The patch-scale distribution pattern of *Stipa capensis* and its affect on annual plant diversity and growth

Overgrazed Sandveld landscape near Vanrynsdorp invaded by *Stipa capensis*

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A project in partial fulfilment of the requirements for a B.Sc. Honours degree in Plant Ecology, University of Cape Town, 2003

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Abstract

Namaqualand is home to an unusually large diversity of plant species the most noticeable component being that of the large flowering annuals. In the last 50 years the annual grass *Stipa capensis* has spread throughout the Vanrynsdorp landscape having previously been restricted to localised areas. This study investigated how the Vanrynsdorp Sandveld environments have changed in the last 100 years through photographic comparison and the implications of this change for *S. capensis* distribution. The distribution of *S. capensis* at a habitat scale in degraded and less degraded sites was also established. Lastly the affect of *S. capensis* on herbaceous annual diversity and growth was assessed. Results indicated that perennial cover was sparser and there were more, large intershrub patches. The degraded Vanrynsdorp landscape could be described by four habitats, 1= heuweltjie with grass, 2= calcrete ring around heuweltjie with no grass, 3= off heuweltjie with grass, 4=off heuweltjie depressions with no grass. *S. capensis* was generally restricted to habitats 1 and 3 and "weedy" annuals were distributed between habitats 1, 3 and 4. High abundance of *S. capensis* and annual plants in habitats 1 and 3 were due to more benign habitat conditions. High annual plant abundance in habitat 4 was due to the presence of an algal crust. Habitat 2 had very low diversity and density of plants. *S. capensis* had no relationship with the diversity or density of "weedy" annual species. It did however retard the growth and maturation of the large annual *Dimorphotheca sinuata* in both drought and optimum moisture conditions. *S. capensis* may impact negatively on the indigenous annuals in the area important to tourism however it performs vital agroecological functions as well. These include amelioration of wind and water erosion effects and providing fodder for livestock. Before considering removal of this grass agroecological impacts should be taken into consideration.

Introduction

Namaqualand is an area that has been under human influence for thousands of years, the land has been used for cropping as well as livestock production. This form of landuse has dramatically altered the landscape. Anthropogenic pressure has not stopped but continues changing the natural ecology of the area. Large annual plants found in Namaqualand provide a floral display every spring, drawing thousands of tourists. The variety of forms and colours provide a visual pleasure to many. It is an area known for its diversity of geophytes and succulent shrubs, 30-40 species have been recorded at a scale of 0.1 ha in the Sandveld habitats such as those of the study area (Cowling *et al.* 1989). This area has a relatively benign temperature regime and receives less than 150 mm of rain a year and although this is particularly low it is regular and the ecology of the area depends on this regularity (Cowling *et al.* 1999a).

In the last 50 years it appears that an invasive grass has spread throughout the area, replacing these displays. This grass was first observed to be occasionally abundant on heuweltjies by Acocks (1953). Heuweltijes are mounds distributed throughout the winter rainfall Succulent Karoo region. They are large, raised termite mounts, which attract a large array of fossorial mammals since the soil on heuweltjies is generally deep and well drained (Cowling 1999). They are regularly distributed throughout the landscape and are sites of high disturbance (Cowling 1999). There appears to have been an increase in the distribution and density of the annual grass in the area over the last 50 years. This grass could be impacting on the indigenous flora. The increase in annual grasses in Namaqualand has been attributed to the spread of alien covercrops from road verges, ploughing and rangeland deterioration caused by domestic livestock (Steinschen *et al.* 1996). There are several grasses present in the area but the major grass, *Stipa capensis*, generally considered to be indigenous, is the most abundant. Currently the conservation of the Namaqualand area is poor only 3.5 % of the area is conserved by three small reserves (Cowling 1999b) and there are no reserves in the Vanrynsdorp area.

Steinschen *et al.* (1996) investigated the abundance of the grasses *Bromus pectinatus* and *Stipa capensis* as well as that of the annual forbs and geophytes for three sites in the

Namaqualand with different disturbance regimes and cover. They found that grazing reduced perennial cover on the heuweltjies and in low-lying areas. They also found low annual abundance was greatest where perennial cover was low and grazing reduced annual diversity. They concluded that the annual flower displays were threatened more by grazing than by grasses invasions.

The purpose of this study was to investigate the distribution of the dominant grass, *Stipa capensis* and the affect of this grass on the growth and diversity of annuals. The following three questions were addressed in this study: How the Vanrynsdorp Sandveld environments have changed over the last 100 years and what are the implications of this change is for *S. capensis* abundance, what the distribution pattern of *S. capensis* in degraded and less degraded environments is and lastly how *S. capensis* affects herbaceous annual diversity and growth.

Study area

The area used for this investigation was Aties farm in the Vanrynsdorp area. The area has been occupied since 1836. For this study two sites were sampled. Site 1 is located S 31 37 43.9, E 1.8 38 53.2 and was less degraded than site 2, S 31 39 22.7, E 18 39 52.2. Total perennial cover for site 1 was 12 % and for site 2 was 5%. The mean distance between shrubs at both sites was 1.8 m for site 1 and 1.9 m for site 2. . Dominant species were *Aridaria noctiflora*, *Asparagus* sp., *Drosanthemum cf. hispidum*, *Galenia affinis*, *Sasola dealata*. and *Zygophyllum microphyllum*.

The landscape could be coarsely divided into four habitats. These habitats became more clearly defined as the intensity of degradation increases. The four habitats can be described topographically as in Figure 1a and b:

1= heuweltjie with grass present

2= exposed calcrete "ring" at the base of the heuweljtie with no grass

3=off heuweltjie with grass

4=off heuweltjie "depressions" with no grass

Figure 1a: Photograph of the four habitats in the degraded Sandveld landscape near Vanrynsdorp.

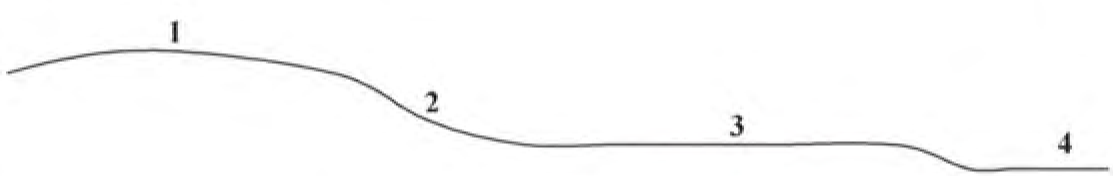

Figure 1b: Major habitats found in the landscape, habitats 1 and 2 are on heuweltjies and habitats 3 and 4 are between heuweltjies.

