The potential of *Cephalophyllum inaequale* for the restoration of degraded arid landscapes in Namaqualand, South Africa

Pippin Anderson
Percy FitzPatrick Institute of African Ornithology,
University of Cape Town, Rondebosch 7701,
South Africa

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Supervisors:
Prof. M. T. Hoffman, Institute for Plant Conservation
Dr P. Holmes, Cape Ecological Services

Abstract

The potential of *Cephalophyllum inaequale* for use in initiating ecosystem restoration in degraded landscapes of Namaqualand, South Africa, was investigated. A bioclimatic envelope was modeled to establish the area in which this species might feasibly be used. The regional bioclimatic potential for *C. inaequale* proved to be extensive, covering an area of approximately 17 500 km^2. A landscape level investigation was carried out to establish *C. inaequale's* abiotic requirements and biotic associations. This comprised a phytosociological survey and soil analysis of the three dominant plant communities of the communal lands of Soebatsfontein in Namaqualand. These three communities were defined as: the Cephalophyllum community, dominated by *C. inaequale* and confined to the flat areas between heuweltjies (raised ±30 m diameter termite mounds); the non-Cephalophyllum community, similarly confined to the flat areas between heuweltjies, but where *C. inaequale* was notably absent; and the heuweljtie community. The Cephalophyllum community grows on slightly acidic soil, with an even mix of coarse, medium and fine sand. The soil on which the Cephalophyllum community grows is most similar to that of the non-Cephalophyllum community, varying significantly only with respect to the high stone content of the soil associated with the non-Cephalophyllum community. Two DCAs of species abundance, and species composition, show that while all three of the communities do best (are most abundant) when confined to their respective habitats, the Cephalophyllum community shares a number of compositional elements with the other two communities. The DCAs demonstrate the heuweltjie community to be the most distinctive of the three communities examined. The heuweltjie community is associated with deep soils that are nutritionally rich, have a high pH and a high percentage of fine sand. *C. inaequale* was excluded from the heuweltjie community, possibly on the basis of the unique soil properties associated with this

community. The community dominated by *C. inaequale* was associated with a diverse plant community, including a cryptogamic crust. A number of the plants associated with this community are highly palatable, and this community can be described as productive for livestock farming. An examination of the functional role of *C. inaequale* showed that it may facilitate a successional process, as evident in improved seedling survival in this community when compared to other communities. A nearest-neighbour study found no evidence of interspecific competitive interactions between *C. inaequale* and its dominant co-occurring species, possibly due to the vertical stratification of their rooting structures. It was demonstrated that *C. inaequale* effectively reduces wind speed and subsequently soil erosion. Experiments to test the feasibility of successfully propagating, re-introducing and establishing this species, showed that it is easily germinated from seed. Cuttings kept under greenhouse conditions, and cuttings transplanted in the field, survived the four month duration of the study, but showed no positive growth during this period. This study demonstrates that *C. inaequale* has several attributes that are desirable in a species to be used in initiating a restoration process, and points to other attributes that may prove to be useful, but need to be explored with further experimental work.

Introduction

Recently there has been an upsurge in interest in restoration as a technique for reversing habitat degradation worldwide (Hobbs and Norton 1996). As human population growth and associated impacts on the earth intensify, so does the threat to biodiversity and productivity. The need for ecosystem repair, both to restore biodiversity and improve productivity, is seen as increasingly urgent (Hobbs and Norton 1996, Webb 1996). In light of this trend, restoration ecology is a growing discipline and an increasingly important tool to conservation biology (Young 2000).

While the implications of the loss of much of the earth's biodiversity are unknown, the loss of ecosystem function frequently has considerable economic cost. It is estimated that 43% of the earth's terrestrial surface has reduced capacity for supporting humanity as a result of the negative effects of human land use management (Webb 1996). In particular, the loss of topsoil through erosion is one of the world's greatest environmental and agricultural problems (Skidmore 1994). It is believed that as much as 75 billion metric tons is lost across the globe every year, with an associated cost of $400 billion (Myers 1993, Pimentel *et al.* 1995). In South Africa, the on site cost of erosion from croplands alone for the year 1992 was estimated at R260 million (Mackenzie 1994). Many different methods are deployed in reducing the loss of topsoil and the vast majority of these entail the maintenance or re-establishment of some form of protective vegetative cover (Pimentel *et al.* 1997).

Restoration ecology is loosely defined as the intentional alteration of a site with the aim of restoring the degraded system to some form of cover that is protective, productive, aesthetically pleasing, or valuable in a conservation sense (Hobbs and Norton 1996). Restoration can be broken down into two approaches. The first is restoration in the strictest sense, which seeks a direct and full return to the indigenous historic ecosystem. The second, broader sense of restoration, often termed rehabilitation, simply seeks to halt degradation and to redirect a disturbed ecosystem in a trajectory resembling its predisturbance state (Aronson *et al.* 1993). The second approach has a stronger emphasis on restoring ecosystem processes, whereas the first may strive more simply to re-introduce species (Aronson *et al.* 1993). This study examined the potential of *Cephalophyllum inaequale* (L. Bolus) for use in arresting ecosystem degradation and redirecting a disturbed Succulent Karoo ecosystem towards a predisturbance state. The focus is on the plant's potential in promoting the restoration of ecosystem functioning, stability and biodiversity. A by-product of such a successful restoration project would be the improved productivity of the environment, in this case for use as a rangeland.

With its combination of high plant diversity combined with large numbers of local endemics, the Succulent Karoo Biome is a region of global botanical importance (Cowling *et al.* 1999). Efforts at expanding the network of protected areas in the Succulent Karoo are well advanced, and recent estimations are that just under 3% of the area is now formally conserved (Mittermeir *et al.* 1999). However, one would have to conserve 58% of the land area to conserve at least one population of each of the biome's 851 Red Data Book species (Lombard, Hilton-Taylor, Rebelo and Cowling unpublished data, cited in Desmet 1999). Combined with the high degree of degradation, this area is considered a global conservation priority, and it is recognised that to achieve the adequate conservation of this biome, efforts must extend beyond the network of formally conserved areas (Desmet 1999). Over the last three centuries the arid and semi-arid regions of South Africa have undergone wide-scale and dramatic change attributed primarily to overgrazing (Yeaton and Esler 1990, Dean and MacDonald 1994). The Succulent Karoo has been used extensively for small livestock farming and recently the impact of this on the diversity, productivity and sustainability of the Succulent Karoo has been raised (Milton and Dean 1995a, Todd and Hoffman 1998, Allsopp 1999). Experience has shown that Karoo rangelands will not revert to their pre-disturbance state simply through resting the rangeland (Milton and Hoffman 1994, Milton and Dean 1995b, Milton *et al.* 1995). Severely disturbed arid landscapes are not easily improved due to species reductions, altered species interactions, and physical degradation such as reduced infiltration or nutrient depletion (Milton *et al.* 1995, Whisenant *et al.* 1995). There is a recognised need for the active restoration of Karoo rangelands to improve productivity and species diversity (Milton and Dean 1995b).

C. inaequale, a perennial shrub, is a member of the succulent Mesembryanthemaceae family, typical of the Succulent Karoo and in particular of the Namaqualand area. There are about 33 species of *Cephalophyllum* in southern Africa of which 25 occur in Namaqualand (Smith *et al.* 1998). Most species of this genus have a prostrate creeping habit and this is evident in their common name '*rankvygie*' meaning 'creeping mesemb' (Smith *et al.* 1998). They commonly form groundcovers on disturbed sites such as roadsides or exposed ground following floods. Species of this genus are described as forming large mats as central runners die away, allowing secondary centres to develop into new plants (Hartmann 1983). In colonizing disturbed areas it is believed that they stabilize exposed ground reducing further soil erosion (Smith *et al.* 1998). *C. inaequale* has a creeping architecture, forms large mats and is associated with disturbed areas. It grows extensively on the communal lands of Soebatsfontein and is a dominant species in this landscape, forming large patches between 'heuweltjies' (large earth mounds reaching diameters of as much as 30 m with average heights of 1 m, created by termites and small burrowing mammals (Lovegrove and Seigfried 1986, Moore and Picker 1991)). This locally adapted and indigenous plant species warrants investigation as a potential primary colonizer in the restoration of the degraded rangelands of Namaqualand.

Historically, restoration projects have often been undertaken on a trial and error basis and with limited success. It is now recognised that greater understanding of the ecology of the system and the biology of the plant species in question is needed at the outset of any restoration project (Call and Roundy 1991, Webb 1996). Restoration studies offer good opportunities to study the ecology of systems, rendering such studies informative beyond their immediate aim (Aronson *et al.* 1993, Palmer *et al.* 1997). In this study, the biology of *C. inaequale* and its role within this ecosystem was explored, simultaneously contributing to our understanding of the dynamics of the vegetation of the Succulent Karoo Biome and potentially identifying an effective species for use in the restoration of degraded rangelands.

The central aim of this study was to explore the potential of *C. inaequale* in the restoration of degraded rangelands in Namaqualand. In order to do this the following key questions were addressed:

1. What is the potential area in which *C. inaequale* could grow? This question aims to develop an understanding of where this species might feasibly be used for restoration on a regional scale.
2. Where does *C. inaequale* grow in the landscape? This question looks at gaining a better understanding of the exact habitat requirements of this species, on a landscape level. This question also sets out to establish the species affiliations of this plant to understand what community it is associated with.
3. What is the functional role of *C. inaequale*? If restoration is to redirect a system towards a predisturbance state, then any species used in restoration should ideally play a role in driving the system. This question examines the role of *C. inaequale* in ecosystem processes, and the successional and competitive dynamics of the community in which it occurs. It also considers whether *C. inaequale* reduces soil erosion, a necessary attribute in the restoration of overgrazed rangelands.
4. How easily is *C. inaequale* propagated? An important characteristic of any plant to be used in restoration is that it should be readily propagated and easily established. This question addresses the practicality of this species for use in restoration.

