

Predicting the decomposition patterns of tree biomass in tropical highland microregions of Kenya*

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Abstract. Decomposition- and nitrogen-release patterns of biomass from three agroforestry multipurpose trees (*Calliandra calothyrsus*, *Cordia africana* and *Grevillea robusta*) were investigated in four contrasting environments (microregions) in the Kenyan tropical highlands during two cropping seasons. Dried leafy biomass was placed in 2-mm litter bags, buried at 15-cm depth and recovered after 2, 4, 7, 10, 15 and 20 weeks. Decomposition patterns were best described by first-order exponential decline curves. The decomposition rate constants ranged from 2.1 to 8.2 yr⁻¹, and the rates of decomposition among the species were in the order: calliandra ≥ cordia > grevillea. There was a species-by-environment interaction during both seasons, but the nitrogen released did not follow such a pattern. Among the three tree species, calliandra released the highest amount of cumulative N, followed by cordia and grevillea. Using multiple regression techniques, decomposition pattern was described as a function of three groups of factors: biomass quality (N, C, lignin and polyphenol), climate (soil temperature and rainfall), and soil conditions (pH, soil organic C, total N and P). For all the species and factors combined, the adjusted R² values were 0.88 and 0.91 for seasons 1 and 2, respectively. Among the three groups of factors, climate and biomass quality had the most influence on decomposition rates. Climatic factors accounted for 75% of the total rate of decomposition in season 1 ('irregular' season with less rainfall and more soil temperature fluctuations), whereas biomass quality factors were more influential in season 2 ('regular' season), accounting for 65% of the total variability.

Introduction

In many agroforestry systems, leaf biomass (litter or leafy prunings) of multipurpose trees (MPT) is added as a source of nitrogen and other nutrients to crops (Nair, 1993). Decomposition and mineralization (nutrient release) of the biomass so added are key processes by which nutrients locked up in plant parts eventually become available to crops. The processes are regulated by a host of variables including physical and chemical properties (quality) of litter, climate, soil properties and decomposer communities consisting of microorganisms and soil invertebrates (Meentemeyer and Berg, 1986; Upadhyay and Singh, 1989). Understanding the extent of influence or control of these variables over biomass decay and nutrient release is an important first step to

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better managing organic inputs that are applied in agroforestry and other related land-use systems (Palm, 1995; Mafongoya et al., 1997).

The influence of litter quality on decomposition and nutrient release has recently been reviewed by Palm (1995). Initial concentrations of nitrogen (N), lignin (LG), polyphenol (PP) and ratios, such as C:N, LG:N, (LG+PP):N and PP:N in the biomass, are some of the chemical factors that have been shown to influence decomposition rates (Frankenberger and Abdelmagid, 1985; Palm and Sanchez, 1991; Tian et al., 1993; Constantinides and Fownes, 1994; Mafongoya and Nair, 1996). However, there is no unanimity of views as to which of the chemical indices and ratios are the best predictors of decomposition and nutrient release, in addition to other factors, such as microclimate and decomposer communities, species differences, contents and proportions of chemical constituents in the plant materials, and the analytical methods employed which are also important (Palm, 1995; Quemada and Cabrera, 1995).

Reports on the role of differing environments and their interaction with litter chemical indices in decomposition and nutrient release are few. Meentemeyer (1978) showed that climatic factors such as actual evapotranspiration (AET) were a better predictor of decay rate than were litter quality factors (e.g., lignin) when considering different climatic regions (subpolar to warm temperate). Other abiotic factors mentioned as influential in determining the rate of decomposition included temperature and rainfall (Upadhyay and Singh, 1989; Upadhyay et al., 1989; Sandhu et al., 1990). These studies dealt mostly with forest litter decay and were often localized on single sites. Studies on how litter quality and abiotic environment affect decomposition on multilocational sites in agroforestry systems are unavailable. The objective of this study was to develop a statistical model that describes the influence of plant chemical qualities, climate and soil characteristics on decomposition patterns across different microregions (subhumid to semiarid) in the tropical highlands of Kenya where agroforestry is being practiced.