Table 1: Proportions of each habitat in each site. Proportions of habitat 2 and 4 increased in site 2 (the more degraded site).

	Site 1	Site 2
Habitat 1	33	30
Habitat 2	7	15
Habitat 3	40	30
Habitat 4	20	25

Methods

Photograph

Botanist Rudolph Marloth took a photograph of the general Vanrhynsdorp landscape probably in the first decade of the 20th century. The precise position from where this early photograph was taken was re-located and a new image taken. Plant cover and species composition were compared between the two photographs providing close to a 100-year record of vegetation change in the region.

Survey of habitats

Perennial cover was measured by recording the distance to the nearest shrub for 30 individuals. Dominant perennials were noted and their percentage cover estimated. Percentage cover of physical characteristics describing each habitat was estimated within random 50 by 50 cm quadrats in each habitat. Physical characteristics included percentage cover of algal crust, non-living crust, loose sand, stones, litter and plant cover. This was repeated 5 times per habitat. At each site the wetting front after 2.5 mm of rain had fallen the night before was measured with 7 replicates per habitat. Soil depth was measured for each site by digging till the hard substrate was reached; this was repeated 3 times per habitat. The mean and standard deviation was calculated for each of the plant and soil variables as well as the wetting fronts and soil depth. A one-way ANOVA and post hoc Tukey test tested for significant differences between the means of the variables for each habitat between each site (Zar 1984).

At each site three, 10 m transects were laid out for each microhabitat yielding a total of 12 transects for each site. For each 1 m interval percentage grass cover was estimated within 16 by 16 cm quadrat. The number of individual grasses and all plants were counted and their growth forms noted. The numbers of each species identified by growth form are presented as total numbers in each habitat for each site. A one-way ANOVA and a post-hoc Tukey test were used to test for significant differences between habitats within and between sites (Zar 1984). Data for grass abundance and distribution and density of annual plants was analyzed using Decorana (Community analysis package 2.13, Pisces Conservation LTD). Sites 1 and 2 were analyzed independently. The two principle axes were used to plot the graphs. The relationship between *Stipa capensis* abundance and number of species for each plot was regressed, as well as the relationship between *S. capensis* abundance and number of "weedy" annual individuals (Zar 1984).

Competition of large annuals with grass

A greenhouse experiment was set up to measure the effects of grass density on the growth of annuals. Soil was taken from a dense grass site between sites 1 and 2 and was used to fill 24 pots with a diameter of 15cm and depth of 22cm. Potting gravel was placed in the bottom of the pots and they were then filled with the soil. *Dimorphotheca sinuata* seed was sown in the middle of each pot. All pots were saturated in order to germinate grass and *D. sinuata* seed on the 1 July 2003. In all pots the grass successfully germinated and grew, however *D. sinuata* seed successfully germinated and grew in only 18 of the pots. After a further 2 weeks, half the pots were set aside for a dry treatment and the grasses were thinned or removed in order to create a grass density gradient. For the wet treatment soil was kept saturated. For the dry treatment soil was left to dry and moistened only when *D. sinuata* started to wilt. Grass and *D. sinuata* were harvested on the 7 October 2003 and above ground biomass harvested, dried at 65 °C for 5 days and then weighed. Root material was too matted to separate and therefore excluded from the analysis. To show the affect of grass cover on the growth of herbaceous annuals, above ground biomass of *D. sinuata* was regressed against grass biomass (Zar 1984). The slopes and elevation of the regressions were compared (Zar 1984).

Results

Environmental History

Differences in cover were compared for the site with the coordinates 31° 39' 42.0 S, 18° 39' 38.6 E, ± 6.1, 132 m asl (Figures 2a and 2b). The first photograph was taken in the 1920's and was retaken on 18 September 2003. Cover was far sparser in 2003 and shrubs were further apart. The landscape in 2003 generally exhibited more bare patches. The perennial *Mesembryanthemum cf. crystallinum*, dominant on the "heuweltjie" in the foreground of the early photograph, has been reduced to sparsely scattered individuals. *Euphorbia schoenlandii*, the erect, ±50 cm tall stem succulent present in the earlier image was no longer present on the "heuweltjie" in 2003. The nearest location for this species was approximately 500m south of the location of the photographs. The dominant shrub in the 2003 photograph was *Salsola cf. tuberculata*. A sparse cover of grass and "weedy" annuals has colonized the bare inter-shrub spaces.

Figure 2a: Photograph taken by Rudolf Marloth in the early 1900's from a location south west of Vanrynsdorp. In the foreground is a heuweltjie with dense perennial cover and in the background is the Matsikammaberg.

Figure 2b: Photograph was retaken by matching the site , coordinates, 31° 39' 42.0"S, 18° 39' 38.6"E 6.1 132 m asl. The location was 1.7 km north of Aties farmhouse on an old road to Vredendal. Cover on the heuweltjie is much sparser.

Figure 3 is a model indicating how the spread of *Stipa capensis* might have occurred and how the colonization of the area by European farmers facilitated this spread. It is probable that perennial shrubs dominated the landscape, while annual species were confined to locally disturbed sites. Regular disturbance in the form of grazing provided a niche for annuals to colonize areas more frequently. Continued heavy grazing and the introduction of *S. capensis* selected for the small, weedy species. This has resulted in a landscape that is homogenous and dominated by *S. capensis*, particularly in dry years.

