this description since the curves with the steepest slopes and the
most linear form i.e. strongest dominance (numbers 4, 10, 12 and 13,
Fig. 44) ominate from samples that are certainly not early
successional. However, as demonstrated by Whittaker (1972) strong
dominance can occur relatively late in a successional sequence
associated with the invasion of grassland by woody plants. In three
of these samples (4, 10 and 13) a previously dominant woody species is
in the process or has already been replaced by a newly dominant
species. For example in site 4, Acacia luederitzii the current
dominant is being replaced by Euclea schimperi, E. divinorum and
possibly later by Spirostachys africana.

The dominance-diversity curves are illustrated from left to right
in order of increasing utilizable biomass (Fig. 44). This gradient
also reflects an increase in the relative proportion of woody plant
biomass. In addition it might seem apparent that the slopes (or
steepness) of the curves increases along this gradient. To explore
this relationship further, the equitability, Ec for each sample was
calculated and correlated with biomass. Equitability was found to be
significantly negatively correlated with the total utilizable plant
biomass ($r = -0.586, p<0.05$) (Fig. 45). This and other plant
diversity relationships and their significance will be explored in
more detail in the next chapter.

6.3.2 Large herbivore biomass and structure

Dry season large herbivore biomass measured at the intensive study
sites had a maximum of 15.9 and a minimum of 1.2 g m$^{-2}$. Species
richness during this time was between a maximum of 9 and a minimum of
5 species recorded per site (Table 13).

Wet season herbivore biomass lay between a maximum of 50.8 and a
minimum of 1.4 g m$^{-2}$ while the number of large herbivore species
utilizing the sites varied from 10 to 3, (Table 13). The confidence
limits of these estimates are difficult to estimate particularly for
plots where rare and very large herbivores (e.g. rhino species and
giraffe) occurred. In these instances a single sighting can make a
big difference to the estimate of biomass at the site but also
increases the confidence interval of these estimates. As a result of
Fig 45  Relation between equitability (Ec) and total utilizable plant biomass ($r = -0.586$, $p < 0.05$)
this, approximate 95% confidence intervals were generally high with a maximum of 73 and a mean of 37% of the mean biomass estimate.

Table 13 Estimated biomass (g m⁻²), species richness (No) and equitability (Ec) of the large herbivore communities utilizing the fifteen intensive study sites in the late dry and wet seasons.

<table>
<thead>
<tr>
<th>Site No.</th>
<th>Biomass</th>
<th>No</th>
<th>Ec</th>
<th>Biomass</th>
<th>No</th>
<th>Ec</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>5.6</td>
<td>8</td>
<td>2.69</td>
<td>20.9</td>
<td>9</td>
<td>3.11</td>
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<tr>
<td>2</td>
<td>7.5</td>
<td>7</td>
<td>2.83</td>
<td>19.8</td>
<td>10</td>
<td>3.48</td>
</tr>
<tr>
<td>3</td>
<td>3.1</td>
<td>9</td>
<td>1.21</td>
<td>16.6</td>
<td>6</td>
<td>2.50</td>
</tr>
<tr>
<td>4</td>
<td>10.5</td>
<td>7</td>
<td>2.22</td>
<td>6.7</td>
<td>7</td>
<td>3.93</td>
</tr>
<tr>
<td>5</td>
<td>15.9</td>
<td>8</td>
<td>2.52</td>
<td>10.1</td>
<td>10</td>
<td>3.92</td>
</tr>
<tr>
<td>6</td>
<td>1.2</td>
<td>8</td>
<td>4.54</td>
<td>4.3</td>
<td>8</td>
<td>3.36</td>
</tr>
<tr>
<td>7</td>
<td>12.9</td>
<td>7</td>
<td>2.72</td>
<td>6.4</td>
<td>8</td>
<td>2.88</td>
</tr>
<tr>
<td>8</td>
<td>3.5</td>
<td>6</td>
<td>3.03</td>
<td>20.1</td>
<td>9</td>
<td>3.12</td>
</tr>
<tr>
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<td>13.7</td>
<td>7</td>
<td>1.89</td>
<td>41.7</td>
<td>10</td>
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</tr>
<tr>
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<td>11.9</td>
<td>6</td>
<td>2.01</td>
<td>3.0</td>
<td>6</td>
<td>3.49</td>
</tr>
<tr>
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<td>4.0</td>
<td>6</td>
<td>3.42</td>
<td>8.6</td>
<td>6</td>
<td>3.01</td>
</tr>
<tr>
<td>12</td>
<td>6.4</td>
<td>5</td>
<td>2.31</td>
<td>1.4</td>
<td>3</td>
<td>2.80</td>
</tr>
<tr>
<td>13</td>
<td>12.4</td>
<td>8</td>
<td>2.88</td>
<td>11.9</td>
<td>7</td>
<td>3.35</td>
</tr>
<tr>
<td>14</td>
<td>4.6</td>
<td>6</td>
<td>3.87</td>
<td>6.3</td>
<td>5</td>
<td>3.96</td>
</tr>
<tr>
<td>15</td>
<td>4.1</td>
<td>8</td>
<td>3.21</td>
<td>50.8</td>
<td>9</td>
<td>2.71</td>
</tr>
</tbody>
</table>

