South African Journal of Botany 95 (2014) 19–23

Contents lists available at ScienceDirect

South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

Livestock paths on Namaqualand quartz fields: Will the endemic flora disappear?

C. Van Tonder *, S.J. Milton, M.J. Cameron

School of Natural Resource Management: Nature Conservation, Nelson Mandela Metropolitan University, Private Bag X6531, George 6530, South Africa

ARTICLE INFO

Article history:
Received 3 April 2014
Received in revised form 9 July 2014
Accepted 16 July 2014
Available online 7 September 2014

Edited by RM Cowling

Keywords:
Succulent Karoo
Endemic species
Soil stability
Livestock paths

ABSTRACT

Quartz fields are rare features that contribute significantly to vegetation diversity and endemism of South Africa's Succulent Karoo Biome. The Riethuis-Wallekraal quartz fields in the north-western Namaqualand area of South Africa contain 17 quartz field specialist species of which seven are endemic to this specific area. Hoof-action by livestock has formed paths of approximately 0.30 m on these quartz fields. It would be important to conservationists to understand whether direct (e.g. trampling) and indirect effects (e.g. burial of flora by sediment movement) associated with the livestock paths holds any threat to the dwarf succulent (<0.05 m) and micro-chamaephytes (0.06–0.15 m) endemic to the quartz fields. We tested the hypotheses that the unique quartz field vegetation and biological soil crusts would be affected by loose soil particles transported downslope from the paths. The soil stability index, total vegetation cover, cover of specialized quartz field species and species diversity were lower on livestock paths but did not differ between upslope and downslope locations. Livestock paths also had lower cover and fewer quartz field specialist species. It is concluded that under conditions of intense and continuous grazing, livestock are likely to have an even stronger negative impact on the specialist quartz field flora.

1. Introduction

The Succulent Karoo is a biodiversity hotspot in the semi-arid winter rainfall region of southern Africa, which contains a high proportion of endemic plant species (Myers et al., 2000). Quartz fields are rare features of South Africa's Succulent Karoo Biome as they are represented in only five of the biome's 63 vegetation units and cover less than 8% of the biome's 111,000 km^2 surface area (Mucina et al., 2006). Despite their small area, quartz fields contribute significantly to plant diversity and endemism in the Succulent Karoo as 155 (10%) of its 1600 endemic species are restricted to quartz fields (Schmiedel, 2004). The dwarf vegetation of quartz fields contains growth forms and species very different from surrounding non-quartz field habitats (Schmiedel, 2002). Microclimate conditions also differ from the surroundings in that the surface covering of angular white stones gives rise to lower air temperatures at the soil surface (Schmiedel and Jürgens, 2004).

Geographic separation of quartz fields has resulted in high levels of plant compositional turnover resulting in six quartz field regions being recognized namely, Little Karoo, Knersvlakte, Riethuis-Wallekraal, Northern Richtersveld, Southern Richtersveld and Bushmanland-Warmbad (Schmiedel, 2004). The Riethuis-Wallekraal quartz fields occur on the lowlands of the Namaqualand region in north-western South Africa. This quartz field area contains 17 quartz field specialist species belonging to the Asteraceae and Crassulaceae as well as to the Mesembryanthema group within the Aizoaceae. Seven species are restricted to these quartz fields (Schmiedel, 2004).

Livestock farming is the dominant land use in the Succulent Karoo (Hoffman et al., 1999). It is likely that prolonged livestock hoof action would have impacted the biological soil crusts of the Riethuis-Wallekraal quartz fields and that this should be noticeable when indexing soil aggregate stability. A study by Kaltenecker et al. (1999) found significant biological soil crust recovery after livestock exclusion in Sagewood plant communities in the arid winter rainfall region of the United States of America. Concostrina-Zubiri et al. (2013) also suggest that heavy grazing by livestock may alter biological soil crust patterns in rangeland landscapes. Biological soil crusts, especially those types at the late succession stage, are indicators of healthy and stable soils as they contribute to soil organic matter, the binding of soil particles (Belnap et al., 2001a), as well as resistance to water and wind erosion (McKenna-Neuman et al., 1996; Eldridge and Leys, 2003).