Perennial vegetation dominant

Annuals confined to locally disturbed sites

→ Sustained heavy grazing Reduces perennials, increases annuals and geophytes

<perennial shrubs >annuals (large and small) >geophytes

Continual heavy grazing → Selection for small weedy annuals → Introduction of grass

Solitary shrubs localised
Few large annuals except in good years
Homogenous in dry years- grass dominant in landscape with weedy annuals and few geophytes

Altered microclimate and microtopographical effects

Figure 3: Facilitation of *Stipa capensis* spread through the area

Microhabitats within the landscape

Soil and plant variables differ between the four habitats and give them distinct characteristics (Table 2). Soil depth did not vary much between habitats 2, 3 and 4 for either site; however, habitat 1 was significantly deeper at site 1 ($n=3$, $f=0.0002$, $p<0.05$). Wetting fronts were significantly deeper for habitats 1 and 4 ($n=7$, $f=0.0002$, 0.0005, 0.0078, 0.0102, $p<0.05$) and very similar for habitats 2 and 3 in both sites. Wetting fronts were generally deeper at site 2. Algal crust was the dominant cover type for habitat 1 and

4 in site 1 but was only dominant in habitat 4 of site 2. Algal crust was significantly more abundant in habitat 4 of both sites (n=5, f= 0.0001, 0.0004, 0.0002, 0.003, 0.0186, 0.002, $p<0.05$). There was little algal crust in habitats 2 and 3. Non-living crust was most abundant in habitat 2 at both sites, and constituted significantly the greatest proportion of cover for habitat 2 in site 1 (n=5, f=0.0001, 0.0002, 0.0004, $p<0.05$) while in site 2 it was not a dominant cover type. Loose sand was most abundant in habitat 2 for both sites, however, it was not significantly so. Stone cover was significantly greater (n=5, f=0.0001, $p<0.05$) in habitat 2 of site 2 and occurred rarely in other habitats. Litter was more common in habitats 1 and 3 of both sites, habitat 3 having the most litter although this was not consistently a significant result. Plant cover was significantly highest for habitats 1 and 3 in both sites and was very low in habitats 2 (n=5,f=0.0001, 0.001, 0.0002, 0.0005, 0.0006, 0.0163, $p<0.05$) while intermediate values were attained for habitat 4 which were not significantly different from habitat 2.

<u>Table 2</u>: Variables (plant and soil) describing the four microhabitats at two sites in the Vanrhynsdorp area of southern Namaqualand. Significant differences between habitats within and between sites were calculated in a one-way ANOVA and compared using a posthoc Tukey test for equal n.

		Site 1				Site 2			
		Habitat				Habitat			
Variable	n	1	2	3	4	1	2	3	4
soil depth (m)	3	0.66^{a} ±0.06	0.09^{b}±0.02	0.16^{b} ±0.01	0.17^{b} ±0.03	0.8^{a} ±0	0.1^{b} ±0.02	0.20^{b} ±0.01	0.17^{b} ±0.03
wetting front (cm)	7	34.7^{a} ±6.6	23.3^{b} ±9.3	25.4^{b} ±5.3	33.9^{a} ±5.4	38.4^{a} ±4.8	31.9^{b} ±4.2	31.3^{b} ±4.5	45.3^{a} ±5.3
% algal crust	5	40^{a} ±21	5^{a} ±3	10^{a} ±11	51^{b} ±11	12^{a} ±17	18^{a} ±20	2^{a} ±2	70^{b} ±25
% non living crust	5	15^{a} ±20	67^{b} ±9	12^{a} ±10	22^{a} ±13	23^{a} ±14	25^{a} ±17	24^{a} ±10	4^{a} ±2
% loose sand	5	6 ±5	24 ±11	8 ±4	12 ±7	22 ±13	39 ±21	9 ±5	16 ±22
% stone cover	5	0^{a} ±0	2^{b} ±1	0^{a} ±0	0^{a} ±0	1^{a} ±1	12^{a} ±5	1^{a} ±1	1^{a} ±1
% litter	5	10 ±6	2 ±2	33 ±11	8 ±6	19 ±7	4 ±4	23 ±12	3 ±3
% plant cover	5	29^{a} ±4	1^{b} ±1	37^{a} ±15	7^{b} ±5	24^{a} ±11	1^{b} ±1	41^{a} ±6	6^{b} ±1

Distribution of *Stipa capensis* and "weedy" herbaceous annuals

Stipa capensis was the most common species in habitats 1 and 3, "weedy" annual species are distributed across the habitats. Samples and species are arranged in space so that similar entities are close together (Figure 4). Dominant species are identified by growth form. Habitats 1 and 3 are grouping together around Gr1 (*Stipa capensis*) and Ha4 (*Erodium* sp.). Habitat 2 is clustering around Ha1 (*Atriplex* sp.), Ge2 (*Oxalis* sp.), Ha7 (*Zuluzianskya* sp.) and to a lesser extent Ha5 (unidentified herbaceous annual). Habitat 4 has a greater spread but is clustering around Ha6 (*Leysera tenella*) and LSA2 (unidentified succulent annual).

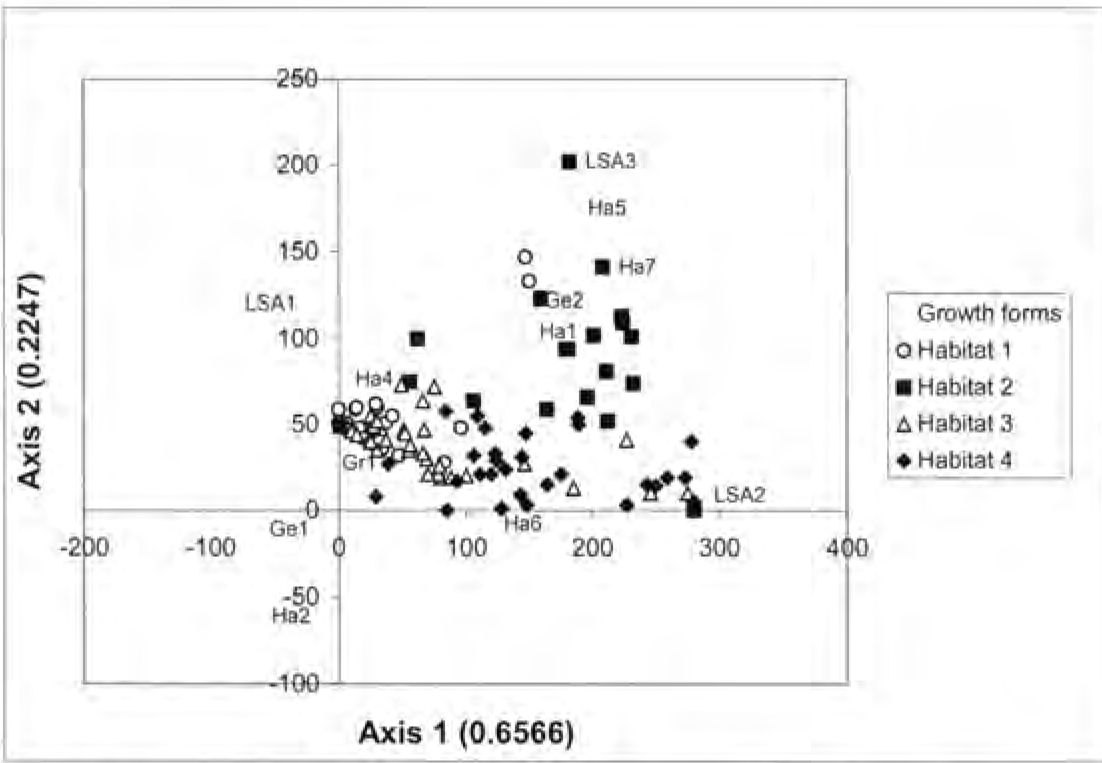

Figure 4: Ordination of the four microhabitats: distribution of *Stipa capensis* and dominant "weedy" annual species, site 1.