Large herbivore data are summarized in the form of relative abundance distributions for each site. During both seasons they are generally linear (i.e. following the geometric series) with some tending to be sigmoidal (Fig. 46). A comparison of these curves with the large herbivore dominance diversity curve for the whole of Mkuizi
Fig. 46 Relative abundance distributions of large herbivores at each intensive study site during the dry (a) and wet season (b) study periods. Relative importance (abundance) is the percentage each species forms of the total estimated biomass at each site. Curves are fitted by eye.
(Fig. 33) (which approaches the lognormal form), would seem to support
the contention that the geometric and lognormal series "represent
extremes of a sample size-dependant continuum of relative abundances"
(McNaughton and Wolf, 1973). The individual site data describes the
partitioning of the realised niche space among co-occurring
populations and hence have geometric dominance diversity curves, while
the curve constructed from the regional abundance of species describes
the partitioning of realised niche space among species and is of the
lognormal form.

The relations between herbivore biomass, species richness and
equitability are weak but give a consistent interpretation. Firstly,
there appears to be no relation between biomass and species richness
in the dry season (Fig. 47). In the wet season, on the other hand,
biomass is positively correlated with species richness ($r = 0.738,$
$p<0.01$) and the relation appears curvilinear (Fig. 47). Secondly,
herbivore biomass is negatively correlated with equitability. In the
dry season the relation is curvilinear ($r = -0.533, p<0.05$), but in
the wet season it appears linear and weaker ($r = -0.402, p>0.05$ (Fig.
47).

These relations indicate that during the wet season at least, the
number of large herbivore species in relation to total herbivore
biomass would seem to reach an asymptote. From this we can infer one
of two things: i) large herbivore biomasses are facilitated by
herbivore communities with high species richness. In this instance,
the increase in biomass is accompanied by an increase in dominance
(decrease in equitability) inferring that although species richness
might increase along this biomass gradient, high biomass was
associated with an increased dominance by a few successful species.
ii) That conditions giving rise to, or allowing, a high herbivore
biomass also allow for co-occurrence of more species.
Fig. 47 Relations between large herbivore species richness ($N_0$) and equitability ($E_C$), and biomass for dry and wet seasons. $\theta$ = two points.
6.4 SUMMARY

This chapter has developed the data base with which the evaluation of the determinants of diversity can be made. This data base consists of dry and wet season estimates of the species composition and biomasses of plants and large herbivores at each of 15 sites selected to represent the major communities of the reserve.

The results of this chapter have illustrated a drop in the biomass of herbaceous vegetation from dry to wet season as a result of below wet season rainfall, utilization by herbivores and increased summer decomposition rates. Since many of the woody plants are deciduous, leaves had regrown by the wet season evaluation and woody biomass showed an increase from dry to wet season.

