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Rapid vegetation regeneration in a seriously degraded *Rhanterium epapposum* community in northern Kuwait after 4 years of protection

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Abstract

A study was carried out in northern Kuwait to investigate vegetation recovery in sandy depressions in the Sabriya oilfield ('Sabriya-IN'), 4 years after it was completely protected from livestock grazing and other anthropogenic activities which have largely depleted the dwarf shrub vegetation. This vegetation was compared with that in seriously overgrazed depressions outside the oilfield ('Sabriya-OUT'), where negative influences persist, and with a sandy site in central Kuwait which has been protected for over 20 years ('Sulaibiya').

There has been a striking recovery of the dwarf shrub vegetation in Sabriya-IN during the 4 years, with cover values of shrubs as high as at Sulaibiya. *Rhanterium epapposum* has been the main species to benefit from protection. However, the shrubs have not regenerated from seed, but rather from underground stumps that have probably remained in the soil for decades.

Cover values of the annual flora at Sabriya-IN were very similar to those at Sulaibiya, and they were significantly higher than at Sabriya-OUT. However, it appears that some species may have disappeared or become extremely rare at Sabriya-IN when compared with Sulaibiya, as Sabriya-IN and Sabriya-OUT are remarkably similar floristically.

Despite the impressive regeneration of the dwarf shrub vegetation at Sabriya-IN, which contradicts the view that vegetation recovery is a slow process in desert ecosystems, it is important to consider what the natural vegetation was in this part of the world. It is suggested that the region was once dominated by an open *Acacia* woodland, in which perennial grasses comprised most of the ground layer, and that the current dwarf shrub vegetation is a response to decades, if not centuries, of moderate to heavy grazing.

Keywords: Desert annuals; Desert ecology; Desertification; Vegetation degradation; Vegetation recovery

1. Introduction

Kuwait has suffered severely from the effects of desertification in recent years, due mainly to overgrazing (Khalaf, 1989; Brown, 2003). The term 'desertification' is somewhat controversial, but in this study is used in accordance with Dregne (1986), referring particularly to a reduction in plant productivity, a decline in species diversity and the loss of soil resources.

About 30 years ago, much of northern Kuwait was occupied by one of two dwarf shrub communities, each referred to by the name of the main woody species present. On shallow, gravelly soils, *Haloxylon salicornicum* (Chenopodiaceae) predominated, whereas *Rhanterium epapposum* (Asteraceae) thrived on deeper, sandier soils (Halwagy et al., 1982). An intergrading of these two communities probably occurred locally where there was a corresponding mosaic of soil conditions. However, both communities have disappeared from many areas, mainly as a consequence of severe overgrazing, but also due to off-road driving, camping and construction activities (Brown, 2003). In many former *Haloxylon* stands, the annual grass *Stipa capensis* is now the main constituent of a species-poor vegetation, particularly in years of plentiful rainfall (Halwagy and Halwagy, 1974b; Brown and Porembski, 1997). On deep, sandy substrates, however, the perennial sedge *Cyperus conglomeratus* appears to have replaced *Rhanterium* as the dominant perennial (Brown, 2003). These changes have led to a general decline in species diversity, especially in the *Haloxylon* community, and have enhanced aeolian sand removal and deposition (Brown,

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2003). For instance, 'sealed' soil crusts (see Le Houérou (2002)) largely lacking surface sand now prevail where *S. capensis* predominates (Brown and Schoknecht, 2001), but in other areas, there has been a marked increase in the formation of mobile dunes (Al-Dhabi et al., 1997).

The vegetation of Kuwait is of particular scientific interest because of the relatively high mean annual rainfall (ca. 120 mm). On the basis of the concept of Shmida (1985), it can therefore be regarded as representing a transition between semi-desert and desert vegetation, corresponding to semi-arid and arid ecosystems, respectively. Such transitional areas are highly sensitive to human-induced change and therefore offer an effective index of human perturbation (Schlesinger et al., 1990).

Vegetation recovery is generally regarded as a slow process in desert ecosystems (Bolling and Walker, 2000). In accordance with the views of some authors (Garner and Steinberger, 1989; Tongway and Ludwig, 1996), we expect that where soil resources have been lost to wind erosion, the process of recovery will be greatly impeded. Conversely, if soil resources are retained and run-off is negligible (i.e. there is little 'nutrient leakage', see Shachak et al. (1998)), recovery of the perennial vegetation can be expected to proceed at a faster rate. Because desert annuals are able to build up substantial permanent seedbanks and then germinate under favourable conditions (Kemp, 1989), we also expect the recovery of the annual flora to be quite rapid on stable sandy substrates, such as in sandy depressions, where seeds are retained in the soil, as opposed to the situation on crusted surfaces.

Given the seriousness of vegetation degradation in north-eastern Arabia and the lack of any detailed studies examining the potential for vegetation regeneration, the main aim of this study was to investigate vegetation recovery in sandy depressions in an oilfield in northern Kuwait that has been enclosed recently and now enjoys complete protection from detrimental activities. These depressions, varying in size from about 0.01 to 0.2 km^2, are interspersed in an otherwise unfavourable matrix of shallow, crusted soils, largely lacking vegetation cover, which predominates over wide expanses, as described by Halwagy et al. (1982) and Brown and Schoknecht (2001). Vegetation characteristics of the depressions were compared inside and outside of the enclosure, 4 years after the fence was erected. Furthermore, to monitor the progress of recovery in the oilfield, the data were compared with those obtained from an enclosure with sandy substrate in central Kuwait that has been protected from grazing and public access for over 20 years.