* Corresponding author at: P.O. Box 1379, Sedgefield 6573, South Africa. Tel.: +27 72 252 8129.
E-mail addresses: cvtonder@capenature.co.za (C. Van Tonder), renukaroo@gmail.com (S.J. Milton), Mike.Cameron@nmmu.ac.za (M.J. Cameron).

http://dx.doi.org/10.1016/j.sajb.2014.07.014
0254-6299/

Biological soil crusts have been observed on the quartz fields of the study area (pers. obs.). It can be expected that changes in biological soil crust composition and functioning, as a result of livestock disturbance on the Riethuis-Wallekraal quartz fields, will be reflected in its vegetation composition. Biological soil crusts are beneficial for plants as they fix atmospheric nitrogen (Aranibar et al., 2003) making this limiting nutrient available to shallow-rooted plants such as quartz field specialists. The destruction of biological soil crusts may also facilitate the establishment of invasive plant species (Hernandez and Sandquist, 2011).

Beside possible damage to biological soil crusts, other likely consequences of trampling are physical damage to plants, soil compaction and accelerated soil erosion. Soil compaction alters soil structure and hydrology which can affect water absorption by plants (Kozlowski, 1999). Depending on the intensity and period of livestock stocking rates these factors can cause vegetation change, as has been observed along a piosphere in the Tanqua Karoo part of the Succulent Karoo biome (Beukes and Ellis, 2003). Haarmeyer et al. (2010) found that intense stocking of livestock reduced species richness and the abundance of endemic species on quartz field vegetation.

Livestock paths approximately 0.30 m wide are present on the Riethuis-Wallekraal quartz fields (Fig. 1). These paths are seemingly denuded of vegetation and appear to have more exposed soil than areas away from livestock paths. Smooth surfaces will offer less resistance to wind and water erosion, and loose soil particles are more likely to be displaced by such erosion forces. More than half of the Riethuis-Wallekraal endemic quartz field flora are dwarf succulents <0.05 m in height (Schmiedel, 2002) (refer to Appendix 1 that lists the flora endemic to the Riethuis-Wallkekraal quartz fields and their growth forms). Because of the undulating terrain on which the Riethuis-Wallekraal quartz fields are located, we sampled quartz field vegetation and soil aggregate stability upslope and downslope of the paths. Loose soil particles dislodged by livestock hoof action are expected to move downslope during rain and such soil deposition could be to the detriment to the unique quartz field vegetation. Burial of dwarf succulent plants is likely to have negative impacts on their growth and survival. Fig. 2 shows a typical example of a dwarf succulent species of the Riethuis-Wallkeraal quartz fields that is vulnerable to trampling and soil burial. Of concern to conservationists is whether plant species unique to quartz field vegetation will be able to persist in the face of livestock pressures.