Total utilizable plant biomass and utilizable woody biomass was shown to increase with an increase in soil depth, an increase in soil sandiness and a decrease in base saturation, or an increase in soil depth accompanied by an increase in B-horizon clay content and soil salinity. Herbaceous vegetation favoured the shallower soils with low salinity. It was suggested that interaction with the woody layer and grazing tended to obscure the actual relation between herbaceous biomass and soils.

The vertical distribution of vegetation varied markedly between sites. In some, herbaceous vegetation dominated all other strata, and in others the upper browse layer dominated. The grass component of the herbaceous layer was negatively related to all other structural components of the vegetation. All four browse strata were found to be positively correlated.

The height class distributions of woody plants indicated that there were trees and shrubs with an apparently stable distribution and these were termed trees or shrubs with replacement. Others had height class distributions with a dearth of seedlings and smaller size classes termed trees or shrubs without replacement, and in some instances tree height class distributions were distinctly bimodal implying periodic recruitment and replacement events. On the basis of these distributions, and characteristics of the plants themselves, it
was apparent that successional changes were taking place at several sites.

Species relative abundance curves of plants were either lognormal or lying between the lognormal distribution and the geometric series. The slopes of these curves (equitability) were shown to be negatively related to utilisable plant biomass suggesting that increased plant biomass was associated with increased dominance of a few species.

The relative abundance curves of large herbivores from each site appeared to be distributed according to the geometric series. The biomass of large herbivores during the wet season was positively related to species richness. Equitability on the other hand was negatively related to herbivore biomass, inferring that although species richness might increase along this gradient, high biomass was associated with an increased dominance by a few successful species.
CHAPTER 7. RELATIONS BETWEEN SOIL, VEGETATION BIOMASS AND
VEGETATION DIVERSITY

7.1 INTRODUCTION
The primary aim of this chapter is to examine the response of
vegetation to what are perceived as the most important environmental
gradients. Vegetation alpha and beta diversity and biomass are
examined in relation to soil properties, estimates of recent grazing
pressure and fire frequency. The interrelations between vegetation
characteristics are also investigated as these might help explain some
of the patterns arising from the above analyses.

More explicitly the aim is to attempt to examine the following:
1) The patterns of beta diversity in the reserve.
2) The patterns of alpha-diversity and more specifically plant
   species richness, in relation to resource and disturbance
   gradients.

7.2 PLANT BETA-DIVERSITY
The length of the ordination axes derived from a detrended
correspondence analysis (DCA) is a real measure of the rate of species
turnover (beta-diversity along that axis (Gauch, 1982; see also
section 3.2.5.1). In this instance beta-diversity is measured in
average standard deviations of species turnover (SD) where a half
change (50% change in sample composition) occurs in about one SD.

The gradient lengths of the first axes of the detrended
correspondence ordinations of woody and herbaceous plants are, 6.5 and
6.0 SD respectively. These are of a similar order to the extremely
diverse sample set reported by Hill and Gauch (1980) derived from a
vegetation survey of south east England, comprising 876 species from
3270 samples. Alternatively, the gradient lengths from the Mkuzi data
are considerably longer than those reported by Witkowski (1983) of 3.8
SD from Klaserie Nature Reserve (Transvaal Lowveld, South Africa) and
Whittaker et al., (1984) of approximately 4.7 SD from Nylovley Nature
Reserve (Northern Transvaal, South Africa). Since beta diversity is
conceptually significant in that it is directly related to species packing along community gradients (Peet, 1978), it is worth analysing the relatively high beta diversity found in MKuzi in more detail.

