Agriculture, Ecosystems and Environment 188 (2014) 12–19

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Seasonal patterns in decomposition and nutrient release from East African savanna grasses grown under contrasting nutrient conditions

Lucy W. Ngatia[a,b], K. Ramesh Reddy[a,*], P.K. Ramachandran Nair[a,c], Robert M. Pringle[b,d], Todd M. Palmer[b,e], Benjamin L. Turner[f]

[a] Soil and Water Science Department, University of Florida, Gainesville, FL 32611 USA
[b] Mpala Research Centre, P.O. Box 555, Nanyuki, Kenya
[c] School of Forest Resources and Conservation, University of Florida, 118 Newins-Ziegler Hall, Gainesville, FL 32611, USA
[d] Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA
[e] Department of Biology, University of Florida, Gainesville, FL 32611, USA
[f] Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama

ARTICLE INFO

Article history:
Received 20 September 2013
Received in revised form 27 January 2014
Accepted 4 February 2014

Keywords:
Aboveground biomass
East Africa
Nutrient cycling
N release
P release
Savanna

ABSTRACT

Litter decomposition and nutrient release is one of the key biogeochemical processes that regulate plant productivity and nutrient cycling in African savanna ecosystems. We examined the influence of nitrogen and phosphorus additions on grass decomposition and nutrient release rates in an *Acacia* savanna ecosystem in central Kenya. Grass was clipped from a factorial nitrogen × phosphorus experiment and decomposed in a common plot that had not received fertilizer. After 20 weeks, including one dry season and one wet season, 50–65% of carbon, 68–75% of nitrogen and 73–83% of phosphorus had been released from the litter. Decomposition was slow in the dry season (mass loss 1–2% wk^{-1}) compared to the wet season (7–11% wk^{-1}). Wet season decomposition was more rapid for grasses that had been fertilized with nitrogen, even though tissue nitrogen was not significantly different from the control grass, indicating that factors other than litter nitrogen concentration influenced decomposition rates under nitrogen enrichment. Surprisingly, nutrient loss from decomposing litter was relatively high during the dry season, suggesting a role for dew in leaching nutrients from dry litter. We conclude that seasonal rain and nitrogen addition (but not phosphorus addition) accelerate decomposition of grass litter, but that nutrient leaching during the dry season can be considerable.

1. Introduction

The balance between net primary productivity and decomposition of organic matter determines carbon (C) stocks in savannas and other terrestrial ecosystems (Valentini et al., 2000). The decomposition of annual litter fall contributes approximately half of the CO_2 released from soils (soil + litter CO_2) (Couteaux et al., 1995) and recycles nutrients for plant uptake (Aerts et al., 1992). Understanding the factors controlling litter decomposition is therefore important to determine the influence on greenhouse gases emission and global warming (Fearnside, 2000).

Both abiotic and biotic processes regulate litter decomposition, including photodegradation, and microbial breakdown (Facelli and Pickett, 1991) and also physical fragmentation (leaching of soluble C) during rainfall events (Ferreira et al., 2006). Decomposition rates are controlled primarily by extrinsic drivers such as climate (Aerts, 2006; Austin and Vitousek, 2000; Gill and Burke, 2002) and soil properties (Gill and Burke, 2002). Intrinsic drivers include plant litter quality (Aerts, 2006; Gindaba et al., 2004; Mugendi and Nair, 1997) and litter physical properties (Meentemeyer, 1978). Temperature is considered to be a major regulator of litter decomposition in cold climates, while litter quality is more important under warmer conditions (Couteaux et al., 1995).

Moisture content is a major regulator of decomposition and nutrient leaching in the arid environments. Rain and irrigation are considered to be the main sources of moisture in agricultural areas, while rain is considered to be the main source in natural ecosystems. In these places other sources of water namely fog, mist and dew are often overlooked (Went, 1955). Dew is mainly deposited in the dry season when the sky is clear and hence an important source of moisture in the semi-arid areas during the dry season compared to other climates (Went, 1955). Duvdevani (1953) conducting an experiment in the coastal plains of Israel, where dew

* Corresponding author. Current address: PO Box 110290, 2181 McCarty Hall A, Gainesville, FL 32611-0290, USA. Tel.: +1 352 294 3154; fax: +1 352 392 3399.
E-mail address: krr@ufl.edu (K.R. Reddy).

http://dx.doi.org/10.1016/j.agee.2014.02.004
0167-8809/

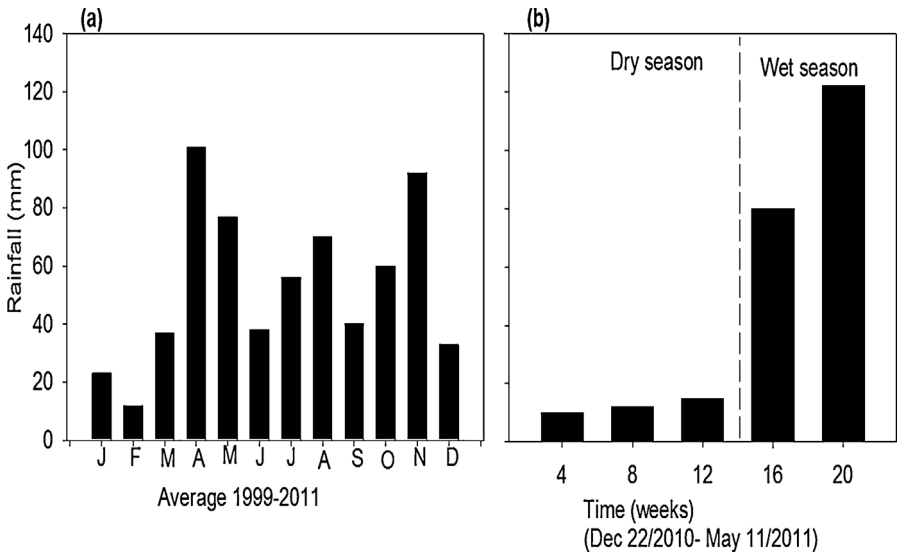

Fig. 1. Rainfall at the Mpala Research Centre, Laikipia, Kenya. Records are presented for a) the long-term rainfall average (1999–2011) and b) during the study period from 12/22/2010 to 5/11/2011. In (b) the data are presented in 4 weeks intervals to emulate the field litter incubation period. The litter was incubated for 20 weeks and the samples were collected from the field after every 4 weeks without replacement.

occurred frequently indicated that most plants grew about twice as much when they received dew during the night. The dew water could run off the leaves and collect in the soil on which it drips (Duvdevani, 1953; Ruinen, 1961). The dripping dew contains both mineral and organic constituents in varying composition, making dew a leaching agent (Ruinen, 1961).