Methods

Study site

The study was conducted in Namaqualand, the winter-rainfall region of South Africa's Succulent Karoo Biome, on communal lands belonging to the Soebatsfoentein community (30° 11'S, 17° 33'E) (Fig 1.). Namaqualand is described as a relatively mild desert, with its proximity to the West Coast and the cold, upwelling Benguela current, serving to temper its climate (Desmet and Cowling 1999). While rainfall in most of Namaqualand is extremely low, often at less than 150 mm per annum, it is characteristically predictable, falling predominantly during the winter months from May to August (Cowling *et al.* 1999). Rainfall recorded in Kammieskroon (48 km east of Soebatsfontein) for 2001 was 332 mm, almost 50 mm above the average over the last ten years, which was 287 mm. Rainfall received during the winter months of July and August 2001 was twice the average recorded for those months over the last ten years (South African Weather Service unpublished data). Wind is a prominent feature of the climatic regime of the region, arising from steep atmospheric pressure gradients associated with the cold ocean and warmer hinterland (Desmet 1996, Desmet and Cowling 1999). Soebatsfontein experiences a strong prevailing south-westerly wind during the summer months.

The communal lands of Soebatsfontein lie to the west of the Kamiesberg, on an apron of colluvial soils intruded by granite-gneiss outcrops (Desmet and Cowling 1999). The soils of this plain are red and yellow and described as weakly structured, apedal soils (Watkeys 1999). Their origin lies in a complex sequence of aeolian sands derived from coastal and inland sources, resulting in a combination of weathered and fine grained deposits of the late Tertiary age and more recent calcareous sands from the coast (Desmet and Cowling 1999). Some of the outcrops rising from the plain are capped with quartzite, which, when weathered, contributes a quartz pebble component to the surrounding soil (Watkeys 1999). The landscape is dotted with earth mounds of biogenic origin. These termitaria, or 'heuweltjies', can reach heights of 3m to 5m with base diameters reaching 30 m (Lovegrove and Siegfried 1986, Moore and Picker 1991). The soil of heuweltjies differs from those of the surrounding area and typically holds more water and is enriched in nutrients (Midgley and Musil 1990, Whitford 1999). The different soil composition of heuweltjies leads to vegetation communities that frequently are distinctive from those of the surrounding area (Midgley and Musil 1990).

The vegetation of the Soebatsfontein area is typical Lowland Succulent Karoo vegetation; the most characteristic and widespread vegetation of Namaqualand (Low and Rebelo 1996). Lowland Succulent Karoo vegetation is found principally along the inner margins of the coastal plain of Namaqualand, below the escarpment, at elevations ranging from 0 to 600 m. This extremely arid vegetation type grows in areas receiving between 50 and 200 mm of rain per year (Low and Rebelo 1996).

Soebatsfontein is a small community of about 250 people. The settlement is situated approximately 80km south-west of Springbok and 48 km west of Kamieskroon. The community was recently awarded 15 000 ha of land as part of South Africa's land redistribution programme. This land was owned for the previous 60 years by the De Beers Mining Corporation. Between 1940 and 1970 the land was leased to one family who used it to farm sheep, the dominant agricultural practice in the region; thereafter it was grazed by Dorper sheep under De Beers management (Surplus Peoples Project 1995). During this period approximately 5000 sheep were grazed on this land. Historic land use practices have resulted in the area being overgrazed. It is estimated that as much as a third of the area is degraded and there is considerable evidence of soil erosion and loss. Since receiving the land in 1999, the Soebatsfontein community has continued the practice of sheep grazing but with considerably reduced stock numbers. The community is keen that the ecological status and productivity of the land be improved and have recently been awarded a Landcare[1] grant to pursue this aim.

Three distinctive plant community types dominate the communal rangelands of Soebatsfontein. *C. inaequale* covers large areas, forming dense mats. Interspersed are patches where *C. inaequale* is notably absent. Other Mesembryanthemaceae shrubs, for example *Eberlanzia docotoma* and *Ruschia leucosperma*, dominate this community. Scattered across the landscape are large heuweltjies, which support a third distinct plant community type, dominated by a different suite of Mesembryanthemaceae shrubs and a high number of annuals. In this report these three community types will be referred to as Cephalophyllum, non-Cephalophyllum and heuweltjie communities respectively.

[1] The Landcare programme originated in Australia to promote sustainable land management and was adopted in South Africa in 1998. The South African Landcare programme is a community-driven and government-supported land management programme, which aims to conserve natural resources through sustainable agricultural resource utilisation by communities (National Department of Agriculture 2000).

Sampling procedure

Bioclimatic envelope

To establish the regional potential range of *C. inaequale*, known spatial distribution points from herbarium records were correlated with five environmental surfaces using the GIS package ArcView 3.2. The five environmental determinants are climatically-derived parameters considered critical to plant physiological function and survival (Schulze *et al.* 1997). The parameters used were: mean minimum temperature of the coldest month; heat units (annual sum of daily temperatures exceeding 18°C); annual potential evaporation; winter soil moisture days; and summer soil moisture days. The bioclimatic envelope, or approximated realised niche space for *C. inaequale* was determined by the upper and lower limits of each of these parameters. This area was then mapped. A brief examination of the known location points in relation to national soil texture covers was also carried out.

Phytosociological survey and abiotic environmental variables

Thirty 25 m^2 quadrats were surveyed in community patches dominated by *C. inaequale*. Ten similar quadrats were surveyed in communities on heuweltjies and a further ten in non-Cephalophyllum communities. Mesembryanthemaceae seeds can be dispersed up to 1.65 m away from the parent plant by raindrops (Parolin 2001). Secondary dispersal by sheet flow may increase this distance (Cowling *et al.* 1999). To reduce the possibility of the absence of *C. inaequale* as a function of the lack of available seed, all non-Cephalophyllum sites sampled were within 2 m of existing *C. inaequale* patches.

In each quadrat, all species, numbers and percentage cover of each species were recorded, as well as total vegetation cover for the entire quadrat. The percentage cover of cryptogamic crusts was also recorded. Sampling was carried out during September and October 2001.

Soil depth and infiltration rates were recorded in each quadrat. Soil depth was measured in open areas by hammering a metal stake (1 cm diameter) into the soil until bedrock was reached. Soil infiltration rates in each quadrat were measured by placing an open-ended cylinder (diameter 75 mm) into the soil to a depth of *c.* 5 mm, taking care not to disturb the soil surface. The time taken for 50 ml of water to penetrate the soil was recorded (see Dean 1992).

In each quadrat, soil samples were taken to a depth of 10 cm from open areas between shrubs. Soil samples were analysed for the following chemical properties: pH; conductivity; total carbon; total nitrogen; potassium; phosphorus and exchangeable cations (Mg, Ca, K and NA). pH was determined in 1M KCl (McClean 1992). Total carbon was determined using the Walkley-Black method and total nitrogen was determined by digestion in a LECO FP-528 nitrogen analyser (Nelson and Sommers 1982). Exchangeable cations were determined in a 1M ammonium acetate extract (Doll and Lucas 1973). Cation exchange capacity (CEC) was determined at pH 7 by saturation with 0.2 M ammonium acetate. Ammonium was displaced with K2SO4 and determined by Kjeldahl distillation (Peech 1965). Soil texture was analysed using the Bouyoucos particle size method (Bouyoucos 1962).

Facilitation of a successional process

Using four random transects, 1 m^2 quadrats, taken at 1 m intervals, were established for the monitoring of seedling survival over a three month period. Where quadrats contained no seedlings or spanned more than one community type, they were discarded. Thirteen quadrats were established for monitoring in each of the three community types. Perennial seedling numbers were counted in October, November and December 2001 and the surviving proportion in each community type over this three-month period established. Seedlings were too small for identification to species level, but the relative proportion of Mesembryanthemaceae seedlings in each community type was recorded.

Nearest-neighbour interactions

To explore the relationships between *C. inaequale* and the dominant co-occurring species in the Cephalophyllum community, a nearest-neighbour study was carried out on *Salsola dealata*, *Tetragonia portulacoides* and *Zygophyllum cordifolium*. Individuals of these plants were randomly selected and their height, average width and distance to the closest *C. inaequale* individual recorded. Shrub volume, *v*, was calculated as if the shrub was an oblate spheroid (Philips and MacMahon 1981):

$$V = \frac{\pi a^2 b}{6}$$

where:

a is the minor axis either height or average diameter, whichever is smaller.

b is the major axis either height or average diameter, whichever is greater.

Three individuals each of *C. inaequale*, and the co-occurring *S. dealata*, *T. portulacoides* and *Z. cordifolium* were excavated and their rooting depths measured and compared.

Control of soil erosion

Wind speed was measured using a hand-held anemometer placed 10 cm above the ground in the three different plant communities. Readings were taken five seconds after the anemometer was placed on the ground. Walking random transects, sixty readings were taken in the middle of patches typical of the Cephalophyllum, non-Cephalophyllum and heuweltjie communities. Readings were taken in the late afternoon over two days in November and December 2001.

