms and soil properties: A common garden test with 14 tree species. Ecol. Lett., 8: 811-818.

Sekamatte MB (2001). Termite situation on crops and rangelands in Nakasongola District. A report submitted to the Environmental Protection and Economic Development (EPED) project, Kampala, Uganda.

Ter Braak JFC, Verdonschot MFP (1995). Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquat. Sci., 57/3.

Waren MW, Zou X (2002). Soil macrofauna and litter nutrients in three tropical tree plantations on a disturbed site in Puerto Rico. For. Ecol. Manage., 170: 161-171.

Webb GC (1961). Keys to the Genera of the African Termites. Ibadan University Press, Ibadan, Nigeria.

Wood GT (1991). Termites in Ethiopia: The Environmental Impact of Their Damage and Resultant Control Measures. Ambio,, 20: 3-4.

XLSTAT (2011). http://www.addinsoft.com.

Yates CJ, Norton DA, Hobbs RJ (2000). Grazing effects on plant cover, soil and microclimate in fragmented woodlands in southwestern Australia: Implications for restoration. Austr. Ecol., 25: 35-47.