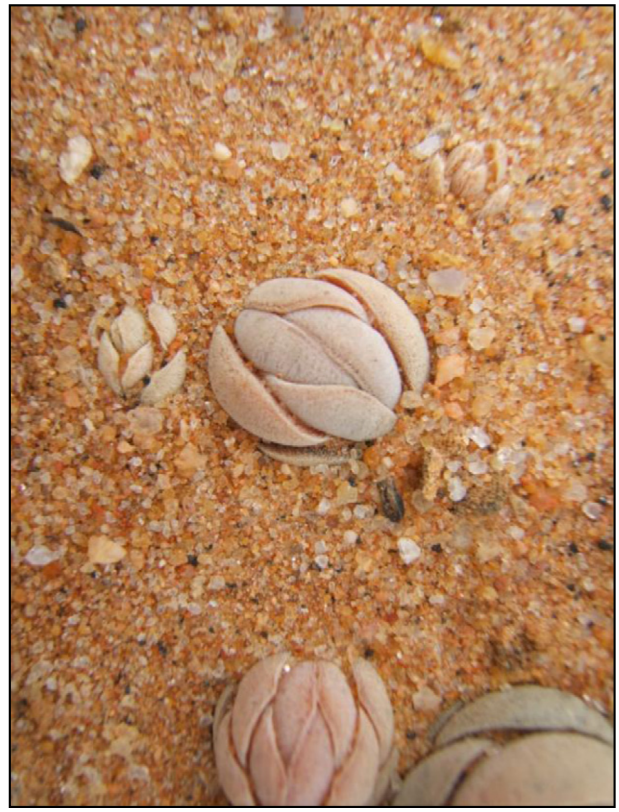

Fig. 2. *Crassula alstonii* a dwarf succulent vulnerable to livestock trampling and soil burial. Photo: Carlo Van Tonder.

Fig. 1. A livestock path formed on a quartz patch in the Riethuis-Wallekraal region. Photo: Carlo Van Tonder.

We tested the following hypotheses relating to presence of livestock paths on the Riethuis Wallekraal quartz fields and their potential impact on species composition:

1. Livestock hoof action affects the soil stability on livestock paths and indirectly also soil stability downslope;
2. Quartz field vegetation is less diverse on livestock paths and on the adjacent quartz field area downslope;
3. Endemic quartz field flora specific to quartz fields is absent from livestock paths and the adjacent quartz field area downslope.

2. Study area

The study was carried out in the Riethuis section of the Namaqua National Park (29°54′–30°11′ South, 17°20′–17°48′ East). Previous landuse of the area included farming with small stock (Dorper sheep) which was removed during 1999 when ownership was transferred to the Namaqua National Park (Matthew Norval, personal communication, June 2014). The stocking rate of sheep by the previous landowner is unknown, but was probably relatively light, at least in comparison to adjacent communally-owned areas. The former National Department of Agriculture's 1993 map estimates that the grazing capacity for this region is 31–45 ha per animal unit.

The study area contains a significant proportion (25%) of the Riethuis-Wallekraal Quartz Vygieveld (SKs10) which is one of 63 vegetation units recognized in the Succulent Karoo (Mucina and Rutherford, 2006). The Riethuis-Wallekraal quartz field vegetation is dominated by low growing leaf-succulents with species belonging to mainly the Asteraceae and Crassulaceae as well as the Mesembryanthema group within the Aizoaceae family (Schmiedel, 2004). The landscape of the Riethuis-Wallekraal quartz fields is characterized by low-lying undulating hills with scattered gneiss outcrops (Watkeys, 1999). Quartz field sizes range from 10 to more than 100 m in diameter and are covered with white angular stones, 0.02–0.60 m in size that have weathered from quartz bedrock or quartz veins (Schmiedel and Jürgens, 1999). The mean annual rainfall for a farm close to the study area (approximately 10 km away) is 137 mm, range: 65–188 mm from 1983 to 2004 (D. Van Niekerk, personal communication, 4 October, 2005). Rainfall is concentrated in the winter months. Temperatures in winter are relatively mild with minimum temperatures above 0 °C whereas summers are hot and dry with maximum temperatures often reaching 35 °C (Desmet and Cowling, 1999).

3. Methods

3.1. Plot layout and vegetation sampling

Field work was carried out from May to July 2005. Plots were laid out for sampling vegetation upslope of, downslope of, and on livestock paths. Thus a natural experimental design was followed whereby the effects of each treatment were tested and therefore could not be randomly allocated. Plots on the livestock paths covered the width of the livestock paths and were flanked by the upslope and downslope plots. The underlying assumption is that hoof action destabilizes soil on paths. It was expected that sediment transported downslope by rain or dislodged by hoof-action resulting from livestock activity would result in burial of dwarf flora and biological soil crusts. Off-path impacts of livestock on soil and vegetation were therefore expected to be greater below than above the path. For each plot the step point method (Evans and Love, 1957) was used to record presence or absence of plant species along a series of transects.