Thirty sand-traps were erected, with ten in each of the three community types. Sand-traps comprised an acetate sheet (20 cm x 30 cm), covered uniformly in Plantex glue, attached to a section of pipe (10 cm x 30 cm) which was in turn attached to the bottom of a stake. These stakes were then erected, with the pipe base 1 cm above the ground, in the centre of patches typical of the three different communities. Sand-traps were left in the veld from 16 November to 18 December 2001. Wind blown sand collected on the sand-traps was removed by dissolving the glue with a solvent and filtering the remaining solution. Insects were removed and the sand was dried and weighed.

Plant propagation, establishment and re-introduction

One hundred cuttings were transplanted in the field on a highly eroded slope. Thirty of these were planted in erosion gullies and seventy were planted on exposed, but flat areas of the eroded slope. These were watered twice, once immediately after planting in September, and again in October 2001. The cuttings did receive rain during the four-month period of this study, with 33.5 mm of rain recorded in Kammieskroon between October and December 2001 (South African Weather Service unpublished data 2001). The survival of these cuttings was recorded in December 2001.

Thirty cuttings of *C. inaequale* were transplanted into soil taken from the three different plant communities, with 10 cuttings in each soil type. These were watered every week under greenhouse conditions. The number of leaves of each cutting, as a measure of successful establishment, were counted in September 2001 and again in January 2002.

Seed from *C. inaequale* capsules was germinated in June 2001 and 180 seedlings were transplanted into individual wells containing randomly arranged soil taken from Cephalophyllum, non-Cephalophyllum and heuweltjie communities. Seedling height, as a measure of establishment success, was recorded in October 2001 and again in January 2002.

Data analysis

Detrended Correspondence Analysis (DCA), an indirect gradient analysis technique, was used to explore the relationships between environmental variables and species incidence and species abundance. The computer programme CANOCO for Windows (version 4.0, Microcomputer Power, Ithaca, NY, USA) was used for the analysis.

DCA is favoured for the analysis of unimodal species data sets with large numbers of zero values, as it avoids the problems of interpretation due to the arch effect produced by correspondence analysis (ter Braak 1996). The eigenvalue scores used to reproduce a sample-environmental variable biplot are linear combinations of the abiotic variables and the regression coefficients (ter Braak and Smilauer 1998). The data in all the analyses were detrended by segments. The environmental variables used in the analysis were those abiotic variables described above.

High variance and occasional lack of normality in the data meant Kruskal-Wallis ANOVAS for non-parametric data were used to test for significant differences in measured biotic and abiotic variables among the three communities. The same test was used in testing for significance difference in the volumes of wind blown sand collected in each community types. Single factor ANOVAs for parametric data were used to test for significant differences in wind speeds and in comparing survival among seedlings in different communities. The proportion of seedlings surviving was arcsin transformed to achieve normality. Significantly different means were separated using the Tukey significant difference test (Zar 1996).

In examining nearest-neighbour relations, distances between individuals were regressed against individual volumes using a simple linear regression.

Results

Bioclimatic envelope

The bioclimatic envelope generated for *C. inaequale* shows that this species could grow across a considerable area of the west coast of the Northern Cape Province (Fig. 1). The potential area extends approximately 345 km in a north-south direction and extends in an east-west direction for 36 km at its narrowest point and 92 km at its widest (a total area of approximately 17 500 km^2). An examination of the known location points in relation to national soil texture covers showed no correlation with the known spatial distribution points from herbarium records. On this basis, soil was excluded in defining the potential area.

Phytosociological survey and abiotic environmental variables

A total of 122 species were recorded in the study, of which 79 were perennial and 43 were annual. The Cephalophyllum community was characterised by *C. inaequale* and the co-occurring perennial species *T. portulacoides, S. dealata* and *Z. cordifolium* in conjunction with large numbers of annual species, in particular *Didelta carnosa var. tomentosa*. The non-Cephalophyllum community was characterised by a high number of perennial shrubs of the Mesembryanthemaceae family, in particular *Eberlanzia dicotoma* and *Ruschia leucosperma*. The heuweltjie community was characterised by a perennial *Ruschia* sp. and two annual species, *Pentzia pilulifera* and *Opophytum hypertrophicum*.

The DCA ordination diagram of species composition shows a scatter plot of the sites and the abiotic variable sample scores (Fig. 2). The eigenvalues of the first two ordination axes of the DCA of species composition data are 0.36 and 0.25 respectively. The heuweltjie sites form the most distinct cluster at the bottom of the diagram. The heuweltjie communities are associated with deep soils, a high percentage of fine-sand, high pH, and high magnesium, calcium and sodium values. The non-Cephalophyllum sites are distinct from the heuweltjie sites and are clustered at the top left-hand side of the diagram. Non-Cephalophyllum communities are associated with high percentage coarse-sand values and high stone content. The Cephalophyllum sites are less clearly grouped, with elements overlapping with both the non-Cephalophyllum and heuweltjie communities, and no particularly strong associated environmental variables.

The DCA ordination diagram of species abundance data, measured as percentage cover, shows a scatter plot of the sites and the abiotic variable sample scores (Fig. 3). The eigenvalues of the first two axes of the DCA of species abundance are 0.81 and 0.23 respectively. Based on species abundance, the three community types sampled form more coherent clusters, with some overlap between the Cephalophyllum and non-Cephalophyllum communities, but no overlap between the heuweltjie community and the other two communities. The heuweltjie sites are associated with deep soils, a high percentage fine-sand, high pH, and high potassium, carbon, nitrogen, magnesium, calcium and sodium. The Cephalophyllum sites are associated with low infiltration rates and coarse sand, and also to a lesser degree with the clay content associated with the non-Cephalophyllum sites. The non-Cephalophyllum sites are associated with a high stone and clay content.

The heuweltjie communities had significantly lower cryptogamic crust cover and fewer plant species than the Cephalophyllum and non-Cephalophyllum communities, which were similar to each other in both annual and perennial species number and in percentage cryptogamic crust cover (Table 1). Cephalophyllum communities had the highest overall percentage plant cover, which is expected given that *C. inaequale* has a prostrate and creeping growth form which forms large mats covering much of the ground. The non-Cephalophyllum community had significantly less plant cover than the other two communities.

Significant differences among the abiotic variables served largely to identify the heuweltjie community as distinctive from the Cephalophyllum and non-Cephalophyllum communities (Table 1). In particular, heuweltjie soils are higher in pH, potassium, exchangeable cations, and are significantly deeper with a faster infiltration rate. The non-Cephalophyllum community was significantly stonier and generally shallower than the other two communities although soil depth was not significantly different from the Cephalophyllum community. The Cephalophyllum community varied significantly from the heuweltjie community with regard to 11 of the abiotic variables measured, and was more similar to the non-Cephalophyllum community, varying significantly only in terms of stone content.

Facilitation of a successional process

The number of perennial seedlings recruited in the non-Cephalophyllum community during the three-month monitoring period was considerably higher than among the Cephalophyllum and heuweltjie communities (Table 2). All three communities experienced seedling deaths over the three-month monitoring period, with the greatest loss for all communities being between November and December 2001. While not significantly different, out of the three communities the seedling survival rate in the Cephalophyllum community was highest ($n = 39$, $F = 2.65$, $p > 0.05$).

The percentage contribution of Mesembryanthemaceae seedlings to the total in each community was as follows: Cephalophyllum = 32%; non-Cephalophyllum = 73%; and heuweltjie = 54%. There was no significant difference in the relative contributions of seedlings of the Mesembryanthemaceae and other, non-Mesembryanthemaceae seedlings to each community ($n = 39$, $H = 0.88$, $p > 0.05$). The majority of the non-Mesembryanthemaceae seedlings were species of the genus *Tetragonia*.

Nearest-neighbour interactions

No significant interactions were recorded between *C. inaequale* and the co-occurring perennial species *S. dealata*, *T. portulacoides* and *Z. cordifolium* (Fig. 4). Rooting depths among these co-occurring species were found to differ, with main root areas occupying different depths of the soil profile (Plate 1). Mean rooting depths (n = 3 for all species) in centimetres (±SD) for the four species are as follows: *C. inaequale* = 8.6 (±1.6); *S. dealata* = 45.2 (±12.6); *T. portulacoides* = 12.9 (±2); and *Z. cordifolium* = 4.6 (±1.3).

Control of soil erosion

Wind speeds ranged between 0 - 15 km per hour during the survey (Fig. 5). Mean recorded wind speeds (±SD) in km hr^{-1} for each community are as follows: Cephalophyllum = 8.5 (±1.8); non-Cephalophyllum = 8.9 (±0.9); and heuweltjie = 9.7 (±1.2). Winds were gusty and as a result wind speed measures were variable. Wind speeds on heuweltjies were significantly higher than in the surrounding communities.

Volumes of sand trapped over the 33 days of monitoring ranged from 2 g to 3.8 g (Fig. 6). Mean volumes of sand in grams (±SD), trapped in each community, are as follows: Cephalophyllum = 2.27 (±0.25); non-Cephalophyllum = 2.55 (±0.39); and heuweltjie = 2.91 (±0.55). Significantly greater volumes of sand were trapped on the heuweltjies.

Plant propagation, establishment and re-introduction

Of the 100 cuttings transplanted in the field, 98 had survived by the end of December 2001. Two cuttings could not be found in December 2002 and had presumably been dislodged by sheep and blown away.

The germination and establishment of *C. inaequale* from seed was extremely successful. However, the majority of transplanted seedlings experienced negative growth rates between October 2001 and January 2002. Approximately one third of the transplanted seedlings died with no significant variation among the three different soil treatments. No significant differences were recorded in the growth rates on soils taken from the three different communities ($n = 180$, $F = 2.089$, $p > 0.05$).