In African savannas, most litterfall occurs in the dry season, yet most decomposition studies have been initiated at the onset of the wet season (Deshmukh, 1985; Jama and Nair, 1996; Mafongoya et al., 1997; Mugendi and Nair, 1997; Mugendi et al., 1999) with few in the dry season (e.g., Fornara and Du Toit, 2008). In addition, most studies involved leguminous forbs and trees (Fornara and Du Toit, 2008; Fosu et al., 2007; Jama and Nair, 1996; Mafongoya et al., 1997; Mugendi and Nair, 1997; Mugendi et al., 1999; Oladoye et al., 2008), and few included grasses (Deshmukh, 1985; Ohiagu and Wood, 1979), even though grasses dominate the aboveground biomass of savanna ecosystems (Bond, 2008). Finally, few studies have examined the role of nutrients in determining the decomposition rates of tropical savanna grasses, yet foliar nutrients can have a marked impact on litter decomposition in other ecosystems such as temperate grassland (Kochy and Wilson, 1997; Moretto et al., 2001), tundra (Bryant et al., 1997; Hobbie and Gough, 2004), temperate forest (Melillo et al., 1982), montane forests (Hobbie and Vitousek, 2000) and tropical forests (Gonzalez and Seastedt, 2001; Kaspari et al., 2008).

The objectives of our study were to determine the influence of N and P addition on plant litter decomposition, N and P release in savanna ecosystem. To do this, we decomposed grasses from a factorial N × P fertilization experiment in a common unenriched site throughout one dry season and one wet season. We hypothesized that decomposition rate, N and P release would be greater in the wet season than in the dry season, and that grasses that had been fertilized with N and P would decompose faster than untreated grasses.

2. Methods

2.1. Site description

The study was conducted in 2010 and 2011 at Mpala Research Centre, Kenya, which encompasses 190 km^2 of semi-arid savanna within the Laikipia County of the Rift Valley Province (37°53′E, 0°17′N). The site is a conservancy where wildlife and livestock co-exist and share resources. The dominant woody vegetation includes *Senegalia (Acacia) brevispica*, *Vachellia (Acacia) etbaica*, *S. (Acacia) mellifera*, *V. (Acacia) nilotica* and *V. (Acacia) gerrardii*, *Croton dichogamus*, *Grewia* spp. and *Rhus vulgaris* (Young et al., 1995). The herbaceous vegetation consists of a discontinuous layer of mostly perennial grasses, which include *Pennisetum mezianum*, *Pennisetum stramineum*, *Digitaria milanjiana*, and *Cynodon dactylon*.

The soils are red sandy loams (Typic Haplustalfs in Soil Taxonomy) derived from metamorphic basement rock (Ahn and Geiger, 1987; Goheen et al., 2013). Prior to fertilization, soil pH was 6.3 (measured in water), total soil P was 230 mg kg^{-1} and available P was 11 mg kg^{-1} (determined by resin bags as outlined by Kouno et al. (1995)). Total soil C and N contents were 10 and 1.1 g kg^{-1}, respectively and the mean annual rainfall was approximately 640 mm over a 13 years period (Fig. 1a) (Goheen et al., 2013). Monthly maximum temperatures range from 25 to 33 °C, while minimum temperatures range from 12 to 17 °C (Young et al., 1998).

This study was conducted in the Ungulate Herbivory Under Rainfall Uncertainty (UHURU) experiment, established in 2008 at the Mpala Research Centre (Goheen et al., 2013). The study was conducted in the southern (wettest) site of the UHURU experiment, which received an average of 638 mm rain $year^{-1}$ from 2009 to 2011.

2.2. Experimental design

Four fertilizer addition plots (16 m^2 each; hereafter "plots") were established in February 2010 in each of three replicate exclosures (1 ha each) which fenced out all herbivores larger than *Lepus spp.* (~2–3 kg). Thus, there were a total of 12 plots arranged across the three exclosures. The 12 plots entailed four fertilizer treatments and three replications of each fertilizer treatment. Within each of the 12 plots, grass was clipped to ground level in a 1 m^2 patch and discarded and fertilizers were applied to the entire 16 m^2 plot on the onset of rainfall (March 2010). This allowed regrowth standing dead grass from the 1 m^2 plot to be used for the decomposition experiment. The fertilizer treatments included: (1) N only, (2) P only, (3) a mixture of N and P, and (4) unfertilized

control (hereafter referred as N, P, NP and control). The fertilizer application consisted of N (urea) at 100 kg N ha^{-1} and/or P (triple super phosphate) at 50 kg P ha^{-1}. All treatments were arranged in a randomized complete block design within each of the exclosures. In November/December 2010, grass regrowth from the 1 m^2 fertilizer-enriched patches was clipped for use in decomposition study.

2.3. Experimental procedure

After fertilization, aboveground standing dead grass was selected from the regrowth, was clipped from each plot and air-dried to a constant weight. Litter bags (15 × 20 cm) were made from 2 mm mesh polyester to allow entry of micro- and mesofauna. Three grams (dry weight basis) of a mixture of grasses from each fertilizer-enriched plot and each of the three treatment replicates was put into each of 10 litter bags, which were heat sealed and placed in the thatch layer in a common unenriched decomposition area away from the plots of origin. After placement on the ground, the bags were lightly covered with litter from the common unenriched plot. This experiment was maintained from 22 December 2010 to 11 May 2011 (5 months). Two litter bags (duplicates) from each of the three treatments replicates were retrieved after 0, 4, 8, 12, 16, and 20 weeks. The bags and their contents were air-dried to a constant weight. Prior to weighing the contents of each bag, soil particles and any other extraneous matter were carefully removed. The content from the duplicate litter bags in each treatment replicate was composited for chemical analysis after weighing. Litter samples were then ground to pass through a 1-mm screen and analyzed for total C, N, P and lignin concentrations. The N and P concentration and remaining litter biomass at any given time were used to estimate the N and P release. The N or P release was the balance between the original N or P mass and the mass at any given time.

2.4. Litter processing and analysis

Total C and N were determined using a Costech Model 4010 Elemental Analyzer (Costech Analytical Industries, Inc., Valencia, CA) coupled to a Finnigan MAT Deltaplus XL mass Spectrometer (CF-IRMS, Thermo Finnigan) via a Finnigan Conflo II interface. Total P was determined by ignition at 550 °C followed by extraction in 1 M H_2SO_4 acid and detection by automated molybdate colorimetry. Digested solutions were analyzed colorimetrically using Shimadzu UV visible recording spectrophotometer UV-160. Lignin was determined by a modified sequential fiber extraction method (Ankom Technology, Fairport, NY) modified from the feed and forage analysis by Van Soest (1970).

