A MULTIVARIATE ANALYSIS OF GRASS (*STIPAGROSTIS* spp) GROWTH AND ITS RELATION TO CLIMATIC FACTORS IN THE NAMIB DESERT.

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Abstract. Heavy rainfall in 1976 in the central Namib desert initiated two discrete periods of grass (*Stipagrostis* spp) growth. Above ground production of dry matter for the three species of grass studied was significantly different during the two growth periods. Stepwise multiple regression analysis has been used to examine relationships between weekly increase in grass height, soil moisture and a number of macro-climatic parameters. Soil moisture at 5 cm was found to be the most common explanatory variable in regression equations; followed by relative humidity at 14h00 and soil surface temperature at 08h00. The average amount of variance in grass height (R^2) that could be accounted for by the derived equations was 76% and 85% for the first and second growth periods respectively. The variation between the species in R^2 value reflected the degree of adaptation to the Namib desert environment.

Key words: Regression analysis; desert grass; macro-climatic factors; environmental adaptation.

Running title: DESERT GRASSES

INTRODUCTION

Rainfall in the western part of the central Namib desert from Gobabeb (23^{0} 24'S; 15^{0} 03'E) to the coast 60 km westward averages less than 15 mm year^{-1} (Seely 1978*a*). During January to March 1976 a total of 103 mm of rain fell, which was the largest amount since 1934. Two events, 28 mm on 21 January and 31 mm on 30 March were in excess of the 20 mm found to be necessary for plant germination (Seely 1978*b*), including species of ephemeral grass: *Stipagrostis subacaulis* (Nees) De Winter, *S. ciliata* (Desf.) De Winter and *S. gonatostachys* (Pilger) De Winter. These two events presented the unusual opportunity of studying grass growth not once but twice, in an area which in normal years is vegetated by succulents and aphyllous shrubs with grasses only sparsely represented (Schulze and Schulze 1976).

The aim of this paper is to compare dry matter production between the two growth periods and to examine the relationship of the weekly height increase of these grass species to soil moisture and to macro-climatic factors measured nearby at Gobabeb. Stepwise multiple linear regression is used to elucidate this relationship and is also useful in coping with multi-colinearities in the data.

Study area

The Namib desert is the only true desert in Southern Africa. It extends along the South Atlantic coast from 13° 10'S in Angola to 31° 10'S in South Africa (Wellington 1955). At its centre it extends eastwards to the base of the Great Escarpment which coincides approximately with the 100 mm isohyet and the 1000 m contour. The desert has no distinct eastern boundary because the rainfall and vegetation increase gradually towards the interior (Scholz 1972, Schulze and Schulze 1976).

The aridity of the Namib desert is caused by the Benguela current which reduces the temperature of the westerly winds thereby reducing their moisture content (van Zinderen Bakker 1975). Over the land the air warms and reduces relative humidity even further. Moisture-laden air from the east warms up adiabatically as it descends over the escarpment into the Namib desert (Logan 1960). As a result, rainfall decreases rapidly towards the Atlantic coast.

This study was carried out near Gobabeb where a first order weather station is maintained. Annual rainfall at Gobabeb averages 17.9 mm (Seely and Stuart 1976) most of which falls in the austral summer between January and April immediately preceding the advent of the desiccating easterly or 'berg' winds. Mean annual temperature of the warmest and coldest months differ by 6.5°C and the average aperiodic range (mean maximum less mean minimum) is about 17°C throughout the year (Seely and Stuart 1976).

MATERIALS

On 23 January immediately following the first rain, when the surface was devoid of vegetation, twenty quadrats (each composed of 4 replicates of 25 cm x 25 cm) were laid out at 20 sites on the gravel plain north and west of Gobabeb (Fig. 1). At the same time 4 quadrats (each composed of 2 replicates of 25 cm x 25 cm) were placed in the interdune valleys to the south of Gobabeb (Fig. 1). Weekly increase of height of the 3 grass species was measured at the same time of day until such time as all grasses had set seed but before the leaves had turned brown. For the first period, following the rain of 21 January, growth was measured on the gravel plain until 7 March and for the second period from 12 April until 24 May. On the interdune valley plots the first period extended from 1 February until 11 March and the second period from 13 April to 25 May. The mean height value of all stems was determined for each species in each plot. For comparative purposes the number of plots on the gravel plain was halved by taking the mean of heights between adjacent plots. After the final measurements were taken, all vegetation was removed from the ground and the dry weight of above ground material was determined.