Habitat 1 and 4 are clustering together around Gr1 (*Stipa capensis*), Ha5 (unidentified herbaceous annual) and LSA1 (*Dorotheanthus* sp.) (Figure 5). Habitat 2 is clustering around Ha1 (*Atriplex* sp.) and LSA3 (*Dorotheanthus* sp.), although LSA1 is also influencing the cluster. Habitat 4 is broadly characterized by the species Ge2 (*Oxalis* sp.), LSA2, Ha4 (*Erodium* sp.), Ge2 and Ha7 (*Zuluzianskya* sp.).

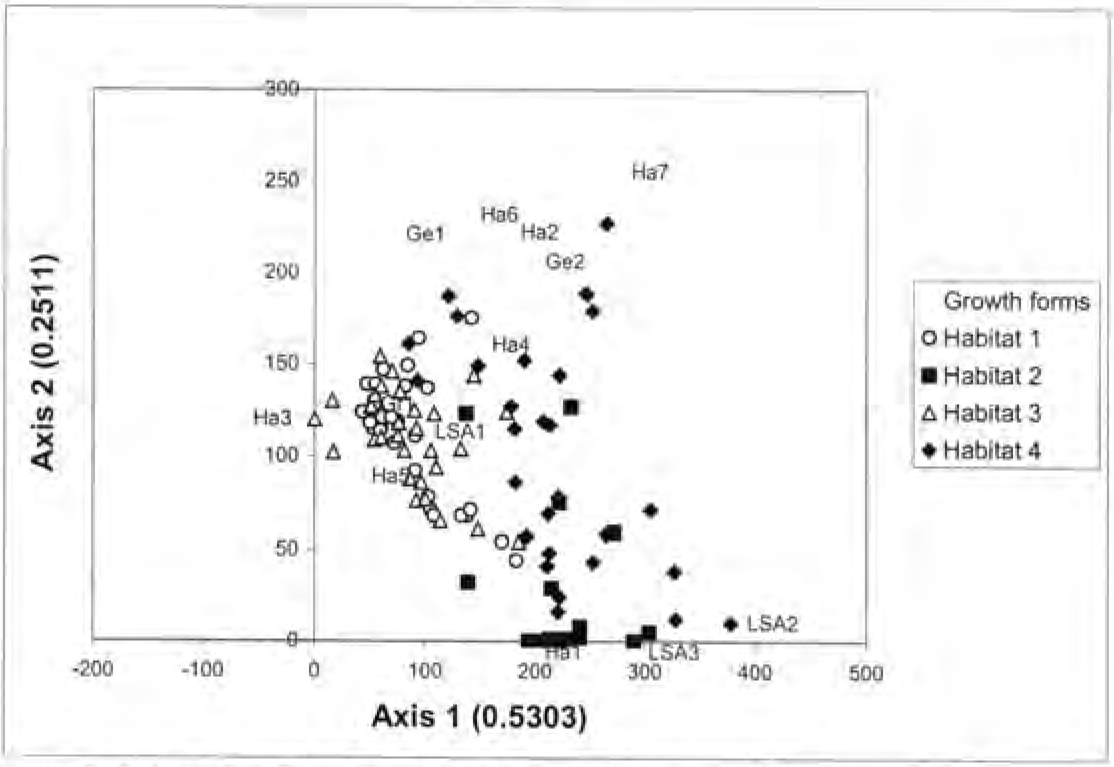

Figure 5: Ordination of the four microhabitats: Distribution of *Stipa capensis* and dominant "weedy" annual growth forms for site 2.

Mean number of species in each habitat (Table 3) was significantly lower in habitat 2 (n=60, f=0.00011, 0.00139, 0.00003, 0.00066, 0.00740, 0.00004, 0.00045, 0.00003, $p<0.05$). Highest number of species was in habitat 3 while the second highest value was in habitat 1.

Table 3: Mean number of species and standard deviation for each habitat.

Habitat 1	Habitat 2	Habitat 3	Habitat 4
8.8 (±2.8)^a	5.3 (±1.2)^b	10.2 (±2.5)^a	7.8 (±1.9)^a

The density of the dominant species varied for all the habitats and occasionally varies between sites (Table 4). *Stipa capensis* was most abundant in habitat 1 followed closely by habitat 3. The density of *S. capensis* was lowest in habitat 2. Site 2 generally had lower numbers of grass than site 1. Ha1 was more common in site 2, whereas Ha6 is more abundant in site 1. Ha7 was evenly distributed between the sites. LSA1 is generally confined to habitat 1. Herbaceous annuals were found in highest densities in habitat 3 and second highest densities were in habitat 4. Habitat 2 had the lowest density of herbaceous annuals. LSA2 was more abundant in habitats 3 and 4 of site 1 and most abundant in habitat 4 of site 2. LSA3 was generally more abundant in site 2 and occurred at greatest densities in habitat 1 of both sites, it was least common in habitat 3. Leaf succulent annuals (LSA) densities in habitat 4 were not as reduced as the other growth forms. Lowest densities of LSA's were found in habitat 2 of site 1 and habitat 3 of site 2. There are far more geophytes present in site 2 where the abundance of grass was lower. In both sites the highest numbers of geophytes were found in habitat 3. Total number of individuals is highest in habitats 1 and 3, with a large decrease to habitat 4 and a further large decrease to habitat 2.

Table 4: Total density of each species and growth form in each habitat for each site.

