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Research Article

Grass species litter have varied trait response to the photodegradation and microbial decomposition in tropical savanna grasslands, South Africa

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Summary

Purpose of the paper: This paper evaluated the effects of microbial and photodegradation on the ten grass species in a tropical grassland ecosystem in South Africa. Despite continuous necromass accumulation in tropical grasslands, the process that governs how the grass litter gets to the soil has often been ignored. In the absence of fire, abiotic factors and biotic factors are drivers of this process of nutrient cycling.

Methods and approaches: A classical litterbag experiment was set up to simulate photodegradation (standing litter) versus microbial (soil surface) decomposition using 10 savanna types of grass from the start of the dry season until the beginning of spring. The rates of photodegradation versus microbial decomposition were compared for tropical savanna grasses and plant traits or predictors of decomposition were also investigated.

Main results: The results showed that the grass litter decomposed more rapidly when exposed to the activity of soil microbes at the soil surface ($k = 0.0028$) than when held above ground ($k = 0.0018$) and subjected to photodegradation only. However, examination of the individual litter species revealed up to 4 fold variation between the slowest (0.0001) and fastest (0.006) decomposing species. Differences in decomposition rates were more pronounced for litter decomposed at the soil surface than held above the soil surface. Multiple linear regression analyses did not resolve clear differences between measures of litter quality as drivers of decomposition in the two treatments.

Implications: Photodegradation appeared to be a rate-controlling step during the process of decomposition in tropical savanna grasslands. Therefore grasslands dominated by photodegradation-resistant grasses were likely to need fire to get rid of moribund litter, which may be the reason why mesic grasslands need to burn to recycle nutrients.

Introduction

Litter decomposition has been shown to be an important process in all terrestrial ecosystems because it controls the recycling of nutrients [1]. The accepted view on decomposition in the past has always been that it was the detachment of litter onto the ground where microbes break down the litter and incorporates it into the soil organic matter. Temperature and moisture were touted as the most important abiotic drivers

of decomposition [2] largely based on how the two drivers affected microbes on the soil surface. The other reason was that leaf litter from trees remained relatively high in forests but not many studies existed in arid and semi-arid systems where the dominant growth forms are often grasses.

The biotic factors include decomposers (for example, micro- and macro-organisms such as bacteria and termites [3-5] and litter quality [3,6-8]. Decomposers, notably termites



and earthworms process a large litter fraction of dead organic matter but in general a small fraction of the tropical grassland ecosystem respiration results directly from detritivores [9]. All these soil fauna move surface litter into the soil and fragment it, thereby speeding decomposition especially when soil moisture has increased. Recent studies investigated the role of termites as an abiotic driver of litter and mammalian dung decomposition [10]. Buitenwerf, et al. [11] focussed on the interaction between large herbivores and litter removal by termites across spatial scales and a rainfall gradient at Hluhluwe-iMfolozi Park in a South African savanna. At the landscape scale, termite consumption depended on an interaction between rainfall and the presence of large mammalian herbivores wherein litter removal by termites was greater in the presence of large herbivores at the drier sites but lower in the presence of large herbivores at the wetter sites. In alpine ecosystems grazing accelerated litter decomposition but was also important that the incubation site had significantly more impact than litter quality on litter decomposition and N release, while litter quality affected decomposition in the early stages [12]. This contributes to why the mesic savanna accumulates litter whereas the arid end of the spectrum has lower litter accumulation as suggested in Masubelele [13]. In a more recent study, Davies, et al. [14] showed that grass decomposition in African savannas varies significantly along precipitation gradients, with different factors becoming influential in different habitats. Their work across Kruger National Park also showed that fire promoted grass decomposition in intermediate rainfall savanna under higher levels of fungus-growing termite activity but not in arid and wetter savannas.

Current research explores a combination of abiotic factors including temperature [2], moisture [15,16], atmospheric water vapor [17] and solar radiation [6,18–21]. These abiotic factors driving decomposition have recently been well studied in arid and semi-arid drylands in Argentina [18] and the United States shrublands and grasslands [6,22,23] after early researchers focussed on wet ecosystems [1,24]. Few studies have been carried out in African savannas where the dominant functional groups are trees and grasses. Earlier work by Scholes & Walker [9] at Nylsvlei Nature Reserve compared decomposition rates of grasses and trees on nutrient-rich versus nutrient-poor soils. They showed that grass litter decomposed faster than tree litter due to lower recalcitrant chemical composition in grasses. Despite the lower rates than trees, standing grass litter is a common phenomenon as mentioned above which results in high carryover and may slow down the decomposition process.