At the same time as weekly height measurements were made, soil samples were taken next to the quadrats for gravimetric determination of water content at the surface and at 4.5 - 5.5 cm. Soil in the study plots was at most 10 cm deep. In the interdune valleys, the soil is a uniform mixture of cemented red-brown aeolic sands with a surface crust of calcium carbonate and a gravel blanket. Soils of the plains range from ochre brown calcareous soil with a slight gypsum crust to ochre brown, partly calcareous gypsum soil, both with a grit blanket, above granite or metamorphic schists (Scholz 1972). Generally more than 90% of root development during the short growing period occurred in the upper 10 cm of soil.

Macro-climatic data were obtained from the meteorological station at Gobabeb. Weekly averages of daily climatic readings were determined for the respective growth periods. Climatic parameters were: soil surface temperature at 08h00 and 14h00 (08h SSfT and 14h SSfT respectively), maximum temperature (MAX T), minimum temperature (MIN T), relative humidity at 08h00 and 14h00 (08h RH and 14h RH respectively), rainfall (Rn) and evaporation (EVAP).

METHOD

Multiple linear regression analysis formulates the interrelationship between a set of independent (explanatory) variables and the dependent (endogenous) variable. The technique assumes a linear structural relationship betwwen Y_i, some dependent variable, and a number of X_{ik} 's, the independent variables, that is:

$$Y_i = \beta_o + \sum_{k=1}^{p} \beta_i X_{ik} + \varepsilon_i \qquad \begin{array}{l} i = 1, \ldots., n \\ k = 1, \ldots., p \end{array} \qquad (1)$$

where p is the number of independent variables in the regression, the β's are the weights or regression coefficients to be determined and ε_i is the i-th residual on Y_i (error term). The stepwise approach was adopted so as to reduce the problem of multi-colinearities among the independent variables (Gillooly and Dyer 1977), and to assess their order of importance to grass height.

In this paper the dependent variable is grass height by the week (GH) and the independent variables are weekly mean values of soil moisture at the surface and at 5 cm (SfSM and 5 cm SM respectively), together with the 8 climatic parameters mentioned above. Using this technique an assumed internal dependence structure (Kendall 1975) between grass height and climate is investigated.

The order of stepwise insertion of variables into the regression is determined by their partial correlation coefficients (r_p) rather than simple correlation coefficients (r) which do not consider those variables already in the model. Using partial coefficients it is possible to examine in turn the ability of each potential determinant in accounting for variance in the endogenous variable both individually and combined with other explanatory variables. The squares of the r_p's give the proportion of the total variance in the endogenous variable unaccounted for by those variables already in the regression. In addition, not all possible determinants are necessarily included in the final equation. At a given level of significance an explanatory variable may later be rejected from a regression as its initial ability to account for variation in GH diminishes with the introduction of other such variables later in the analysis.

More possible determinants (p = 10) were available than were weeks of height measurements (n = 7). To solve this problem an iterative regression procedure, which does not rely upon the solution of normal equations, was used (Veldman 1967). Only those quadrats which produced grass in both growth periods were analysed. *S. subacaulis* had 6 plots common while *S. ciliata* and *S. gonatostachys* both had 4 quadrats common to the two growth periods.

RESULTS

Several points emerge on comparison of the two growth periods. The number of plants growing per metre^2 was not significantly different between the two intervals but the production of dry matter did vary significantly for the 3 species of *Stipagrostis* over the two periods (Table 1). Prior to the first fall of rain, there was no sign of previous grass growth on the surface and the seeds had lain dormant for an unknown period. It is not known whether it was ungerminated dormant seed or newly produced seed that gave rise to the second crop.

Mean soil moisture for each period, expressed as a percentage water by eight, varied significantly on the plains (SfSM - period I : 1.04%, period II : 0.25%, $p < 0.001$; 5 cm SM - period I : 3.92%, period II : 0.88%, $p < 0.001$) although in the interdune valley the SfSM difference was not significant (period I : 0.11%, period II : 0.14%) the difference at 5 cm was signficant (period I : 0.57%, period II : 0.32%, $p < 0.001$).

Representative results from the regression analysis are presented separately for each growth period. For explanatory purposes details of *S. subacaulis* (plot 1-2) during the first growth period are given.