While all the transplanted cuttings survived in the different soil types, none of the cuttings experienced positive growth between the months of October 2001 and January 2002. No significant difference was recorded among soils taken from the three different communities ($n = 30$, $F = 0.341$, $p > 0.05$).

Discussion

Historically the revegetation of semi-arid rangelands has developed more as an agronomic technology than as a science (Call and Roundy 1991). Research has emphasised the rapid establishment of vigorous, and often exotic species on specific sites, as opposed to focussing on the processes of plant establishment and the development of diverse and persistent plant communities in functioning ecosystems (Call and Roundy 1991). Many revegetation projects attempted in the arid winter rainfall regions of southern Africa have failed, frequently at great expense (Desmet 1996, Milton 2001). It is now recognised that the processes responsible for the origin and maintenance of natural systems must be understood as a pre-requisite for ecological restoration. A more mechanistic approach to revegetation and restoration is called for. Ecosystem restoration should strive to reinstate those processes that contribute to the development and maintenance of sustainable ecosystems as a whole, ideally through the use of indigenous species and the salvaging of living components of the landscape (Milton 2001). The approach adopted in this study, which explores the potential of one indigenous plant species for use in revegetation and ultimately restoration, strives to adopt this more comprehensive and scientific approach.

The regional potential of *C. inaequale*

An examination of the geographic potential of a species is a sensible first step to exploring its feasibility for use in restoration. The extensive bioclimatic envelope modeled for *C. inaequale* demonstrates that this species has a wide geographic potential, and lends support for its further investigation. The creation of bioclimatic envelopes is used extensively in modeling the effects of climate change on plant distribution patterns (Rutherford *et al.* 1995), but could have a number of further applications in the restoration arena. By correlating the bioclimatic envelope of *C. inaequale* with a map of land degradation across Namaqualand, target areas for using this species, could be identified. Furthermore, much of the exceptional diversity of the Namaqualand flora can be attributed to the high number of species of the Mesembryanthemaceae family (Cowling *et al.* 1999). The dispersal distances of this family, which predominantly have hygrochasitic capsules and water dispersed seed, are typically short (< 2 m) (Parolin 2001). The relatively short dispersal distances of many of these species of Mesembryanthemaceae, which dominate this flora, suggest it may be useful to use such a model to prioritise areas for restoration in relation to their proximity to patches of remnant vegetation. Remnant patches of vegetation would act as sources for potential colonists and their proximity to restoration sites could improve success rates (Bell *et al.* 1997). There is also scope to explore the potential of other species of *Cephalophyllum* that could be used outside the feasible area identified for *C. inaequale*. Given the threat that climate change poses to the Succulent Karoo, it may be sensible to take this model one step further to ensure that a species is only considered for use in areas where it will feasibly grow 20 years from now (Midgley and O'Callaghan 1993)

This model was generated at a coarse scale and in reality the landscape is more finely partitioned. The feasibility of growing this species in the potential area identified should be tested experimentally by planting *C. inaequale* in areas across the boundary of the modeled bioclimatic envelope. This would serve to demonstrate the accuracy of the envelope modeled in this particular case, and the value of adopting this approach in similar studies in future.

The position of *C. inaequale* in the landscape

Gaining an understanding of the position *C. inaequale* occupies at a landscape level clarifies its abiotic habitat requirements, and gives clearer insight as to exactly where it could be used in restoration projects. The soils collected and analysed in this study, taken from the three different plant communities, showed considerable spatial heterogeneity, which is a common feature of many desert systems (Stock *et al.* 1999). This heterogeneity is most pronounced between those soils associated with the heuweltjies, and those of the surrounding area, with considerably less variation between the soils associated with the Cephalophyllum and non-Cephalophyllum communities. The soil on which the Cephalophyllum community grows is a slightly acid soil, with an even mix of coarse, medium and fine sand. The soils of the heuweltjie community are alkaline, nutrient rich and deep. Those of the non-Cephalophyllum community are strongly acidic, have a high coarse-sand and stone content, and are typically shallow.

The DCAs show no particular association between the Cephalophyllum community and any set of environmental variables. Based on species composition, the DCA indicates that the Cephalophyllum community shares a number of elements with the more distinctive non-Cephalophyllum and heuweltjie communities. The more obvious segregation of the Cephalophyllum community on the basis of abundance in the DCA, demonstrates that this community is most successful (as measured by species abundance) when confined to a specific habitat as defined by those abiotic parameters measured. This shows that while the Cephalophyllum community favours a specific habitat, many species within this community are tolerant of a wide range of soil conditions.

In the flatlands between the heuweltjies, the Cephalophyllum and non-Cephalophyllum communities form adjacent patches. The DCA of compositional data shows that a number of species are shared between these two communities. The soils of these communities are similar, differing significantly only in terms of stone content. While not significantly different, the non-Cephalophyllum community grows on shallower soil than that associated with the Cephalophyllum community, which were generally deeper, but also highly variable in their depth. Survival to date of *C. inaequale* cuttings and seedlings on soil taken from the non-Cephalophyllum community gives no indication of preference for soil properties. The shallow soils of the non-Cephalophyllum community, a feature lost in the greenhouse transplants, may be an important factor limiting the success of *C. inaequale* in this community. It is also possible that typically shallow rooted species, which are a feature of the Namaqualand flora (Cowling *et al.* 1999, Eccles 2000), dominate this shallow habitat, limiting the success of *C. inaequale* through a competitive interaction, in this otherwise similar environment.

Of the three communities examined in this study, the heuweltjie community was the most unique. This community had distinctive physical and chemical soil properties and a particular plant community, with few compositional elements overlapping with the Cephalophyllum and non-Cephalophyllum communities. The alkaline soils and high infiltration rates of heuweltjie soils aid decomposition of organic matter and nutrient cycling rendering these soils eutrophic (Midgley and Musil 1990, Miller and Donahue 1990, Desmet 1996). As evident from the DCA based on species composition, the Cephalophyllum community is largely excluded from heuweltjies, and *C. inaequale* is not found growing on heuweltjies. Despite the evidently unique soil environment of the heuweltjie community, the survival to date of *C. inaequale* cuttings on soil taken from this community does not conclusively demonstrate that this exclusion is a function of soil chemistry. Exclusion of *C. inaequale* from heuweltjies could simply be a function of seed dispersal, where this water-dispersed species would struggle to colonize higher ground. *C. inaequale* may also be absent from heuweltjies due to competitive exclusion by those species dominating this community. The fact that *C. inaequale* is excluded from heuweltjies attests to the fact that the landscape is finely partitioned. While the bioclimatic envelope generated may show this species to be viable across a large area on a regional level, it is important to consider the finer landscape level to identify a species' exact habitat requirements. In a landscape dominated by heuweltjies, *C. inaequale* would only be an ideal candidate for use in restoration in those areas between heuweltjies.

In keeping with previous studies in semi-arid areas of southern Africa (Midgley and Musil 1990, Esler and Cowling 1993), soils do appear to play a role in determining transitions between the communities in this study. However, of the three communities examined the Cephalophyllum community seems to be the least defined on the basis of soil properties, and the best tolerant of the more extreme soil environments measured in this landscape.

The functional role of *C. inaequale* in the landscape

Ecosystem processes

In order to initiate a restoration process and redirect a disturbed ecosystem towards a predisturbance state, plants used in restoration must play a functional role in the landscape. For example, plants that create or maintain habitats (Eccles 2000), or have positive associations with other organisms (Callaway 1995), make good candidates for use in restoration ecology.

The Cephalophyllum community was marked by the presence of a cryptogamic crust, which formed a dark mat covering as much as sixty percent of the bare soil between the plants. Cryptogamic crusts are established through a rich association of lichens, bryophytes, cyanobacteria, green algae and fungi in the upper most layer of soil (Leys and Eldridge 1998). The presence of cryptogamic crusts is reported to favour the success of vascular plants by increasing nutrient availability and moderating soil temperature (Callaway 1995, Gold and Bliss 1995, Leys and Eldridge 1998). Cryptogamic crusts are also noted for their role in controlling wind erosion as they bind soil particles with exudates and filaments, aggregating soils and reducing the potential for soil loss (Verrecchia *et al.* 1995, Hodgins and Rogers 1997). Cryptogamic crusts have also been recorded to increase water runoff and reduce infiltration, in particular at the start of a rainfall event, when the crust is still dry (Verrecchia *et al.* 1995). However, once water has penetrated the crust, it is protected from excessive evaporation (Verrecchia *et al.* 1995). While their worth in the agricultural arena could be debated, the positive association between the Cephalophyllum community and cryptogamic crusts may add to its attributes, enhancing its potential for use in ecosystem restoration. These crusts are easily lost to rangelands through trampling, and their successful re-establishment would aid in restoring ecosystem function and add to overall biodiversity (Hodgins and Rogers 1997).