Materials and methods

Characterization of microregions

The study was conducted in the central highlands of Kenya, East Africa, during two rainy seasons of 1995. Season 1 was the so-called long rain season (LR) that extends usually from mid-March to July, and season 2, the so-called short rain season (SR), extending usually from mid-October to January. Four contrasting environments (microregions) were selected in accordance with Jaetzold and Schmidt's (1983) agroecological zonation of the area: microregions 1–4 correspond to Jaetzold and Schmidt's classification of upper midlands 1–4 (UM1–UM4). The geographic and climatic details of the four microregions (henceforth referred to as Reg1, Reg2, Reg3 and Reg4) are

presented in Table 1. The average daily soil temperatures (recorded using soil thermometers for the 0–15 cm top soil layer) and total rainfall (from daily readings) in the different microregions during the experimental period are presented in Table 2. The soil properties of the sites are shown in Table 3.

Table 1. Geographic and climatic^a descriptors of the four microregion sites of the central highlands of Kenya.

Region	Altitude (m)	Average air temperature (°C)			Average total rainfall (mm)		
		Max	Min	Mean	LR	SR	Total
1	1700	23.5	12.6	18.0	1050	700	1750
2	1400	25.0	14.1	19.5	800	600	1400
3	1320	27.6	16.9	21.2	540	460	1000
4	1596	31.0	13.3	19.0	400	350	750

^a Climatic data represent ≥ 10 years.

Abbreviations: LR = long rain season; SR = short rain season.

Source: Jaetzold and Schmidt (1983).

Table 2. Average soil temperature and total rainfall in the four microregions during the two study seasons in the central highlands of Kenya.

		Week	0–2	2–4	4–7	7–10	10–15	15–20
Season 1 (LR 95)								
Temperature (°C) (0–15-cm depth)	Reg1		21.0	19.2	18.6	17.9	16.3	13.0
	Reg2		23.8	22.1	20.1	19.3	17.1	16.0
	Reg3		27.9	27.3	25.0	24.4	20.9	21.1
	Reg4		Data not recorded					
Rain (mm)	Reg1		80	179	450	64	32	118
	Reg2		80	140	251	30	9	39
	Reg3		93	167	162	34	5	14
	Reg4		Data not recorded					
Season 2 (SR 95)								
Temperature (°C) (0–15-cm depth)	Reg1		12.2	11.5	10.8	11.1	11.9	13.0
	Reg2		18.8	18.0	17.8	16.7	15.5	17.0
	Reg3		25.4	25.1	25.9	23.5	23.0	25.0
	Reg4		24.6	23.0	22.5	21.7	23.6	25.0
Rain (mm)	Reg1		336	292	92	119	101	3
	Reg2		145	119	73	67	68	9
	Reg3		111	61	49	82	42	13
	Reg4		99	26	19	69	12	29

Season 1, 24 March–11 August 1995; Season 2, 19 October 1995–5 March 1996.

Abbreviations: LR = long rain season; SR = short rain.

Table 3. Soil properties for the decomposition sites in the different microregions in the central highlands of Kenya.

Region	Site	Soil type	pH	C (%)	N (%)	P (%)
1	Kavutiri	Orthoxic Palehumult	4.8 b	2.41 a	0.41 a	0.11 a
2	Embu	Typic Palehumult	5.8 a	1.95 ab	0.23 b	0.09 a
3	Murinduko	Typic Palehumult	5.6 a	1.44 bc	0.16 bc	0.08 a
4	Machakos	Kandic Rhodustalfs	6.1 a	1.17 c	0.09 d	0.09 a

Values followed by the same letter within a column are not significantly different from each other at $P < 0.05$.

Experimental procedures

Biomass of three tree species were chosen for the study: calliandra (*Calliandra calothyrsus* Meissner), cordia (*Cordia africana* Lam.) and grevillea (*Grevillea robusta* Cunn. ex. R. Br.). The species are common in the study region and are popular among the important multipurpose trees in tropical agroforestry systems (Nair, 1993). Calliandra (originated from tropical America) was introduced in the study area in the early 1980s as a source of fodder and for soil fertility enrichment. Cordia is indigenous and is found frequently scattered in crop lands; farmers allow it to grow on farms because of its perceived ability to improve soil fertility. Grevillea was introduced from Australia in the 1920s. It is now the most common tree found on farms throughout the Kenyan highlands; it is used for fuelwood and as a building material. Its prunings are spread on coffee farms or used as bedding in cowsheds.

