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Testing the Ecosystem Productivity- Diversity Hypothesis in a Grassland

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Abstract

Globally, the academic debate about the relationship between species diversity and ecosystem productivity has been widely contested. While some researchers support the positive relationship between ecosystem productivity and diversity, others propose the reverse. However, mechanisms that play a role in this relationship remain unclear. As such a study was conducted in Lilongwe plain, in Malawi to test the theory of ecosystem productivity and diversity in a grassland ecosystem to make a humble contribution to this debate. Methodologically, five transects of 25metres each, were systematically drawn across the area. Each transect had 14 quadrats that were randomly placed at a distance of 10 meters apart. The data sets (moisture content, distribution and composition of plant species were collected in 5 transects located in two contrasting areas of dry and waterlogging conditions. Alpha diversity was computed to determine variations in species diversity between dry and the water logged areas. The results show that moisture content and species composition were the main productivity influencing factors with P-values <0.05. Results further show that there is indeed a relationship between productivity and diversity which was affected by variations in the availability of water, legume species that initiates nitrogen fixation, and nature of the mixture of the grass stands within the study area. Despite few numbers of species in areas of high water concentration, the results show that the biomass production was considerably high. The higher diversity in the upper and middle areas of the land indicates more species that survive as well as facilitate and complement each other.

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Such areas support the concept of complementarity which result from interspecific differences in resource requirements and that of facilitation which result from certain species helping or allowing other species to grow by modifying the environment in a way that is favorable to co-occurring species. The findings suggest that the correlation between productivity and diversity cannot be disputed. But the specifics as to when and how this relationship exhibits need to be clearly understood since this relationship is influenced by factors such as species composition as well as conditions in that particular area where the species exist, (in this case the grassland). Perhaps in this study the relationship was influenced by the presence of water in some areas which exhibited higher biomass but little diversity, as well as the presence of leguminous grasses that fix nitrogen and benefits surrounding species hence increasing the biomass as well.

Keywords*:* Ecosystem Diversity; Productivity; Grassland; Species

1. Introduction

1.1 Overview of species diversity and productivity hypothesis

Biological diversity has attracted public attention recently addressing issues associated with disappearing species around the world and the need to conserve them. Discussions of the value of diversity has been intense involving different concepts such as genetic diversity, habitat diversity, species diversity; and mostly this is not specified when the issues of diversity conservation are being discussed or addressed [1]. Species engage themselves in three kinds of interaction; competition, symbiosis, predation-parasitism; and these interactions affect ecosystem productivity in one way or another [1]

This study defined diversity as the number of different species within a community or an ecosystem. In other words, areas of high diversity are characterized by great variety of species. Productivity on the other hand is defined as a measure of relating quantity of output or a measure of ecosystem function.

In the face of declining biodiversity, the question of how species diversity relates to productivity of ecosystems has become critically important. Researchers have long been examining how biodiversity controls rather than simply responds to the production of biomass in an ecosystem [2]. Other researchers have proposed that diversity and productivity must somehow exhibit bi-directional causality [3,4]. But in all this, the mechanism by which this might occur remains uncertain.

These differing perspectives on productivity-diversity relationship have stimulated a lively debate about whether biodiversity is the cause or the consequence of ecosystem production. As this is the situation, scientists have begun to ponder as to how this query can be resolved and it is thought that these perspectives can be determined by recognizing that historical research has focused on how resource supply regulates both productivity and diversity where as more recent studies have focused on how the richness of an ecosystem regulates the efficiency by which these resources are being put to use [6].

This paper therefore presents a contribution of this debate in the context of the local conditions of Malawi focusing on the factors affecting the composition as well as distribution of the species within the study area. It further gives insight into how diversity-productivity relationship is affected not only by the soil conditions as in water logged, wet and dry conditions within an area, but also the relationship amongst the species themselves.

1.2 Productivity- Diversity relationship

Some researchers have done some remarkable work in contributing to this research though most experiments documented on productivity- diversity relationship have mostly been done rather at a larger scale and in controlled and marine ecosystems. Little has been done in the terrestrial ecosystem. For example, diversity and productivity in long-term grassland experiment [7], and also productivity-diversity hypothesis in streams [2].

As such, it is unclear whether conclusions can be readily extrapolated to the smaller scales and whether the results can hold true irrespective of scale and of type of ecosystem. Doing experiments in the larger scale may have missed variations in productivity. In fact, depicting changes in the ecological systems is generally challenging as it requires capturing various spatial- temporal scales. Hence, generalizations of study outcomes can be questionable.