Population dynamics

Seedling recruitment recorded in October 2001 showed recruitment to be lowest in the Cephalophyllum community. The comparatively high recruitment recorded in the non-Cephalophyllum community could be a function of the degree of available space in this community (Milton and Dean 1995a). Germination microsites are more frequently a function of seed dispersal biology, where passively dispersed seed tends to germinate in the open, and wind-blown seed is actively trapped by other plants or litter, and then germinates in these sites (Esler 1999). This study supports these findings, where seedlings recruited in the non-Cephalophyllum community, which had the most bare ground, were predominately of the Mesembryanthemaceae, the majority of which have hygrochasitic capsules and water-dispersed seed (Parolin 2001). In contrast, recruitment in the Cephalophyllum community was predominately of other perennials, mostly species of the genus *Tetragonia*, which frequently have winged seeds that are wind dispersed. The extensive patches created by *C. inaequale* trap wind-dispersed seeds. There is also the possibility that *C. inaequale*, with its creeping structure, may prevent water-dispersed seeds of the Mesembryanthemaceae from being washed into the midst of this community. The high number of Mesembryanthemaceae seedlings in the non-Cephalophyllum community is also due to the diversity of Mesembryanthemaceae species established as adults in this community. A study of the population dynamics of several Cephalophyllum species noted a trade-off between runner formation (vegetative reproduction) and seedling recruitment (sexual reproduction) (Hartmann 1983). Vegetative reproduction appeared to be at the cost of sexual reproduction. It is possible that the low number of Mesembryanthemaceae seedlings recruited in the Cephalophyllum community is a function of this dynamic, where the dominant Mesembryanthemaceae species, *C. inaequale*, is reproducing vegetatively and not producing large amounts of seed.

Of those seedlings that germinated, survival over the three-month period of this study was highest in the Cephalophyllum community. Studies of perennial seedling survival in arid rangelands show that few seedlings reach reproductive maturity (Milton 1993, Esler 1999). The most recent count of seedlings in this study was in December 2001 and survival in all communities was still above 50%. These are considerably higher than previously recorded values in similar studies, which range from less than 5%, to 25% in exceptional years of rain (Milton 1995, Esler 1999). The higher overall survival rate recorded in this study may be a function of time, and that with the ensuing late summer months there will be further mortality. The timing and amount of rain is also known to influence seedling survival (Esler 1999). The exceptionally high rainfall experienced in the winter of 2001, may have aided seedling survival in this study. Further monitoring of these seedlings will be carried out and will give more conclusive results.

Through *C. inaequale's* role as a 'nurse' plant (Beukman 1991, Dean and Yeaton 1992) it appears to facilitate a successional process at this site. Seedlings that germinate under an adult 'nurse' plant generally experience less abiotic stress and are better protected against herbivory, and subsequently stand a better chance of survival (Beukman 1991). The mat-like architecture of *C. inaequale* both reduces the abiotic stress of seedlings as well as the threat of herbivory. This trend of improved seedling survival in close proximity to adult *C. inaequale* plants, is in contrast to findings in other studies. Milton and Dean (1995b) concluded that seedling survival was a function of moisture availability, which increased with distance from adult plants, and subsequently seedling survival was also improved with distance to adult plants. To establish whether the trend of improved seedling survival in the Cephalophyllum community would persist with time, survival would have to be monitored for a longer period.

Competitive interactions

C. inaequale is associated with a diverse plant community. A number of the co-occurring dominant perennial shrub species associated with this community, for example *S. dealata*, *T. portulacoides* and *Galenia sarcophylla*, are described as highly palatable and extremely well grazed (Shearing 1994). Successful restoration with the establishment of *C. inaequale* and its associated community would also serve to improve agricultural productivity.

Studies examining nearest-neighbour relationships in desert shrub communities have concluded that a strong correlation between nearest-neighbour distance and plant size is evidence of interspecific competition between species (Yeaton *et al.* 1977, Phillips and MacMahon 1981). The interaction between interspecific nearest-neighbours in this study demonstrated no such dynamic between *C. inaequale* and its co-occurring dominant species. It is suggested that where individuals of different species are able to grow more closely there must be some mechanism acting to reduce competition, such as the vertical stratification of root systems (Yeaton *et al.* 1977, Phillips and MacMahon 1981, Cody 1986). In this study, the lack of any evidence of a significant relationship between co-existing plants is in keeping with the suggestion that the flora of Namaqualand has weakly developed competitive interactions due to the relatively high turnover rate of individuals in this vegetation (Eccles *et al.* 1999). However, when viewed in combination with the apparent vertical stratification of their rooting systems, this may be an example of this mechanism of reducing interspecific competition, maintaining coexistence between the species in this association. Contrary to the proposal that the typically shallow rooting depths of the Namaqualand flora are too shallow for partitioning (Eccles 2000), the findings of this study suggest that co-existence and weak interspecific competition is achieved through partitioning.

Erosion control

Live vegetation cover has long been recognised as protecting soil against wind erosion (Miller and Donahue 1990, Skidmore 1994). In this study *C. inaequale*, with its prostrate and creeping growth form and resulting high density of plant cover, has been shown to reduce wind speeds and subsequently soil erosion. The thinning and death of vegetation with excessive grazing, in particular during dry periods, increases the extent of bare ground (Maestre *et al.* 2001). Surface soil conditions deteriorate as the wind physically removes the most fertile portion of the soil, and lowers productivity (Skidmore 1994). Soils low in clay and high in fine sands, a feature of the soils analysed in this study, are described as weakly structured and especially vulnerable to wind erosion (Miller and Donahue 1990). The ability of *C. inaequale* to hold soil is an essential attribute in considering its potential for use in the restoration of this landscape.

In circumstances where the most fertile and active soil layer is lost, the goal of restoration must be to not only halt soil erosion, but to strive to ameliorate soil conditions. Soil processes that give rise to the biologically active surface layer, essential as a rooting medium and nutrient source for plants, are a key component in the functioning of ecosystems (Desmet 1996, Webb 1996). Erosion altered soil surfaces have been recorded in the Karoo, where increased runoff and hardened surfaces preclude plant establishment (Palmer *et al.* 1999). *C. inaequale* evidently reduces wind erosion and promotes the deposition of aeolian load, as is apparent in the mounding of soil around the base of this plant to depths of around 7 cm. Once successfully established, and possibly even as newly planted cuttings, this species would serve to focus resources such as seed, sand, microbial spores and organic matter, improving the nutrient status of the soil, and in turn become the foci for plant establishment (Tongway 1994, Milton and Dean 1995b, Desmet 1996, Milton 2001). Even if they die, translocated plants or cuttings contribute to the improvement of soil health as their roots include microbes and fungi that re-establish decomposition and symbiotic processes (Milton 2001). Such nutrient enriched zones which result from the concentration of nutrients and biotic activity accumulating beneath shrubs, are termed 'fertile islands' (Maestre *et al.* 2001), a phenomenon which has been recorded, albeit weakly, in Namaqualand (Stock *et al.* 1999). In this manner, transplanted plants may act as 'ecosystem engineers' (Eccles 2000), initiating the creation of 'fertile islands', and there is a good case for actively planting cuttings into eroded or exposed sites to achieve this end.

Given the evidence of mounding around the base of this species, it is very likely that *C. inaequale* also plays a role in reducing water erosion. The role of *C. inaequale* in reducing the effects of water erosion could be readily tested with the erection of pit traps prior to the rainy season. Such an experiment should be carried out to further establish the value of this species for use in restoration.

The feasibility of *C. inaequale* for propagation, re-introduction and establishment

Simple propagation techniques were explored in this study. The seeds of this species apparently germinate with ease. Seedlings transplanted after four months, and monitored under greenhouse conditions were less robust and experienced high mortalities. While no positive growth has been recorded from either the cuttings in the field or those kept in the greenhouse, survival has been close to a hundred percent. While these cuttings would need to be monitored further to assess the success of propagation, early results suggest this species may be successfully propagated. Effective propagation and establishment are central to the success of any revegetation exercise. The ability to successfully propagate *C. inaequale* would need to be confirmed with continued and additional experimental work.

One of the advantages of restoration ecology as a discipline is that it provides one of the most accessible ways in which local communities can become actively involved in nature conservation (Cairns 1993, Hobbs and Norton 1996, Young 2000). By improving agricultural productivity, restoration projects will offer direct benefits to local communities and can also serve to create employment (Cairns 1993). Any restoration project involving the use of *C. inaequale* would be labour intensive and require little technology, making it an attractive prospect to simultaneously address unemployment and landscape degradation in Namaqualand.

Conclusions

The findings of this study suggest that *C. inaequale* is a potentially useful plant for restoring the degraded arid landscapes of Namaqualand. A simple bioclimatic model demonstrates the regional potential of this species to be extensive. It is suggested that the validity of this potential area be tested experimentally. At a landscape level, the abiotic habitat requirements of *C. inaequale* are not highly specific. This species forms part of a generalist community that occupies an intermediate habitat in the landscape, and is associated with a diverse and productive plant community. Furthermore, this species may act as an 'ecosystem engineer' within the landscape, facilitating seedling survival and potentially creating 'fertile islands' by trapping wind blown sand, seed and organic matter. It also does not appear to have a strongly competitive dynamic with co-occurring dominant plants. Early results show that it is easily established from seed and that cuttings survive transplanting. Further research and monitoring are required to conclude the exploration initiated in this study, and to definitively declare this species effective for use in ecosystem restoration.

There is considerable scope for work in the identification of new species and mechanisms for use in the restoration of the degraded lands of Namaqualand. It is proposed that similar exploratory studies are carried out, and given the promising findings of this study, it is suggested that the consideration of sister species may be an appropriate starting point.

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Table 1 Environmental variables for three different plant communities in Soebatsfontein; data are means ± SD. Results of Kruskal-Wallis one-way ANOVAS comparing the three plant communities are shown, * = $p < 0.05$, ** = $p < 0.01$, *** = $p > 0.001$, NS = not significant ($p > 0.05$). The small superscript letters indicate significantly different means.