Leafy biomass used in each microregion was obtained from mature trees found in that region or near the respective study sites. Leaves and twigs (no more than 2 mm in diameter) were collected and sun-dried to constant weight, after which samples of 50 g each were transferred to litter bags of 2-mm mesh-size. The bags were then buried in the ground at a depth of 0–15 cm (plow-layer). The experiment was installed as a randomized block design, replicated three times within each region. One bag, containing residues of each species, was randomly removed from each block (in each region) after 2, 4, 7, 10, 15 and 20 weeks. The contents of the bag were carefully cleaned free of soil and oven-dried at 65 °C (for about 48 h) to constant weight (Anderson and Ingram, 1993). The dry weight of the litter remaining undecomposed was recorded.

Decomposition rate constants (k) were estimated using the Wieder and Lang (1982) first order exponential equation:

$$L_R/L_1 = e^{-kt},$$

where: L_R = the litter weight remaining at a given time, L_1 = the initial litter weight at time zero, t = the time interval of sampling L_R expressed in years, and k = the rate constant (decomposition rate per year). The fraction of the

material remaining (L_R/L_1) declined with time. The k values were estimated using a non-linear module in SAS (1988).

Nitrogen released over time was calculated following the formula by Giashuddin et al. (1993):

$$\% \text{ N released} = 100 - \% \text{ of original N content remaining}$$

$$\% \text{ original N} =$$

$$\frac{(\% \text{ N remaining at time } t)}{(\% \text{ N at time } 0)} \times \% \text{ of the original weight remaining.}$$

The data were analyzed as a three-way factorial study with region, species and time (expressed in years) as fixed effects. Tree biomass samples were analyzed for initial contents of N, C, lignin and polyphenols by methods outlined by Anderson and Ingram (1993). The plant and soil analyses data were subjected to ANOVA using SAS. Means were separated by Tukey's mean separation procedure at $P < 0.05$. Regression and correlation analyses were also performed relating the rate of decomposition to three groups of factors: biomass quality (N, C, lignin and polyphenol contents, and the ratios between some of them), climate (soil temperature and rainfall), and soil conditions (pH, total N, organic N and total P). Statistical models were then developed relating the rate of decomposition to the three groups of factors. The contribution of each group toward the rate of decomposition was estimated by partitioning its percentage contribution to the overall variability (R^2) obtained in each model.

Results

Reg1 was the coolest site and received the highest amount of rainfall, whereas Reg3 and Reg4 yielded the highest temperatures and received the lowest amounts of rainfall (Table 2). In season 1, the temperatures were highest at the initiation of the experiment (0–2 weeks) and decreased progressively as the season advanced. The amount of rain received in this season increased from the start of the study reaching a maximum at weeks 4–7, and declined thereafter. Soil temperatures recorded in season 2 did not vary greatly across the season (for each region); however, the highest amount of rainfall was recorded during the first two weeks of the experiment (Table 2). Reg1 had the lowest soil pH and highest carbon and nitrogen contents compared to all the other sites (Table 3).

The MPT biomass used in this study showed some variation in chemical composition (Table 4). Calliandra obtained from the different regions had the highest concentration of N (though not significantly different from that of cordia) and polyphenols (PP) and the lowest concentration of lignin (LG). Nitrogen, C and the C:N ratio for calliandra and cordia biomass were similar. Grevillea biomass had the lowest concentration of N and the highest con-

Table 4. Initial chemical properties and ratios of different tree biomass incorporated in different regions in the tropical highlands of Kenya.