Woody vegetation

A trace of the accumulated beta diversity along the first ordination axis from the DCA of the woody vegetation (Fig. 48a) indicates an extremely high species turnover rate in the last fifth of the gradient. The environmental interpretation of this axis is a gradient from base rich, poorly drained, clay soils with extremes in the moisture regime (i.e. water logging during the rainy season to extremely dry during the dry season) to a base poor, well drained sandy soil with less variability in the seasonal moisture regime. The sites occurring in the last fifth of the trace are all primarily broadleaf woodlands and closed woodlands associated with the Quaternary sand deposits. The sites forming the first four-fifths of the trace are predominantly microphilous wooded grasslands, woodlands, bushlands and thickets on soils ranging from clays to sandy clay loams and clayey lithosols. This part of the soil gradient illustrates a slow, evenly spaced turn-over in woody species indicative of a continuum (Fig. 48a). The transition to the sandy soils is characterised by a sharp discontinuity in species followed by a rapid turnover in these species to the end of the gradient. This latter portion of the gradient accounts for 64 per cent of the total species turnover along this axis.

The gradient length along the second axis is 3.9 SD. The trace of the accumulated beta-diversity along this axis (Fig. 48b) again illustrates a relatively low turnover in species in the first four fifths of the gradient. A smaller discontinuity to that observed along the first axis then occurs, followed by a short continuum before rising steeply again at the end of the gradient. The discontinuity in this case is between the wide variety of woody communities on the deeper (>20 cm) lithosols containing a small proportion of rock and influenced by a high degree of herbivory, and the wooded grassland communities on shallow (<20 cm) lithosols influenced by a low
**Fig. 48a** Detrended correspondence analysis trace for woody plants from 118 sample sites.

**Fig. 48b** Detrended correspondence analysis trace for woody plants from 118 sample sites.
intensity of herbivory but subject to fire at three to four yearly intervals. The increased woody species turnover rate at the end of this axis (accounting for approximately 20% of the beta-diversity) is due to three samples which are dominated by *Acacia karroo* and at least in one instance has a history of past disturbance.

**Herbaceous vegetation**

The gradient length of the first DCA ordination axis of herbaceous vegetation is 6.0 SD. The trace of the accumulated beta diversity indicates two regions of high species turnover (Fig. 49a). The first, is at the end of the gradient, accounts for approximately 39% of the total length of the gradient and is associated with a regular, frequent (3 - 5 yearly) fire treatment, a high site exposure and large amount of rock in the already rocky soil. All of these sites are found on the top of the Lebombo Mountains and thus experience higher rainfall and lower degrees of herbivory than sites further to the east and at lower altitudes. The second occurs at the beginning of the gradient, accounts for 12% of the total length of the gradient, and is associated with sites found in bottom land situations, on seasonally waterlogged clay to clay loam calcareous soils that experience little or no fire and high degrees of herbivory. The intermediate area of the gradient between the end groups shows a relatively even replacement of species with no major discontinuities (Fig. 49a).

The gradient length of the second axis is 4.2 SD. The environmental interpretation of this axis is a gradient from poorly drained base rich clay soils in bottomland positions to free draining, moderately leached sandy soils. A single area of extremely high species turnover is evident at the sandy end of the gradient, and accounts for 20% of the total accumulated beta diversity (Fig. 49b).

The two sites which account for this area of high beta-diversity are dominated by *Eragrostis pallens*. However, a high proportion (39%) of the total beta-diversity) was accounted for by the sites on sandy substrates.

It is interesting that although both the woody and herbaceous vegetation have beta-diversities of similar orders, the highest beta-diversities in each are associated with different environments.
Fig. 49a  Detrended correspondence analysis trace for herbaceous plants from 118 sample sites.