2.5. Statistical analysis

Statistical differences in treatments were determined using analysis of variance (ANOVA) for a randomized complete block design using Tukey HSD test at $\alpha = 0.05$. Sidak adjustment for multiple comparisons test was used to determine the significant difference for the multiple phase regression model at $\alpha = 0.05$. A nonlinear procedure of SAS (SAS 9.2) for multiphase regression models was fitted for C release during decomposition; parameters include intercept and slope of each phase, and the spline. The slope of the linear regression represents the decomposition rate constant (k). The spline point is the end of phase 1 and beginning of phase 2 (Jama and Nair, 1996). For C release half-life was calculated from multiple regression model by determining the time (x) that half of the original C mass had been released.

3. Results

3.1. Pattern of litter decomposition

Plant litter decomposition followed a biphasic pattern, with an initial phase of slow decomposition rates followed by faster rates (Fig. 2a–d) after the onset of the rains in April. Within nutrient enrichment treatments, the decomposition constants (k1 and k2) for the two phases differed significantly between dry and wet seasons (phase one is hereafter referred to dry phase and phase two as wet phase). Sidak adjustment for multiple comparisons test indicated that the decomposition rate constant was higher in the wet phase than the dry phase for all treatments ($P < 0.0001$ for the control and N enrichment treatments $P = 0.0003$ for the P enrichment treatment, $P = 0.04$ for the NP enrichment treatment) (Fig. 2). The decomposition rate was two times greater for the enriched treatments than for the control (Fig. 2). For the wet phase, the decomposition constant was significantly higher for N enriched grasses (11% wk^{-1}; $P = 0.0008$), whereas P, NP-enriched grass and control grass did not differ significantly from one another (Fig. 2a–d).

The decomposition rate of grass from the control treatment was 10 g kg^{-1} $week^{-1}$ in the dry phase and 70 g kg^{-1} $week^{-1}$ in the wet phase (Fig. 2a). This corresponds to a half-life of 39 weeks. The wet phase of decomposition started at 13 weeks at 88% initial C mass. At the end of the study (after 20 weeks), 50% of the total C remained. The decomposition rate of N-only enriched grass was 20 g kg^{-1} $week^{-1}$ in the dry phase and 110 g kg^{-1} $week^{-1}$ in the wet phase, (Fig. 2b), corresponding to a half-life of 35 weeks. The wet phase of litter decomposition commenced on week 14 with 75% of the initial C remaining. At the end of the study, 35% of the initial C remained.

The decomposition rate of the P-only enriched grass was 20 g kg^{-1} $week^{-1}$ in the dry phase, and 90 g kg^{-1} $week^{-1}$ in the wet phase (Fig. 2c), with a half-life of 40 weeks. The wet phase of decomposition began at 16 weeks with 73% of the initial C mass remaining. At the end of the study, 45% of the initial C mass remained.

The NP-enriched grass decomposition rate was 20 g kg^{-1} $week^{-1}$ in the dry phase and 80 g kg^{-1} $week^{-1}$ in the wet phase (Fig. 2d) with a half-life of 42 weeks. Wet phase decomposition started at 16 weeks (Fig. 2d) with 73% of the initial C remaining. Although there were no significant differences between the initial nutrient concentrations of the enriched grasses (Table 1), Sidak adjustment for multiple comparisons test indicate that N-enriched grasses had higher decomposition rates in the second (wet) phase ($P = 0.0008$; Fig. 2b) compared to other treatments, with the N-enriched grasses having the least amount of C mass remaining at the end of the study. The seasonal rainfall positively correlated with decomposition rate ($R^2 = 0.80$; $P < 0.0001$).

3.2. Trends in nitrogen and phosphorus release from the grass litter

Nitrogen release was high in the initial 8 weeks of the decomposition (dry season). The control, N, P and NP treatments released 45%, 48%, 41% and 55% respectively, of the initial N mass (Fig. 3). By the end of the study (20 weeks), the N, P and NP treatments had each released 75% of the initial N mass, while the control released 68% of initial N mass (Fig. 3a–d).

Phosphorus release was rapid in the initial 8 weeks (dry season) of the study. In this period, the control, N, P, and NP treatments released 49%, 61%, 58% and 70% of the initial P mass, respectively. By the end of the study (20 weeks), these four treatments had released 73%, 80%, 77%, and 83% of initial P mass, respectively (Fig. 3e–f).

