TEMPORAL AND SPATIAL VARIABILITY OF GRASS PRODUCTIVITY IN THE CENTRAL NAMIB DESERT

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ABSTRACT The production of grass was investigated on the gravel plains of the Central Namib Desert, Namibia, during 10 rainfall seasons sampled between 1989–2003. The aim was to evaluate the rainfall-productivity relationship, to elucidate the relationship between temporal and spatial variability, and to examine the spatial scale of patchiness. We compared two different methods and found that a less accurate rapid assessment of grass cover correlated well with measurements of biomass. Our data were in agreement with previous determinations of the desert end of the curve of grassland productivity, and productivity was closely related to the rainfall of the particular season. There was high variability between years at study sites, especially in the west (CV=279%), where it rained more seldom than in the east (CV=86%). During all years rainfall was very patchy at a spatial scale of 5 km, which apparently reflected the storm path of individual rain clouds. Long-term monitoring should be continued in order to detect changes of pattern in this rainfall-driven system.

Key Words: Rainfall-productivity relationship; Rapid assessment; Grass biomass; Storm cloud size; Patchy rainfall.

INTRODUCTION

Tropical arid regions are characterized by high temporal variation of rainfall (Tyson, 1986; Nichols & Wong, 1990). Temporal variability of rainfall at a particular site is negatively correlated with mean rainfall, and the more arid a site, the higher the variability (Tyson & Dyer, 1975). Similarly, high spatial variability of rainfall characterizes arid regions (Sharon, 1981; Noy-Meir, 1981; Dean & Milton, 1999; Ward *et al*., 2004). These patterns result in frequently-changing temporal and spatial concentration of primary production. The current study elucidates these responses along a steep gradient of aridity in the Namib Desert (Fig. 1).

Previous studies conducted in the Namib Desert demonstrate that temporal patterns of local rainfall affect abundance of plants and animals (e.g. Holm, 1970; Seely, 1973, 1978a, 1978b, 1990, 1991; Seely & Louw, 1980; Nel, 1983; Hamilton, 1985, 1986; Yeaton, 1988; Boyer, 1989; Berry & Siegfried, 1991; Günster, 1992; Southgate *et al*., 1996; Henschel & Seely, 2000). It is also known that distribution of rainfall affects spatial patterns within the ecosystem

(Robinson, 1976; Seely, 1978a, 1978b; Tilson & Henschel, 1986; Günster, 1992, 1995; Brain, 1993; Kilian, 1995; Kok & Nel, 1996; Burke, 1997; Hachfeld, 2000). In the Central Namib, epiphenomena in the form of heavy rainfall events of >100 mm per annum have occurred only four times in a century (1934, 1976, 1978, 2000). In a first approximation, strong, rapid increases in abundance of many plants and animals were demonstrated (Seely & Louw, 1980). These big events can have effects that last for decades (Southgate *et al*., 1996; Henschel *et al*., in press). Winds that shift surface material blow for >50% of the time (Lancaster *et al*., 1984), continuously redistributing detritus and renewing its availability on the surface, where detritivores feed on it (Crawford, 1979; Crawford & Seely, 1994).

Biomass of Namib plants is normally extremely low except at inselbergs (Burke *et al*., 1998), in washes (Robinson, 1976) and in ephemeral rivers (Seely *et al*., 1980; Jacobson *et al*., 1995), as well as in the fog zone, where succulents and lichens increase primary productivity (Schieferstein & Loris, 1992; Hachfeld, 2000). Most primary productivity on the Namib gravel plains is in the form of ephemeral grasses that flush briefly after effective rainfalls from dormant seedbanks (Robinson, 1976; Seely, 1978a, 1978b; Günster, 1992, 1995; Jacobson, 1992, 1997; Burke, 1997; Hachfeld, 2000).