Fig. 49b  Detrended correspondence analysis trace for herbaceous plants from 118 sample sites.
With regard to the woody plant gradient, highest beta-diversity occurs on the sandy, moderately leached soils with, in some instances an impeded drainage within rooting depth. Although profile available moisture (P.A.M.) is not appreciably different on these soils when compared to soils with a higher clay content (Fig. 18c), moisture conditions would be more favourable on sandy soils due to better infiltration and permeability properties, the effect of which would be enhanced by impeded drainage conditions (Tinley 1982). Furthermore, the extremes in moisture conditions experienced are greater at the clay end of the gradient, being waterlogged during high rainfall events and becoming extremely dry during low rainfall periods. By contrast, the consistently lower nutrient status of the sandy soils would tend to make these soils less favourable for plant growth when compared with the base saturated clay soils. Notwithstanding the latter, it is suggested that the sandy end of the environmental gradient has a lower variability, and has more predictable conditions for plant growth than any other sampled. In addition utilizable woody biomass which in this instance may be considered an index of production potential and thus a measure of the favourability of a site, is highest on sandy soils and lowest on base rich clays (Fig. 36). Exceptions to this are soils with high B−horizon clay contents, high salinity and an improved moisture status due to water run on. This suggests that moisture status is an important factor determining the favourability of a site, in which case highest beta-diversity is indeed associated with the most favourable end of the woody plant growth gradient.

With regard to the herbaceous plant gradient represented by the first DCA axis, it would seem that the area of highest species turnover might possibly be located in the area with the least favourable and predictable growth conditions for grass growth. However grazing intensity does change from extremely high in the lower and middle areas of the axis to extremely low at the end of the axis. Grazing animals tend to be diversifiers of grassland communities (Harper, 1977), but at extremely high levels of herbivory, it is likely that this effect is reversed. In this respect, the effect of
grazing on plant species composition can override quite major nutritional differences between sites (Harper, 1977).

The depression of beta-diversity in the middle area of this axis is therefore thought to be due to heavy grazing pressure. This has reduced the herbaceous sward to one which is characterized by the same procumbent annuals or unpalatable perennials on all soil types, thus reducing beta-diversity. In contrast the sites on the crests and slopes of the Lebombo's are subject to a slightly higher rainfall, light grazing pressure and regular burning thus maintaining plant species diversity and vigour. Consequently beta-diversity has remained high and is thought to reflect mainly species turnover under moderate and fairly predictable levels of defoliation as well as up an altitudinal gradient. Once the effects of defoliation and altitude are largely removed (Fig. 49b), the trend in herbaceous species turnover mirrors to a large degree that of the woody vegetation.

7.3 PLANT SPECIES RICHNESS AND RESOURCE GRADIENTS

Species richness and its relation to resource gradients is explored using data from the descriptive analysis of vegetation (Chapter 3), and the vegetation biomass and diversity data presented in Chapter 6. Tilman (1982) asserts that species richness should be greatest in relatively resource poor habitats. The analyses in this section will be undertaken with this assertion in mind.

7.3.1 Species richness and soil gradients

The variation in species richness over the whole reserve and in response to the major soil gradients was examined by ranking the plant total species richness of each stand as either very low, low, intermediate, high or very high and then plotting these ranks in the relevant positions on the plane created by the first two axes of the soil ordination (Fig. 50). The soil ordination diagram was then subjectively partitioned into sub-units based on apparent discontinua in sample distribution in ordination space (Fig. 50). The mean position of samples within each sub-unit was determined with respect to the first and second principal component axes, and plotted against the mean species richness of samples within the sub-unit.
Fig. 50 Total plant species richness at each site in the ordination space created by the first two axes of the principal component analysis of soils. Dotted lines indicate partitioning of ordination space used for Figs. 51 to 55.

Key to symbols.

Species range

- $\leq 38$ - very low
- $39 - 49$ - low
- $50 - 60$ - intermediate
- $61 - 71$ - high
- $\geq 72$ - very high
The variation in total species richness relative to the major soil gradients, although highly variable, does suggest some general trends. At the base rich clay bottom land extreme of the first ordination axis species richness is low (Figs. 50 and 51a). This gradually increases with a decrease in the proportion of clay and a decrease in base saturation. Maximum species richness is attained close to the base poor sandy extreme of this gradient. From here it drops again at the sandy extreme. This latter apparent drop in species richness must be viewed with some doubt since it is derived from a small and highly variable sample.