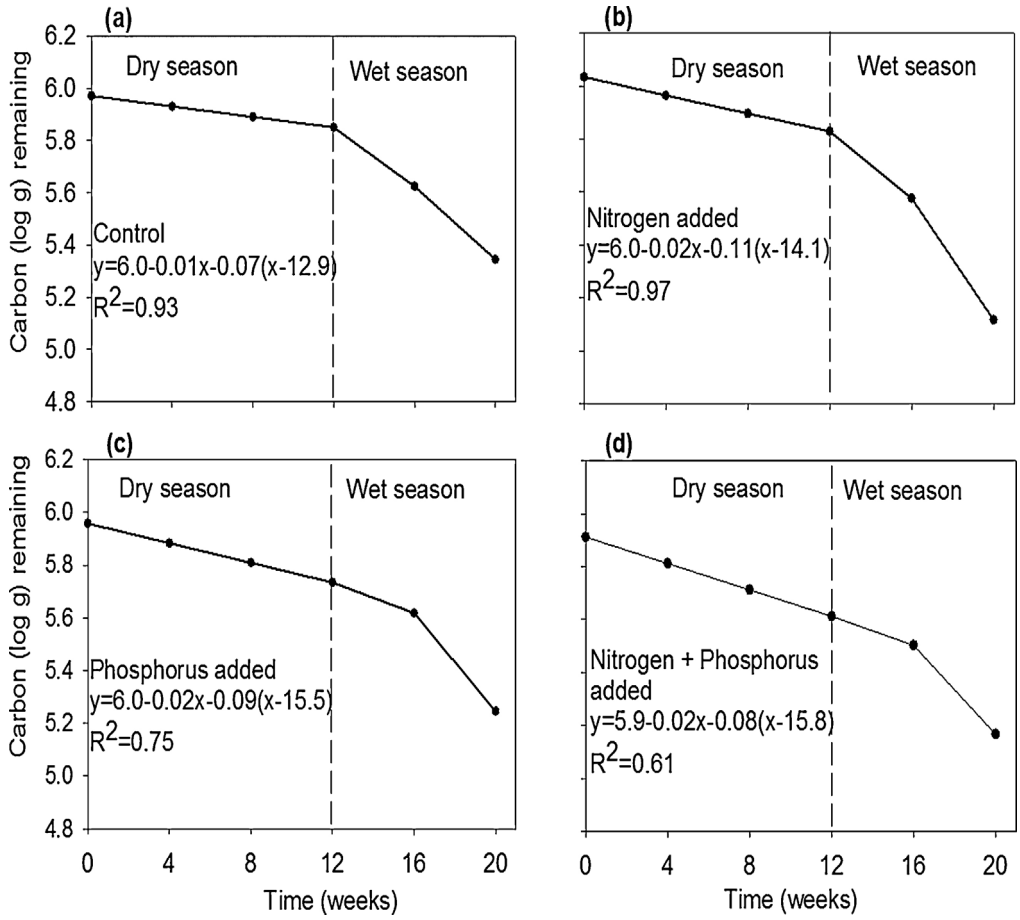

Fig. 2. Decomposition pattern over time for a) control, b) nitrogen-enriched, c) phosphorus-enriched, and d) nitrogen + phosphorus enriched grass placed on the unenriched soil surface. The means are replicates of three composite samples ± one standard error. The samples were collected from the field after every 4 weeks for a period of 20 weeks without replacement.

Table 1
Aboveground biomass, biomass C (carbon), N (nitrogen) and P (phosphorus) storage. Chemical composition of the initial grasses biomass after fertilization and ratios of initial aboveground biomass. The values are means of three composite replicates ± one standard error. There were no significant differences between the treatments for all parameters.

Treatment	Control	N	P	NP
Aboveground storage (kg ha^{-1})				
Aboveground biomass	1155 ± 187	1494 ± 407	1602 ± 490	2411 ± 735
Carbon	472 ± 77	620 ± 170	663 ± 193	974 ± 313
Nitrogen	14.7 ± 2.7	25.6 ± 3.6	27.3 ± 5.2	33.4 ± 17.6
Phosphorus	1.4 ± 0.2	1.9 ± 0.6	2.0 ± 0.4	4.1 ± 0.9
Chemical composition of the initial aboveground biomass (g kg^{-1})				
Carbon	404 ± 5	415 ± 7	414 ± 6	404 ± 9
Nitrogen	13 ± 1	17 ± 2	17 ± 2	14 ± 2
Phosphorus	1.3 ± 0.1	1.5 ± 0.3	1.4 ± 0.1	1.2 ± 0.2
Lignin	250 ± 30	210 ± 25	250 ± 5	230 ± 13
Nutrient ratios of the initial aboveground biomass				
Lignin: N	19 ± 0.8	13 ± 3.1	15 ± 1.8	17 ± 3
C:N	32 ± 3	25 ± 3	25 ± 3	30 ± 3.6
C:P	326 ± 23	276 ± 49	300 ± 22	335 ± 46
N:P	10.2 ± 0.8	12.2 ± 3.3	12.5 ± 1.4	12.2 ± 3.0

Although the C:N ratio of the litter was >25 throughout the study, except for the N and P treatment in the initial litter (Fig. 4a), the C:N ratio increased throughout the study. However, the C:N ratio of the mass loss (<25) was much lower than the C:N of the remaining litter over time (Fig. 5a) and the N and P loss was closely correlated ($P < 0.0001$; $R^2 = 0.88$) (Fig. 5b). For all treatments, the C:P ratio was >300 throughout the decomposition study, apart from the initial litter from the N-enriched treatment (which was 275; Fig. 4b). However, there was a continuous increase in C:P ratio throughout the study period.

4. Discussion

The study assessed litter decomposition in the dry and wet seasons of a semi-arid African savanna by emulating the timing of processes involved in natural decomposition. Our results are