	Site 1				Site 2			
	Habitat				Habitat			
Growth form and species	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
Geophytes								
Androcymbium sp. (Ge1)	2	0	3	0	27	1	9	14
Oxalis ecklonia (Ge2)	1	0	12	5	2	0	24	18
Unidentified geophyte (Ge3)	0	0	3	0	0	0	0	0
Ledebouria sp. (Ge4)	0	0	0	0	0	0	1	0
Unidentified geophyte (Ge5)	0	0	0	0	0	0	1	0
Unidentified geophyte (Ge6)	1	0	0	0	0	0	0	0
Albuca sp. (Ge7)	0	1	1	0	2	1	0	0
Total geophytes	**4**	**1**	**19**	**5**	**31**	**2**	**35**	**32**
Grass								
Stipa capensis (Gr1)	824	28	520	74	683	16	491	40
Unidentified grass (Gr1)	0	0	0	0	0	0	8	0
Total grasses	**824**	**28**	**520**	**74**	**683**	**16**	**499**	**40**
Herbaceous annuals								
Atriplex sp. (Ha1)	7	11	54	16	222	126	196	190
Unidentified herb. annual (Ha2)	0	0	0	1	0	0	11	11
Ursinia sp. (Ha3)	0	0	0	0	0	0	175	1
Erodium sp. (Ha4)	0	0	20	0	0	0	3	1
Unidentified herb. annual (Ha5)	3	0	0	5	28	2	3	2
Leysera tenella (Ha6)	196	17	404	270	54	4	58	75
Zuluzianskya sp. (Ha7)	24	61	29	36	14	13	17	112
Unidentified herb. annual (Ha8)	1	0	0	0	0	0	0	0
Unidentified herb. annual (Ha9)	1	0	3	0	0	0	0	0
Crotalaria sp. (Ha 10)	1	0	0	1	9	0	1	2
Crotalaria sp. (Ha 11)	0	0	0	0	0	0	1	0
Amsinckia calycina (Ha 12)	1	0	0	0	0	0	0	0
Acanthopsis disperma (Ha 13)	0	0	0	0	2	0	0	0
Total herbaceous annuals	**234**	**89**	**510**	**329**	**329**	**145**	**465**	**394**
Leaf succulent annuals								
Dorotheanthus sp. (LSA1)	52	0	0	0	47	0	1	9
Unidentified suc. annual (LSA2)	0	37	135	275	14	31	12	141
Dorotheanthus sp. (LSA3)	25	14	2	3	36	28	6	33
Aizoon sp. (LSA4)	0	0	0	0	1	0	0	0
Unidentified suc. annual (LSA5)	0	2	0	0	0	0	0	0
Unidentified suc. annual (LSA6)	1	0	0	0	0	0	0	0
Total leaf succulent annuals	**78**	**53**	**137**	**278**	**98**	**59**	**19**	**183**
Total number of individuals	**1140**	**171**	**1186**	**686**	**1141**	**222**	**1018**	**649**

Relationship between *Stipa capensis* and indigenous herbaceous annuals

Figure 6 indicates that there was no relationship between the numbers of "weedy" species and abundance of *Stipa capensis* for both sites (n=240, R^2= 0.0258, $p>0.05$).

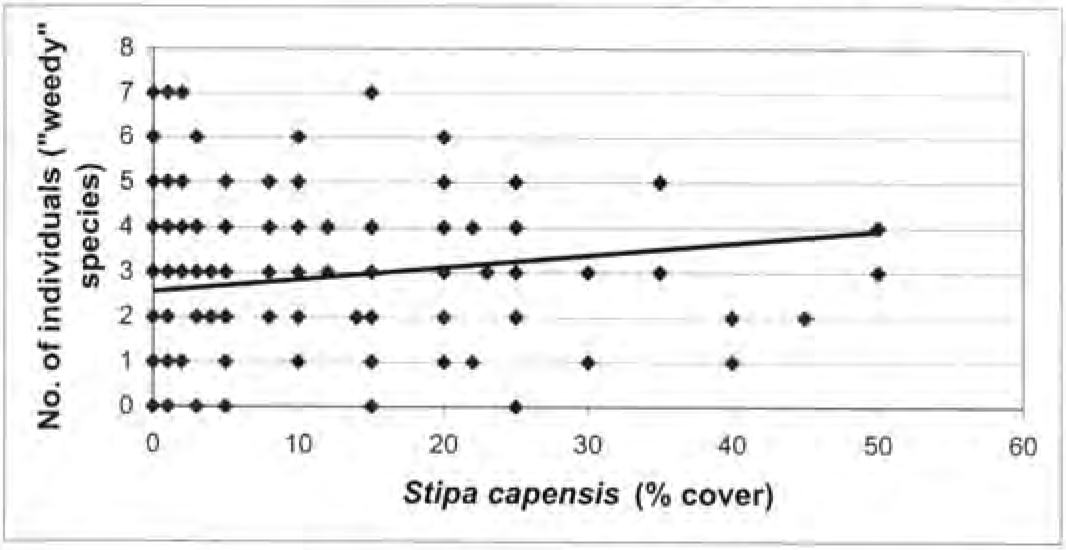

Figure 6: Relationship between abundance of *Stipa capensis* and number of species.

There was no relationship between the number of individuals of "weedy" species and the % cover of *Stipa capensis* (Figure 7) for both sites (n= 240, R^2=0.0086, $p>0.05$).