South African mesic grasslands similarly to other types in the world, such as the tall-grass prairie experiences a decline in productivity in the following growing season, due to high carryover of standing dead material from the previous season [13,25]. This necromass goes through a series of processes including decomposition from fragmentation by the sun and other abiotic factors to breakdown by fungi into soil organic matter. For example, Mlambo & Mwenje [26] looked at the effects of shading by Mopani tree cover on litter decomposition of the same species and suggested that this shading retarded photodegradation in a semi-arid savanna. Photodegradation is

the breakdown of litter or any living organism by light [19,22]. Photodegradation is likely to be important in the long dry seasons encountered in many savanna grasslands. For example, Austin and Vivanco, 2006 concluded that photodegradation is a dominant control of the aboveground litter decomposition in the semi-arid Patagonian steppe. In order to understand how this standing litter gets to the soil, methods currently employed need to be rectified especially since their assumptions that grass litter gets to soil despite it being understood that unless the fire was applied in most grasslands, necromass does not get incorporated into the soil. Throop & Archer [6] suggest that standing dead material in drylands would be subject to decomposition via photodegradation and leaching while breakdown by decomposers would be minimal. In this paper, we investigate if photodegradation was an important abiotic driver in savanna grasslands. The question we asked did the rates of photodegradation of standing dead materials of savanna grasses differ from surface soil microbial decomposition? The variation of decomposition rates among the different savanna grasses is not yet understood in spite of a couple of studies mentioned above having related decomposition rates to a number of factors [27]. We, therefore, decided to compare the relative rates of decomposition by photodegradation versus microbial breakdown and to test whether these rates differ between different species in savanna grasslands.

Secondly, Plant traits have been shown to determine the productive capacity of the vegetation and the rates of decomposition and nutrient mineralization [28]. Plant traits include lignin content, carbon to nitrogen (C/N) ratio, leaf thickness, and tannin or polyphenolic content of decomposing material [20,24,29]. C/N ratio, lignin, and lignin/N ratio have been reported as the most important in studies from Australia [30], New Zealand [31], and America [2,29]. Decomposition rates are known to vary among species with different litter properties, but experimental evidence has been limited to soil-placed litterbags not sun-exposed litterbags. The other key question addressed in this paper was which of the different leaf properties were the best predictors of savanna grass decomposition at various stages. If the relative rates of decomposition for different species were similar for decomposition in the sun versus the soil, then similar leaf traits may determine the conversion of standing litter to surface litter on the soil.

Methods and materials

The standard protocol for studying decomposition rates uses litterbags placed on the soil (Meentemeyer, 1978), and therefore persisting standing dead material's rate of reaching the ground has often been ignored in litterbag studies. In this paper, we compared decomposition rates in litterbags placed above the ground, simulating standing litter versus litterbags placed on the soil surface, which is the standard procedure.

Study area

The decomposition study started with a collection of grass litter harvested in April 2002 at the start of the dry season in a savanna grassland at Hluhluwe iMfolozi Park (HiP), which

lies ($28^{\circ}00'S$ and $28^{\circ}26'S$; $31^{\circ}43'E$ and $32^{\circ}09'E$), in KwaZulu Natal Province of South Africa. This park formerly known as Hluhluwe Umfolozi Park and the oldest proclaimed nature reserve in Africa consists of two reserves, the Hluhluwe Game Reserve (HGR) (225km²) to the north, the iMfolozi Game Reserve (iGR) (447km²) to the south and a corridor (227km²) joining the two (Whateley and Porter, 1983). The park has a varied hilly topography with altitudes ranging from 60m to 450m above sea level. The mean minimum temperature is 13 °C and the maximum temperature is 35 °C (Balfour and Howison, 2002). Annual rainfall has a unimodal pattern and the driest time of year is between June and August. Rainfall increases with altitude so that Hluhluwe, which is at higher elevations, supports a mesic whereas iMfolozi is a semi-arid savanna. The mean annual rainfall near the highest point in Hluhluwe (Egodeni) is 980 mm (a 68-year record) with a coefficient of variation of 28.4%. In iMfolozi, the mean annual rainfall at Mpila, an elevated site, is 728 mm (a 36-year record) with a coefficient value of 29.9%. However, most of iMfolozi is at lower elevations and has much lower rainfall less than 650 mm.