Rainfall in the Namib usually comes from isolated convective clouds, that are spaced widely apart (Sharon, 1981). Rainfall is unpredictable to the degree that the occurrence of effective rain stimulating plant growth cannot be predicted for any year (Pietruszka & Seely, 1985), nor any location (Sharon, 1981). Individual rain clouds moving from east to west across the Namib leave a green path of grass. The width and length of each rainfall path and the number of annual rainfall days varies greatly (Sharon, 1981; Burke, 1997; Ward *et al*., 2004). Hence, adjacent locations may not have the same productivity in a given year, and, via the seedbank and accumulated detritus, this effect may be cumulative over the years.

In the current paper we elucidate the relationship between temporal and spatial variability in rainfall and plant productivity. In particular we determine the spatial scale across which variability in productivity is expressed in each season, and how this may introduce heterogeneity across an otherwise relatively homogeneous plain. We asked the following questions: (1) are rapid (grass cover) assessments good indicators for grass biomass, (2) what is the rainfall-productivity relationship in this desert, (3) what is the relationship between temporal and spatial variability, (4) what is the spatial scale of grass patchiness.

STUDY AREA

The study was conducted across the gravel plains of the Central Namib (Günster, 1995; Wilkinson, 1990; Henschel *et al*., 2003) between latitude 22°58’ S and 23°34’S, longitude 14°34’E and 15°43’E (Fig. 1). The study area extended from 9–125 km inland of the coast, and extended about 50 km from north to south. Altitude at study sites ranged from 27–1000 m above mean sea level (a.m.s.l.). This area crosses several climatic zones from west to east (Besler, 1972; Hachfeld, 1996; Henschel *et al*., 1998; Lancaster *et al*., 1984) and the study area was subdivided accordingly (Fig. 1).

The central Namib's gravel plains are characterised by wide expanses of plains, intersected by a network of drainage areas and shallower drainage lines and several inselbergs (isolated mountains). These inselbergs rise 10 to about 200 m above the surrounding plains. The gravel plains slope gently from the

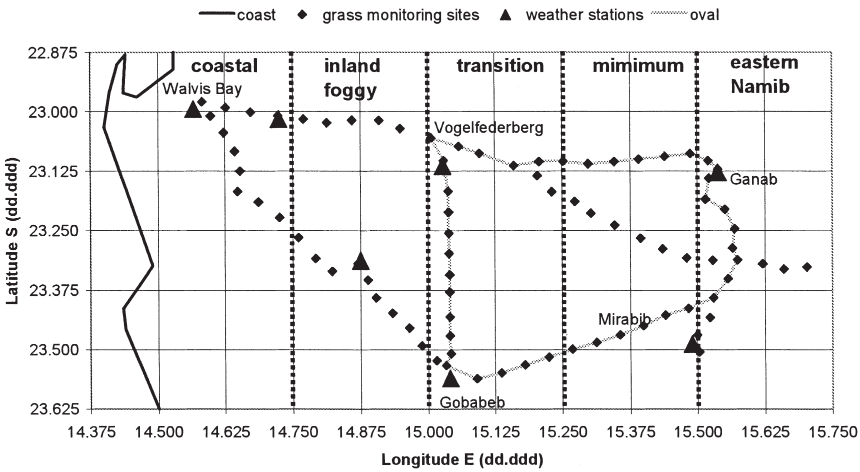

Fig. 1. Map of study area, showing position of 87 study sites, climatic zones, weather stations, and the Gobabeb-Mirabib-Ganab-Vogelfederberg oval of sites.

Table 1. Grasses recorded in the study area.

Aristida parvula	(Nees) De Winter
Brachiaria glomerata	(Hack.) A.Camus
Centropodia glauca	(Nees) T.A.Cope
Enneapogon desvauxii	P.Beauv.
Eragrostis annulata	Rendle ex Scott-Elliot
Eragrostis nindensis	Ficalho & Hiern
Stipagrostis ciliata	(Desf.) De Winter
Stipagrostis dinteri	(Hack.) De Winter
Stipagrostis gonatostachys	(Pilg.) De Winter
Stipagrostis hirtigluma	(Steudel ex Trin. & Rupr.) De Winter
Stipagrostis lutescens	(Nees) De Winter
Stipagrostis obtusa	(Delile) Nees
Stipagrostis subacaulis	(Nees) De Winter
Stipagrostis uniplumis	(Licht.) De Winter
Triraphis pumilo	R.Br.
Triraphis purpurea	Hack.

coast towards the east, with an increase in altitude from 0 to approximately 1000 m a.m.s.l. The soils on the plains are poorly developed calcisols and gypsisols, which are characterised by underlying calcrete crusts and high gypsum content in the fog zone (Fig. 1) (Scholz, 1972).