Two quartz fields located approximately 300 m apart, with a gently sloping (2–3°) north-facing aspect were sampled. Within each quartz field three plots were laid out per treatment, which differed in distances from one another (range approximately 5–45 m). The three treatments consisted of upslope, livestock path and downslope plots. In total there were six replicates per treatment. Transects within plots were spaced 0.5 m apart and each was 10 m long. Points along each transect were sampled every 0.2 m. As the livestock paths do not follow a straight line only points actually on the livestock path were sampled. The dimensions, number of transects and number of points for the three respective plots were as follows:

- Upslope plots: 5 m × 10 m, 10 transects, 500 points sampled per plot, replicated three times on two quartz fields = 3000 points.
- Downslope plots: 3 m × 10 m, 6 transects, 300 points sampled per plot, replicated three times on two quartz fields = 1800 points.
- Livestock path plots: 0.3 m × 10 m, 3 transects, the following number of points were located on livestock paths: 51, 62, 71, 53, 37 and 50 = 324 points.

Plant species nomenclature followed that of Germishuizen and Meyer (2003). Species richness was expressed as number of species per total number of points recorded. In order to get a measure of vegetation cover it was recognized that the probability of encountering small plants (<0.02 m in width) on a point sample is low; therefore, in the event of no plant being present at a point, the nearest dwarf succulent within a 0.10 m radius of the point was recorded. It is important to understand that this led to an over estimation of dwarf succulent cover and, therefore, cannot directly be compared to cover for the other growth forms. Total cover estimation and cover estimation by growth form were expressed as a percentage of the total number of points per plot.

Total species richness and specialist quartz field species richness were calculated by tallying the number of species per total number of points recorded per plot. Species diversity for each plot was calculated by using the Shannon–Wiener diversity index (Zar, 1984).

3.2. Soil stability index

In order to quantify soil stability the slake test (Tongway and Hindley, 2004) was performed. Six replicates were completed for each of the three treatments within the same plots as for the vegetation sampling. A replicate consisted of a plot with 10 × 10 m transects spaced 0.5 m apart. One slake test was performed in the middle of each transect for the upslope and downslope replicates. For the livestock path replicate a slake test performed along the length of each livestock path at 0.5 m intervals. The following number of slake tests were performed per treatment:

- Upslope replicates: 10 transects per replicate = 10 slake tests, replicated 6 times = 60 slake tests.
- Downslope replicates: 6 transects per replicate = 6 slake tests, replicated 6 times = 36 slake tests.
- Livestock path replicates: 6 transects per replicate = 10 slake tests, replicated 6 times = 60 slake tests.

The objective of the slake test was to assess the stability of natural soil fragments to rapid wetting (Tongway and Hindley, 2004). Performing the slake test involved lifting a standard sized (approximately 1 cm^3) soil crust fragment from the soil crust and observing its behavior after being immersed in rainwater. The behavior of the soil crust was indexed according to the time taken for the soil crust fragment to dissolve and/or the size of soil crust fragment that slumped (Table 1).

3.3. Statistical analysis

One-way analysis of variance (ANOVA) (Zar, 1984) was used to test for differences between means for the soil stability index, vegetation diversity and plant cover. Data were tested for normality using the Kolmogorov–Smirnov test; all data sets were normally distributed. STATISTICA computer software was used to perform statistical analysis (StatSoft, Inc., 2004).

Table 1
Classification of soil crust fragment behavior for the slake test used as an indication of soil stability (Tongway and Hindley, 2004).

Soil crust fragment behavior	Soil stability index
No coherent fragments available e.g. sand	0
Fragment collapses in less then 5 s	1
Fragment substantially collapses within 5–10 s; a thin surface crust remains. >50% of the sub-crust material slumps	2
Surface crust remains intact with some slumping of the sub-crust but less then 50%	3
Whole fragment remains intact with no swelling	4

Table 3
Mean values (±standard deviation) for the soil stability index, Shannon Wiener diversity index and plant cover categories for the three respective treatments. Post-hoc Scheffés tests were used to determine differences between group means (95% confidence limit). Identical superscripts indicate that means do not differ.