Region	Spp	N	C	LG	PP	C:N	LG:N	PP:N	(LG+PP):N
----- g 100 g ⁻¹ -----									
1	Call	2.9 a	45 b	12.4 b	11.0 a	15.9 b	4.4 c	3.9 a	8.2b
	Cord	2.8 a	46 b	28.1 a	4.3 b	16.4 b	10.1 b	1.5 b	11.7 b
	Grev	1.4 b	47 a	23.8 a	4.6 b	32.7 a	16.5 a	3.2 ab	18.8 a
	Call	3.6 a	45 b	12.4 c	11.2 a	12.6 c	3.5 c	3.1 ab	6.6 c
2 and 4	Cord	2.7 b	46 b	31.3 a	2.6 c	16.9 b	11.5 b	1.0 b	12.4 b
	Grev	1.3 c	48 a	23.7 a	6.1 b	39.4 a	19.7 a	5.1 a	24.8 a
	Call	2.3 a	45 b	13.5 b	15.4 a	19.3 b	6.0 c	6.6 a	12.6 b
3	Cord	2.2 a	45 b	26.0 a	6.0 b	20.4 b	12.0 b	2.8 b	14.8 b
	Grev	1.3 b	48 a	26.2 a	6.5 b	38.1 a	21.0 a	5.2 a	26.8 a

Values followed by different letters in a column within each region are different from each other at $P < 0.05$.

Abbreviations: LG = lignin; PP = polyphenol; Call = *Calliandra calothyrsus*; Cord = *Cordia africana*; Grev = *Grevillea robusta*.

centration of carbon and, therefore, the highest C:N ratio. Lignin and polyphenol concentrations for grevillea were similar to those of cordia; however, its LG:N, PP:N and (LG+PP):N ratios were significantly higher than for the biomass of the other two species in all the regions.

Decomposition patterns of the biomass were affected by both the region (environment) and the type of species (region-by-species interaction). Figure 1 shows an example of the decomposition patterns obtained during the two seasons of experimentation. Decomposition rates were in the order calliandra $>$ cordia $>$ grevillea (Table 5).

Patterns of cumulative mineralized N (N released) of the biomass of the three species was influenced by region and species. An example of the different patterns during the 20-week study period is shown in Figure 2. Calliandra and cordia tree-biomass showed a pattern of rapid N release whereas grevillea showed an initial net N immobilization followed by a slow release. The highest amounts of cumulative mineralized N were given by calliandra biomass, though in some regions they were not significantly different from those of cordia. Grevillea biomass released the lowest amounts of cumulative N in both seasons and in all the regions. The cumulative amounts of N released after 20 weeks ranged from 1.68 to 3.47 g 100 g⁻¹ for calliandra, 0.98–1.78 g 100 g⁻¹ for cordia and 0.17–0.44 g 100 g⁻¹ for grevillea (Table 6); representing amounts of N released of 65–96%, 48–66% and 12–34% of the initial N contents for calliandra, cordia and grevillea biomass, respectively.

Correlation coefficients relating the rate of decomposition to plant, climate and soil characteristics are shown in Table 7. In both seasons, rainfall, N, C:N, LG:N and (LG+PP):N, and, in addition, temperature for season 1 and lignin for season 2 significantly correlated with the rate of decomposition.