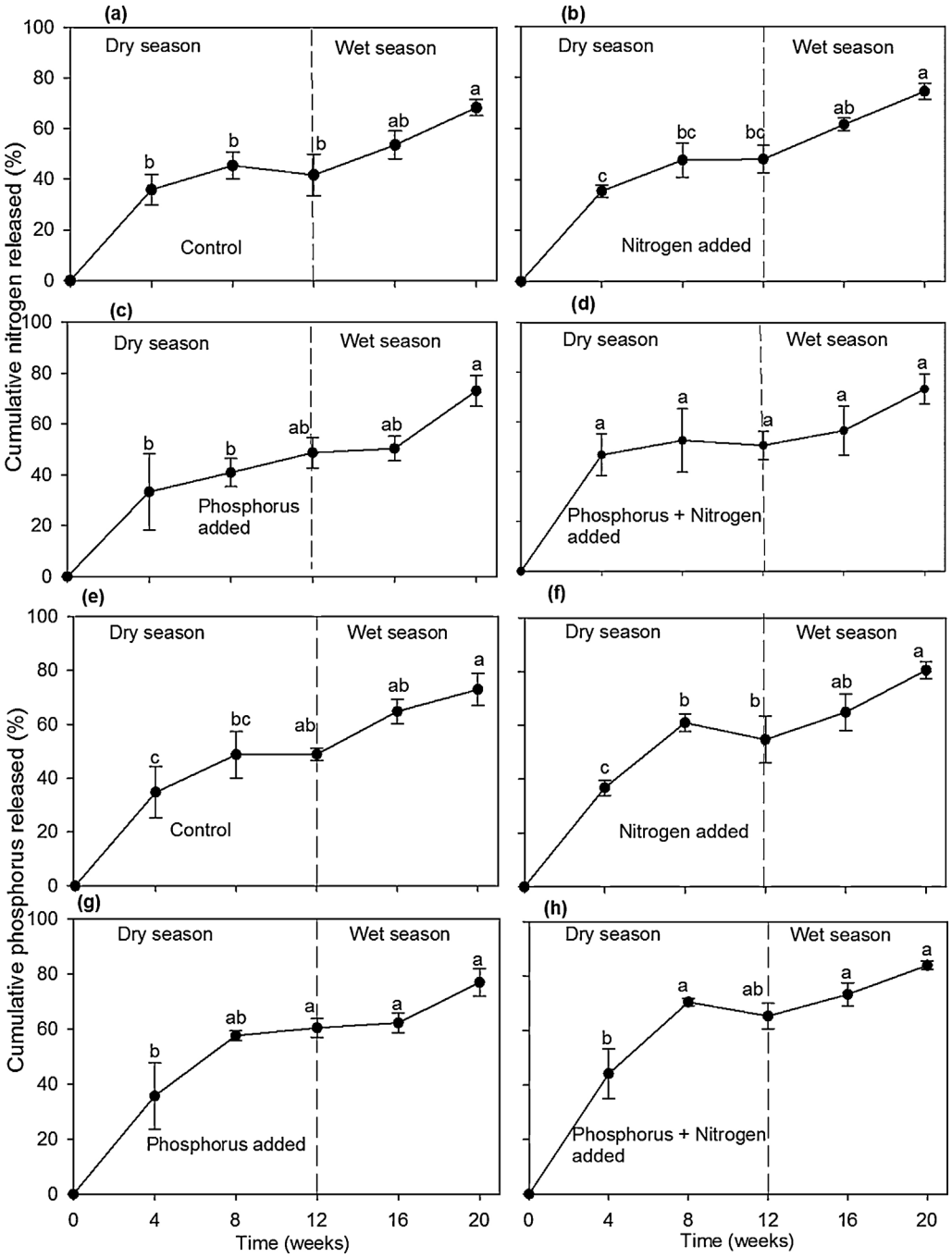

Fig. 3. Cumulative percent nitrogen and phosphorus release pattern over time. For nitrogen; a) control, b) nitrogen, c) phosphorus, d) nitrogen + phosphorus enriched grasses. For phosphorus; e) control, f) nitrogen, g) phosphorus, h) nitrogen + phosphorus enriched grasses. The means are replicates of three composite samples ± one standard error. Different letters along the line graph indicate significant difference between the means at $P < 0.05$. The samples were collected from the field after every 4 weeks for a period of 20 weeks without replacement.

consistent with previous work initiated in a wet season (Dubeux et al., 2006; Hamadi et al., 2000; Jama and Nair, 1996), which reported a biphasic litter decomposition pattern. However, the order was reversed in our study, initiated in the dry season, with an initial slow decomposition rate in the dry season followed by a faster decomposition rate on the onset of rainfall. This is consistent with moisture being the main factor influencing decomposition rates (Austin and Vitousek, 2000; Epstein et al., 2002; Mugendi and Nair, 1997; Vitousek et al., 1994), further supported by the positive correlation observed between the decomposition constant (k) and rainfall. Notably, however, C and N in our study did not mineralize simultaneously as observed in several previous studies in which patterns of both C loss and N release followed a multiphase regression model (Hamadi et al., 2000; Jama and Nair, 1996). In our study, litter decomposition followed a multiphase regression model, whereas N release did not; this was similar to the findings of Dubeux et al. (2006) in sub-tropical Florida, USA. Minimal C was lost in the dry season: in the first 4 weeks, only 6–24% C was lost, whereas 33–47% N was released in the same period. This contrasts with the findings of Austin and Vitousek (2000), who reported that proportional release of C was faster than release of nutrients, which is expected in a decomposition process. One possibility is that, although moisture limits the decomposition process in the dry season, dew promotes nutrient leaching from decomposing

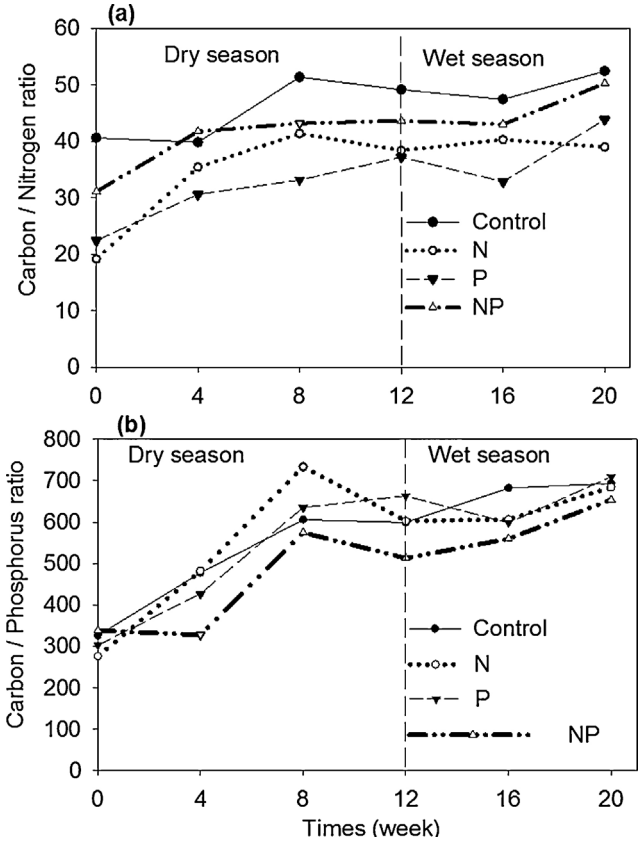

Fig. 4. C:N and C:P ratio over time for a) carbon/nitrogen ratio. b) Carbon/phosphorus ratio of the litter over time. The litter is from fertilized plots and decomposed in a common unfertilized site. The means are replicates of three composite samples. The samples were collected from the field after every 4 weeks for a period of 20 weeks without replacement.

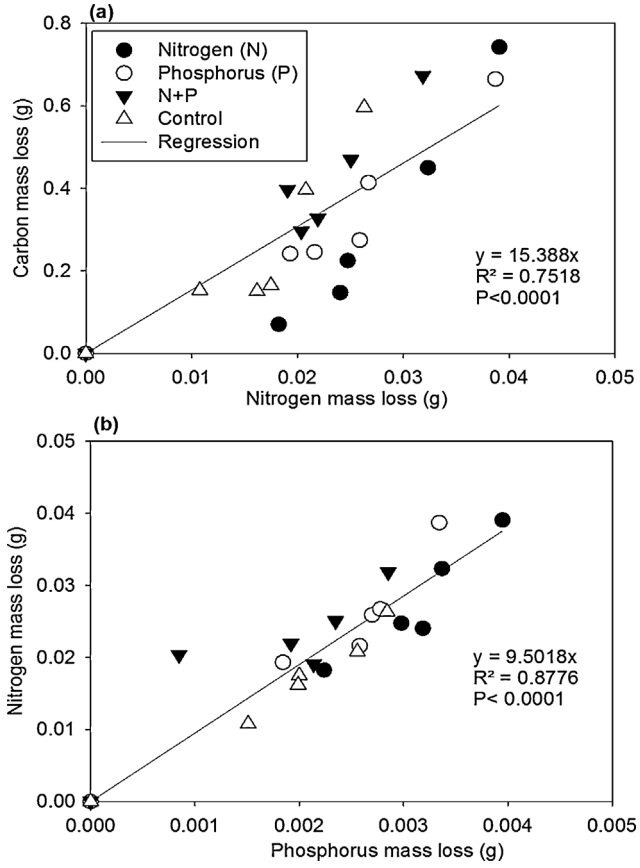

Fig. 5. Nutrients losses over time for a) carbon versus nitrogen losses. b) Nitrogen versus phosphorus losses. The litter is from fertilized plots and decomposed in a common unfertilized site. The means are replicates of three composite samples. The samples were collected from the field after every 4 weeks for a period of 20 weeks without replacement.

litter in the dry season (see also Leonard and Fluckiger, 1989; Tukey, 1970).