On a national scale the vegetation has been classified as Central Namib (Giess, 1971) and at a landscape level several grass communities were characterised (Nel & Opperman, 1985). We recorded 16 species of grass in the study area (Table 1).

CLIMATE

The study area contains 6 automatic weather stations of the Gobabeb Training & Research Centre (Fig. 1).

Most rain comes from summer monsoons. These come from the distant Indian Ocean, and rainfall becomes patchier as moisture decreases across the African continent. Only seldom do individual rain clouds cross westwards over the Namibian Great Escarpment and into the Namib. Therefore, rainfall decreases and temporal variability of rainfall increases from the Namib escarpment westwards towards the coast (Seely, 1978a, 1978b; Gamble, 1980; Sharon, 1981; Lancaster *et al*., 1984; Günster, 1992; Mendelsohn *et al.*, 2002). Most rain falls during the hottest season between January and April (austral late summer). This period is followed by a dry period (May-August) dominated by berg winds. Relatively heavy precipitation of fog occurs in the western half of the Namib most commonly during the cool early summer (September–December).

METHODS

A network of 87 study sites, approximately 5 km distant from each other, was marked with GPS along 420 km of gravel roads crossing the Central Namib gravel plains (Fig. 1). The survey was conducted 2–3 weeks after the final rain of the season, i.e. during late April or early May. Between 1989–1995 changes in grass productivity were mapped along continuous transects bordering the roads and classified according to a visually-assessed index of grass cover (Günster, 1995; Burke, 1997) (Table 2). For comparison with later data, point

Table 2. Grass cover indices based on visual assessment of cover from a vehicle (following Burke 1997) compared to grass biomass.

Index	% Grass Cover	Grass biomass ($g \cdot m^{-2}$)	Conversion of Index to Biomass ($g \cdot m^{-2}$)
0+	only in drainage lines	1–2	1
1	1–5	3–9	5
2	5–25	10–19	15
3	25–50	20–29	25
4	>50	>30	35

data for the 87 study sites were extracted from the transect data.

Between 2000–2003, grass productivity was measured as follows. From each marked site along a road, we walked off 60 m perpendicular to the road (S for E-W roads, W for N-S roads). There we determined a random spot by tossing a stone backwards across the shoulder away from the road. If the spot was unsuitable, the process of stone-throwing was repeated at another location 20 m parallel to the road. A spot was unsuitable if it fell into a drainage line, a rocky ridge or included a large perennial plant. We measured grass height and density with a point-frequency frame of 1 m width with guide holes at 1 m height (Mueller-Dombois & Ellenberg, 1974; Ward *et al*., 1998). The point-frequency frame was positioned perpendicularly to the road with the closest leg standing on the designated spot. Then we took readings of grass height by lowering the ruler rod through a guide hole until its tip touched a blade of grass, and this height was measured (grass height). Ten measurements were recorded at 10-cm intervals and the average grass height was calculated. An area of 1 m^2 was demarcated with the point-frequency frame as mid-diameter, and all grasses inside this area were identified to species. The next spot was located 20 m parallel to the road (westwards for E-W roads, northwards for N-S roads). After measuring five spots on one side of the road, we measured another five spots 60 m off the other side of the road until the last spot was located opposite the first spot. The mean and CV of grass height from ten different spots (100 measurements) at a site constituted the measure of grass production and its patchiness at the site.