First growth period

Simple correlation matrices were determined for all species in all plots. In general, GH was highly negatively correlated with SfSM and 5 cm SM. The high correlation is not unexpected since moisture is the growth limiting factor in deserts (Noy-Mier 1973). The reason for the inverse association is initially a little puzzling but a look at Figure 2 explains why. Figure 2 illustrates GH data for *S. subacaulis* in plot 1-2 and the curves for SfSM and 5 cm SM. In this example, the simple correlation coefficients (r) between GH and SfSM and 5 cm SM were -0.85 and -0.69 respectively. It is evident that as GH increases, moisture supplies are progressively depleted because replenishment did not take place until the second fall of rain on 30 March. In this way a strong inverse relationship is generated.

When GH and climatic data were subjected to a stepwise regression analysis, the first variable taken into the equation was that with the highest r value with GH. In the case of *S. subacaulis* (plot 1-2) this variable was 5 cm SM, r = -0.85. The order of entry for subsequent variables is based on their r_p values which give a better indication of inter relationships between the variables than do the r values. This process continues until no further variables are inserted or rejected.

Table 2 gives the final regression equations of *S. ciliata, S. subacaulis* and *S. gonatostachys* during the first growing period. The proportion of the total variance in GH (coefficient of determination, R^2) that could be accounted for by the regression was, on average, 59%, 81% and 87% respectively. In most cases, no more than two explanatory variables were significant to GH and still the R^2 values are substantial ($p < 0.10$).

Taking the first period as a whole, the most common explanatory variable is 5 cm SM, selected in 35% of all cases, followed by 08h SSfT which constitutes an additional 26% of all the final determinants. Variations in the relative importance of SM between sites may be a function of differences in soil type. This may explain the presense of *S. ciliata* and *S. subacaulis* on the gravel plain whilst *S. gonatostachys* is found only in the interdune valleys.

The connection between GH and 08h SSfT is related to the fact that *S. ciliata, S. gonatostachys* (Vogel and Seely 1977) and *S. subacaulis* (Schulze and Schulze 1976) are C-4 plants adapted to a hot, dry climate. The mean MAX T's, $30^{\circ}C$ and $31^{\circ}C$ for the two growth periods respectively, are in the lower range of photosynthetic efficiency. This may account for the response of GH to 08h SSfT, mean values of which are $23^{\circ}C$ and $18^{\circ}C$ for the two periods respectively.

Second growth period

Two interesting points emerge from the results of the second growth period. Firstly, in all 3 *Stipagrostis* species the final regression equations account for larger amounts of variance in GH than was found in the first growth period. Final regression equations for the 3 species of *Stipagrostis* are given in Table 3. Taking means of individual R^2 values for each species, the proportion of the total variance in GH accounted for is 79%, 83% and 94% respectively.

Secondly, different climatic factors are incorporated into the later regressions. We find that now 14h RH comprises 32% of all final determinants, followed by 5 cm SM and 08h SSfT which constitute 21% and 18% of the final explanatory variables respectively.

Vapour pressure may have been a better measure of atmospheric moisture than RH. However, the high degree of association between GH and 14h RH is unexpected and we therefore consider it worthy of discussion. There are at least two possible explanations for the appearance of 14h RH as the most common determinant during this period: One explanation is that although 5 cm SM was significantly less ($p < 0.001$) during the second growth period, SM may not have been a limiting factor as the demand for water from the less vigorous vegetative growth (Table 1) would also have been less. Thus other factors such as 14h RH become limiting. Another related possibility is that the presence of sunken stomata in these *Stipagrostis* species (Bornman, pers. comm.) may enable more efficient use of available atmospheric moisture. It was found that 14h RH decreased significantly ($p < 0,001$) from the first growth period to the second, average values were 42% and 18% respectively. Thus stomatal response controlled by ambient moisture, which has been demonstrated in other plants (Schulze *et al* 1975, Larcher 1975) may be effecting overall grass growth, and acting as a limiting factor during the second period.

DISCUSSION

Multiple linear regression analysis has elucidated relationships between ephemeral grass growth, soil moisture and macro-climatic factors. Generally, the proportion of the total variance in grass height that could be accounted for was high. Nonetheless, differences between species of *Stipagrostis* during the two intervals were clear. The smallest values of R^2 were found in *Stipagrostis ciliata*, 59% and 79% respectively, in the two periods, followed by *S. subacaulis* with 81% and 83%, while the highest values were consistently obtained for *S. gonatostachys*, 87% and 94% for the early and late periods respectively.