The three main vegetation types according to Mucina & Rutherford (2006) are the Northern Zululand Sourveld (SVI22), Zululand Lowveld (SVI23), and Scarp Forest (FOz5). The vegetation is characterized by fine-leaved Acacia savanna with a continuous grass layer and a fairly open tree canopy. The most prevalent grassland types are tall-grass dominated by members of the Andropogoneae subfamily, especially species such as *Themeda triandra*, *Cymbopogon plurinodis*, *Hyparrhenia filipendula* and *Heteropogon contortus* (Downing 1974; Brooks & Macdonald 1983). Other tall grass communities are also present where members of the Chlorideae tribe such as *Sporobolus pyramidalis* and *Eragrostis curvula* (Gibbs-Russell, 1986). These tall, tussock-forming grasses grow fast, produce a high fuel load (400–700g/m²), and promote frequent fires. These tall-grass areas do not support high numbers or a high diversity of grazing animals except after fire; only Buffalo (*Syncerus caffer*) was a tall grass specialist at Hluhluwe (Page & Walker, 1978). Thus these grass communities are most dominant in areas of frequent fire and relatively low grazing pressure. The tall grass species mentioned above remain dominant in the higher elevation areas of iMfolozi whereas lawn grass species from the tribe Chlorideae including *Dactyloctenium Australae*, *Chloris gayana*, *Sporobolus nitens*, or members of the tribe Paniceae (sensu Gibbs-Russell & Spies, 1988) such as *Urochloa mosambicensis*, *Cenchrus ciliaris*, *Digitaria longifolia* and *Panicum coloratum* are common in drier areas. Lawns are grazed by white rhinos (*Ceratotherium simum*), Burchell's zebra (*Equus burchelli*), blue wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*), and nyala (*Tragelaphus angasii*) both mixed feeders and warthog (*Phacochoerus africanus*). Therefore fire is not as common in iMfolozi compared to Hluhluwe. All grass species mentioned above were collected at the start of the dry season.

Field experiments

The litterbag experiment was conducted on a large grass patch in the dry season at the University of Cape Town in the

Western Province, South Africa. The site lies at latitude and longitude (33.953856 and 18.462702). The site is at an altitude of 83m above sea level. The monthly mean daily temperature is highest in January and February (21 °C) but lowest during the month of April (18 °C). The three months also have the highest amount of vapor pressure. Monthly solar radiation and heat units gradually decrease from December to April. There was no rainfall during the month of December 2002. Late January and mid-February of the same year received less than 10 mm of rainfall each, with the most rainfall falling in the middle of March. No rainfall fell during the month of April.

Ten grass species common in the savanna grassland were used (Table 1). The collected grass litter was air dried for 48 hours packed and transported to Cape Town where they were stored and sorted at room temperature and, finally put out during the dry season in December 2002 until the end of April 2003 when the first rains started. Litterbags used for the experiment had a mesh size of 2mm with dimensions of 20x20 cm². The litterbags were made not to be flat but oval-shaped to allow the grass species material to be loose in the bag. An ingenious table (more than 20 cm above the soil) was then designed to simulate standing litter by placing litterbags horizontally on top of the chicken wire fencing with a mesh size of less than 5cm to allow the litter material to fall out freely to the ground. Two treatments were used; one simulated decomposition of standing litter and contained 20 litter bags per species placed horizontally on a chicken mesh table. The other treatment simulating soil surface decomposition contained 20 litterbags placed on the soil shielded from the sun for most of the day under trees but also buried within the grassy layer. Dry leaves material weighing 2.5 g was inserted into each litter bag. Twenty litter bags of each species were placed on a table and on the ground giving a total of 400 litter bags. The decomposition rate was obtained by removing five litterbags for each species on the ground and on the table every month during the dry season of December 2002 moving into an early wet season of April 2003 on a grass patch in Cape Town. The litter bag contents were removed and weighed using Mass Balance. A hundred litter bags, 10 for each species, with 2.5 g were also set aside for chemical and structural analysis in the laboratory at the start of the experiment.

Laboratory analysis

The leaf materials used in this experiment were air-dried green leaves collected as to samples at the start of the litterbag experiment. All the samples were analyzed for C/N ratio using the Mass Spectrophotometer at the Archaeology Department at the University of Cape Town. The method was adopted by Chimpango, et al. [34]. Concentrations of Carbon (C) and Nitrogen (N) in all the different grass leaves were measured as %C and %N using a Carlo Erba NA 1500 elemental analyzer (Fisons Instruments SpA, Strada Rivoltana, Italy) coupled with a Finnigan MAT 252 mass spectrometer (Finnigan MAT GmbH, Bremen, Germany) via a Conflo II open-split device. The amount of C and N per grass leaf was estimated from the product of %C and %N and the dry matter weight. For lignin determination, the ANKOM method was used. This is a stepwise



Table 1: The best five models for k for photodegradation vs soil surface decomposition during the initial and final stages were selected from the multiple linear regression using an information theoretic approach [32,33].