	Plant community			
Environmental variable	**Cephalophyllum** (n = 30)	**Non-Cephalophyllum** (n = 10)	**Heuweltjie** (n = 10)	**H-statistic**
pH (KCl)	5.8 ±0.6[a]	5.4 ±1.1[a]	7.6 ±0.6[b]	24.0***
Conductivity (ohms)	122.8 ±115.9	164.5 ±190.5	233.7 ±272.5	NS
Carbon (vol %)	0.9 ±0.5	0.9 ±0.4	1.1 ±0.6	NS
Nitrogen (vol %)	0.1 ±0.03	0.1 ±0.02	0.1 ±0.04	NS
Potassium (mg/kg)	425.5 ±117.4[a]	334.8 ±105.5[a]	1118.6 ±344.7[b]	25.4***
Phosphorus (mg/kg)	32.9 ±17.3	26.4 ±8.4	34.2 ±16.9	NS
Magnesium (cmol(+)/kg)	2.4 ±1.6[a]	2.6 ±2.4[a]	4.4 ±1.6[b]	10.1**
Calcium (cmol(+)/kg)	3.2 ±2.5[a]	1.8 ±1.0[a]	25.0 ±5.3[b]	25.7***
Potassium (cmol(+)/kg)	1.1 ±0.3[a]	0.9 ±0.3[a]	2.9 ±0.9[b]	25.4***
Sodium (cmol(+)/kg)	1.8 ±1.7	2.1 ±2.4	5.3 ±5.7	NS
Stone (vol %)	3.3 ±3.8[a]	10.1 ±4.3[b]	0.4 ±0.7[a]	25.9***
Coarse sand (vol %)	29.1 ±5.1[a]	33.9 ±5.4[a]	17.7 ±3.9[b]	23.9***
Medium sand (vol %)	23.1 ±4.1[a]	21.0 ±3.8[a]	26.0 ±4.0[b]	7.6*
Fine sand (vol %)	33.3 ±3.9[a]	27.1 ±3.9[a]	38.8 ±6.7[b]	18.0***
Silt (vol %)	4.6 ±3.2[a]	6.0 ±2.5[a]	7.2 ±1.9[b]	7.6*
Clay (vol %)	9.3 ±2.5	10.4 ±2.6	8.6 ±3.3	NS
Soil depth (cm)	23.6 ±38.3[a]	15.0 ±4.6[a]	58.7 ±21.3[b]	24.1***
Infiltration rate (minutes)	1.1 ±1.3[a]	1.1 ±1.5[a]	0.2 ±0.4[b]	6.6*
Crust (%)	59.5 ±21.2[a]	51.5 ±35.1[a]	31.5 ±26.5[b]	6.9*
Plant cover (%)	67.2 ±11.2[a]	40.3 ±11.2[b]	51.6 ±16.2[a]	18.8***
Species number (total)	24.6 ±4.83[a]	23.2 ±2.49[a]	12.1 ±1.73[b]	2.4***
Species number (annuals)	12.5 ±3.8[a]	10.5 ±1.8[a]	5.2 ±2.7[b]	21.4***
Species number (perennials)	12.2 ±2.6[a]	12.8 ±2.6[a]	6.9 ±1.4[b]	21.4***

Table 2 Perennial seedling numbers, and percentage survival, monitored in 1 x 1 m plots for the months October to December 2001 in the Cephalophyllum, non-Cephalophyllum and heuweltjie communities; data are means ±SD.

	Plant Community		
	Cephalophyllum (n = 13)	**Non-Cephalophyllum** (n = 13)	**Heuweltjie** (n = 13)
No. perennial seedlings			
October	22.92 (±10.5)	51.15 (±54.09)	29.45 (±29.03)
November	17.38 (±10.26)	43.69 (±51.46)	19.73 (±13.84)
December	16.92 (±11.2)	35.85 (±47.98)	13.45 (±13.62)
% Seedling survival			
Oct – Dec 2001	71.4 (±30.9)	58.3 (±34.3)	43.1 (±20.9)

Captions to figures

Figure 1 Map showing the bioclimatic potential of *Cephalophyllum inaequale* (shaded area) in relation to the west coast of South Africa. This study was carried out in Namaqualand, on the communal lands of Soebatsfontein, situated south-west of Springbok.

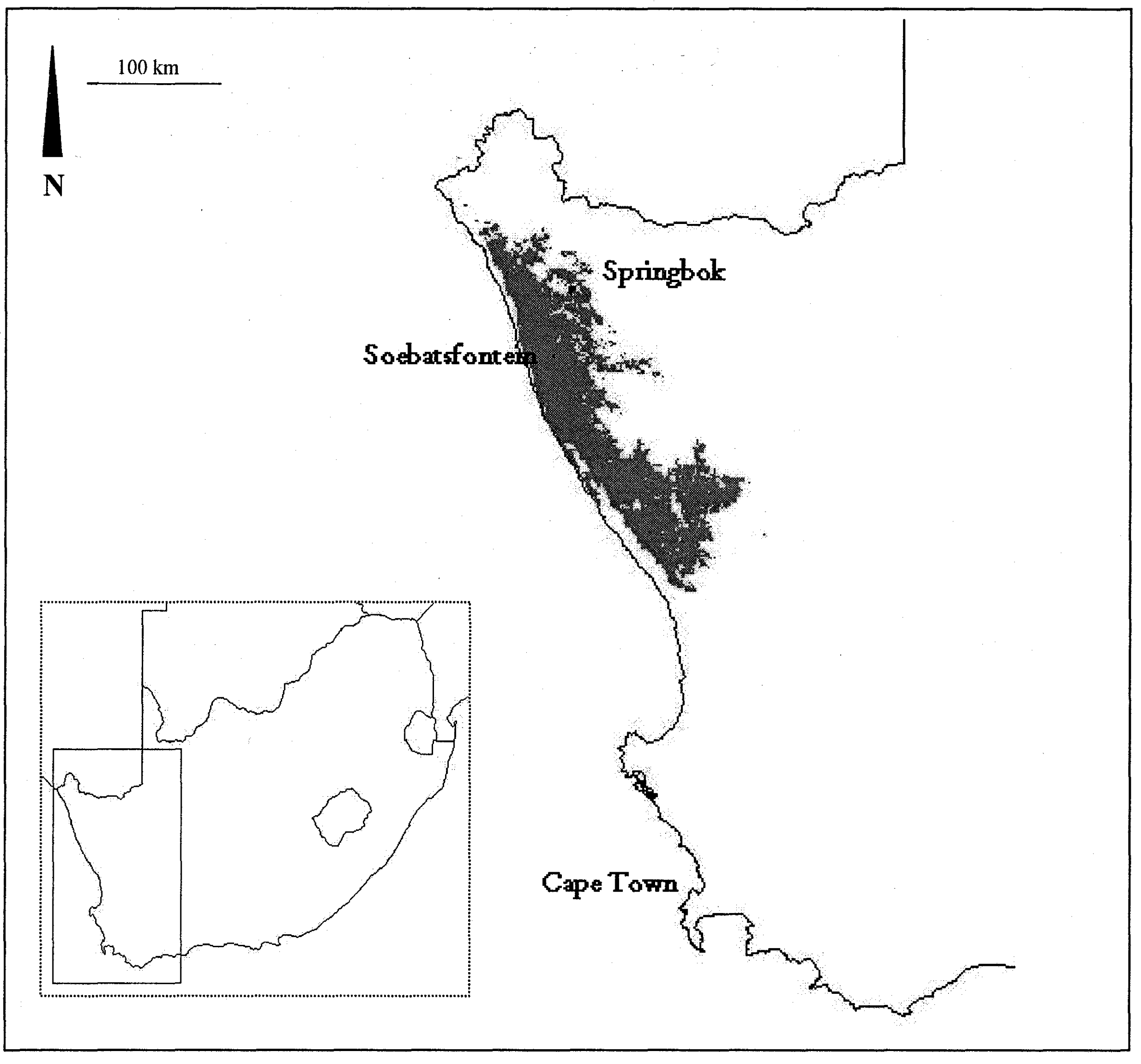
Figure 2 Detrended correspondence analysis (DCA) ordination of species composition from the 50 sites sampled with environmental variables. Cephalophyllum sites are indicated by the letter 'C', non-Cephalophyllum sites by 'N' and heuweltjie sites by 'H'. The length of arrow is indicative of the strength of the relationship.

Figure 3 Detrended correspondence analysis (DCA) ordination of species abundance from the 50 sites sampled with environmental variables. Cephalophyllum sites are indicated by the letter 'C', non-Cephalophyllum sites by 'N' and heuweltjie sites by 'H'. The length of arrow is indicative of the strength of the relationship.

Figure 4 Plant size (volume cm^3) in relation to distance from co-occurring *Cephalophyllum inaequale* for *Salsola dealata*, *Tetragonia portulacoides* and *Zygophyllum cordifolium*, $p > 0.05$ in all cases.

Figure 5 Wind speeds measured over two days in November and December 2001. Measurements were taken 10 cm above the ground in Cephalophyllum (C), non-Cephalophyllum (N) and heuweltjie (H) communities ($n = 360$, $H = 42.31$, $p < 0.000$).

Figure 6 Amount of sand (g) trapped on sticky plastic film used to measure wind erosion in Cephalophyllum (C), non-Cephalophyllum (N) and heuweltjie (H) communities ($n = 30$, $H = 8.9$, $p < 0.01$).