Importantly, the productivity-diversity relationship may depend on the type of the ecosystem. Hence this study was conducted in grassland since different species are adapted to different environments. Core to the understanding of this relationship is its implications not only to agriculture but also to the maintenance of ecosystem resilience to disturbances.

2. Literature Review

2.1 Diverse communities and productivity

More diverse communities increase the chances that at least one species is highly productive. The basis of this is that more diverse communities may be able to tap resources more effectively because they differ in strategies for resource acquisition [1]. Though there have been a lot of arguments back and forth, to some extent it is clear that this explanation contribute to the phenomenon. In other words, there is something about more diverse community that can at least make it more productive and may as well make it stable.

Two things commonly measured in relation to changes in diversity are productivity and stability. Productivity is a measure of ecosystem function. It is generally measured by taking the total aboveground biomass of all plants in an area. Many assume that it can be used as a general indicator of ecosystem function and that total resource use and other indicators of ecosystem function are correlated with productivity [2,7]. Creating the need for a study that does not focus on stability but the productivity with particular emphasis on the influence of the diversity on the grassland ecosystem

2.2 How diversity influence ecosystem productivity

Authors in [8,9,5] have described how diversity might influence ecosystem productivity and this is explained as follows:

Complementarity

Plant species coexistence is thought to be the result of niche partitioning, or differences in resource requirements among species. By complementarity, a more diverse plant community should be able to use resources more completely, and thus be more productive. Also called niche differentiation, this mechanism is a central principle in the functional group approach, which breaks species diversity down into functional components.

It has been hypothesized that niche complementarity, which result from interspecific differences in resource requirements and in spatial and temporal resource and habitat use, or from positive interaction, is predicted to allow stable multispecies coexistence and sustainably greater productivity at higher diversity.

Facilitation

Facilitation is a mechanism whereby certain species help or allow other species to grow by modifying the environment in a way that is favorable to co-occurring species. Plants can interact through an intermediary like nitrogen, water, temperature, space, or interactions or herbivores among others. Some examples of facilitation include large desert perennials acting as nurse plants, aiding the establishment of young neighbors of other species by alleviating water and temperature stress and nutrient enrichment by nitrogen-fixers such as legumes.

It is suggested that primary productivity in more diverse plant communities is more resistant to and recovers more fully from, a major drought [10,7]. In their experiments, these ecologists found that more diverse communities are more resistant than less diverse communities but they do not have to be very diverse. In addition to that, Authors in [5] suggests that plant cover is an increasing function of species richness and lower concentration of inorganic soil nitrogen, presumably because of greater nitrogen uptake in more diverse communities.

2.3 Variation of species in different places

Species diversity varies greatly from place to place because of differences in species richness and their relative abundance. One system can support more species than another in several basic ways. A greater variety of available resources will support more species than a less diverse resource base. More species can be packed in on the same range of available resources if, on average, species use a narrower range of resources (i.e., they are more specialized and have narrower niches). Resource partitioning among species reduces competition and promotes diversity. More species can be packed in on the same range of available resources if, on average, species share more resources (i.e., they tolerate greater niche overlap), [8,9]. Each of these mechanisms contributes to local diversity. Another way in which two systems can differ is in the degree to which they support as many species as possible, or the degree of saturation with species.

2.4 Factors influencing the structure and composition of plant communities

Plant abundance, structure and composition vary with nutrient and water availability [11,12]. In grasslands, slope influences soil properties such as texture and depth, which in turn influence the distribution of vegetation communities [6,9]. It is hypothesized that in a wetland ecosystem, variations in waterlogging period will influence variations in nutrient availability and chemical properties which will ultimately influence the distribution of plant communities, their composition and stricture. However, the composition and structure of plant communities change also in response to disturbance factors such as flooding, grazing and fire [12].

Authors in [2,9,14] stipulate that there are three pathways that operate concurrently to generate productivity diversity relationship in nature and these are; resource supply directly limits the standing biomass and/ or rate of new production;, producer biomass is directly influenced by the richness of species that locally compete for resources; resource supply rates indirectly affects producer biomass by influencing the fraction of species that locally coexist.