The interspecific variations highlighted by the regression results could perhaps reflect the degree of adaptation of the three grass species to the Namib environment. The distribution of *S. ciliata* includes Africa and Asia (Merxmüller 1970). *S. ciliata* grows more commonly in the higher rainfall areas of the central Namib and in areas where it can assume an annual or perennial growth form (Seely 1978*b*). In the interdune valleys it replaces *S. gonatostachys* towards the east where the rainfall is regularly greater (Seely, pers. obs.). *S. ciliata* is probably less well adapted to the particularly extreme Namib environment under consideration and therefore has a more variable growth pattern. *S. subacaulis* exhibits a somewhat more northerly range of distribution, occurring mainly in districts bordering the northern Namib (Merxmüller 1970). Its degree of adaptation to the study area, as reflected by the role of climatic factors in determining growth patterns, appears to be intermediate between *S. ciliata* and the dune grass, *S. gonatostachys*. The distribution of *S. gonatostachys* is restricted to the western Namib, mainly in the interdune valleys of the Namib dune field (Merxmüller 1970; Seely, pers. obs.). Annual rainfall here is usually limited to an average of 15 mm or less (Seely 1978*a*). Thus this species probably responds readily to any available moisture. That the analysis for this species includes soil moisture as an explanatory variable to a lesser extent than for the other two species, suggests that an apparently low level of soil moisture is less of a limiting factor for growth of *S. gonatostachys*.

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CAPTIONS

FIG. 1. Location of quadrats on the gravel plain north of the Kuiseb River (1-16) and those on the interdune valleys to the south of Gobabeb (1-4). Inset shows position of study area on the Southern African subcontinent.

FIG. 2. Graph of height of *Stipagrostis subacaulis* and soil moisture levels at the surface and at 5 cm in plot 1-2 during the first growth period.

TABLE 1. Comparison of the above ground production of dry matter for the 3 *Stipagrostis* species during the two growth periods. Significance of difference between means over two periods indicated by SIGNIF.

SPECIES	PERIOD 1		PERIOD 2		SIGNIF.
	Number of plants m^{-2}				
	No.plants	No. plots	No.plants	No. plots	
S. ciliata (plains)	15.7	15	20.0	14	N.S
S. subacaulis (plains)	34.5	19	29.3	12	N.S
S. gonatostachys (dunes)	175.5	8	172.0	8	N.S
	Grams dry weight m^{-2}				
S. ciliata	23.9		0.8		.01
S. subacaulis	4.4		0.6		.01
S. gonatostachys	22.0		3.9		.01
	Grams dry weight $plant^{-1}$				
S. ciliata	1.5		0.04		.001
S. subacaulis	0.1		0.02		.001
S. gonatostachys	0.1		0.02		.05

TABLE 3. Final regression equations for 3 species of *Stipagrostis* grown during the second growth period. Overall fit of all regression equations is significant at $p < 0.10$.

PLOT	FINAL REGRESSION EQUATIONS	R^2
	S. ciliata	
1-2	GH = -309.5 - 113.6 (5 cm SM) + 12.8 (14h SSfT)	.95
3-4	GH = 433.8 - 6.3 (14h RH) - 12.8 (08h SSfT)	.86
7-8	GH = 169.4 - 90.8 (5 cm SM)	.79
13-14	GH = 147.1 - 4.6 (14h RH)	.57
	AVERAGE R^2 (4 plots)	.79
	S. subacaulis	
1-2	GH = 216.7 - 1.1 (08h RH) - 3.8 (MAX T)	.82
3-4	GH = 281.2 - 2.3 (14h RH) - 3.2 (EVAP)	.71
5-6	GH = 71.1 - 23.5 (5 cm SM)	.65
9-10	GH = 182.2 - 9.4 (5 cm SM) - 5.8 (08h SSfT) - 1.7 (14h RH)	.95
11-12	GH = 74.8 - 3.1 (14h RH) + 54.4 (SfSM)	.88
15-16	GH = 208.9 - 24.6 (5 cm SM) - 1.9 (14h RH) - 3.2 (14h SSfT)	.99
	AVERAGE R^2 (6 plots)	.83
	S. gonatostachys	
1	GH = 113.4 - 2.7 (14h RH) - 2.4 (08h SSfT) + 56.1 (5 cm SM)	.95
2	GH = 228.1 - 4.5 (14h RH) - 5.0 (08h SSfT)	.91
3	GH = 41.1 - 12.8 (08h SSfT) + 7.9 (MAX T)	.89
4	GH = 129.8 - 3.2 (14h RH) - 1.6 (MIN T)	.99
	AVERAGE R^2 (4 plots)	.94

TABLE 2. Final regression equations for 3 species of *Stipagrostis* grown during the first growth period. Overall fit of all regression equations is significant at $p < 0.10$.