We compared grass height (cm) with above-ground oven-dried (60°C) biomass (range 1.424 – 46.294 $g \cdot m^{-2}$) of ephemeral plants clipped from 1 m^2 that surrounded the point-frequency frame at 53 sites in 2000. The following regression equation (r^2=0.85, p<0.001) was used to convert grass height to grass biomass ($g \cdot m^{-2}$):

$$grass\ biomass = 1.12 \times (grass\ height) + 2.79$$

At 60 sites in 2000, we simultaneously applied Burke's visual index of grass cover and measured grass height. This enabled us to combine the two data sets obtained with the index and by measuring grass height.

To determine the rainfall-productivity relationship data for a rainfall event in March 2000 were obtained from the Botany Department of the University of Hamburg, which maintains rain gauges located at 10 km intervals along the Walvis Bay–Kuiseb Canyon road. In April 2000, we determined grass biomass at 12 sites located <5 km from these rain gauges.

In order to establish the spatial scale at which grass biomass changed, sites were compared to their nearest neighbour. To examine the differences in grass biomass across distance in a given year, we used a subset of 44 sites situated along a continuous oval of roads Gobabeb–Mirabib–Ganab–Vogelfederberg–Gobabeb (Fig. 1). To avoid re-sampling when comparing all sites, comparisons were made only in one direction half-way around the oval. Each site was compared with the first 22 sites in an anti-clockwise direction, with the minimum distance between sites being 5 km and maximum 110 km. Grass biomass from site (i) was subtracted from the next (i+1), then the next after (i+2) ... until the most distant site (i+22) was reached. Absolute differences were recorded and the mean difference for each distance calculated.

RESULTS

I. Biomass-cover Relationship

Burke's (1997) visual index of grass cover was highly correlated ($r=0.96$, $p<0.01$, $n=60$) with categories of grass biomass (derived from height) (Table 2). We used the midpoint of the range of grass biomass to convert the cover index to biomass. The threshold for visual assessment of patchiness was at 67% CV for grass height at a site.

II. Rainfall-productivity Relationship

Dry biomass of grass was significantly correlated with rainfall ($r^2=0.58$, $p=0.0025$, $n=12$) and the relationship was:

$$\textit{grass biomass} = 0.5872 \times (\textit{rain} - 10.93).$$

The mean grass biomass varied between years, being highest in the good rainfall year, 2000, and lowest in 2003, when biomass was only 4.5% of the amount recorded in 2000 (Fig. 2). There were eight sites at which no grass was ever recorded and four sites that had fresh grass every year. Across all 87 sites, the mean frequency of grass occurrence at a site was 4.7 ±SD 3.1 years.

III. Spatio-temporal Variation

The distribution of grass productivity varied strongly across the study area and between years (Fig. 3). Mean biomass increased over 70-fold from west to east. The maximum biomass at sites in each zone was recorded during 2000, ranging from 2.8 $g \cdot m^{-2}$ in the coastal zone, to 30.5 $g \cdot m^{-2}$ in the east. Temporal variability, as indicated by the mean coefficient of variation of grass biomass at sites that fall into each zone, was extremely high, ranging from 279% in the coastal zone to 86% in the eastern Namib (Table 3). During the 10 years of

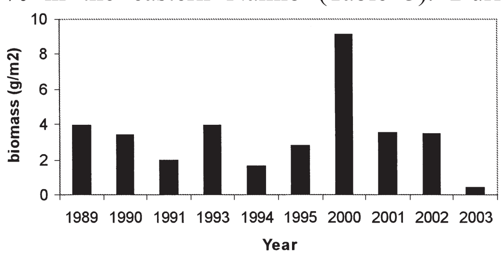

Fig. 2. Mean biomass of grass ($g \cdot m^{-2}$) at all sites over the entire study area in each year.