2.5 The Functional diversity hypothesis

Though most of the literature supports the productivity-diversity relationship, others have a different view as well [5,9]. For example explain about functional diversity, saying that experiments concerning this relationship just focus only on the numbers of species present, not on the functions they play in an ecosystem. They summarize evidence from a variety of studies suggesting that ecosystem processes depend on functional diversity far more strongly than on species diversity per se. They suggest two plausible explanations:

Functional redundancy

Two or more species in a particular ecosystem may play essentially the same role in ecosystem processes. It may for example, make relatively little difference to the nitrogen dynamics as to which particular species of legumes are present, only that there are some nitrogen-fixing plants available. The loss of species with similar functional effects should have relatively little effect on ecosystem processes.

Functional insurance

The more divergent species in an ecosystem are with respect to their influence on ecosystem processes, the smaller number is required to buffer an ecosystem against change. Species with similar functional effects that differ in functional response may buffer ecosystems against externally imposed change because the species that influence each ecosystem response may respond differently.

3. Methodological Approach

The study was conducted at Bunda College, Sakhula farm grassland (100m^2). This area is located in Lilongwe, the southern region of Malawi, and it is 32km from the Lilongwe city. The type of soil is pellivicvertisols characterized by high clay content [15]. Usually good for grazing though it had not been grazed during the time of the study.

The land type units in the study area were categorised as upper, middle and lower areas depending on their slope and moisture content. The upper was drier than the middle, and the lower part had had much moisture content.

In other words, moisture content increased with reducing distance towards the dambo. Sample lay out was as figure 1

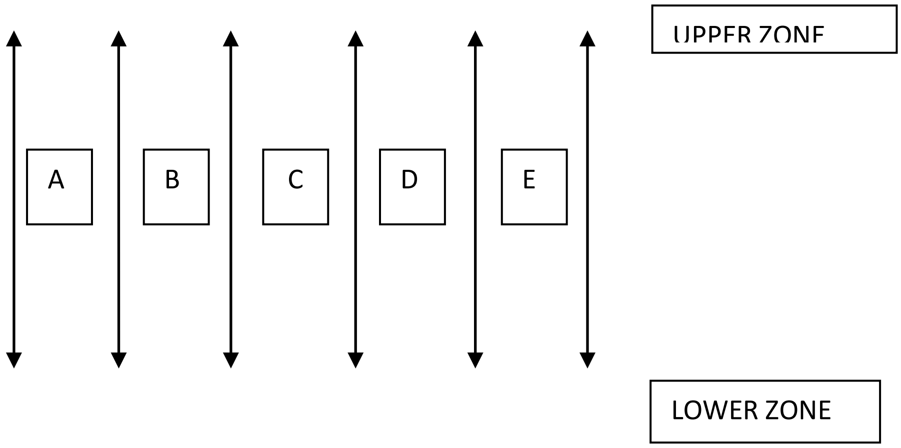

Figure 1: Lay out of the study area

The climate is tropical continental with two distract season, the rainy season from November to April and the dry from May to October. However, from May to July, it is relatively cool and even drizzles sometimes. Annual rainfall ranges from 700 to 1800mm and annual minimum and maximum temperature ranges from 12 ºC to 32ºC.

3.1 Sampling design

The study site was systematically stratified, specifically to address questions related to the influence of the moisture content (water availability) on the vegetation. Stratification was done based on drainage as well as the slope of the area; thus three zones: the upper (being drier), middle (relatively moist), and lower zone (water logged).

Five transects at regular intervals of 25metres were made and 14 quadrats at regular intervals of 10 meters were made along each transect. Although quadrats were used in the sampling of the vegetation, in the analysis of data, transects were regarded as the main experimental units.

3.2 Measurements of diversity and productivity variables

A measure of the diversity of species in a given area is used to answer questions in ecology and to document patterns important to conservation. Species diversity is typically measured in one of two ways, either as a simple count of the number of species in an area (species richness) or by an index that takes account of the importance of each species. In the study, Alpha and beta diversity measures were used.

Alpha diversity

It is defined as number of species per unit area within a homogenous plant community, or as the total number of species in a homogenous stands of vegetation [16]. So by observation and counting, alpha diversity was determined. This method was also used by Jean and Bouchard [12].

4. Results and Discussion

4.1 Variations in Species composition and their distribution

Table1show the names and a range of the different species along line transects and their respective distribution according to categories upper, middle and lower zones. It appears that the species in the grassland have a defined niche either occurring on the upper, middle and lower zones of the area.