Model	Initial photodegradation					Initial surface decomposition					Later photodegradation					Later surface decomposition				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Lignin			X	X		X	X			X	X		X	X		X		X		
Polyphenolic	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X		
C/N ratio	X			X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X
SLA				X		X	X			X		X		X		X	X	X		X
Tensile strength	X	X	X	X	X	X	X	X			X	X	X	X	X	X	X	X	X	X
df	3	2	3	4	4	4	5	4	2	3	4	3	5	4	4	4	3	4	3	3
AIC	59.4	59.8	59.9	60.7	61.1	44.5	46.5	49.9	50.3	51.3	50.1	51.5	52.0	52.6	53.4	54.8	56.0	56.1	56.3	56.4
Delta AIC	0	0.46	0.56	1.3	1.71	0	1.98	5.41	5.78	6.75	0	1.45	1.96	2.52	3.37	0	1.27	1.32	1.55	1.6
w (AIC)	0.16	0.13	0.12	0.08	0.07	0.63	0.23	0.04	0.03	0.02	0.33	0.16	0.12	0.09	0.06	0.16	0.08	0.08	0.07	0.07

procedure that starts by removing proteins, then hemicellulose, cellulose, crude fiber, and lastly acid lignin. This was done using the ANKOM Fibre Analyzer. The last step of this method involves ashing the samples to determine the loss at ignition. A comprehensive description of the method can be found on the ANKOM website (www.ankom.com). The method was similar to that used by Rowland & Roberts [35]. The Prussian blue assay method [36] was used to assay the polyphenolic content of the ten different grass species in this study. In addition, we measured tensile strength and specific leaf area (SLA) for each species. We followed the method of Balsamo, et al. [37] for measuring tensile strength. Tensile strength was calculated by dividing the failure load (force) by the cross-sectional area of the leaf blade. The specific leaf area (SLA) was the projected leaf area per dry mass. The leaf areas of thirty leaves per species were measured using the LI-3000 Area Meter (LI-COR inc., Lincoln, Nebraska, USA). It was then divided by the dry weight measured using a mass balance to establish SLA, which was then correlated with the decomposition rate.

Data analysis

Variation in decomposition rates: Decomposition was measured as mass loss as well as the decomposition constant (k). k is obtained from the equation $B_t = B_0 e^{-kt}$. Weight loss and decomposition constant were used as the dependent variable to determine whether there was variation in decomposition rates between different species and treatments. All data were first tested for homogeneity of variance using a Goodness of fit distribution histograms in JUMP 5.01 and data transformations were applied where appropriate. Data were analyzed using the Fit Y by X routines of the JMP to compare differences between species and treatments at the different stages of either microbial or photodegradation. A One-Way ANOVA was used for comparison of rates at different stages of decomposition following the All Pairs Tukey-Kramer test.

Variation in plant traits: A regression analysis was performed to determine which variables best predicted decomposition either in the sun or on the soil. Comparing predictor variables using Pearson correlation coefficients we checked multicollinearity between the variables. Six predictor variables were

used for this analysis, that is, lignin, polyphenolics, C/N ratio, SLA, and tensile strength. Polyphenolics were also adjusted by dividing values by 1000. Generalized linear models, stepwise regressions, and other multiple linear regressions [39] were employed to predict the best possible model that predicts decomposition rate in this study. We ran the best sub-sets model with the Akaike Information Criterion ((AIC)) [32,33] was used to select the best model. This method works out which variables are most consistently entered into the best models that have $\Delta AIC < 4$ and also have the lowest AIC but more importantly the model with the fewest variables was selected to be the “best” in the decomposition process.

Results

Variation in photodegradation and microbial decomposition

The decomposition rate for the soil treatments was significantly higher than for the standing treatments (Figure 1). Initial and late decomposition stages were significantly higher for the soil treatment than for the standing treatment. Differences in decomposition rates among the treatments were more pronounced at the later stage of decomposition.