Along the second soil gradient, species richness is relatively low at the base rich bottom land clay loam extreme (Figs. 50 and 51b), increases to a peak on pediment lithic soils and then declines on the higher lying Lebombo lithosols. In this instance, the pediments form a moist ecotone between the lithosols and the lower lying clay loams of the coastal plain.

Woody plant species richness, in contrast to the above trend, increases along the base rich bottom land clay to base poor sand soil gradient (Fig. 52a) and declines along the second major soil gradient (Fig. 52b). Herbaceous plants mirror the total species richness trends with respect to both major soil gradients (Figs. 53a and 53b). Within the herbaceous layer, trends in grass and forb species richness are similar along the primary soil gradient (Figs. 54a and 55a). However, forbs show a consistent decline in species richness along the second axis, whereas grasses indicate a general increase in species richness from base rich bottom land clay loam soils through the rocky pediment soils and ending on the upland lithosols (Figs. 54b and 55b).

In summary, the three major plant growth forms (woody plants, grasses and forbs) all show an increase in species richness along the major soil gradient. However, at the base poor sandy extreme of this gradient, woody plants achieve greatest species richness while both forbs and grasses decline to their lowest. The decline in grass species richness could at least be due to the shading effect of the dense woody plant canopy which characteristically develops at this end of the soil gradient. The decline in the herbaceous plant richness in this area dominates the plant community trend. Along the second major
Fig. 51 Mean and range of plant species richness from 0.1 ha sample sites plotted against mean position of sample plots along the first (a) and second (b) axis extracted by a principal component analysis of soils.
Fig. 52 Mean and range of woody plant species richness from 0.1 ha sample sites plotted against mean position of sample plots along the first (a) and second (b) axes extracted by the principal component analysis of soils.
Fig. 53 Mean and range of herbaceous plant species richness from 0.1ha sample sites plotted against mean position of sample plots along the first (a) and second (b) axes extracted by the principal component analysis of soils data.
Fig. 54 Mean and range of grass species richness from 0.1ha sample sites plotted against mean position of sample plots along the first (a) and second (b) axes extracted by the principal component analysis of soils data.
Fig. 55  Mean and range of forb species richness from 0.1ha sample sites against mean position of sample plots along the first (a) and second (b) axes extracted by a principal component analysis of soils.
soil gradient, woody plants and forbs both show a decline in species richness. Grasses on the other hand show an increase.

There is evidence for interaction between the major plant growth forms, (namely woody plants, grasses and forbs) and these interactions need investigation. Correlations between species richness and cover for the three plant growth forms have been examined using the Spearman rank correlation statistic with corrections for tied observations (Siegel, 1956) (Table 14).

Table 14. Spearman rank correlation matrix for species richness and percentage cover within major plant growth forms (woody plants, grasses and forbs). Data were from 0.1 ha sample sites.

<table>
<thead>
<tr>
<th></th>
<th>Woody Cover</th>
<th>Forb Cover</th>
<th>Grass Cover</th>
<th>Woody Species</th>
<th>Forb Species</th>
<th>Grass Species</th>
</tr>
</thead>
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<tr>
<td>WDCO</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>FBCO</td>
<td>0,106</td>
<td>1,000</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>GRCO</td>
<td>-0,273</td>
<td>-0,394</td>
<td>1,000</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>TOSP</td>
<td>0,213</td>
<td>0,255</td>
<td>-0,228</td>
<td>1,000</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>WDSP</td>
<td>0,540</td>
<td>0,020</td>
<td>-0,288</td>
<td>0,603</td>
<td>1,000</td>
<td>-</td>
</tr>
<tr>
<td>FBSP</td>
<td>0,046</td>
<td>0,440</td>
<td>-0,194</td>
<td>0,787</td>
<td>0,178</td>
<td>1,000</td>
</tr>
<tr>
<td>GRSP</td>
<td>-0,330</td>
<td>-0,019</td>
<td>0,153</td>
<td>0,480</td>
<td>-0,169</td>
<td>0,392</td>
</tr>
</tbody>
</table>