Table 1: composition and distribution of different species within transects

	upper		middle	Lower				
Imperatacylindica								
Terrannus species								
Sporabolaspyramidalis								
Setariaspacelata								
Stylosanthesguyanesis								
Paspalumdilitatum								
Desmodiumuncinatum								
Desmodiumintortum								
Brachiariamutica								
Leervia								
Joint vetch								
Sedges								
Digitaria grass								

Amongst all the grass species, sedges of different types and green leaf as well as silver leaf *desmodium* was found to be common in all transects. For sedges, they dominated the lower part of each transect, where there were water logged conditions, in some parts, with a mixture of *desmodium.* Sedges might be adapted to varying environmental conditions such that variations in water levels within the study area did not negatively impact on its distribution. The thick stem might be an adaptive mechanism that allow it to survive in various conditions of the studied area from waterlogged to fairly well drained upper areas of the grassland.

4.2 Species productivity amongst transects

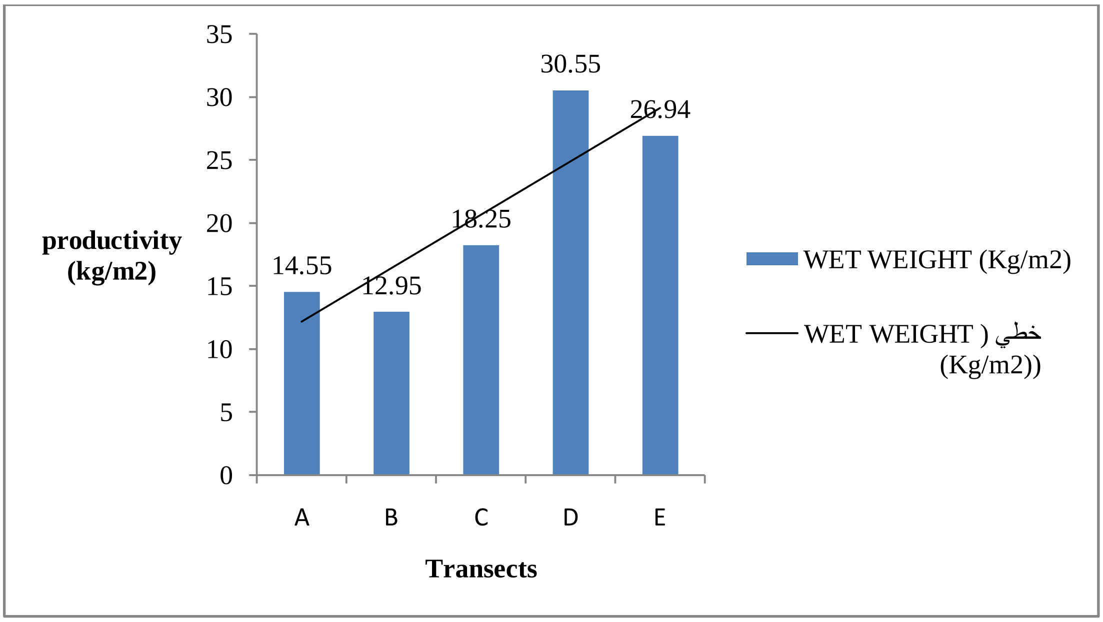

Figure 2: Productivity

Figure 2 shows the graph of species productivity in transects. A significant Species productivity relationship was observed from the upper down to the lower zone of the area. The biomass increased with moisture content from 14.55 to 26.94 kg/m$^{2.}$

The species productivity increase as we move down the slope may suggest that the lower areas keep moisture over a long time as the upper side dries first. The longer period of water availability may correspond to increased productivity as the species grow as long as water is available for growth. Those on drier lands may have had a shorter growing period and thus producing less matter in comparative terms. This observation was similar as we went down transect where the upper quadrats weighed lesser than the lower quadrats probably because of the same effect related to moisture content that allows for growth beyond rainy season.

4.3 Species diversity in the transects

Alpha diversity was used to determine diversity in the quadrats and beta (Whittaker's index) [16] to determine the diversity per transect. Figure 3 shows variations in the species diversity between similar ecological zones where the upper drier land exhibited large number of species (6) as compared to the lower wetland (3). The middle zone had an average number of species of (5), dominated by leguminous grasses.

The results demonstrated that the species diversity decreases along a gradient with more species on the upper slope and less species down the slope. This may suggest that some of the plants on the upper side do not tolerate being submerged as compared to the few ones found on the lower waterlogged site.