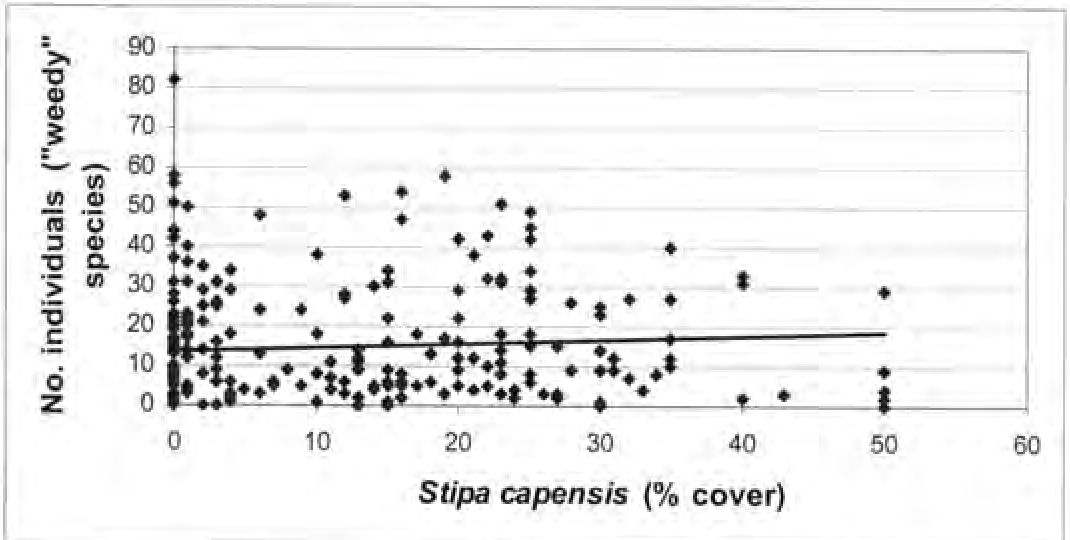

Figure 7: Relationship between abundance of *Stipa capensis* and number of individuals.

The relationship between above ground biomass of *Dimorphotheca sinuata* and above ground biomass of grass for dry and wet treatments (Figure 8) was significant (dry treatment; n=9, R^2= 0.7414, p< 0.025, wet treatment; n=7, R^2= 0.7401, p<0.05). Biomass of the large flowering annual was inversely related to biomass of the grass and the wet treatment had a steeper gradient than the dry treatment although not significantly (f=2.48, p=0.1416, p>0.05). The elevations of the regressions are significantly different (f=14.13, p=0.0024, p<0.05).

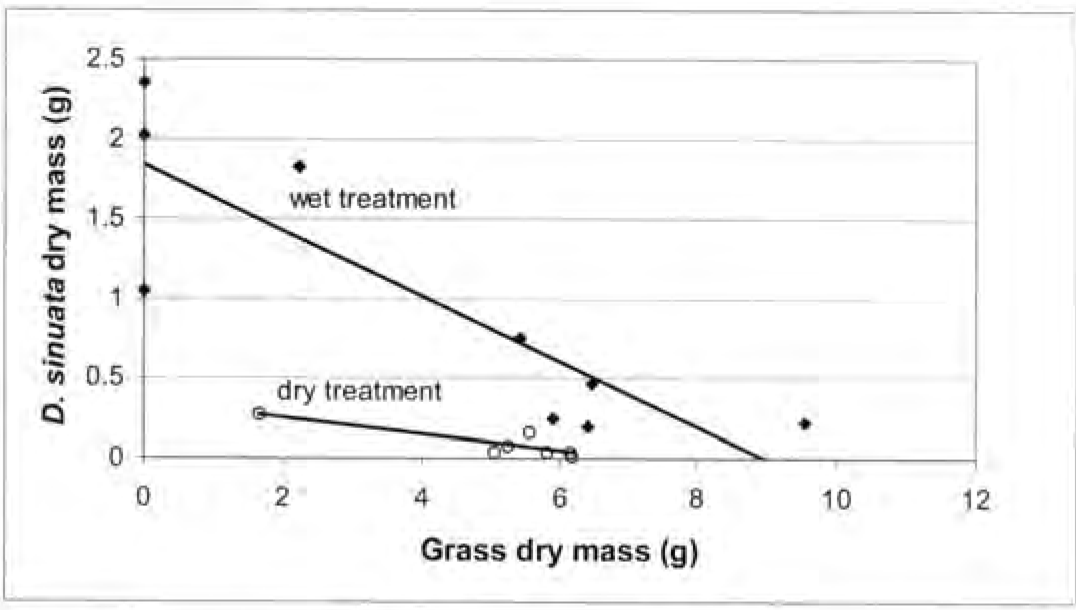

Figure 8: Relationship between above ground grass biomass and above ground *Dimorphotheca sinuata* biomass.

Discussion

Environmental History

Perennial cover has decreased significantly since the photograph by Marloth was taken in the early 1900's. In the period between the photographs the area has been heavily grazed and often overstocked. There was a relationship between perennial cover and grazing intensity and perennial cover has been proven to decrease with increased grazing intensity (Steinschen *et al.* 1996). Perennials are unable to reproduce successfully and recruitment is poor under heavy grazing (Dean and Milton 1991), this explains why there are patches in the recent photograph with no perennial cover. Photographic evidence concurs with the observations from the resident landowner (Willem van Niekerk). *Stipa capensis* was less widespread in the 1950's and the site used for this study did not have grass at that time. According to van Niekerk, *S. capensis* is widely distributed throughout his farm although it does not grow in the redder sands, preferring the calcrete areas. In his opinion the red sands are too hot for the grass. He also felt that perennial cover had been vastly reduced, the perennial *Salsola tuberculata* (a well grazed species) being a species that has decreased most noticeably. Steinschen *et al.* (1996) found perennials constituted approximately 40% of the cover on good rangeland and less than 5 % on poor, overgrazed rangeland and this agrees with observations from September 2003.

The model predicts how the continual disturbance of the landscape and the sparser cover of perennials created the space for annuals including *Stipa capensis* to colonise. Removal of perennial cover by grazing or other forms of disturbance leaves the environment open to colonisation by annuals and geophytes which are otherwise unable to successfully compete with the perennial shrubs particularly for space (Dean and Milton 1991). The overall effect of competition is that the abundance of plants is higher when competitors are present only in low densities (Brooks, 2000). It follows that there was an increase in annuals and geophytes with the decrease in perennial cover and competition. It has been observed that there are dense patches of large flowering annuals in old wheatfields and ploughed lands (Cowling 1999) this concurs with the predictions of the model. The continual overstocking and heavy grazing however eventually affects recruitment and growth of the large flowering annuals negatively. This allowed the faster growing grass (*Stipa capensis*) to colonise bare patches. The severe degradation in combination with low rainfall years is a hostile environment, even for the large flowering annuals. The survival and maturation of these annuals depends on the rainfall (Van Rooyen *et al.* 1992). If the required climatic conditions are not met the annuals do not occur in large abundance. Invasive grasses have been found to outcompete indigenous annuals for resources and to have faster growth rates. In a study by Defalco *et al.* 2003, the efficiency of water and nitrogen uptake as well as biomass increase was compared between the invasive annual grass *Bromus madritensis* subsp. *rubens* and two indigenous annuals. *B. rubens* was able to outcompete the indigenous annuals in all three categories over a larger range of available N and a larger range of plant densities.