Decomposition rates of grass species across treatments

The grass species used in this study had different rates of decomposition during initial and late decomposition (Figure 2). The rates of decomposition were highest for *Dactyloctenium Australe* and *Urochloa mosambicensis* but slowest for *Digitaria longiflora* and *Sporobolus pyramidalis*. The former species were not significantly different from each other but were significantly different from the latter species. During the initial decomposition stage, three species showed significant differences between the standing and soil treatment. These species include *Dactyloctenium australe*, *Themeda triandra* and *Bothriochloa insculpta*. *Hyparrhenia filipendula* was the only species that had higher rates (although not significant) for standing than soil treatment only during the initial decomposition stage. Most species showed treatment differences at a later stage of decomposition except *Eragrostis curvula*, *Cymbopogon excavatus*, *Digitaria longiflora*, *Sporobolus pyramidalis*, and *Hyparrhenia filipendula*.

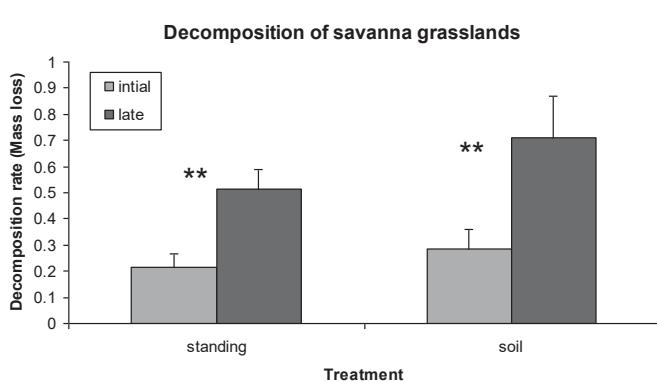


Figure 1: Photodegradation versus microbial decomposition rates of savanna grasses during 63 and 124 days of decomposition (initial & late). The following symbol (**) shows ($p<0.01$) significant differences between grass functional types.

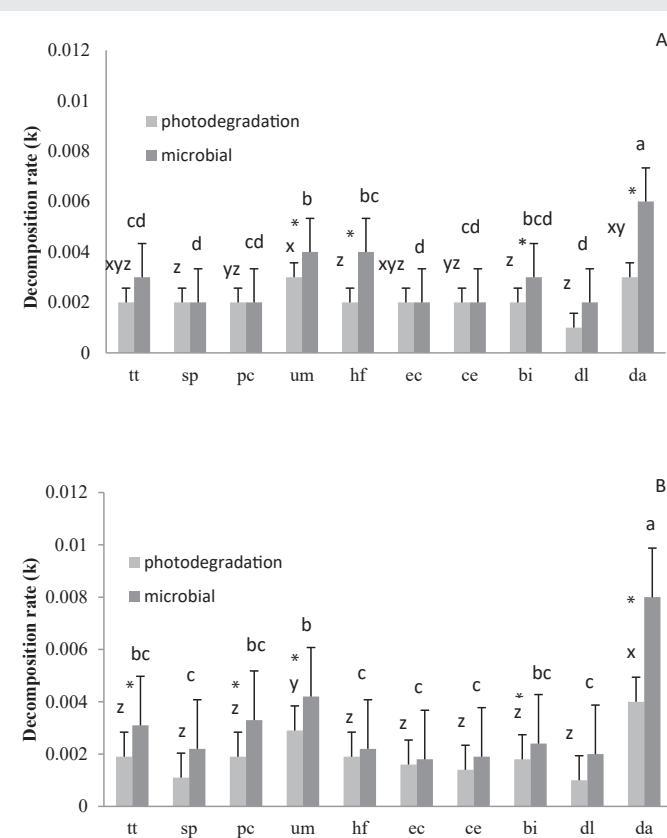


Figure 2: Variation in decomposition rates of individual grass species compared between photodegradation and microbial decomposition during the initial stage (a) and final stage (b). The letters (a-d) depict significant grass species from others in the sun treatment while (x-y) depicts significant grass species from others in the soil treatment whereas * shows treatment differences. Species codes are explained in the study area section under the methods and materials.

Plant traits differences

The species used in this experiment had different chemical and physical leaf traits at the beginning of the experiment (Table 2). Chemical traits include lignin, polyphenolic content, and C/N ratio. The species that had the highest mean lignin content by far was *Sporobolus pyramidalis* with *Digitaria longifolia* having the least mean lignin content. *Themeda triandra* had the highest mean polyphenolic content followed

by *Bothriochloa insculpta* with *Urochloa mosambicensis* having the least polyphenolic content. *Eragrostis curvula* had the highest C/N ratio with *Dactyloctenium australe* having the lowest C/N ratio. Physical leaf traits included specific leaf area and tensile strength. The highest mean specific leaf area was obtained in *U. mosambicensis*. It was followed by *Panicum coloratum* and the lowest mean specific leaf area was found in *E. curvula*. The tensile strength of some species exceeded the tensiometer's force; the values for *S. pyramidalis*, *E. curvula*, and *C. excavatus* could actually be double the obtained values. The highest mean tensile strength was obtained in *D. longifolia* followed by *H. filipendula*, *E. curvula*, and *S. pyramidalis*.