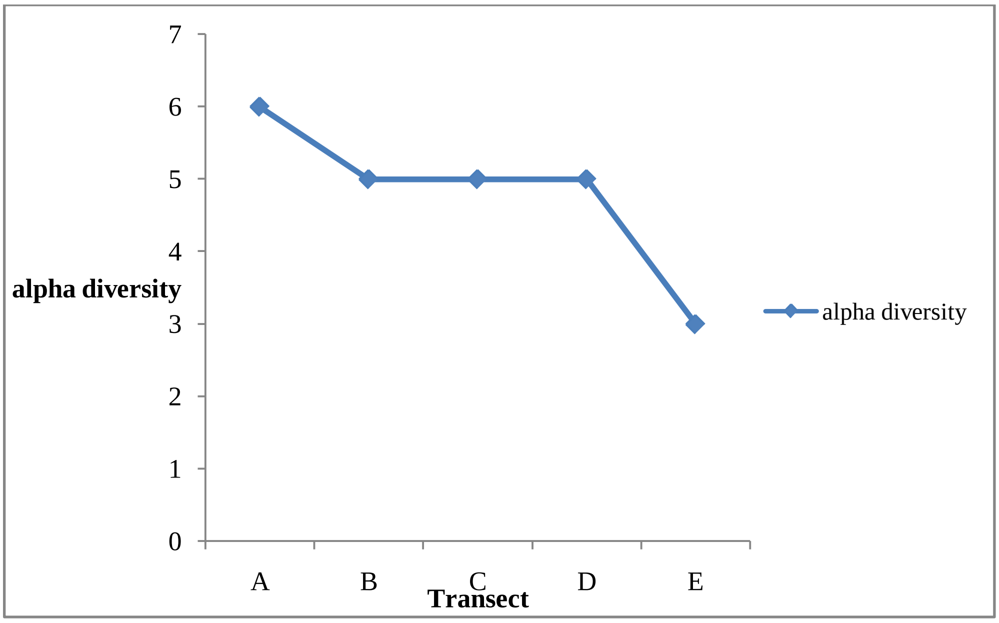

Figure 3: Alpha Diversity

4.4 The effect of grass mixture in areas of equal diversity (5) -transect 2,3,and 4

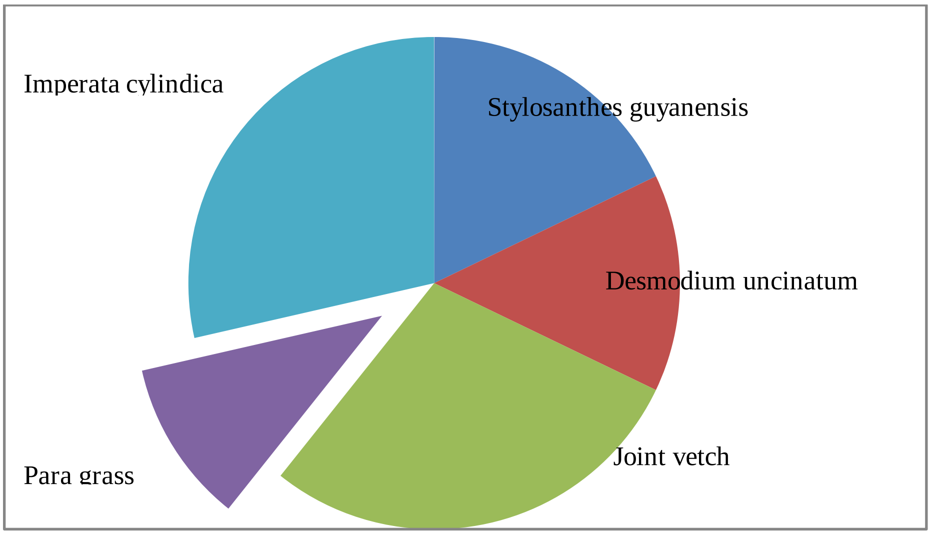

Figure 4: The contribution of *Para* grass in the mixed stand of grasses of transects 2. The productivity (12.95kg/m^2) of the stand was compromised by the presence of the Para grass which is known to inhibit the growth of other species as it produces cyanide.