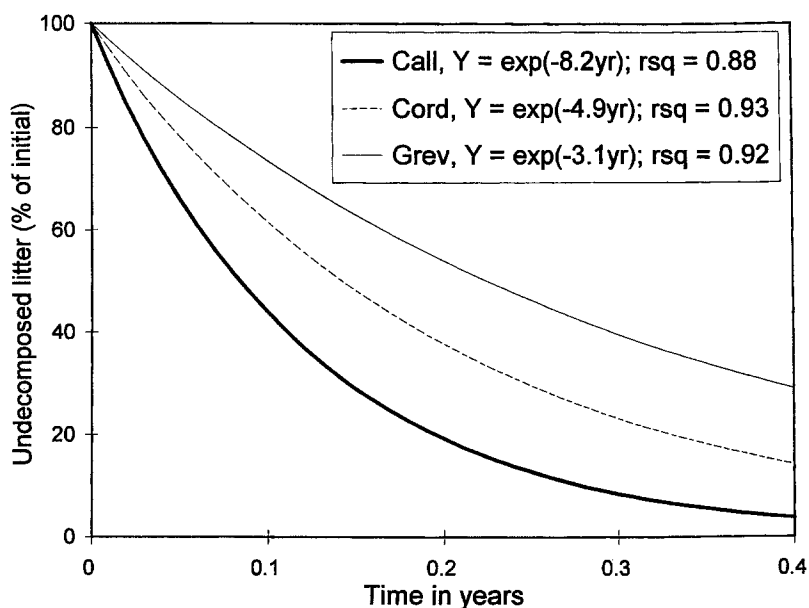


Figure 1. Decomposition patterns of calliandra, cordia and grevillea leafy biomass for season 2 in the different microregions of the tropical highlands of Kenya. call = calliandra; cord = cordia; grev = grevillea.

Table 5. Decomposition rate constants and R^2 for the different tree-biomasses as influenced by different microregions in the central highlands of Kenya.

Species	Season 1 (LR 95)							
	Reg1		Reg2		Reg3			
	k	R^2	k	R^2	k	R^2		
Call	4.4 a	0.68	5.9 a	0.84	6.2 a	0.90		
Cord	3.7 a	0.65	5.3 a	0.79	5.6 a	0.89		
Grev	2.8 b	0.75	3.5 b	0.72	3.7 b	0.82		
Species	Season 2 (SR 95)							
	Reg1		Reg2		Reg3		Reg4	
	k	R^2	k	R^2	k	R^2	k	R^2
Call	7.4 a	0.66	6.9 a	0.86	5.9 a	0.86	8.2 a	0.88
Cord	5.7 a	0.71	5.4 a	0.79	3.2 b	0.89	4.9 b	0.93
Grev	2.1 b	0.54	3.2 b	0.82	2.7 c	0.78	3.1 c	0.92

k is decomposition rate constant, per year; a higher value of k indicates faster decomposition rate.

Values followed by the same letter within a column are not significantly different from each other at $P < 0.05$.

Abbreviations: Call = *Calliandra calothyrsus*; Cord = *Cordia africana*; Grev = *Grevillea robusta*; LR = long rain season; SR = short rain season.

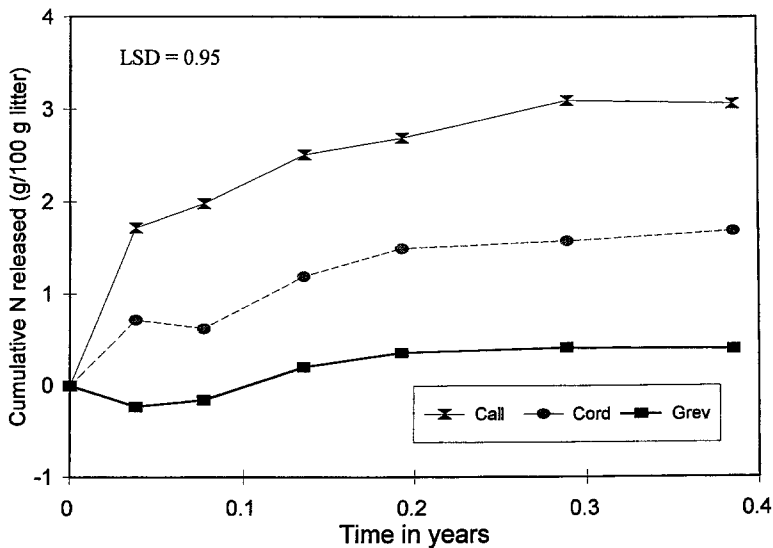


Figure 2. Cumulative N released during the 20-week period by calliandra, cordia and grevillea leafy biomass for season 1, Reg2 in the different microregions of the tropical highlands of Kenya. call = calliandra; cord = cordia; grev = grevillea.

Table 6. Cumulative nitrogen released at week 20 by biomass from different tree species in different regions of the central highlands of Kenya.

Spp	Season 1 (LR 95)			Season 2 (SR 95)			
	Reg1	Reg2	Reg3	Reg1	Reg2	Reg3	Reg4
----- Nitrogen released (g 100 g ⁻¹) -----							
Call	1.88 a	3.07 a	1.71 a	1.97 a	3.40 a	1.68 a	3.47 a
Cord	1.53 a	1.68 b	0.46 a	1.78 a	1.30 b	0.98 b	1.62 b
Grev	0.43 b	0.40 c	0.44 b	0.17 b	0.30 c	0.40 c	0.44 c

Values followed by the same letter within a column are not significantly different from each other at $P < 0.05$.