Dew is important in leaching nutrients from litter in seasonally dry climates and deserts (Tukey, 1970,1969). In the dry season, plant litter that is otherwise dry during the day is frequently wet with dew at night (Yang et al., 2001). Nash (1996) argued that although it is rarely quantified, dew water can represent a significant hydrological input in dry places or seasons. Ruinen (1961) indicated that in both Indonesia and Surinam wetting by dew and ground mist takes place for 10–12 h per day whereby in the early morning the vegetation drips wet and in the shade the dew remains visible until mid-morning. Data on the incidence of dew are scarce and spatially variable; however, Ruinen (1961) reported that dew occurred on an annual mean of 249 nights in Yangambi, Congo and 254 nights in South Cameroon. Further, Ruinen (1961) reported that nitrogen concentrations in dew were 25–80 mg L^{-1}, compared to 9–19 mg L^{-1} in rain. In our study, over the dry season which lasted for first 12 weeks of the study, rain fell for only 3 days and each day the rain was ~10 mm. However, the dew is expected to form almost every night over the dry season because the sky is clear (Went, 1955). Hence, in the dry season there is a higher frequency of dew formation compared to rainfall. Tukey et al. (1957) indicated a close relationship between light intensity and carbohydrates loss by leaching from bean leaves with and the losses being cumulative with time of wetting. We conclude that leaching by dew is a plausible mechanism to explain the loss of nitrogen and phosphorus from litter during the dry season in our study.

With the initial litter containing C:N ratios >25 and C:P ratios >300, immobilization was expected to take place (Palm and Sanchez, 1990; Swift et al., 1979), yet the ratios increased continuously throughout the experiment, while the C:N ratio of the mass loss was <25. Dubeux et al. (2006) suggested that higher tissue C:N ratios indicate lower N concentration in tissues rather than changes in C concentrations. The decrease in litter N over the study period contrasted with the findings of several previous studies (Deshmukh, 1985; Dubeux et al., 2006; Hamadi et al., 2000; Liu et al., 2011), which reported increased nitrogen masses over the study period. The 68–75% N and 73–83% P of the initial mass released by the end of our 20-week study were higher than the 20–30% N and 60% P mineralization reported by Dubeux et al. (2006) for 18-week incubation in sub-tropical Florida, USA. However, the N release in our study contrasted the N immobilization reported by Mtambanengwe and Kirchmann (1995) throughout the 75 days study in Zimbabwe woodland savanna. This suggests that microbial decomposition was not the dominant process leading to N and P release.

Considering that the initial grass biomass had 400–410 g C kg^{-1}, of which 21–25% was lignin, the initial slow rate of decomposition in the dry season likely results from the loss of very soluble C compounds that can decompose even under minimal moisture. The subsequent phase of higher decomposition rates with the onset of rain suggests that the more recalcitrant compounds need more moisture for breakdown to be accomplished (Meentemeyer, 1978). Overall, the disappearance of C was greater in the wet season than the dry season. These findings contrast with Ohiagu and Wood (1979), who reported 69% of grass litter disappearance over a 4-month dry season in Nigerian savanna, and indicated this loss was

due to consumption by fungus-growing termites. Termites were excluded in our study, which might explain this discrepancy.

However, in a similar study in Kenya's Nairobi National Park, where termites were absent and the decomposition study was initiated in the wet season, only 50% of the grass litter was lost over a 23-month study period, in spite of a greater rainfall and the use of litter bags with larger aperture mesh (5 mm) that would have allowed in arthropods (Deshmukh, 1985). In the current study, 50% of C in the control treatment was lost in only 20 weeks. This suggests the influence of factors other than just rainfall and the absence of termites on the decomposition process, such as the mixture of grass species used in the study. In our study site, the grass mixture was dominated by *P. mezianum*, *P. stramineum, D. milanjiana* and *C. dactylon*, while the study site of Deshmukh (1985) was dominated by *Themeda triandra* and *Setaria phleoides*, which might have responded differently to decomposition. Both physical and chemical changes in leaf mixes can influence rate of decomposition directly (physically) and indirectly through the decomposer community and its activities (Gartner and Cardon, 2004). Likewise, rates of C loss in our study were higher than the 50% *Zoysia japonica* grass litter mass loss reported by Nakagami et al. (2010) in Japan over a 1 year incubation period.

Nevertheless, our findings of 50–65% C biomass loss were comparable to the findings of Dubeux et al. (2006), who reported 40–60% biomass loss of *Paspalum notatum* Flueggé (Bahia grass) in Florida in a study period of the same length. The findings were also comparable to 36–55% *Cynodon dactylon* (L.) Pers. (Bermuda grass) organic matter loss reported by Liu et al. (2011) within 18 weeks of incubation in Florida.

We acknowledge that the use of the 2-mm litter bags in this study could have altered the litter micro-climate (Meentemeyer, 1978; Witkamp and Olson, 1963) and excluded the larger macrofauna (Elkins and Whitford, 1982), thus reducing the fragmentation of the leaves and causing the bagged leaves to decompose at a different rate compared to non-confined leaves. Our study assumes that these effects did not mask the differences resulting from climatic conditions and litter quality.

Nutrient enrichment increased grass-biomass production, but there was no significant difference in nutrient concentration between initial incubated litters from different treatments. For example, the N-enriched litter lost the highest amount of biomass C (65%) and had significantly higher rate of decomposition in the second (wet) decomposition phase (11%). These findings agree with previous observations (Liu et al., 2011; Lupwayi and Haque, 1999) that N fertilization increases biomass decomposition, but suggest that factors other than litter N concentration accelerate decomposition in N-enriched litter. An example of such a factor is an increase in C lability resulting from N enrichment (Peyraud and Astigarraga, 1998), which is a result of N promoting growth of succulent herbage with a low cell wall content (Waite, 1970).