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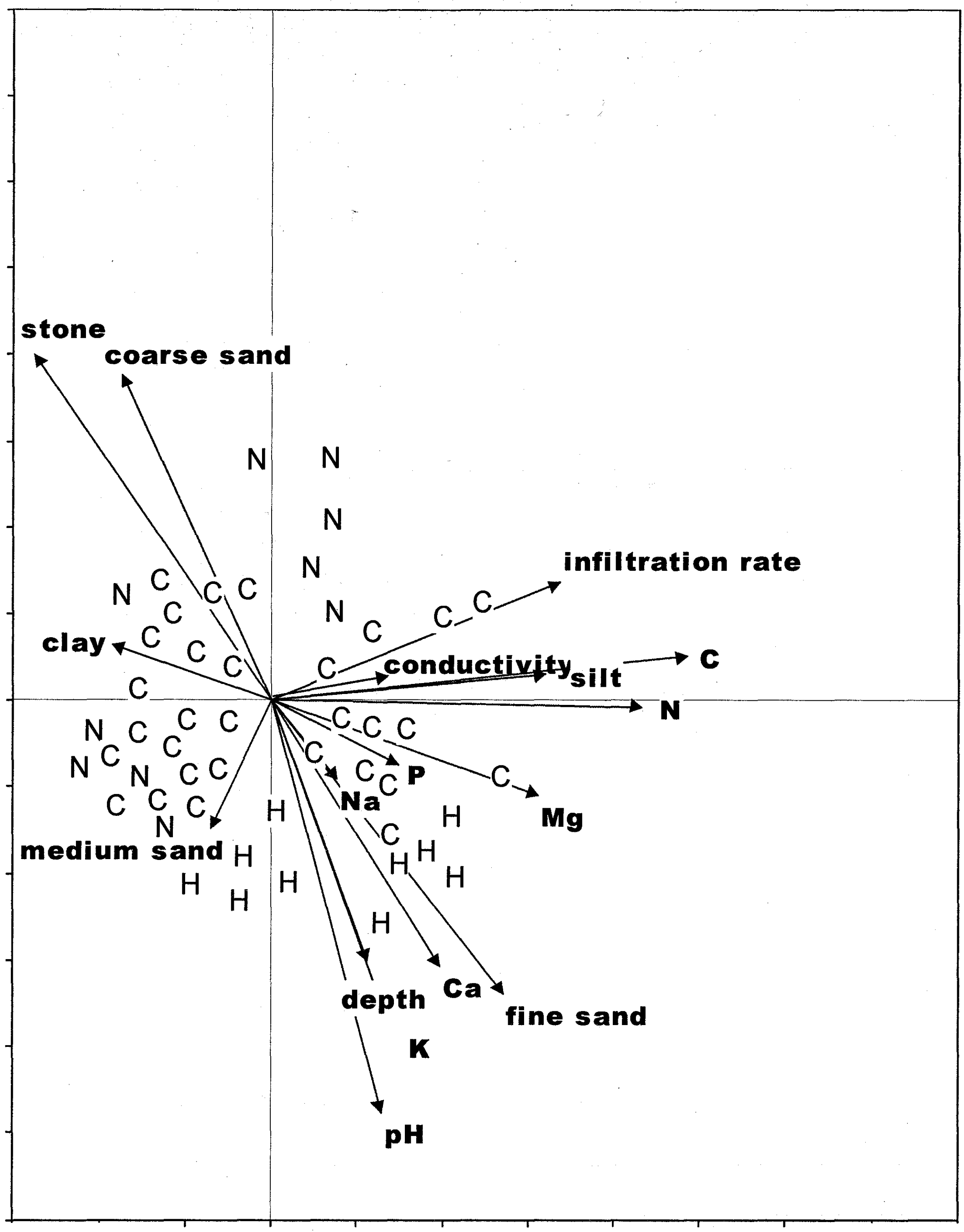

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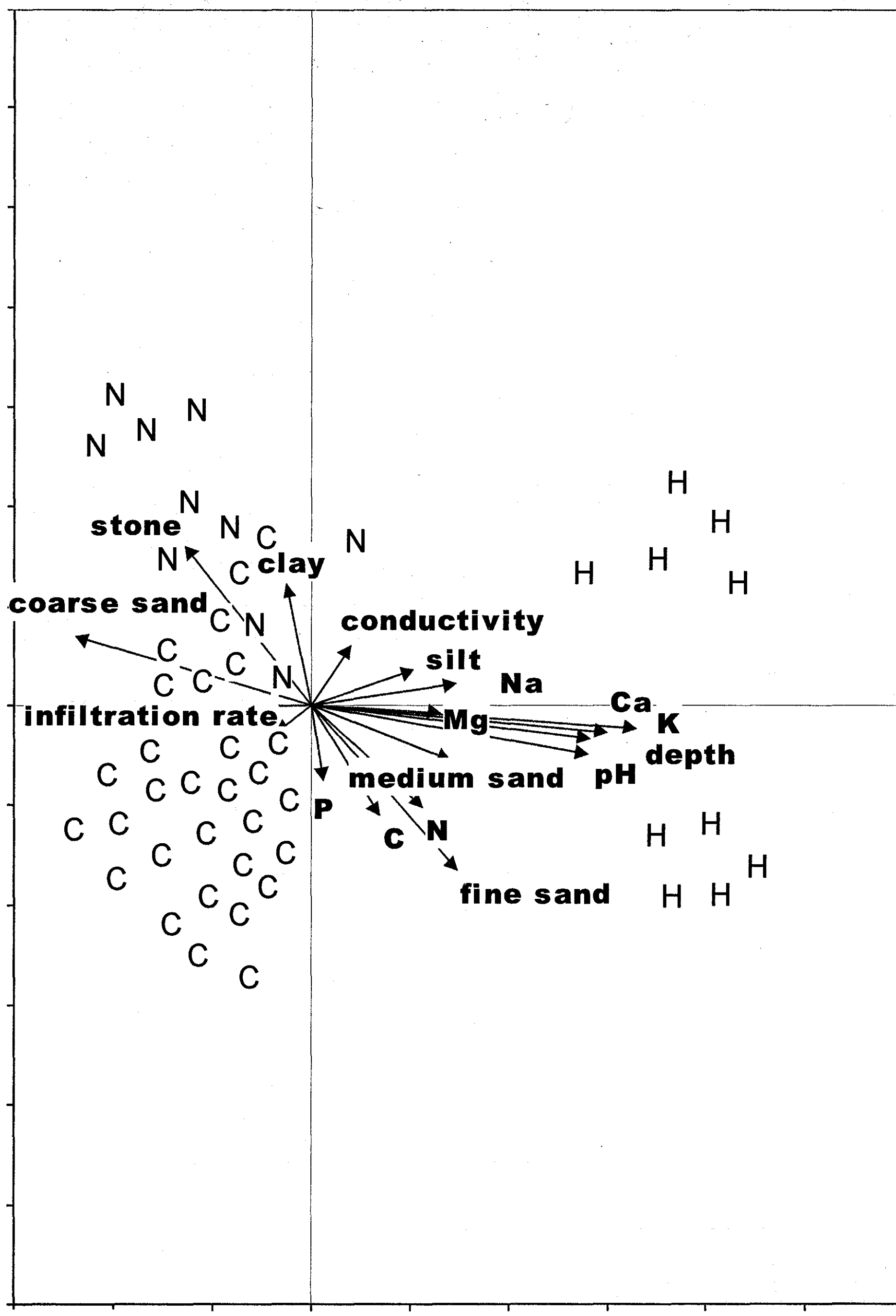

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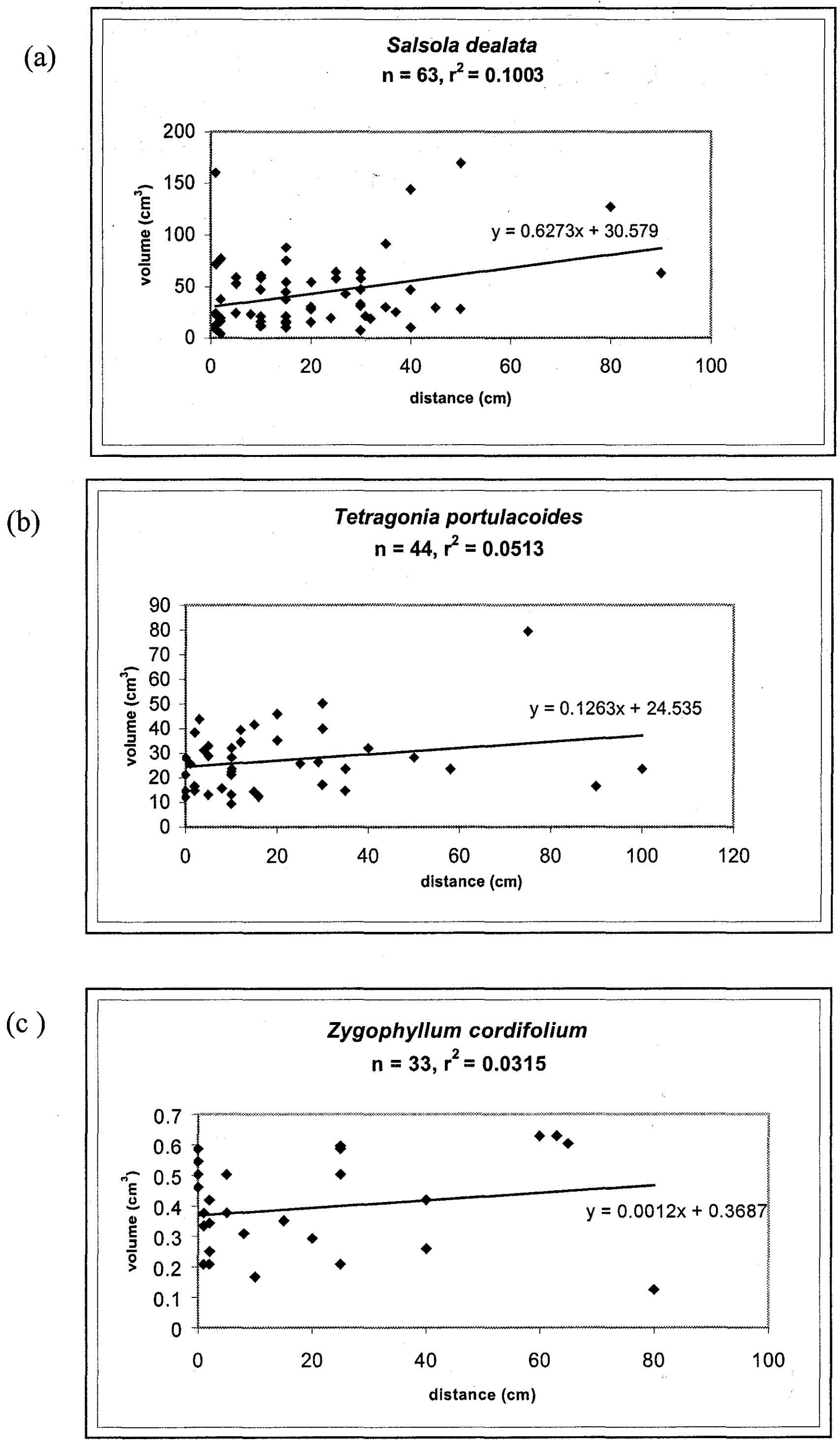