n = 118  df = 117  Critical values alpha 0.05 = 0.180  0.01 = 0.235

Woody plant cover is negatively correlated with grass cover and there is an indication of a positive (though not statistically significant) correlation with forb cover (Table 14 and see also Table 12). This suggests that with increasing woody cover, grass growth (possibly through shading and competition for other resources) is inhibited. Woody cover is strongly positively correlated with woody species richness but negatively correlated with grass species richness (Table 14). This would tend to indicate that as conditions for woody
plant growth improve, so does the species richness of woody plants. Furthermore, increased woody cover and thus shading decreases grass richness probably through exclusion of shade intolerant species. Forb richness however appears unaffected by increased tree competition.

Forb and grass cover are negatively correlated suggesting competition for resources in similar niches (Table 14 and Table 12 for biomass). Forb cover and species richness are strongly positively correlated, suggesting a positive relation between an improvement in growth conditions and species richness for these plants. Forb cover shows no relation with grass species richness.

Grass cover is significantly negatively correlated with woody plant and forb species richness and positively (though not significantly) correlated with grass species richness. Grass and forb species richness are significantly positively correlated. This is despite possible competition for resources suggested by the negative relations between forb and grass biomass and cover.

7.3.2 Species richness and plant performance

In order to explore the relation between plant species richness and resources further, some measure of absolute or relative resource status at each site is required. Since the status of resources is likely to have a significant influence on plant production, a measure of utilisable biomass may be assumed to give a good indication of the resource status of the site. This assumption needs to be applied with caution however, since the amount of utilisable plant biomass of the herbaceous layer in particular may be considerably modified by factors unassociated with resource status, for example grazing and fire.

Estimates of species richness and utilisable biomass from the intensive study sites are used to make this evaluation. Only wet season data are presented (Figs. 56, 57 and 58) since in the case of woody plants, wet season utilisable biomass would be a better estimate of production potential than dry season biomass. In addition, in some instances, the utilization of herbaceous vegetation by large herbivores could have reduced the wet season utilisable biomass.
Fig. 56  Species richness vs utilizable wet season biomass of all plants.

Fig. 57  Species richness plotted against utilizable wet season biomass for woody plants.
substantially and resulted in an underestimate of the site's production potential. To compensate for this the unutilized herbaceous biomass was re-constructed using an estimate of the utilization and the method of Walker (1976).

Total plant species richness is weakly negatively related to total utilizable biomass ($r = -0.415$, $p>0.05$) with only 17 percent of the variation in species richness being accounted for by the biomass (Fig. 56). The significance of this relation however is in the suggestion that relatively resource-poor habitats (low utilizable biomasses) should have higher species richness than resource rich habitats, thus providing some support for Tilman's hypothesis.

Total woody plant richness on the other hand shows a significantly positive linear relation to utilizable woody biomass ($r = 0.666$, $p<0.01$) with 44% of the variation in species richness being associated with by biomass (Fig. 57). The relation between total herbaceous biomass and species richness is curvilinear; (second degree polynomial fit $r = 0.731$, $p<0.01$) with 53 percent of the variance in species richness being accounted for by biomass (Fig. 58a). The first term of the polynomial is positive and large compared to the negative but much smaller second term. Thus these data indicate an increase to greatest species richness in the upper half of the range in biomass and then a slight decline in richness at peak biomass (Fig. 58a).

Grass species richness also shows a significant curvilinear increase against grass biomass ($r = 0.769$, $p<0.01$), with 59 percent of the variance in the former being associated with the latter (Fig. 58b). Greatest species richness is predicted to be close to the upper end of the biomass range.

The relation between forb species richness and biomass is similar to, but less clear than that for all herbaceous plants. A two term polynomial curve fits the data best and accounts for 20 percent of the variance ($r = 0.456$, $p>0.05$), indicating that the peak in species richness occurs around the middle of the biomass range (Fig. 58c).