The high N and P release in the dry period compared to the wetter period contrasted with the suggestion by Swift et al. (1979) that precipitation can control the physical process of leaching through accelerated breakdown of surface litter by increased rainfall. After the first 8 weeks of the incubation period (i.e. in the dry season), 40–50% of N and 50–70% of P had been released. The rapid N and P release that did not match the C loss and suggest that in the long term, both N and P are likely to limit the microbial decomposition process unless there is an external source of nutrients to drive the decomposition process or photodegradation would prevail and short-circuit the decomposition process leading to direct C loss to the atmosphere (Austin and Vivanco, 2006). On the other hand, Couteaux et al. (1995) suggested that decrease in litter quality could lead to increased production of ligninolytic enzymes, leading to increased degradation of recalcitrant compounds. However, the extent to which lowering the N concentration would influence lignin degradation is still unknown.

5. Conclusions

Our study showed that both N enrichment and rainfall accelerate the decomposition of plant litter in African savanna, indicating the importance of nutrient release in support of plant productivity. The effect of N addition appears to occur independently of an increase in the N concentration of the litter, suggesting internal cycling and rapid N turnover in the system. Previous studies projected increased atmospheric N deposition and rainfall variability in the savanna where both soil moisture and N availability limit plant productivity.

The litter N and P released during the dry season are deposited in the soils for plant uptake on the onset of wet season, supporting plant growth and production in the next growing season. Release of N and P during the dry season was not in parallel with C release suggesting an enhanced C storage in litter when N and P release limits the decomposition rates in the long term. However, future studies need to consider the role of photodegradation on carbon loss and ligninolytic enzymes on lignin degradation. The balance between plant production and litter decomposition will determine the carbon sequestration, carbon dioxide emissions and the feedback to global climate change.

Acknowledgments

Funding for the research was provided by the University of Florida, the Swiss National Centre of Competence in Research (NCCR) and a Smithsonian Tropical Research Institute – Levinson Fellowship. We thank Elkanah Korir for field assistance, the Mpala Research Centre for logistical support, CETRAD and the University of Nairobi for providing access to laboratories, James Colee for statistical support, the Wetland Biogeochemistry Laboratory for analytical support, and the Office of the President in Kenya for allowing us to conduct this research in Kenya. Jacob R. Goheen provided helpful comments on the paper.

References

Aerts, R., 2006. The freezer defrosting: global warming and litter decomposition rates in cold biomes. J. Ecol. 94, 713–724.
Aerts, R., Bakker, C., Decaluwe, H., 1992. Root turnover as determinant of the cycling of C, N, and P in a dry heathland ecosystem. Biogeochemistry 15, 175–190.
Ahn, P.M., Geiger, L.C., 1987. Soils of Laikipia District. Kenya Soil Survey Project, Reconnaissance Soil Survey Report no. R-13. Ministry of Agriculture, National Agricultural Laboratories, Nairobi, pp. 128, p. ISN: 11427.
Austin, A.T., Vitousek, P.M., 2000. Precipitation, decomposition and litter decomposability of Metrosideros polymorpha in native forests on Hawaii. J. Ecol. 88, 129–138.
Austin, A.T., Vivanco, L., 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. Nature 442, 555–558.
Bond, W.J., 2008. What limits trees in C4 grasslands and savannas? Annual review of ecology. Evol. Syst. 39, 641–659.
Bryant, D.M., Holland, E.A., Seastedt, T.R., Walker, M.D., 1997. Analysis of litter decomposition in an alpine tundra. Can. J. Bot. 76, 1295–1304.
Couteaux, M.M., Bottner, P., Berg, B., 1995. Litter decomposition, climate and litter quality. Trends Ecol. Evol. 10, 63–66.
Deshmukh, I., 1985. Decomposition of grasses in Nairobi-National-Park, Kenya. Oecologia 67, 147–149.
Dubeux, J.C.B., Sollenberger, L.E., Interrante, S.M., Vendramini, J.M.B., Stewart, R.L., 2006. Litter decomposition and mineralization in Bahia grass pastures managed at different intensities. Crop Sci. 46, 1305–1310.
Duvdevani, S., 1953. Dew gradients in relation to climate soil and topography, in desert research. In: Proceedings of the Desert Symposium, Jerusalem, pp. 136–152.
Elkins, N.Z., Whitford, W.G., 1982. The role of microarthropods and nematodes in decomposition in a semi-arid ecosystem. Oecologia 55, 303–310.
Epstein, H.E., Burke, I.C., Lauenroth, W.K., 2002. Regional patterns of decomposition and primary production rates in the US Great Plains. Ecology 83, 320–327.
Facelli, J.M., Pickett, S.T.A., 1991. Plant litter – its dynamics and effects on plant community structure. Bot. Rev. 57, 1–32.