Initial photodegradation (after 63 days)

A two-factor model number 2, in table 1 including polyphenolics and tensile strength was the best predictor of initial photodegradation. This model had the highest predictive power although it had a higher ΔAIC value than the lowest three-factor model (model 1). No other two-factor model had comparable predictive power. Models 1, 3-5, which include various combinations of the other three plant traits, were also acceptable predictors ($\Delta AIC < 4$, [33]. The estimated regression coefficients for model 2 were -0.46 (polyphenolics) and -0.31 (tensile strength). The estimated standard errors for the regression parameters were 0.09 and 0.16 respectively. The selected model had an R^2 value of 0.69 and a p -value of 0.002.

Initial soil surface decomposition (after 63 days)

A two-factor model, number 4 in Table 1 including C/N ratio and polyphenolics, was the best model. This model had the highest predictive power but not the lowest ΔAIC value. A single-factor model number 6 not included in Table 1 with only a C/N ratio had comparable predictive power. Model number 1 which includes various combinations of the other plant traits was also acceptable, especially since $\Delta AIC < 4$. The estimated regression equation was $k = \text{intercept} - 0.67 (\text{C/N ratio}) - 0.42 (\text{polyphenolics})$ with an estimated standard error of 0.19 and 0.09. The selected model had an R^2 value of 0.60, $p = 0.002$.

Table 2: Plant traits differences among the savanna grasses used in the paper.

Species name	Lignin	Polyphenolics	C/N ratio	SLA	Tensile strength
<i>Themeda triandra</i>	5.0	35604.3	51.8	98.9	21.1
<i>Sporobolus pyramidalis</i>	6.7	19238.1	59.3	62.4	33.1
<i>Panicum coloratum</i>	4.4	24217.3	40.7	102.9	12.9
<i>Urochloa mosambicensis</i>	5.4	5610.1	44.3	147.3	13.1
<i>Hyparrhenia filipendula</i>	4.0	22941.5	64.3	68.1	39.3
<i>Eragrostis curvula</i>	4.6	11274.6	74.1	32.1	35.2
<i>Cymbopogon plurinoides</i>	4.8	24429.2	72.3	57.4	24.9
<i>Bothriochloa insculpta</i>	4.7	33473.4	57.4	93.8	13.2
<i>Digitaria longifolia</i>	3.1	15154.5	60.2	74.2	66.0
<i>Dactyloctenium australe</i>	4.1	17536.9	18.1	97.5	20.0

Mean values are shown in this instance.



Late photodegradation (after 124 days)

A three-factor model, number 2 in table 1 including lignin, polyphenolics, and tensile strength, was the best predictor of late photodegradation. This model had the second lowest AIC value of all models. Models 1, 3–5, which include various combinations of all the plant traits, were also acceptable predictors ($\Delta\text{AIC} < 4$, (Burnham and Anderson, 2002). The estimated regression equation was $k = \text{intercept}-2.02$ (lignin)-0.26 (tensile strength)-0.25 (polyphenolics). The estimated standard errors for the regression parameters were 1.39, 0.10, and 0.14, respectively. The selected model had an R^2 value of 0.74, $p = 0.003$.

Late surface decomposition

In Table 1 a three-factor model number 4 including C/N ratio, tensile strength, and polyphenolics was the best predictor of decomposition rate in the soil over 124 days. This model was among those with the lowest AIC values. Model 9 not included in the table with two factors that included C/N ratio and tensile strength, was the best two-factor model and might have more predictive power than model 4. All the models except model 10, which include a combination of the two plant traits, were also acceptable predictors ($\Delta\text{AIC} < 4$, [33]. The estimated regression equation for model 3 was $k = \text{intercept}-0.41$ (C/N ratio)-0.32 (tensile strength)-0.24 (polyphenolics). The estimated standard errors for the regression parameters were 0.08, 0.08, and 0.14, respectively. The selected model had an R^2 value of 0.94, $p = 0.000$.

Discussion

Ungrazed grass often becomes moribund, reducing the amount of plant material that enters the decomposition subsystem [13,27]. Nutrients are locked up in the aboveground compartment rendering them unavailable, negatively influencing the soil-based microbial abundance and activity [41] and thus litter decomposition [27,42]. The importance of standing litter carryover in influencing grass productivity has been recognized [13,25], but not much was documented on its control on decomposition in ecosystems where this was prevalent. This persistence of grass material not grazed by herbivores (termites included) as standing dead litter may take several years before being incorporated into the surface litter pool unless fire was applied [25].