This winter rainfall area is becoming increasingly sensitive to invasions. Factors such as changing land use, heavy grazing, atmospheric pollution and natural disturbance are interacting and influencing the distribution and abundance of alien grasses (Richardson *et al.* 2000). C_3 grasses such as *Stipa capensis* are good at dispersing over limited distances, some have hooks enabling attachment to the coats of animals (Richardson *et al.* 2000). Small natural disturbance at a patch scale allows scattered metapopulations of alien grasses to establish (Richardson *et al.* 2000). In Vanrynsdorp grazing causes regular disturbance in the area allowing annuals, the grass *S. capensis* in particular, to establish. Cutting and intensive grazing is often implemented to improve the displays of spring flowers but in fact the diversity of indigenous flora has been found to decrease (Van Rooyen *et al.* 1996). Finally climate change and changes to the soil could promote these invasions at patch or landscape scale (Richardson *et al.* 2000). In this area, the combination of heavy grazing and low rainfall years prevents many species from germinating. In these years only the "weedy" annuals and grasses like *S. capensis* occur. With neither the perennial species' nor the large flowering annuals colonising the area only the "weedy" species and the grass *S. capensis* remain in the landscape, the grass forming a dominant component. The ultimate result is a homogenous landscape filled primarily with "weedy" annuals and grass especially in dry years. This landscape is unusual for the area which is well known for its high local and regional plant diversity (Cowling *et al.* 1999).

Distribution of *Stipa capensis* and "weedy" herbaceous annuals in the major habitats

Characteristics of the four habitats, along with species distribution and plant density changed slightly from the less degraded site (site 1) to the more degraded site (site 2). Habitats were distributed more evenly in site 2 whereas in site 1 habitat 1 and 3 constituted a greater proportion of the total area. This could be because of increased degradation at site 2. The higher degree of degradation could be attributed to the fact that site 2 is lower on a soil catena than site 1. More erosion occurs, as the slope is steeper.

Habitats 1 and 3 were more benign habitats supporting the greatest number of species and highest densities of plants. Habitat 1 had deep soil thus creating space for more extensive root structures and increased water infiltration. Soil depth was much greater for habitat 1 because this habitat was on heuweltjies which are disturbed by animals thus preventing compaction of the soil. The wetting fronts in habitat 1 confirm the soil depth results as water penetrates deeper than in habitats 2 and 3. The large proportions of plant cover and litter were evidence of a far more favourable environment in habitats 1 and 3. It is possible that seeds become trapped in the litter and grass and this organic cover provides shading and traps moisture allowing plants to colonize these habitats with greater success. Habitats 1, 3 and 4 had similar numbers of species although they supported different suites of plants. *Stipa capensis* along with several other annual species preferred the benign environment of habitats 1 and 3. *S. capensis* did occur in the other two habitats but at very low densities. Geophytes and herbaceous annuals occurred at highest densities in the benign habitat 3 where fewer grasses were present. Habitat 1 on heuweltjies is usually the most heavily grazed habitat and this could be why there are lower numbers of geophytes and herbaceous annuals even though it is a benign habitat. Spatial heterogeneity of habitats has been found to influence how *S. capensis* responds to rainfall (Kadmon 1993), germination success after rainfall was determined by habitat in this study. It is possible therefore that *S. capensis* is restricted to habitats 1 and 3 through an interaction of the late rainfall season of 2003 and specific habitats.

Habitat 2 was on the edge of the heuweltjies and was easily recognisable because of the band of white quartz stones and exposed calcrete found in it. This band was evidence of the degree of erosion in the site. It is part of the calcrete base of the heuweltjies which becomes exposed as the area erodes. It was more noticeable at site 2 where there was a higher degree of erosion. Habitat 2 was the shallowest with a hard, inhospitable substrate beneath a shallow covering of soil. Lowest species numbers were found in this habitat. Herbaceous annuals and geophytes occurred at lowest densities in the harsh environment of habitat 2 and only the leaf succulent annuals were able to colonise this habitat with any success. Namaqualand leaf succulents commonly have shallow root systems, this is possibly why they are able to survive in the shallow soil characteristic of habitat 2 (Esler *et al.* 1999).

Habitat 4 occurred in depressions with species number almost equivalent to habitat 1, it also had a surprisingly deep wetting front. The density of herbaceous annuals was second highest, leaf succulent annuals were most dense while *Stipa capensis* was observed at low densities. The algal crust that dominates habitat 4 is probably responsible for the high density of plants found in it. Biological crusts alter the resources present in the soil consequently influencing the plant communities which establish in the same habitat (Defalco *et al.* 2001). Crusts increase infiltration (Fletcher and Martin 1948) (hence the deep wetting front) and so there is more water available to plants. This crust also provides a less stressful microclimate for seedlings as it stores not only water but nutrients as well (Lesica and Shelly 1992). Nitrogen fixing bacteria increase the N and P uptake of plants (Pauli 1964; Rogers *et al.* 1966), consequently higher densities of plants are found in the crust habitats. Plant density was found to be 77 % greater on crusts compared to bare soils (Defalco *et al.* (2001). The algal crust creates a more habitable environment but however appears to favour the herbaceous annuals and exclude *Stipa capensis*.

Geophytes occurred in high abundance in habitat 1 and 4 in site 2 whereas in site 1 they occurred in low numbers in habitats 1 and 4. This difference could be due to the increased degradation at site 2 or it could be related to the lower density of *Stipa capensis* in site 2.

Relationship between *Stipa capensis* and indigenous herbaceous annuals

There was no relationship between number of "weedy" species and grass abundance at the annual recruitment stage. This indicates that competitive effects are weak and the distribution of "weedy" annuals is most probably due only to factors in the physical environment. Eccles *et al.* 1999 found that there were neutral associations when pairwise relationships between the most common annuals and indigenous annuals in the short Strandveld communities were analvzed. In medium Strandveld communities they found positive associations in addition to the neutral associations. They also compared plant volumes to an index of neighbourhood competitiveness, no relationships were found in the short Strandveld and there were weak relationships in the medium Strandveld. The results from this study for the "weedy" herbaceous annuals are consistent with the findings of *Eccles et al.*, in that relationships between abundant annual species are weak.