Abbreviations: Call = *Calliandra calothyrsus*; Cord = *Cordia africana*; Grev = *Grevillea robusta*; LR = long rain season; SR = short rain season.

Statistical models were developed, using SAS to describe decomposition pattern as a function of three groups of factors: litter quality (N, C, lignin, polyphenol and various ratios), climate (soil temperature and rainfall) and soil characteristics (pH, total N, organic C and total P). for each season, the best ten regression models based on adjusted R^2 were listed in a descending order. The best of the ten models (listed first in each case) for both seasons are presented in Table 8. In both seasons, temperature, rainfall, N, C:N, (LG+PP):N, pH and soil total N were significant indices for predicting the rate of decomposition; in addition, LG and LG:N were also important in

Table 7. Correlation coefficients (r) relating the rate of decomposition to plant, climate and soil factors in the tropical highlands of Kenya during the two seasons of 1995.

Season	Temperature	Rain	N	LG	PP	C	C:N	LG:N	(LG+PP):N	pH	TC	TN	TP
1 (LR)	0.45***	0.39***	-0.30***	0.22	-0.22	0.24	0.32*	0.31*	0.29*	-0.21	-0.19	-0.21	-0.22
2 (SR)	0.12	0.40**	-0.55***	0.33*	-0.27	0.32	0.50***	0.51***	0.52***	-0.04	-0.02	-0.10	-0.08

Levels of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Abbreviations: LG = lignin; PP = polyphenol; TC = total soil organic carbon; TN = total soil nitrogen; TP = total soil phosphorus; LR = long rain season; SR = short rain season.

Table 8. Statistical models predicting decomposition rates across different regions in the highlands of Kenya in seasons 1 (LR 1995) and 2 (SR 1995).

Season	Model
1	$Y = \text{Exp}(Yr \times (-10.4 - 0.2T + 0.04R + 0.8N - 0.07C:N + 0.4(LG+PP):N + 0.2pH + 6.8TN)); R^2 = 0.91$
2	$Y = \text{Exp}(Yr \times (-2.4 + 0.03T - 0.01R + 4.4N - 0.3C:N + 4.2LG:N - 3.6(LG+PP):N + 0.2pH - 1.2TN)); R^2 = 0.93$

Abbreviations: Y = fraction of biomass remaining undecomposed; yr = time expressed in years; T = soil temperature ($^{\circ}\text{C}$); N = plant nitrogen concentration (%); R = rainfall (mm); LG:N = lignin:nitrogen ratio; (LG+PP):N = (lignin + polyphenol):nitrogen ratio; pH = soil pH; TN = soil total nitrogen (%).

season 2. The adjusted R^2 values were 0.88 and 0.91 for seasons 1 and 2, respectively. Figure 3 presents the overall contribution of climatic factors, litter quality and soil characteristics to decomposition rate in each season. Climate was the dominating factor in season 1 accounting for almost 75% of the total rate of decomposition, whereas in season 2, biomass quality was more influential accounting for 65% of the total variability.

Discussion

Biomass quality and decomposition

The decomposition patterns of calliandra and cordia were somewhat similar and distinctly different from that of grevillea (Figure 1 and Table 5). N-release patterns were also similar to decomposition patterns; however, they could not be adequately described by simple equations due to observed variations of net release and net immobilization from one sampling period to the next. These variations did not follow any definite pattern. Among the plant indices that were shown to be effective in determining the rate of decomposition (Table 7), N, C:N, LG:N and (LG+PP):N were best correlated with the rate of decomposition for both seasons. Past studies have indicated initial N content and C:N ratio of plant materials to be reliable predictors of decomposition and N release (Sandhu et al., 1990; Tian et al., 1992b; Mugendi et al., 1994; Thorup-Kristensen, 1994; Quemada and Cabrera, 1995; Jama and Nair, 1996).