Variable	Upslope	Downslope	Livestock paths
Soil stability index	$3.76^{a} \pm 0.17$	$3.56^{a} \pm 0.27$	$0.88^{b} \pm 0.13$
Species diversity index	$0.92^{a} \pm 0.12$	$1.00^{a} \pm 0.07$	$0.66^{b} \pm 0.08$
Total plant cover	$34.43^{a} \pm 10.81$	$35.78^{a} \pm 8.82$	$14.33^{b} \pm 9.41$
Quart field specialist plant cover	$12.76^{ab} \pm 5.50$	$18.89^{a} \pm 9.18$	$5.12^{b} \pm 5.94$
Dwarf succulent cover	$5.93^{a} \pm 5.97$	$4.80^{a} \pm 3.25$	$2.23^{a} \pm 2.12$

4. Results

A total of 61 species were recorded with 12 of these being quartz field specialist species (Table 2). Five species endemic to the Riethuis-Wallekraal quartz field species were found. A total of nine specialist quartz field species was found on upslope and downslope locations, respectively, with one species unique to each location (Table 2). Fewer (6) specialist quartz field species were recorded on livestock paths.

The soil stability index for samples taken on the livestock paths was significantly lower (ANOVA: $F(2,12) = 327.20$, $p < 0.01$) than for samples taken up or down slope from the path, but did not differ significantly between plots sampled above and below the paths (Table 3).

Plant species diversity recorded on the livestock paths was significantly lower (ANOVA: $F(2,15) = 9.18$, $p < 0.01$) than for the points off livestock paths, but did not differ significantly between plots sampled above and below the paths (Table 3). Total plant cover recorded on the livestock paths was significantly lower (ANOVA: $F(2,14) = 8.06$, $p < 0.01$) than for the points off livestock paths, but did not differ significantly between plots sampled above and below the paths (Table 3). The total cover of quartz field specialist species recorded on the livestock paths was significantly lower (ANOVA: $F(2,13) = 4.91$, $p < 0.05$) than for the points off livestock paths; however, upslope quartz field specialist species cover was intermediate between the two other positions (Table 3). Dwarf succulent cover was lower for the livestock paths compared to upslope and downslope (Table 3); however, this difference was not statistically significant (ANOVA: $F(2,14) = 1.24$ $p = 0.32$).

5. Discussion

5.1. Soil stability

The livestock paths on the study site were characterized by low soil stability indices, interpreted to be a consequence of fragmentation of biological soil crusts on the soil surface caused by livestock trampling. In the semi-arid Nama Karoo and Succulent Karoo biomes of South Africa the influence of livestock trampling is manifested by negative trends observed in soil absorption rates (Dean, 1992) and under extreme influence, a shift in biological soil crust composition (Rutherford and Powrie, 2010). We believe that the biological soil crusts on the livestock paths in our study area were altered sufficiently to reduce soil stability. Our argument is supported by Belnap and Eldridge (2001) who described the disturbance and recovery of biological soil crusts by looking at research conducted across the world. They state that mechanical disturbance such as trampling by livestock, people and vehicles are known to cause severe compositional changes of biological soil crusts. Biological soil crusts are important for stabilizing soils by increasing resistance to wind and water erosion (McKenna-Neuman et al., 1996; Eldridge and Leys, 2003). Changes in biological soil crust composition are critical as there is a resistance gradient to disturbance through the stages of biological soil crust succession based on morphological and reproductive attributes (Belnap et al., 2001b). For example, cyanobacteria that occur at an early successional stage are more tolerant to disturbance than certain late succession mosses and lichens but provide less protection against disturbances (Belnap et al., 2001b).

Table 2
Specialist quartz field plant species recorded per treatment (X = presence of species).