Recent studies have shown that the process of decomposition starts prior to that, which is during the dry season when litter is still attached as standing dead material. Breakdown by abiotic drivers such as the sun through a process called photodegradation as well as from water vapor before litter reaches the soil have now been recognized [17,19]. Most studies assume that grass litter gets to soil and therefore ignore whether standing litter decomposition was different from microbial decomposition in the soil. The paper showed that standing grass litter decomposition was slower than soil decomposition in savanna grasslands. Standing litter first has to reach the soil and this was discovered to be a slow process. Photodegradation appeared to alter the rate at which plant

litter reaches the soil. Other studies have shown that solar radiation plays an important role in soil surface decomposition [6,18–20,43] but did not simulate standing litter. The fact that standing litter decomposition was significantly slower than soil decomposition implies that microbial decomposition occurs at much faster rates than photodegradation. This further suggests that belowground decomposition (soil organic matter) may be different [44]. Bontti, et al. [45] have shown the latter statement to be true in the US Great Plains as belowground decomposition was significantly faster than aboveground decomposition in their study with litterbags placed on the ground and therefore not simulating standing litter.

Photodegradation although highly important in drylands [19], appeared to be a rate-controlling step throughout the process of decomposition in savanna grasslands in this paper. This happens at the start of the dry season during the initial phase of decomposition until the final stages of decomposition at the beginning of a wet season. This was an important finding in terms of understanding nutrient cycling in tropical savanna grasslands in the world where necromass was common. Throop & Archer [6] showed that litter in drylands would be subject to decomposition via photodegradation (processes such as photo-oxidation [21,43] and leaching while breakdown by decomposers would be minimal, these may probably be the case in tropical grasslands.

An understanding of grass species dynamics throughout the process of decomposition in savannas had not been carried out to our knowledge before the project was started in 2003. In this study, we showed significant differences in decomposition rates amongst the various dominant grass species at Hluhluwe iMfolozi Park, with some more common throughout tropical savannas. Davies, et al. [14] show that grass litter varied among the four grass species in their study at Kruger National Park with only one of their species not investigated in our study. Litter decomposition has been shown recently in South Africa [27] and Inner Mongolia (China) to be dependent on the species or species type. Other focussed on savanna tree species to come to the same conclusion in Brazil [44] and Kenya [46]. In this paper, species that were able to resist physical breakdown accumulated more standing litter than those that didn't and hence quicker rates of decomposition. Therefore the former species will inhibit productivity in the wet season unless fire was applied prior to the rains. For example, *U. mosambicensis* and *D. australis* decomposed at greater rates and were unlikely to accumulate standing litter while *Digitaria longiflora* and *Sporobolus pyramidalis* were likely to. This was true for mesic and semi-arid savanna grasslands in the Hluhluwe iMfolozi Park where the latter species were commonly found moribund throughout the park but largely in the mesic areas [13]. For some species such as *Themeda triandra* and *Bothriochloa insculpta*, the trick was to get to the soil, since when on the soil the rates of decomposition were clearly quicker than when standing. When standing the latter species was able to resist photodegradation and hence the process was an important rate-controlling step. The grass species with either structural or chemical protection mechanisms against sun breakdown had slower decomposition rates.

In American grassland, the accumulation of dead material has been shown to be due to the fact that their grasslands were dominated by tussock grasses [25] while in mesic savanna grasslands in South Africa species like *Themeda triandra* and *Andropogon* spp, which belong to a subtribe Andropogoneae were also responsible for litter accumulation [13]. Scientists have found some species to resist both physical and microbial breakdown due to the fact that they are heavily armed with polyphenolics and have a recalcitrant litter [26]. Litter quality has long been recorded as an important contributor to variation in decomposition rates among species [24]. Plant traits responsible for photodegradation in savanna grasslands include polyphenolics and tensile strength. There was a negative relationship between the two predictors and decomposition rate which suggests that during initial photodegradation species with higher polyphenolics content and tensile strength had slower rates of decomposition. For example, *Digitaria longiflora* and *Sporobolus pyramidalis* with the slowest rates of decomposition had the highest tensile strength while the other slow decomposing species while standing such as *Bothriochloa insculpta* and *Themeda triandra* had the highest polyphenolics content. The two plant traits together with the C/N ratio and lignin were also important at the later stage of photodegradation. Since Bonatti, et al. [45] showed that decomposition belowground was faster than aboveground, and then plant traits responsible for soil organic matter decomposition are likely to be different from that responsible aboveground (photodegradation & microbial decomposition). Lignin together with moisture (precipitation) was the best predictor of soil organic matter decomposition in their paper.