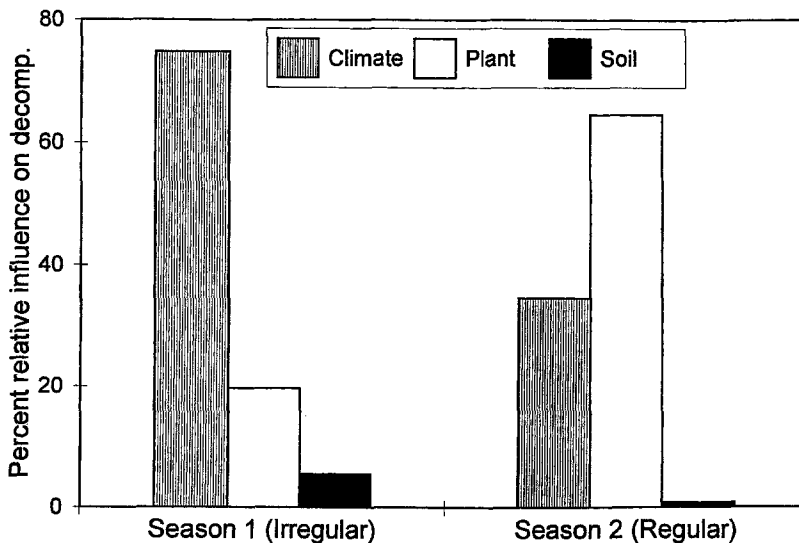


Figure 3. Influence of climatic, litter-quality and soil factors on decomposition rates of plant biomass in four microregions of the tropical highlands of Kenya.

In our study, the N and C:N ratio were significantly correlated with decomposition during both seasons (Table 7). Both calliandra and cordia biomasses had high concentrations of N compared to that of grevillea (Table 4). The biomass from these two species showed a faster rate of decomposition, whereas grevillea biomass showed an initial N immobilization in all the sites during the two seasons, and released the lowest amount of N over the entire 20-week study period. The results of this study corroborate the reports of others that N content serves as a useful preliminary index of decomposition and N release when materials of different categories (e.g. leguminous and non-leguminous) are grouped together (Tian et al., 1992a; Constantinides and Fownes, 1994; Palm, 1995).

Lignin had a significant positive correlation with the rate of decomposition during season 2 only. Whereas lignin content in itself was not a strong predictor of decomposition rate, lignin-derived variables (ratios) were important predictors (Table 7). Lignin is known to be highly resistant to microbial decomposition (Melillo et al., 1982). It may also slow down N mineralization due to lignin-bound N. The lignin concentration of cordia biomass (26–31%) was significantly higher than that of calliandra (12–13%), though both species had almost identical N concentration and C:N ratios (Table 4). This may explain partly why cordia biomass decomposed and mineralized at a relatively slower pace compared to calliandra. The influence of lignin on decomposition is widely reported in literature (Melillo et al., 1982; Fox et al., 1990; Palm and Sanchez, 1991; Oglesby and Fownes, 1992; Tian et al., 1992a; Stump and Binkley, 1993; Becker et al., 1994). Lignin, however, seems to affect the rate of decomposition and N release only if the species used have relatively high levels of lignin concentration and are structurally different (Taylor et al., 1989; Mafongoya and Nair, 1996).

Polyphenol content in the plant biomass had no significant correlation with decomposition in this study. This corroborates the work of Fox et al. (1990), Becker et al. (1994), Handayanto et al. (1994) and Mafongoya (1995) who found no relationship between cumulative N released and soluble polyphenol content. This, however, disagrees with the work of Palm and Sanchez (1991), Oglesby and Fownes (1992) and Tian et al. (1992a). As already mentioned, the initial N content seems to be a better predictor of decomposition rate in materials that are very different in chemical composition. When materials are similar in nature (e.g. legumes), then other indices, such as polyphenols, become important predictors (Constantinides and Fownes, 1994; Palm, 1995). Plant carbon by itself had no significant correlation with the rate of decomposition. The range of C in the biomass of the tree species was very narrow (45–48%), and this may explain why this constituent was not an important index; however, its ratio with N was significant in both seasons.