Taxon	Upslope	Downslope	Livestock paths
Aspazoma amplectens	X	X	
Conophytum concavum[a]	X	X	X
Conophytum obscurum subsp. *vitreopapillum*[a]	X	X	
Crassula alstonii	X	X	X
Crassula barklyi		X	
Dicrocaulon ramulosum[a]	X		
Jacobsenia vaginata	X	X	X
Meyerophytum globosum[a]	X	X	X
Meyerophytum meyeri	X	X	X
Monilaria scutata subsp. *obovata*[a]	X	X	X

[a] Endemic to the Riethuis-Wallekraal quartz fields (according to Schmiedel, 2004).

5.2. Plant diversity

Having already shown that the livestock paths in this study have low soil stability it is significant that Pohl et al. (2009) demonstrated a positive relationship between plant diversity and soil aggregate stability in an alpine environment. They argued that different plant growth forms have different root systems and because of this structural variability, play an important role in soil stabilization. Most leaf-succulent plants of the Succulent Karoo have fairly uniform structure and relatively shallow (<20 cm deep) root systems (Esler and Rundel, 1999) with those of quartz field vegetation considered to be even more limited in structure and depth (Schmiedel, 2002). The role of root systems of quartz field flora is therefore believed to have a limited role in supporting the formation of stable soils on quartz fields.

Quartz fields are generally small (approximately 10 to 100 m diameter) and the associated vegetation differs markedly from the taller vegetation that is on adjacent substrata (Schmiedel, 2002). It would be incorrect to assume that not much time and energy would be spent by livestock to forage on quartz fields, due to the small size of the plants and the absence of more palatable and accessible growth forms such as shrubs, grasses and annual forbs. Indeed, Haarmeyer et al. (2010) showed that quartz field vegetation is utilized by small livestock under high stocking rates. Our study found significant differences in plant species diversity and soil stability on and off livestock paths, but no consistent differences between upslope and downslope locations. This suggests that impacts were limited to livestock paths only and not downslope sites, as predicted.

5.3. Quartz field specific species

Haarmeyer et al. (2010) have shown that the abundance and species richness of certain endemic quartz field species decreased under heavy grazing by livestock irrespective of rotational or continuous grazing regimes. In our study we found fewer quartz field specialists on the livestock paths. Our results suggest that the transformation of soil properties, and hence the edaphic microenvironment, as a result of the livestock path formation happened at a small scale and played a limited role in reducing quartz field taxa overall. However, it is important to note that in the current study the past stocking rate is unknown, but being a commercial farm — is likely to be lower than in communal areas where the heaviest impacts of livestock on plant community structure have been recorded (Allsopp, 1999; Todd and Hoffman, 1999; Riginos and Hoffman, 2003).

Acknowledgments

Carlo Van Tonder acknowledges the National Research Foundation (Grant number GUN 2053674) and Nelson Mandela Metropolitan University for the funding. We thank Dr. W.R.J. Dean for providing a vehicle for the field work. Annelise le Roux of CapeNature and Ute Schmiedel provided valuable assistance with the plant specimen identification. The authors thank the South African National Parks Scientific Services and staff and students of the Namaqua National Park for their support. Dr. Alan Wheeler is thanked for providing comments on the initial draft, and the reviewers for providing constructive comments.

Appendix 1. Specialist quartz field taxa of the Riethuis-Wallekraal phytochorion and their growth forms (adapted from Schmiedel, 2004)