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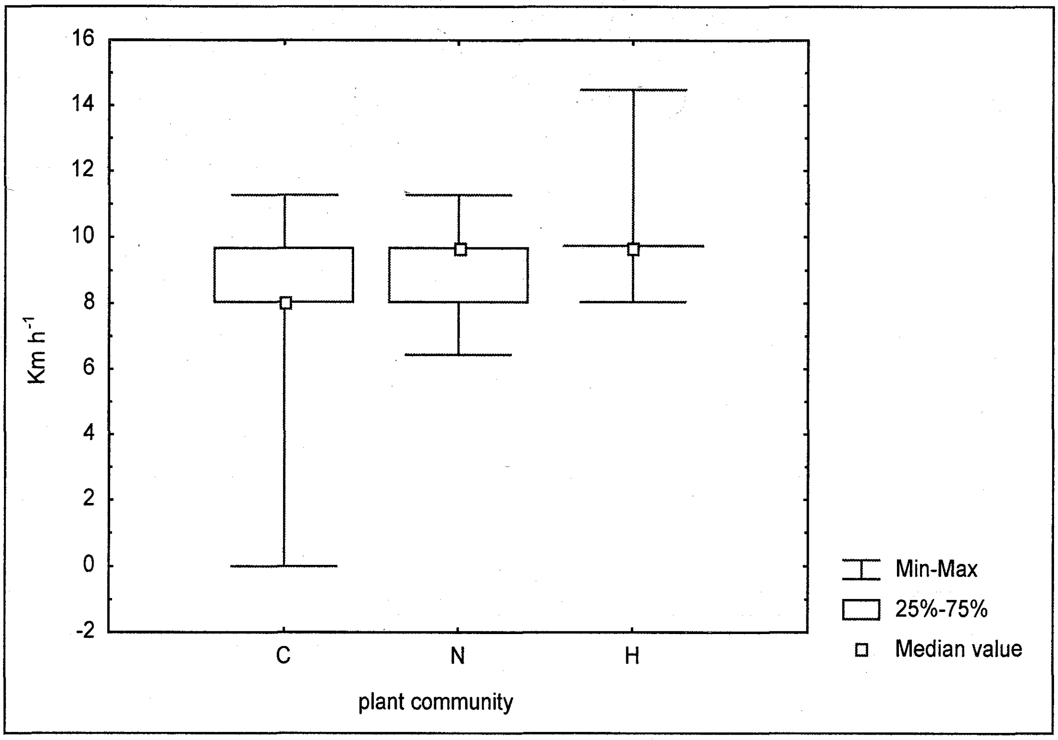

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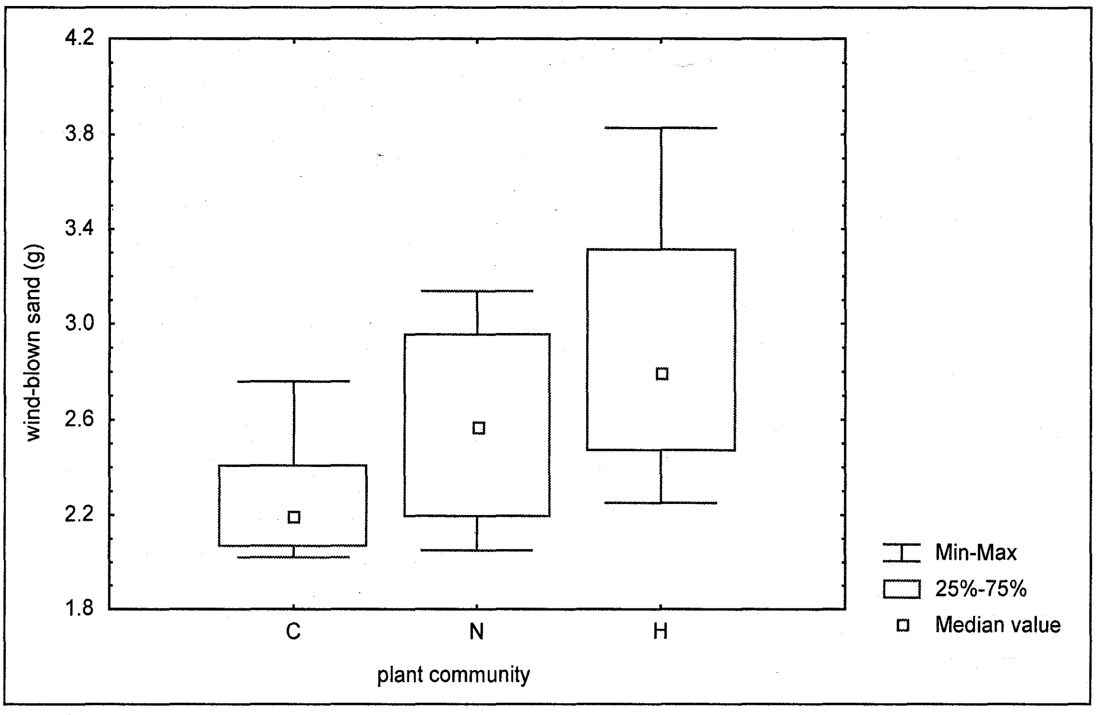

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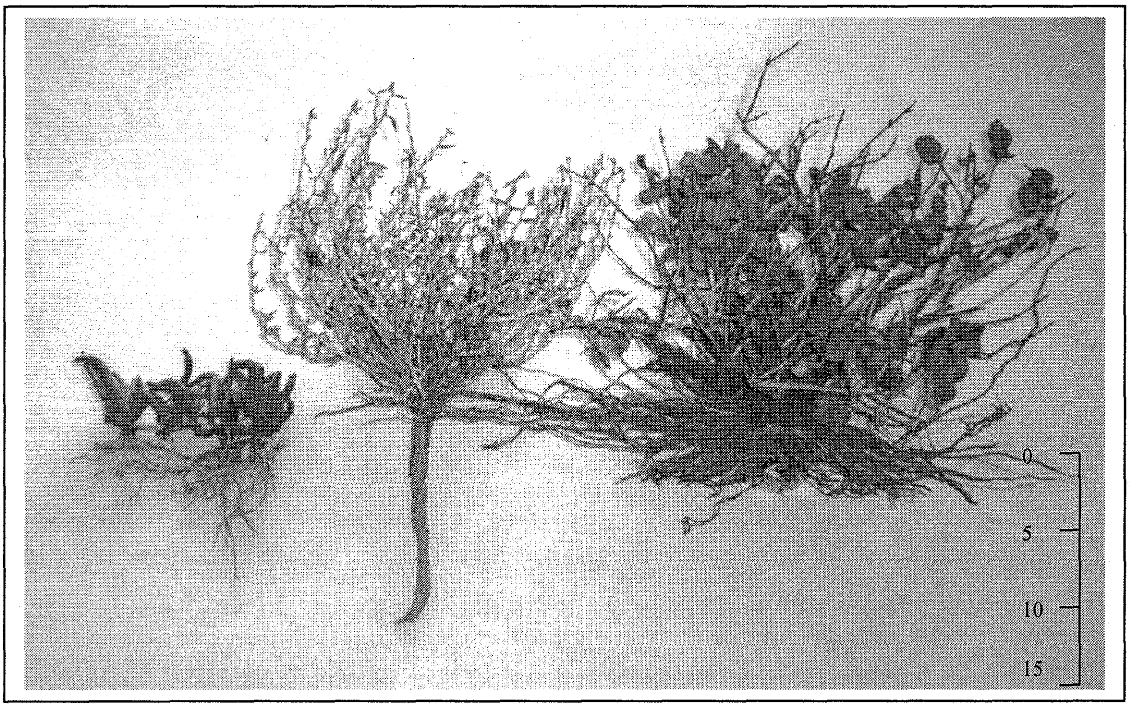
Captions to plates

Plate 1 Photo showing variable rooting depths of (from left to right) *Cephalophyllum inaequale*, *Tetragonia portulacoides* and *Zygophyllum cordifolium*. The scale bar to the right of the picture is in centimetres. The rooting system of *Salsola dealata*, the other species examined in this study, was considerably deeper and too extensive to include in this representation.



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