In summary these data are divergent in regard to the relation between species richness and biomass. The relation between the species richness of all plants and total biomass is negative and thus lends support to Tilman's (1982) hypothesis. However, the relations
Fig. 58 Species richness plotted against reconstructed usable wet season biomass (See text for explanation). a) herbaceous, b) grass and c) forbs.
between species richness of individual components of the vegetation on the one hand and their respective biomasses on the other are largely positive and therefore contrary to Tilman’s hypothesis, in that peak species richness is achieved in the resource rich portion of the resource gradient. In this evaluation, by reconstructing herbaceous biomass the effect of disturbance has only been partially accounted for. In the short term, utilization and fire can substantially reduce above ground biomass whilst in the longer term, prolonged intensive grazing or frequent fire can effectively depress plant species richness at a site by elimination of palatable or utilization sensitive species (Harper, 1977), or fire sensitive species.

7.4 DISTURBANCE AND DIVERSITY

The disturbance regime experienced by a plant community can be characterised by the rate or frequency of disturbance (Huston, 1979), the phasing of the disturbance (Abugov, 1982), the aerial size of the disturbance (Miller, 1982), the intensity, distribution, predictability, severity and synergism (Pickett and White, 1985) of each disturbance event. The intention of this section is to determine the effect of disturbance on species diversity of vegetation.

Two sources of disturbances to Mkuzi’s vegetation were readily quantified, namely short term herbaceous utilization and fire frequency. Considered independently, neither disturbance accounts for all four components of the disturbance regime. However, cumulative herbaceous utilization is a combined measure of rate and intensity of disturbance which is unphased (Abugov, 1982) and in which areal size is probably unimportant. Fire frequency on the other hand is a relatively crude measure of disturbance in which phasing, areal size and intensity of each disturbance event is ignored.

7.4.1 Utilization and diversity of herbaceous vegetation

The utilization of each species of grass and forbs in general was visually estimated in each herbaceous sample quadrat at each of the intensive sites. The weighted mean percentage utilization at the end of the dry season for grasses, forbs and the herbaceous layer as a whole was calculated for each intensive site using the method of Walker (1976). These were then plotted and regressed against their
corresponding estimates of species richness and diversity ($N_0$, $N_2$ and $E_c$). The dry season utilization estimate was used since this is most likely to reflect the long term utilization pressure experienced by each site.

Herbaceous species richness ($N_0$), diversity ($N_2$) and equitability ($E_c$) were all positively correlated with grass utilization. Significant correlations were with species richness ($r = 0.573$, $p<0.05$) and equitability ($r = 0.683$, $p<0.01$).

Grass species richness was positively correlated with grass utilization ($r = 0.446$, $p<0.05$) with only 20% of the variation in richness being accounted for by utilization (Fig. 59a). Grass diversity ($N_2$) and equitability ($E_c$) were both positively correlated with grass utilization ($r = 0.574$ and $r = 0.537$ respectively, $p<0.05$), with 33 and 29% of the variation in diversity being accounted for by utilization, respectively (see Fig. 59b for an example).

Forb species richness was positively correlated with grass utilization ($r = 0.543$, $p<0.05$), grass utilization accounting for approximately 30% of the variation in forb species richness (Fig. 59c). Estimates of forb diversity incorporating relative importance were not made since the relative importance of each forb species in each site was only visually assessed and allocated a broad importance category. Diversity estimates incorporating these estimates of relative importance are thus likely to be biased since the evenness in each case would be exaggerated.

Forb species richness is negatively correlated with forb utilization ($r = -0.438$, $p<0.05$) (Fig. 60). Although this relationship is not statistically significant, the highest forb species richness is found on sites with the lowest utilization, and the lowest forb richness is found on sites with the highest utilization. Consequently, it is reasonable to conclude that in contrast to grasses, forb species richness declines with increased forb utilization. This difference in response to utilization may be explained by differences in grass and forb structure. The former have
Fig. 59 Relations between dry season grass utilization and a) grass species richness ($N_0$) b) grass diversity ($N_2$) and c) forb species richness ($N_0$).