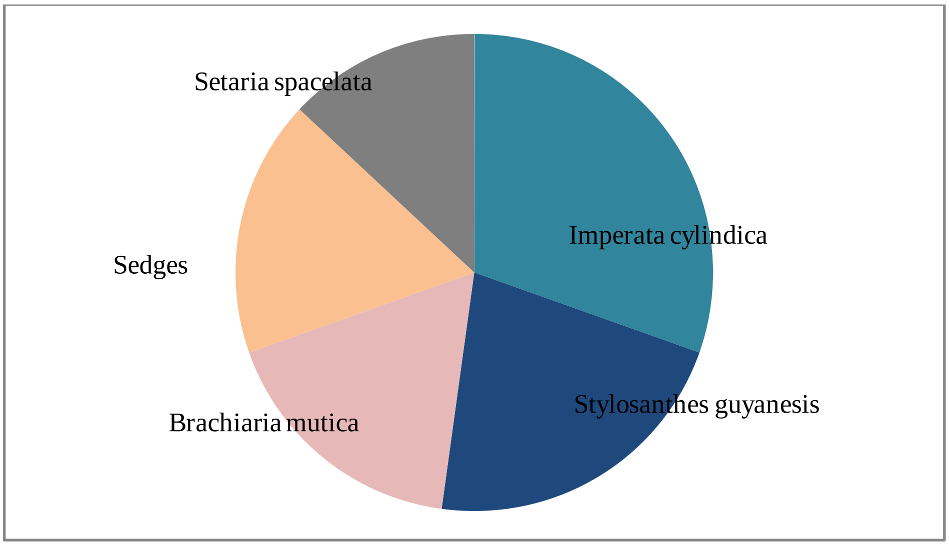

Figure 5: the contribution of the legumes in the mixed stand of grasses of transects 3 with productivity of (18.25kg/m^2). The stand exhibited positive relationship because of complementarity and synergism.

4.5 The productivity-diversity relationship

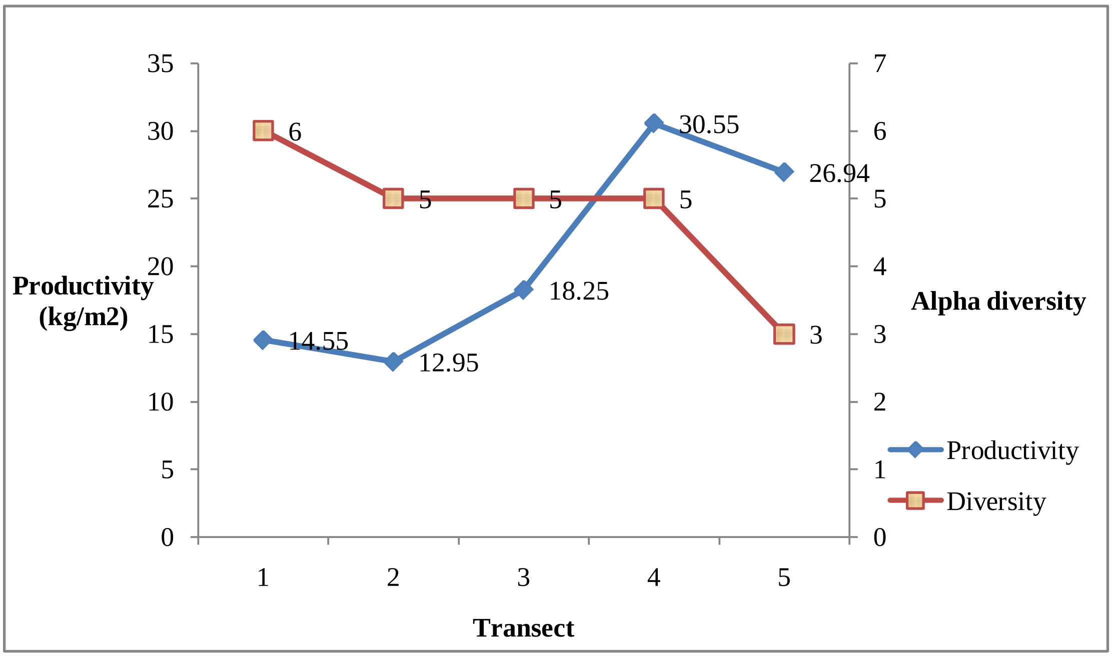

Figure 6: the productivity- diversity relationship graph indicating higher diversity (6) in the area of lower productivity (15 kg/m2), and vice versa.

Different flora differ in so many ways in terms of both moisture requirement and nutrient uptake [17], and differentiation in the use of various nutrients in each species contribute to not only the diversity but even the productivity as well since they have their own peculiar requirements. For example, in transect A, the average number of species was higher than the rest (6) and looking at its productivity, it started out higher than transect B (14.55WW & 4.13DW) before it picked up to higher productivity levels (Figure 6). The possible explanation to this may be because of higher numbers of leguminous species that were found in transect A which fix nitrogen and thus increase nutrient availability for growth of those species growing together with them.