PLOT	FINAL REGRESSION EQUATIONS	R^2
	S. ciliata	
1-2	GH = 360.5 - 41.1 (5 cm SM)	.64
3-4	GH = 391.5 - 43.3 (5 cm SM)	.49
7-8	GH = 554.6 - 149.1 (5 cm SM) + 63.6 (SfSM)	.80
13-14	GH = 875.8 - 33.4 (08h SSfT)	.41
	AVERAGE R^2 (4 plots)	.59
	S. subacaulis	
1-2	GH = 237.0 - 13.5 (5 cm SM) - 2.1 (EVAP)	.86
3-4	GH = 531.5 - 16.2 (08h SSfT) - 1.4 (08h RH)	.84
5-6	GH = 74.7 - 7.5 (5 cm SM)	.73
9-10	GH = 174.2 - 5.1 (08h SSfT) - 3.6 (5 cm SM)	.76
11-12	GH = 181.5 - 1.3 (14h RH) - 4.1 (08h SSfT)	.83
15-16	GH = 215.9 - 1.5 (14h RH) - 5.1 (08h SSfT)	.84
	AVERAGE R^2 (6 plots)	.81
	S. gonatostachys	
1	GH = 1807.1 - 9.1 (14h RH) - 19.0 (EVAP)	.77
2	GH = 607.3 - 153.8 (5cm SM) - 16.2 (08h SSfT)	.96
3	GH = 430.7 - 5.3 (14h RH) - 1474.2 (SfSM)	.85
4	GH = 160.0 - 78.4 (5 cm SM)	.91
	AVERAGE R^2 (4 plots)	.87

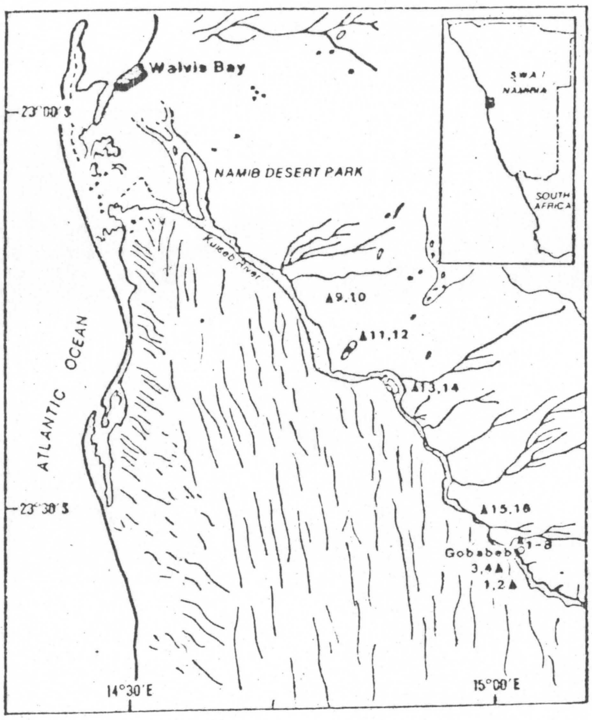
Walvis Bay
23°00'S
NAMIB DESERT PARK
Kuiseb River
ATLANTIC OCEAN
▲9,10
▲11,12
▲13,14
▲15,16
5-8
Gobabeb
3,4▲
1,2▲
23°30'S
14°30'E
15°00'E
SWA / NAMIBIA
SOUTH AFRICA

FIG 1

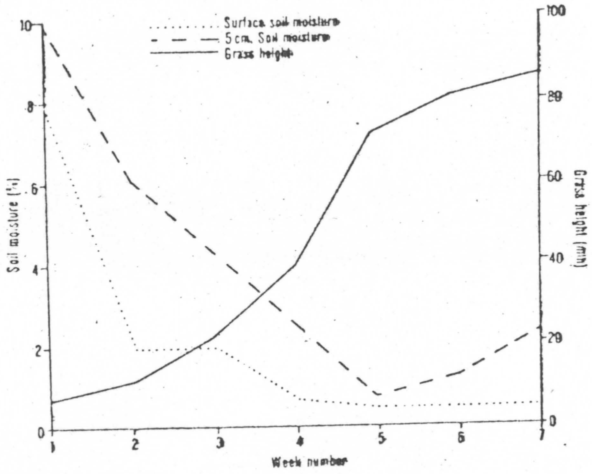
Surface soil moisture
5 cm. Soil moisture
Grass height
Soil moisture (%)
Grass height (mm)
Week number
10
8
6
4
2
0
100
80
60
40
20
0
1
2
3
4
5
6
7

Fig 2