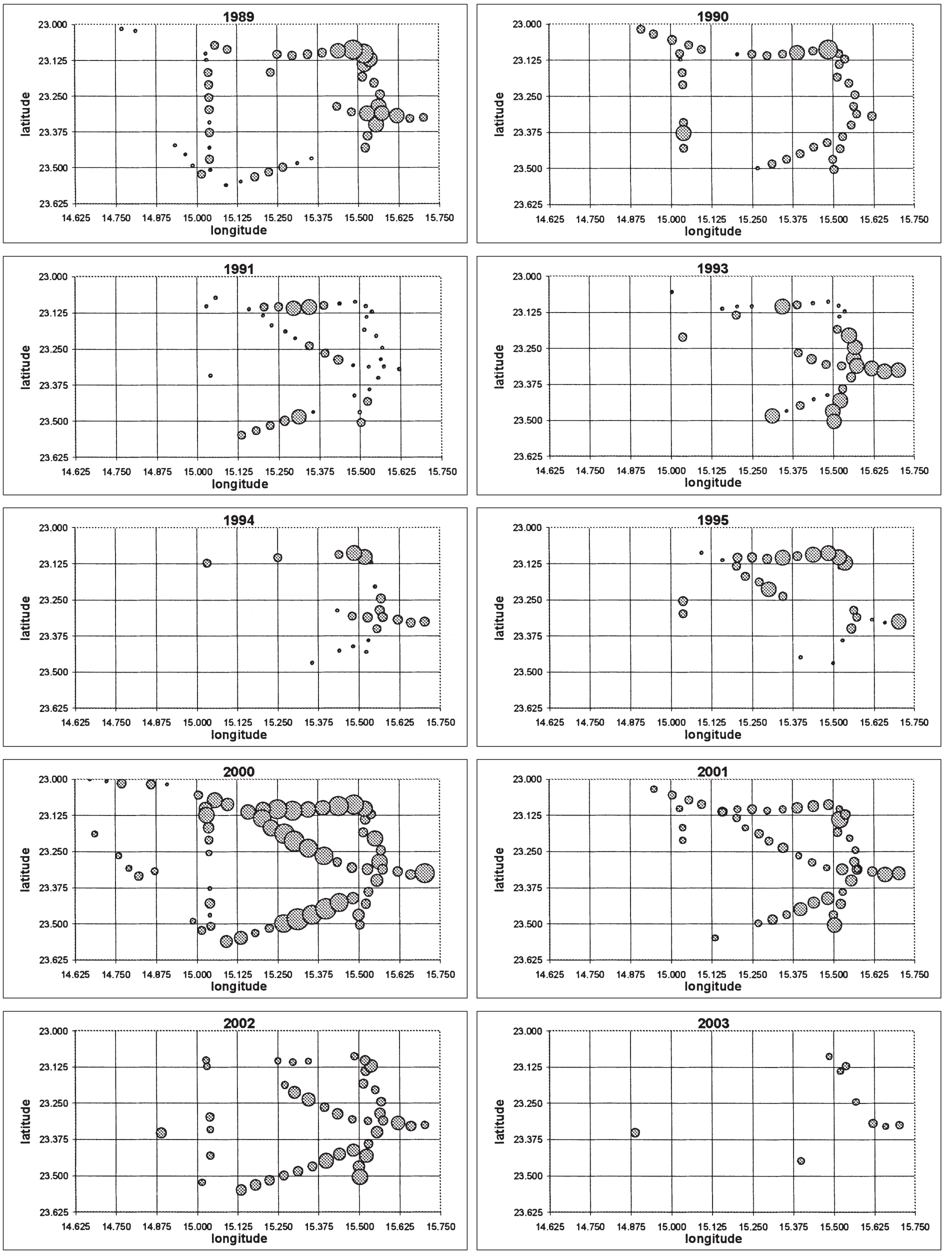

Fig. 3. Map of grass biomass in different years across the study area. Point size (area) is scaled to biomass ranging from 1 to 30 $g \cdot m^{-2}$.

Table 3. Mean grass biomass ($g \cdot m^{-2}$), mean coefficient of variation (%CV) and probability of grass per site in five zones of the Namib.