Results were however different for the large annuals. There was a negative relationship between the biomass of the *Dimorphotheca sinuata* and that of the grass. There was also a negative impact on the time to maturity as the individuals that were grown with no grass in the wet treatment had flower buds whereas individuals growing with grass did not in either treatment. The slope for the wet treatment is steeper than the dry treatment and this could be an indication that under more benign conditions the competitive effect of grass plays a greater role in the growth of annuals than when conditions are harsher. This agrees with the observations of the local farmer. Dominant annuals he picked out included *Ursinia speciousa, Felicia, Gorteria, Gazania* and *Dimorphotheca* species. According to him the grass suppresses these annuals, they are smaller and have fewer flowers when they grow with the grass. The extent of this impact depends largely on the rainfall. If the rain comes early in the year (April, May) the large showy annuals are able to establish, when the rain is late it becomes too cold for the flowers to establish.

In this highly degraded environment competitive effects of the grass probably do not become important to the abundance and diversity of the "weedy" annuals present. The physical environment probably plays a more important role in the distribution of plants in the harsh degraded landscape. Van Rooyen *et al.* (1991) found that annuals growing under moisture stress remained small compared to individuals grown in optimum moisture conditions. They also found that moisture stress delays flowering. This agrees with the results obtained in this study. Plants can germinate in autumn or winter (whenever rain occurs) if they germinate later they will only flower later (Van Rooyen *et al.* 1992). If the rainy season starts in March the annuals germinate and temperatures are still reasonably warm allowing then to accumulate biomass, if the rain only comes in June temperatures are lower and annuals accumulate less biomass and therefore produce fewer flowers (Van Rooyen *et al.* 1992).

Other studies that have investigated the interaction between invasive grasses and annual plants have been done in the Mojave Desert. Brooks (2000) investigated the impact of the grasses *Bromus* sp. and *Schismus* sp. on indigenous annual species. He found negative correlations between the invasive species and indigenous plants, indicating suppressive competitive effects. Through the thinning of the invasive grass the density and biomass of native annuals increased although this result varied over different years and was most noticeable during years of high productivity and species richness. Brooks (1998) found that the biomass of alien plants negatively correlated with biomass and species richness of native annuals, taking into account factors such as disturbance and soil nutrient levels.

Role of *Stipa capensis* in the environment

Stipa capensis has several agroecological roles in the environment, with both positive and negative implications. According to the local landowner: "If there was no grass there would be nothing". In very dry years when not even the grass has been able to survive, wind erosion is problematic. When the grass cover is present it effectively prevents erosion. It is the one of the most resilient species, present during the unusually late winter season of 2003 while many other annuals did not grow. It is the major type of cover in between the perennial shrubs and therefore plays a major role in stabilizing the soil. The dominant wind in this area originates from the southeast. In winter berg winds can reach velocities of 120km an hour (Cowling 1999) and be exceptionally erosive. The possibilities of climate change impacts also need to be considered. There is a 2-4°C mean annual temperature increase predicted by global change models and changes to the patterns of precipitation, most importantly summer rainfall is predicted to increase (Milton 1990). Increased summer rainfall is expected to result in an increase in grass cover and a reduction in species diversity (Hoffman *et al.* 1990). *S. capensis* also influences the reproductive ecology of indigenous annuals. The most common pollination vectors are insects (Cowling 1999), it is therefore very important that flowers are visible for pollinators to locate them. There are also impacts on the livestock grazing in the area. The Willegas (*Stipa capensis*) is palatable until it flowers, however once it drys the livestock will eat it again according to the local landowner. These factors together make it difficult to assess whether *S. capensis* is desirable in the landscape or not.

Services	**Disservices**
Stabilises soil and assists amelioration of wind and water erosion	Retards growth and reproduction of large showy annuals which are important for tourism
Provides fodder for livestock, especially during the grass' pre-reproductive and post-reproductive phases	Awns pierce the skin of livestock and reduce wool quality
Acts as a litter trap and seed trap	Difficult to drive through grasses for a few months as they are very tall and dense
Resilient and therefore in dry years it is particularly useful as little else grows	Influences pollination success as pollinators are unable to locate flowers between grasses

Table 5: Positive and negative impacts of the grass, *Stipa capensis* on the agroecological environment of the sandveld.

Recommendations for further work

The distribution of the grasses in the area could be mapped and the environmental envelope (eg climate and soils) for them established. The potential competitive effects of the grass on the showy annuals could be measured in the field by setting aside matched plots and removing all the grasses from one with a grass specific herbicide and measuring the growth and reproduction of the annuals. The impact of the grasses on wind erosion and water erosion could also be measured in this way. This could be particularly meaningful in a dry year.

Conclusion

The landscape of Vanrynsdorp has changed in the last 100 years, there has been a visible decrease in perennial cover and an increase in the distribution of the grass *Stipa capensis*. The degraded environment can be described by four microhabitats with different characteristics. Within these four habitats *Stipa capensis* was generally found in only two, while the indigenous annuals were found in three of them. The habitat in which the indigenous annuals were present but the grass was not are depressions between "heuweltjies" characterized by an algal crust. This algal crust creates a more favourable habitat. The last habitat was exceptionally harsh, it is a "ring" around the "heuweltjies" in the area and supports very few species. No significant relationship was found between abundance of "weedy" annual species and the abundance of *Stipa capensis* at the recruitment stage, however there was a negative relationship between grass biomass and large annual biomass.

Stipa capensis is a species that has become a major feature in the landscape of Vanrynsdorp. Before any management decisions are made regarding its removal the services and disservices it is responsible for (Table 5) should be carefully considered. Although it probably does have a negative impact on the large annuals that attract tourism, it also provides important services. The uncertainty of future climate and possibility of alterations to the rainfall regime means that the removal of this species could result in an even more unstable and barren landscape. In Southern Arizona *Eragrostis lehmanniana* has been introduced (since 1932) in order to ameliorate the impacts of erosion and to increase the grass cover for livestock grazing (Annable *et al.* 1992). This has been done at great cost. Before removing this stabilizing grass because of the possible threat to the floral display that draws tourists a scenario like that of Southern Arizona should be considered.

Acknowledgements

Thanks to all the members of the Institute of Plant Conservation for all of their advice and support. Particular thanks to Timm Hoffman who supervised this project and was a constant source of motivation and advice.

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