The species diversity seems to reflect moisture availability with lower species where water is available for a long period of time and increasing diversity in drier areas. The higher diversity in the drier areas may reflect the ecosystem resilience to harsh conditions by allowing for greater number of species while where growth is assured with adequate water fewer species allow for survival of species and the ecosystem is stable with such few species. An important observation, which agrees with the findings of Author [12] who showed where areas have higher biomass and higher number of species.

Lower zone vegetation was floristically poor in terms of composition as shown by lower species composition as compared to the upper dry area (Table 1). This observation agreed with the findings of studies elsewhere in South Africa, where a wetland vegetation community was noted to have low species richness [10]. These findings also concurred with the general models of an inverse relationship between species richness and resource gradient [18] and in conflict with the productivity hypothesis [12,17]. Low species diversity in waterlogged areas may be explained with respect to differences in adaptation of plant species. Few species found in this study area can withstand extreme wet conditions and this was probably the reason behind this observation.

5. Conclusion

The correlation between productivity and diversity cannot be disputed. But the specifics as to when and how this relationship exhibits need to be clearly understood since this relationship is influenced by factors such as species composition as well as conditions in that particular area where the species exist, (in this case the grassland). Perhaps in this study the relationship was influenced by the presence of water in some areas which exhibited higher biomass but little diversity, as well as the presence of leguminous grasses that fix nitrogen and benefits surrounding species hence increasing the biomass as well.

5.1 Knowledge contribution

For the experiments that have been conducted, emphasis has been made with regards to the relationship, in terms of area effects, time theories, climatic stability, and competition as well as disturbance hypothesis. The effect of the legumes in the productivity-diversity relationship seems to have been missed or vaguely explained in most of the experiments done, hence a humble contribution towards this debate.

6. Management Implications

The results contain useful information for the management of grasslands especially in rangeland management. The results highlighted conditions for the positive and negative relationship between diversity and productivity which can be used in the successful management of rangeland (in terms of livestock feed).

Understanding this relationship is equally important in agriculture for considering mixed cropping where the mixture has to complement and not compete with one other.

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APPENDIX

Appendix 1: Species productivity

As already explained, the productivity of the species per quadrat was determined by measuring both wet and dry biomass on a scale at the students' animal farm and the soil laboratory respectively.

Table 1: variations in wet and dry biomass of the species in all the quadrats of transect A.

Quadrat no.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**total**
Wet weight (kg)	1.25	1.60	1.80	1.20	1.20	1.75	1.05	1.50	1.40	0.80	0.40	0.40	0.20	**14.55**
Dry weight (kg)	0.35	0.45	0.51	0.34	0.34	0.50	0.30	0.43	0.40	0.23	0.11	0.11	0.06	**4.13**

Table 2: Variations in wet and dry biomass of the species in all the quadrats of transect B.

Quadrat no.	1	2	3	4	5	6	7	8	9	10	11	12	13	TOTAL
Wet weight (kg)	1.00	1.70	1.05	1.05	1.20	0.90	1.20	1.40	1.10	0.60	0.80	0.45	0.50	**12.95**
Dry weight (kg)	0.28	0.48	0.30	0.30	0.34	0.26	0.34	0.40	0.31	0.17	0.23	0.13	0.14	**3.68**

Table 3: Variations in wet and dry biomass of the species in all the quadrats of transect C.

Quadrat no.	1	2	3	4	5	6	7	8	9	10	11	12	13	Total
Wet weight (kg)	3.20	4.25	2.90	2.75	2.60	1.85	2.25	2.00	2.00	1.85	1.70	1.70	1.50	**30.55**
Dry weight (kg)	0.91	1.20	0.82	0.78	0.74	0.52	0.64	0.57	0.57	0.52	0.48	0.48	0.43	**8.66**

Table 4: Variations in wet and dry biomass of the species in all the quadrats of transect D.

Quadrat no.	1	2	3	4	5	6	7	8	9	10	11	12	13	Total
Wet weight (kg)	3.20	4.25	2.90	2.75	2.60	1.85	2.25	2.00	2.00	1.85	1.70	1.70	1.50	**30.55**
Dry weight (kg)	0.91	1.20	0.82	0.78	0.74	0.52	0.64	0.57	0.57	0.52	0.48	0.48	0.43	**8.66**

Table 5: Variations in wet and dry biomass of the species in all the quadrats of transect E.