In the present study, LG:N and (LG+PP):N ratios were also observed to be significantly correlated with decomposition. These observations agree with those of others in which these ratios were found to be among the best descriptors in predicting weight losses and N released from plant materials (Melillo

et al., 1982; Fox et al., 1990; Kachaka et al., 1993; Stump and Binkley, 1993; Thomas and Asakawa, 1993; Becker et al., 1994; Contnifo et al., 1994; Constantinides and Fownes, 1994; Handayanto et al., 1994; Lehmann et al., 1995; Mafongoya and Nair, 1996).

Influence of climate and soil

Rainfall and soil temperature were significantly correlated with decomposition rate (Table 7). Total soil N and pH, though not significantly correlated with the rate of decomposition, were included in the multivariate mathematical models in Table 8. Literature is scarce on the combined use of climatic, plant and soil indices in the prediction of decomposition and nutrient release, especially in agroforestry systems. In the present study, the combined effects of the three groups of factors (climate, plant-quality and soil) on the influence of the rate of decomposition indicated that climate played a key role in regulating the rate of decomposition in season 1 (Figure 3) when temperature and rainfall fluctuated (Table 2) much more than in season 2, which was dominated by plant-quality factors. Soil factors played a minimal role in both seasons. This finding corroborates the work of Meentemeyer (1978), who indicated that climate was a more important predictor of decomposition than litter quality when dealing with multilocal sites that had differing climates. However, when dealing with a particular region that had a reasonably uniform microclimate and terrain, litter quality indices were excellent predictors of the rate of decomposition. Other studies by Meentemeyer and Berg (1986) indicated that about 90% of a first-year litter mass loss could be explained by a simple model combining the influence of climate and nutrient concentration of the litter. Sandhu (1990) also found a significant correlation between the rate of decomposition of various portions of leucaena with moisture content and mean maximum litter temperature in the dry tropics. Similarly, Upadhyay et al. (1989) predicted monthly rainfall to be a more reliable factor regulating monthly weight loss of litter on individual sites in the Central Himalayan forests as opposed to annual temperature, actual evapotranspiration and altitude, which were better indices of annual weight loss. Vanlauwe et al. (1994) reported that the number of rainfall events gave a better correlation with the percentage dry matter loss than was the total amount of precipitation.

Predictive models

From the statistical predictive models presented in Table 8, it appears that most of the indicators that had a significant correlation with the rate of decomposition (Table 7) were also the best indices in predicting decomposition rates. After apportioning the contribution of each index to the total variability in each model, it was observed that, in season 1, climatic factors were more influ-

ential in regulating the rate of decomposition as they accounted for almost 75% of the total variability (Figure 3). The influence of temperature was especially marked during this season when there was a very clear trend of decreasing temperature as the season progressed (Table 2). Plant-quality factors played a major role in season 2 accounting for almost 65% of the total variability. Soil factors accounted for a very small variability in either of the two seasons. None of the soil factors correlated significantly with the rate of decomposition.

This study indicates that the principal factors regulating the rate of decomposition in the different microregions in the Kenyan tropical highlands are climate (soil temperature and rainfall) and the quality of tree biomass (N, C:N, LG:N, and (LG+PP):N). The main difference between seasons 1 and 2 of this study was that climatic conditions (rainfall and temperature) were more 'regular' and evenly distributed in season 2 (as in a normal season), than in season 1 (Table 2). This indicates that, during 'good' seasons with average climatic conditions (as in season 2), biomass decomposition is governed predominantly by plant quality factors, whereas climatic factors (rainfall and temperature) are more important during seasons of uneven or irregular conditions. Thus, the prevailing general assumption that decomposition of plant litter in a given region is determined predominantly by plant quality factors may not necessarily be true. During seasons of erratic climatic changes (e.g. erratic rainfall and fluctuating temperatures as is common in most semiarid tropics), climatic factors become more important than plant quality factors in determining litter decomposition rates. More research that includes other plant materials that are used in these regions as organic soil amendments by farmers is needed to improve further on the predictability of these models and the validity of the findings.

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