Zone	Sites	Biomass	CV	Probability of Grass (%)*
Coastal	12	0.085	279	4
Inland Fog	14	0.672	233	13
Transition	26	2.214	170	45
Middle	19	5.729	126	67
East Namib	16	6.108	86	86

* mean percent of number of years that a site in a zone had fresh grass

recording, the number of years with fresh grass at a site ranged from 0–1 in the coastal zone, to 7–10 in the eastern Namib, and the probability of effective rainfall occurring at a site in a given year increased over 20-fold from west to east (Table 3).

IV. Spatial Scale

Within a given season, differences in grass biomass between adjacent sites (5 km apart) were smaller than between more distant sites. At the distance of 5 km, the difference was 50% of the difference in biomass that is reached at the asymptote distance of 50–80 km (Fig. 4). Differences continued to increase steeply at distances of 10–20 km, and then the rate of difference declined to the plateau level (Fig. 4).

The size of the area of greatest similarity differed little between years. Beyond 5 km distance the shapes of the curves differed, but in all cases its slope declined beyond 15–20 km, which was a second radius of similarity.

The spatial pattern of difference between adjacent sites was independent of the amplitude of grass biomass. There was no relationship between the overall grass biomass in the area in a given year (indicative of the extent of rainfall in the season) and the degree of similarity of sites 5 km apart (r^2=.074, p>0.05). In 2000, an exceptionally wet year, the first radius of similarity (50% difference) was 5 km and the second radius 20 km (change in slope) (Fig. 4), indicating that even when grass is most widespread, spatial variability still occurs at a similar spatial scale as in drier years.

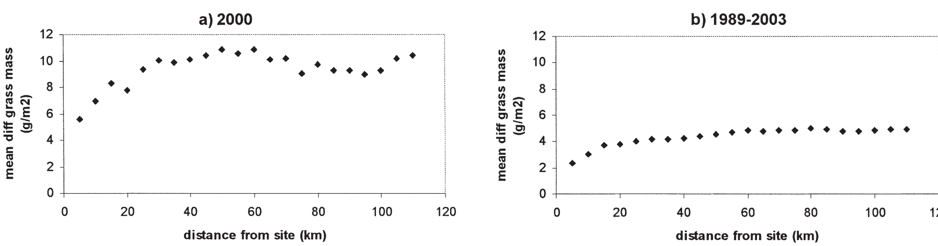

Fig. 4. The mean difference in grass biomass between sites located at different distances apart.

DISCUSSION

I. Biomass-cover Relationship

Plant biomass measurements based on harvesting techniques provide a more accurate measure of productivity than estimates of plant cover (Kent & Coker, 1992). However, based on one year of data, this study showed a highly significant correlation between these two measures, indicating that plant cover estimates, if calibrated and done by the same person(s), can provide a reasonable surrogate for productivity. Taking the high temporal variability into account this relationship should, however, be tested in a less favourable season than 2000, in order to establish that this correlation also holds during normal to below average seasons. The use of cover estimates versus biomass measurements results in enormous savings in time and expense. In areas where little research funding is available for long-term studies, use of cover estimates may make such monitoring possible.

II. Rainfall-productivity Relationship

Seely (1978a, 1978b) determined a relationship of grass standing crop to annual rainfall:

$$\textit{grass biomass} = 0.5476 \times (\textit{rain} - 11.30)$$

The study site used by Seely (1978a, 1978b) in 1974 fell into our own study area, and we found a very similar relationship during 2000 with a much smaller sample size than Seely's.

Our study also agrees with the zero intercept of grass germination in the order of 11 mm rainfall within a period of a week found in other empirical studies in the Central Namib Desert (Jacobson, 1992, 1997; Günster, 1992). This validates the Seely (1978a, 1978b) equation, at least for the desert end of the curve with annual rainfall less than 100 mm, where annual grass dominates. Given that perennial grasses are rare on the open gravel plains of the Central Namib, productivity here should only be related to the rainfall of a particular season and it would be invalid to apply average annual rainfall as is done in areas of higher rainfall (Rutherford, 1980; Ward & Ngairorue, 2000). Conversely, grass biomass in the Namib is indicative of the quantity of rainfall at a site within the range 11–100 mm, although at the upper half of that range in the Namib, nutrient availability becomes a limiting factor (Louw, 1990).