Fearnside, P.M., 2000. Global warming and tropical land-use change: greenhouse gas emissions from biomass burning, decomposition and soils in forest conversion, shifting cultivation and secondary vegetation. Clim. Change 46, 115–158.
Ferreira, V., Graça, M.A.S., de Lima, J.L.M.P., Gomes, R., 2006. Role of physical fragmentation and invertebrate activity in the breakdown rate of leaves. Arch. Hydrobiol. 165, 493–513.
Fornara, D.A., Du Toit, J.T., 2008. Browsing-induced effects on leaf litter quality and decomposition in a southern African savanna. Ecosystems 11, 238–249.
Fosu, M., Kuhne, R.F., Vlek, P.L.G., 2007. Mineralization and microbial biomass dynamics during decomposition of four leguminous residues. J. Biol. Sci. 7, 632–637.
Gartner, T.B., Cardon, Z.G., 2004. Decomposition dynamics in mixed-species leaf litter. Oikos 104, 230–246.
Gill, R.A., Burke, I.C., 2002. Influence of soil depth on the decomposition of *Bouteloua gracilis* roots in the short grass steppe. Plant Soil 241, 233–242.
Gindaba, J., Olsson, M., Itanna, F., 2004. Nutrient composition and short term release from croton macrostachyus Del. and *Millettia ferruginea* (Hochst) Baker leaves. Biol. Fert. Soils 40, 393–397.
Goheen, J.R., Palmer, T.M., Charles, G.K., Helgen, K.M., Kinyua, S.N., et al., 2013. Piecewise disassembly of a large-herbivore community across a rainfall gradient: The UHURU Experiment. PLoS ONE 8 (2), e55192, http://dx.doi.org/10.1371/journal.pone.0055192.
Gonzalez, G., Seastedt, T.R., 2001. Soil fauna and plant litter decomposition in tropical and subalpine forests. Ecology 82, 955–964.
Hamadi, Z., Steinberger, Y., Kutiel, P., Lavee, H., Barness, G., 2000. Decomposition of Avena sterilis litter under arid conditions. J. Arid Environ. 46, 281–293.
Hobbie, S.E., Gough, L., 2004. Litter decomposition in moist acidic and non-acidic tundra with different glacial histories. Oecologia 140, 113–124.
Hobbie, S.E., Vitousek, P.M., 2000. Nutrient limitation of decomposition in Hawaiian forests. Ecology 81, 1867–1877.
Jama, B.A., Nair, R.K.R., 1996. Decomposition and nitrogen mineralization patterns of *Leucaena leucocephala* and *Cassia siamea* mulch under tropical semi-arid conditions in Kenya. Plant Soil 179, 275–285.
Kaspari, M., Garcia, M.N., Harms, K.E., Santana, M., Wright, S.J., Yavitt, J.B., 2008. Multiple nutrients limit litterfall and decomposition in a tropical forest. Ecology 11, 35–43.
Kochy, M., Wilson, S.D., 1997. Litter decomposition and nitrogen dynamics in aspen forest and mixed-grass prairie. Ecology 78, 732–739.
Kouno, K., Tuchiya, Y., Ando, T., 1995. Measurement of soil microbial biomass phosphorus by an anion exchange membrane method. Soil Biol. Biochem. 27, 1353–1357.
Leonard, S., Fluckiger, W., 1989. Effects of cation leaching on mineral cycling and transpiration: investigations with beech seedlings *Fagus sylvatica* L. New Phytol. 111, 173–179.
Liu, K., Sollenberger, L.E., Silveira, M.L., Vendramini, J.M.B., Newman, Y.C., 2011. Grazing intensity and nitrogen fertilization affect litter responses in 'Tifton 85' Bermuda grass pastures: II. Decomposition and nitrogen mineralization. Agron. J. 103, 163–168.
Lupwayi, N.Z., Haque, I., 1999. Leucaena hedgerow intercropping and cattle manure application in the Ethiopian highlands. I. Decomposition and nutrient release. Biol. Fert. Soils 40 (28), 182–195.
Mafongoya, P.L., Nair, P.K.R., Dzowela, B.H., 1997. Multipurpose tree prunings as a source of nitrogen to maize under semiarid conditions in Zimbabwe. Agroforest. Syst. 35, 57–70.
Meentemeyer, V., 1978. Macroclimate and lignin control of litter decomposition rates. Ecology 59, 465–472.
Melillo, J.M., Aber, J.D., Muratore, J.F., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63, 621–626.
Moretto, A.S., Distel, R.A., Didone, N.G., 2001. Decomposition and nutrient dynamic of leaf litter and roots from palatable and unpalatable grasses in a semi-arid grassland. Appl. Soil Ecol. 18, 31–37.
Mtambanengwe, F., Kirchmann, H., 1995. Litter from a tropical savanna woodland (miombo): chemical composition and C and N mineralization. Soil Biol. Biochem. 27, 1639–1651.
Mugendi, D.N., Nair, P.K.R., 1997. Predicting the decomposition patterns of tree biomass in tropical highland micro regions of Kenya. Agroforest. Syst. 35, 187–201.
Mugendi, D.N., Nair, P.K.R., Mugwe, J.N., O'Neill, M.K., Swift, M.J., Woomer, P.L., 1999. Alley cropping of maize with calliandra and leucaena in the sub-humid highlands of Kenya Part 2. Biomass decomposition, N mineralization, and N uptake by maize. Agroforest. Syst. 46, 51–54.
Nakagami, K., Sakanoue, S., Takahashi, S., 2010. Estimation of nitrogen release from decomposing *Zoysia japonica* litter using its relationship to mass loss. Jpn. Grassl. Sci. 56, 177–182.
Nash III, T.H., 1996. Nutrient elemental accumulation and mineral cycling. In: Nash III, T.H. (Ed.), Lichens. Cambridge, United Kingdom, pp. 136–153.
Ohiagu, C.E., Wood, T.G., 1979. Grass production and decomposition in Southern Guinea Savanna, Nigeria. Oecologia 40, 155–165.
Oladoye, A.O., Ola-adams, B.A., Adedire, M.O., Agboola, D.A., 2008. Nutrient dynamics and litter decomposition in *Leucaena leucocephala* (Lam.) De Wit plantation in the Nigerian derived savanna. West Afr. J. Appl. Ecol. 13, 96–103.
Palm, C.A., Sanchez, P.A., 1990. Decomposition and nutrient release patterns of the leaves of 3 tropical legumes. Biotropica 22, 330–338.
Peyraud, J.L., Astigarraga, L., 1998. Review of the effect of nitrogen fertilization on the chemical composition, intake, digestion and nutritive value of fresh herbage: consequences on animal nutrition and N balance. Anim. Feed Sci. Tech. 72, 235–259.
Ruinen, J., 1961. The phyllosphere. Plant Soil XV (2), 81–109.
Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. Blackwell Scientific Publications, Oxford.
Tukey Jr., H.B., Wittwer, S.H., Tukey, H.B., 1957. Leaching of carbohydrates from plant foliage as related to light intensity. Science 126, 120.
Tukey Jr., H.B., 1969. Implications of allelopathy in agricultural plant science. Bot. Rev. 35, 1–16.
Tukey Jr., H.B., 1970. The leaching of substances from plants. Annu. Rev. Psychol. 21, 305–324.
Van Soest, J.P., 1970. Forage and Fiber Analysis Handbook No. 379. USDA, Washington, DC.
Valentini, R., Matteucci, G., Dolman, A.J., et al., 2000. Respiration as the main determinant of carbon balance in European forests. Nature 404, 861–865.
Vitousek, P.M., Turner, D.R., Parton, W.J., Sanford, R.L., 1994. Litter decomposition on the Mauna-Loa environmental matrix, Hawaii – patterns, mechanisms, and models. Ecology 75, 418–429.
Waite, R., 1970. The structural carbohydrates and the in vitro digestibility of a ryegrass and a cocksfoot at two levels of nitrogenous fertilizer. J. Agric. Sci. 74, 457–462.
Went, F.W., 1955. Fog, Mist, Dew, and Other Sources of Water. Yearbook of Agriculture.
Witkamp, M., Olson, J.S., 1963. Breakdown of confined and nonconfined oak litter. Oikos 14, 138–147.
Yang, C., Crowley, D.E., Borneman, J., Keen, N.T., 2001. Microbial phyllosphere populations are more complex than previously realized. PNAS 98, 3889–3894.
Young, T.P., Patridge, N., Macrae, A., 1995. Long-term glades in acacia bushland and their edge effects in Laikipia Kenya. Ecol. Appl. 5, 97–108.
Young, T.P., Okello, B., Kinyua, D., Palmer, T.P., 1998. KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia Kenya. Afr. J. Range Forage Sci. 14, 94–102.