Taxon	Family	Growth form
Crassula alstonii Marloth	Crassulaceae	Dwarf succulent
Crassula barklyi N.E.Br.	Crassulaceae	Dwarf succulent
Crassula columnaris Thunb. ssp. *prolifera* Friedrich	Crassulaceae	Dwarf succulent
Crassula susannae Rauh & Friedrich	Crassulaceae	Dwarf succulent
Aspazoma amplectens (L.Bolus) N.E.Br.	Aizoaceae	Micro-chamaephyte
Conophytum concavum L.Bolus	Aizoaceae	Dwarf succulent
Conophytum obscurum N.E.Br. ssp. *vitreopapillum* (Rawe) S.A. Hammer	Aizoaceae	Dwarf succulent
Dicrocaulon ramulosum (L.Bolus) Ihlenf.	Aizoaceae	Micro-chamaephyte
Jacobsenia vaginata (L.Bolus) Ihlenf.	Aizoaceae	Micro-chamaephyte
Meyerophytum globosum (L.Bolus) Ihlenf.	Aizoaceae	Micro-chamaephyte
Meyerophytum meyeri (Schwantes) Schwantes	Aizoaceae	Micro-chamaephyte
Monilaria scutata (L.Bolus) Schwantes ssp. *obovata* Ihlenf. & Jörg.	Aizoaceae	Micro-chamaephyte

References

Aranibar, J.N., Anderson, I.C., Ringrose, S., Macko, S.A., 2003. Importance of nitrogen fixation in soil crusts of southern African arid ecosystems: acetylene reduction and stable isotope studies. Journal of Arid Environments 54, 345–358.

Allsopp, N., 1999. Effects of grazing and cultivation on soil patterns and processes in the Paulshoek area of Namaqualand. Plant Ecology 142, 179–187.

Belnap, J., Eldridge, D., 2001. Disturbance and recovery of biological soil crusts. In: Belnap, J., Lange, O.L. (Eds.), Biological Soil Crusts: Structure, Function and Management. Springer, Berlin, pp. 363–383.

Belnap, J., Kaltenecker, J.H., Rosentreter, R., Williams, J., Leonard, S., Eldridge, D., 2001a. Ecological roles. In: Peterson, P. (Ed.), Biological Soil Crusts: Ecology and Management. Technical reference 1730-2. United Sates Department of the Interior, Colorado, U.S.A., pp. 29–40.

Belnap, J., Kaltenecker, J.H., Rosentreter, R., Williams, J., Leonard, S., Eldridge, D., 2001b. Response to natural impacts and human actions. In: Peterson, P. (Ed.), Biological Soil Crusts: Ecology and ManagementTechnical reference 1730-2. United Sates Department of the Interior, Colorado, U.S.A., pp. 41–64.

Beukes, P.C., Ellis, F., 2003. Soil and vegetation changes across a Succulent Karoo grazing gradient. African Journal of Range and Forage Science 20, 11–19.

Concostrina-Zubiri, L., Huber-Sannwald, E., Martínez, I., Flores Flores, J.L., Escudero, A., 2013. Biological soil crusts greatly contribute to small-scale soil heterogeneity along a grazing gradient. Soil Biology and Biochemistry 64, 28–36.

Dean, W.R.J., 1992. Effects of animal activity on the absorption rate of soils in the southern Karoo, South Africa. Journal of the Grassland Society of South Africa 9, 178–180.

Desmet, P.G., Cowling, R.M., 1999. The climate of the karoo — a functional approach. In: Dean, W.R.J., Milton, S.J. (Eds.), The Karoo — Ecological Patterns and Processes. Cambridge University Press, Cambridge, pp. 3–16.

Eldridge, D.J., Leys, J.F., 2003. Exploring some relationships between biological soil crusts, soil aggregation and wind erosion. Journal of Arid Environments 53, 457–466.

Esler, K.J., Rundel, P.W., 1999. Phenological and growth form divergence in convergent desert ecosystems: a Succulent Karoo and Mojave desert comparison. Plant Ecology 142, 97–104.

Evans, R.A., Love, R.M., 1957. The step-point method of sampling — a practical tool in range research. Journal of Rangeland Management. 10, 208–212.

Germishuizen, G., Meyer, N.L. (Eds.), 2003. Plants of Southern Africa: An Annotated Checklist. National Botanical Institute, Pretoria.

Haarmeyer, D.H., Schmiedel, U., Dengler, J., Bösing, B.M., 2010. How does grazing intensity affect different vegetation types in arid Succulent Karoo, South Africa? Implications for conservation management. Biological Conservation 143, 588–596.