III. Spatio-temporal Variation

Total grass productivity across the entire study area varied by more than an order of magnitude, reflecting conditions of extreme temporal variability across the Namib (Fig. 3). The pattern in this variability was that it decreased with increasing annual rainfall from west to east across the study area. In North

American deserts, not only regional rainfall gradients, but also particular storm paths, induced by topography, can be observed (Beatley, 1974). The possible effect of storm paths was initially also indicated during the first three years of study of Central Namib plains (Günster, 1995), but not maintained when longer-term data were included (Fig. 3).

Temporal variability was extremely high and a trend of decreasing variability from the coast to the inland areas was indicated, closely following the west-east gradient of variation in annual rainfall (Mendelsohn *et al*., 2002). This confirms that rain events that can trigger development of grass only occur about once in a decade in the extreme arid coastal areas.

Changes in spatial and temporal variability of productivity in arid areas are expected as a result of climate change. This would particularly affect areas at the interface of grassland and shrubland (Huenneke *et al*., 2002). Livestock grazing will exacerbate these effects (Huenneke *et al*., 2002) and the Central Namib plains, which are free of livestock impacts, may be extremely important study areas in future to monitor changes and separate the effects of climate change from those of overgrazing.

In arid environments temporal changes need to be investigated over long time spans to generate meaningful results. This was also confirmed in this study when trends detected in the first three years of surveys (Günster, 1995) were re-analysed using six years of data (Burke, 1997), and now again with ten years of data.

IV. Spatial Scale

The 5 km distance from a site where grass biomass was about 50% different to that site indicates that the scale of rainfall-induced variability in productivity has a radius of 5 km or less (a more exact estimate is limited at the current level of resolution). This is approximately the width of a cumulus cloud (Sharon, 1972, 1981). This area appears to be bigger when it is crossed obliquely, which may explain the secondary spatial scale of 15–20 km in our measurements.

No two study sites had exactly the same pattern of productivity over the years, except for several sites in the extreme north-west of the study area where only one or no rainfall events occurred (Fig. 3). Since the minimum scale of our study was 5 km (distance between adjacent study sites), this indicates that the observed spatial scale of individual rain clouds that have a radius of about 5 km determine the spatial pattern of productivity over the season. Even in wet years, idiosyncrasies of rain clouds determine the overall pattern, which is thus essentially random and unpredictable. Ward *et al*. (2004) reached a similar conclusion when comparing arid rangelands in Namibia, where productivity of annual and perennial grass is not only affected by rainfall, but also by livestock. In our case, the entire study area has the same type of land use (national park frequented by sparse herds of grazers), and differences can essentially be attributed to rainfall.

CONCLUSIONS

This study (1) indicated a good correlation between rapid grass cover assessments and more elaborate biomass harvesting techniques (2) confirmed a previously established relationship between rainfall and productivity, (3) illustrated extreme spatial variability of grass productivity at the regional scale on the Central Namib plains, (4) showed within-patch variability which is likely related to the extent of rain clouds.

By elucidating the implications of extreme temporal and spatial heterogeneity over long periods of time, desert ecology can advise the interpretation of biodiversity in heterogeneous environments in general. One implication is that the hydrological status of even nearby areas will usually be quite different, which could be a kind of virtual portioning of habitats. Primary productivity varies across a scale of 5–10 km and even nearby sites will have different patterns across a sequence of years. So, for instance, populations of detritivores would experience different conditions of food availability across a relatively small scale, which could give rise to different demographic statuses at this spatial scale.

The understanding of spatio-temporal patterns is important for comparing environmental changes induced by climate versus humans. Arid regions, such as Namibia, are particularly vulnerable to anthropogenic disturbance leading to high proportional loss of productivity. In view of this, it is very important to understand the consequences of variability in drylands (Henschel *et al.*, 2000). We recommend that long-term monitoring be continued in undisturbed areas for comparison that will improve interpretation of data from rangelands.

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