Many studies have shown that plant species that produce a large quality of polyphenolics deter herbivores and save themselves from being heavily grazed [47,48]. Other studies found that light levels profoundly influence foliar phenolic levels including polyphenolics [49] despite the often held view of defense against herbivores (Robbins, et al. 1987). However since there is a close link between litter decomposability and vegetation response to herbivory [31], polyphenolics may influence decomposition rate. In forest soils, chemical factors like polyphenolics interfere with the enzymatic functioning or decomposer metabolism resulting in a reduction in litter decomposition rate [50]. But in this instance, polyphenolics may be responsible for the blockage of sunlight and therefore slower photodegradation, as well as interfering with microbial decomposition. A recent laboratory experiment by Lee, et al. [21] suggested photodegradation was not only about photo-oxidation or photochemical breakdown of litter but other processes may need to be explored as well.

In terms of microbial decomposition, the most important predictor is the C/N ratio, but tensile strength was also important. Microbial organisms seem to favor species with a lower C/N ratio. This implies that there was less N for microbes to use on the soil when there was a high C/N ratio. Nitrogen has been determined to be very crucial for microbial organisms in the soil [8,24,51] and therefore greater availability of nitrogen in the litter speeds up decomposition. This was similar to results found by other ecologists investigating decomposition

and nutrient cycling in other terrestrial ecosystems [29]. This implies that a loss of C from the plant litter leads to an increase in decomposition rate especially when microbes feed on plant litter. For example, *D. australis* with a high nitrogen content or low C/N in its litter showed greater decomposition rates than *S. pyramidalis* with a low nitrogen litter or high C/N. Chapin [28] reported the same trend of litter decomposition in association with nitrogen content. They suggested that this was caused by the fact that microbes were seldom N limited below a C/N ratio of 25:1. The N in excess of microbial demands for growth was released into the soil where it becomes available to plants [52].

Structural leaf traits like tensile strength and specific leaf area have been shown to be important in explaining ecosystem processes, especially in the US [28]. Tensile strength was a strong predictor of decomposition in this paper whereas SLA was not. Studies on the mechanical properties of grass leaves have elucidated much useful information such as the relationship of leaf tensile strength and stem flexibility to palatability to livestock [53] and more recently, drought tolerance [38]. The latter paper suggested that a grass species with high tensile strength will tolerate drought compared to grass with low tensile strength, therefore photodegradation might be lower for species with high tensile strength. Our study confirmed that initial photodegradation was influenced by tensile strength too; this implies that grass species that were less brittle took longer to break down under the influence of the sunlight, and therefore will accumulate more standing dead biomass. Theron & Booyse [53] suggested that the tensile strength of grasses was determined by the percentage of strengthening the tissue. In most cases, lignin has been found to be the strengthening tissue. It was also related to tensile strength in this paper. Several authors have shown a negative linear relationship between initial lignin concentration and the rate of mass loss during litter decomposition [29]. Some authors have found that decomposition at the later stages was determined by lignin [15,45,54] with the latter authors showing below ground decomposition was affected by recalcitrant material. However, lignin content did not contribute significantly to the initial decomposition rate in this study except at the later stages of decomposition since it was included in the models that governed standing and soil decomposition at a later stage. Litterbag mesh size did not alter the microbial composition, perhaps due to a failure to exclude decomposers, as mites and springtails were more or equally abundant in fine-mesh bags [55-59].

Conclusion

Decomposition of standing grass litter was half the rate of decomposition on the soil, though litterbags are known to underestimate decomposition rates. Rates of decomposition as found elsewhere were species-dependent. When grasses are still standing in the field, photodegradation may be more important than the microbial process. Decomposition rates were not always correlated for standing versus soil, especially during the initial stage of decomposition. Therefore different factors operate or govern the different stages of decomposition in savanna grasslands. This further suggests conversion



of standing to surface litter may not be the same process as the conversion of surface litter to humus (needs further investigation). Photodegradation was governed by different leaf traits from those predicting microbial decomposition in the soil and therefore soil organic matter decomposition is likely to be governed by different traits. These traits include polyphenolics and tensile strength for photodegradation and the C/N ratio for microbial decomposition in both mesic and arid tropical savannas.

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