Quadrat no.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**Total**
Wet weight (kg)	2.00	2.60	2.10	2.00	2.00	2.00	2.70	2.34	2.20	2.10	1.90	1.60	1.40	**26.94**
Dry weight (kg)	0.57	0.74	0.60	0.57	0.57	0.57	0.77	0.66	0.62	0.60	0.54	0.45	0.40	**7.66**

Appendix 2: Data collection sheets

Transect A

Quad number	**Species Identified(Alpha diversity)**	**Wet weight/quad (kg)**	**Dry weight/quad (kg)**	**Beta Diversity (βw=s/α-1)**
1	8	1.25	0.35	
2	9	1.6	0.45	
3	8	1.8	0.51	
4	6	1.2	0.34	
5	6	1.2	0.34	
6	6	1.75	0.50	
7	6	1.05	0.30	
8	5	1.5	0.43	
9	5	1.4	0.40	
10	4	0.8	0.23	9/4-1 =3.00
11	4	0.4	0.11	
12	4	0.4	0.11	
13	4	0.2	0.06	

Transect B

Quad number	Species Identified (Alpha diversity)	Wet weight/quad (kg)	Dry weight/quad (kg)	Beta Diversity (βw=s/α-1)
1	5	1	0.28	
2	5	1.7	0.48	
3	6	1.05	0.30	
4	6	1.05	0.30	
5	7	1.2	0.34	
6	7	0.9	0.26	
7	7	1.2	0.34	
8	7	1.4	0.40	
9	6	1.1	0.31	
10	4	0.6	0.17	7/3.75-1 = 2.55
11	4	0.8	0.23	
12	4	0.45	0.13	
13	3	0.5	0.14	

Transect C

Quad number	Species Identified(Alpha diversity)	Wet weight/quad (kg)	Dry weight/quad (kg)	Beta Diversity (βw=s/α-1)
1	3	0.25	0.07	
2	3	0.4	0.11	
3	5	2.5	0.71	
4	5	2.4	0.68	
5	5	2.0	0.57	
6	5	1.7	0.48	
7	6	1.65	0.47	
8	6	1.65	0.47	
9	5	1.5	0.43	
10	5	1.6	0.45	
11	4	1.4	o.40	6/4-1 =2.00
12	4	1.2	0.34	
13	4	1.2	0.34	

Transect D

Quad number	Species Identified(Alpha diversity)	Wet weight/quad (kg)	Dry weight/quad (kg)	Beta Diversity (βw=s/α-1)
1	6	3.2	0.91	
2	5	4.25	1.20	
3	5	2.9	0.82	
4	6	2.75	0.78	
5	6	2.6	0.74	
6	6	1.85	0.52	
7	5	2.25	0.64	
8	5	2	0.57	
9	4	2	0.57	6/3.6-1 =2.31
10	4	1.85	0.52	
11	4	1.7	0.48	
12	3	1.7	0.48	
13	3	1.5	0.43	

Transect E

Quad number	Species Identified(Alpha diversity)	Wet weight/quad (kg)	Dry weight/quad (kg=)	Beta Diversity (βw=s/α-1)
1	2	2	0.57	
2	2	2.6	0.74	
3	2	2.1	0.60	
4	3	2	0.57	
5	3	2	0.57	
6	4	2	0.57	
7	4	2.7	0.77	
8	4	2.34	0.66	
9	4	2.2	0.62	
10	3	2.1	0.60	4/3-1 = 2.00
11	3	1.9	0.54	
12	3	1.6	0.45	
13	3	1.4	0.40	

Appendix 3: The means, standard deviations and standard errors of transects of the Sakhula grassland ecosystem

		N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean	
						Lower Bound	Upper Bound
3	transect	13	5.76923	1.690850	.468957	4.74746	6.79100
	Diversity	13	5.46154	1.391365	.385895	4.62074	6.30233
	Biomass	13	4.61538	.960769	.266469	4.03480	5.19597
	4.00	13	4.76923	1.091928	.302846	4.10939	5.42908
	5.00	15	3.06667	.703732	.181703	2.67695	3.45638
	Total	67	4.68657	1.519659	.185656	4.31589	5.05724
2	transect	13	2.072	.3521	.0977	1.860	2.285
	Diversity	13	.996	.3544	.0983	.782	1.210
	Biomass	13	1.496	.6530	.1811	1.102	1.891
	4.00	13	2.350	.7735	.2145	1.883	2.817
	5.00	15	1.996	.3850	.0994	1.783	2.209
	Total	67	1.789	.7010	.0856	1.618	1.959