Hernandez, R.R., Sandquist, D.R., 2011. Disturbance of biological soil crust increases emergence of exotic vascular plants in California sage scrub. Plant Ecology 212, 1709–1721.

Hoffman, M.T., Cousins, B., Meyer, T., Petersen, A., Hendricks, H., 1999. Historical and contemporary land use and the desertification of the Karoo. In: Dean, W.R.J., Milton, S.J. (Eds.), The Karoo — Ecological Patterns and Processes. Cambridge University Press, Cambridge, pp. 257–273.

Kaltenecker, J. H., Wicklow-Howard, M. C. and Rosentreter, R. 1999. Biological soil crusts in three Sagebrush communities recovering from a century of livestock trampling. In: McArthur, E. D., Ostler, W.K., Wambolt, C.L., (comps.). *Proceedings: shrubland ecotones*; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Kozlowski, T.T., 1999. Soil compaction and growth of woody plants. Scandinavian Journal of Forest Research 14, 596–619.

McKenna-Neuman, C., Maxwell, C.D., Boulton, J.W., 1996. Wind transport of sand surfaces crusted with photoautotrophic microorganisms. Catena 27, 229–247.

Mucina, L., Rutherford, M.C. (Eds.), 2006. The vegetation of South Africa, Lesotho and SwazilandStrelitzia. 19. South African National Biodiversity Institute, Pretoria, pp. 220–299.

Mucina, L., Jürgens, N., le Roux, N., Rutherford, M.C., Schmiedel, U., Esler, K.J., Powrie, L.W., Desmet, P.G., Milton, S.J., 2006. Succulent Karoo Biome. In: Mucina, L., Rutherford, M.C. (Eds.), The Vegetation of South Africa, Lesotho and SwazilandStrelitzia. 19. South African Biodiversity Institute, Pretoria, pp. 220–299.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Pohl, M., Alig, D., Körner, C., Rixen, C., 2009. Higher plant diversity enhances soil stability in disturbed alpine ecosystems. Plant and Soil 324, 91–102.

Riginos, C., Hoffman, M.T., 2003. Changes in population biology of two succulent shrubs along a grazing gradient. Journal of Applied Ecology 40, 615–625.

Rutherford, M.C., Powrie, L.W., 2010. Severely degraded rangeland: Implications for plant diversity from a case study in Succulent Karoo, South Africa. Journal of Arid Environments 74, 692–701.

Schmiedel, U., 2002. The Quartz Fields Of Southern Africa: Flora, Phytogeography, Vegetation and Habitat Ecology. Ph.D. Thesis University of Köln, Germany.

Schmiedel, U., 2004. The phytogeography of the obligate quartz field flora of southern Africa. Biodiversity and Ecology 2, 181–205.

Schmiedel, U., Jürgens, N., 1999. Community structure on unusual habitat islands: quartz-fields in the Succulent Karoo, South Africa. Plant Ecology 142, 57–69.

Schmiedel, U., Jürgens, 2004. Habitat ecology of southern African quartz fields: studies on the thermal properties near the ground. Plant Ecology 170, 153–166.

StatSoft, Inc., 2004. STATISTICA (data analysis software system), version 7. www.statsoft.com.

Todd, S.W., Hoffman, M.T., 1999. A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. Plant Ecology 142, 169–178.

Tongway, D.J., Hindley, N.L., 2004. Landscape Function Analysis: Procedures for Monitoring and Assessing Landscapes. With Special Reference to Minesites and Rangelands. CSIRO, Canberra.

Watkeys, M.K., 1999. Soils of the arid south-western zone of Africa. In: Dean, W.R.J., Milton, S.J. (Eds.), The Karoo — Ecological Patterns and Processes. Cambridge University Press, Cambridge, pp. 17–26.

Zar, J.H., 1984. Biostatistical Analysis. Prentice-Hall Inc., Englewood Cliffs, New Jersey.