2. Material and methods

2.1. Natural environment of Kuwait

Kuwait is a small, mainly flat country situated in the north-eastern part of the Arabian Peninsula. It rises from sea-level to reach a maximum elevation of about 280 m on the western border with Saudi Arabia.

On a monthly basis, potential evapotranspiration far exceeds precipitation throughout the year (Halwagy and Halwagy, 1974a). During the hot summers, daytime temperatures regularly reach 50 °C. The winters are relatively cool, with mean daily temperatures between 10 and 20 °C, and sometimes quite wet. Rainfall is usually restricted to the period between October and April, and mean annual precipitation is in the region of ca. 120 mm. However, there is much variation in total rainfall from one year to another, ranging from about 28 to 260 mm (Halwagy et al., 1982).

Due to the harshness of the climate, pedogenesis is light, leaving the sandy or gravelly parent material little altered. In most southern areas, Torripsamments are prevalent, whereas Petrogypsids, Calcigypsids or Haplocalcids predominate in many northern and western parts of the country (Omar, 2000).

Perennial vegetation cover is sparse, and usually less than 10% (Brown, 2001). Dwarf shrubs are the most conspicuous elements of the desert vegetation, and although exceptions exist, the composite *R. epapposum* occurs on deep, sandy soils in central and southern parts of Kuwait, and the chenopod *H. salicornicum* predominates on the shallower soils in the north and west. Native trees are virtually absent.

2.2. Study areas

The Sabriya study area is located in north-eastern Kuwait, and has been described by Brown and Schoknecht (2001). In 1997, a large section of this area (ca. 20 km^2) was fenced off to protect the installations of the Sabriya oilfield (ca. 29.51N, 45.54E). Ever since, access to this newly formed enclosure ('Sabriya-IN') has been severely restricted, so that grazing and other detrimental activities ceased overnight. As the oil installations are situated in one corner of the enclosure, most of the area (ca. 80%) has remained undisturbed. Before enclosure, perennial woody shrubs were largely absent or chewed back to such an extent that they were barely recognisable, and this is still the situation outside of the enclosure ('Sabriya-OUT') (see Fig. 1).

The main soil type at Sabriya is represented by Gypsids, and these are usually developed as firm crusts, lacking any significant accumulation of surface sand. The surface is typically a sealed mineral crust, rich in $CaCO_3$ (Brown and Schoknecht, 2001). However, shallow drainage channels and other depressions (in some cases possibly former bomb craters) are interspersed, in which a Torripsamment, characterised by a loose, sandy substrate, has developed (see diagram in Brown and Schoknecht (2001)).

The KISR Sulaibiya Research Station is located in a sandy area about 20 km south-west of Kuwait City, and has been protected from unauthorised access and grazing since

Fig. 1. Typical view of a sandy depression outside the protected enclosure (Sabriya-OUT). Compare with Fig. 7.

1978 (Omar, 1991). The elevation is ca. 120 m asl. The vegetation consists mainly of an open dwarf shrub community dominated by the composite *R. epapposum*. This species attains a maximum cover of about 15–20% in favourable situations, although it is usually much less (5–10%). *Farsetia aegyptia* (Brassicaceae) is now an exceedingly rare perennial in most of Kuwait, but is locally common at Sulaibiya. A Typic Torripsamment is the main soil type in this area (Omar, 2000), the same as that found in the depressions at Sabriya.

2.3. Climatic situation in 2001

The winter of 2000/2001 can be regarded as being reasonably favourable for vegetation development, as rainfall during the main growth season was 106 mm (Fig. 2). This rainfall was recorded at Kuwait International Airport, but due to its close proximity to Sulaibiya, and the fact that weatherfronts bringing rain move over Sulaibiya and the airport at the same time, rainfall or is virtually identical for the two locations, as demonstrated in earlier studies (Brown, 2001). Precise rainfall data from Sabriya were not available, but the degree of vegetation cover by desert annuals (see below) suggests that the amount of precipitation was not substantially different from that at Sulaibiya, and if anything was slightly higher.

2.4. Vegetation sampling

The study was conducted during the first weeks of March, 2001, when development of the annual vegetation was at its prime. A stratified sampling procedure was adopted to examine vegetation characteristics. Within a 6 km^2 section of the Sabriya oilfield near the southern and eastern perimeter fence, five rectangular blocks, each 20 m^2 (10 × 2 m^2), were randomly selected in five depressions that also continued well beyond the protected oilfield (Sabriya-IN) into the grazed site (Sabriya-OUT). For each block in Sabriya-IN, one was also selected at random within the same depression outside the fence, so that comparable data for both ungrazed and grazed sites were obtained.

In addition, five blocks were randomly selected in a 10 km^2 area of the KISR Sulaibiya Research Station where the same sandy substrate as in depressions at Sabriya occurred, giving a total of three investigated sites.

In each block, the location of all perennial shrubs and grasses was mapped to an accuracy of 10 cm, and the area of each perennial calculated. The number of *R. epapposum* and *F. aegyptia* seedlings were also registered and mapped. Seedlings of the perennial grass *Stipagrostis plumosa* were not counted in the blocks due to the prohibitive amount of labour this process would have entailed, but they were recorded in the 0.25 m^2 quadrats (see below).

To investigate potential differences in the floristic composition of the annual flora (including a few small

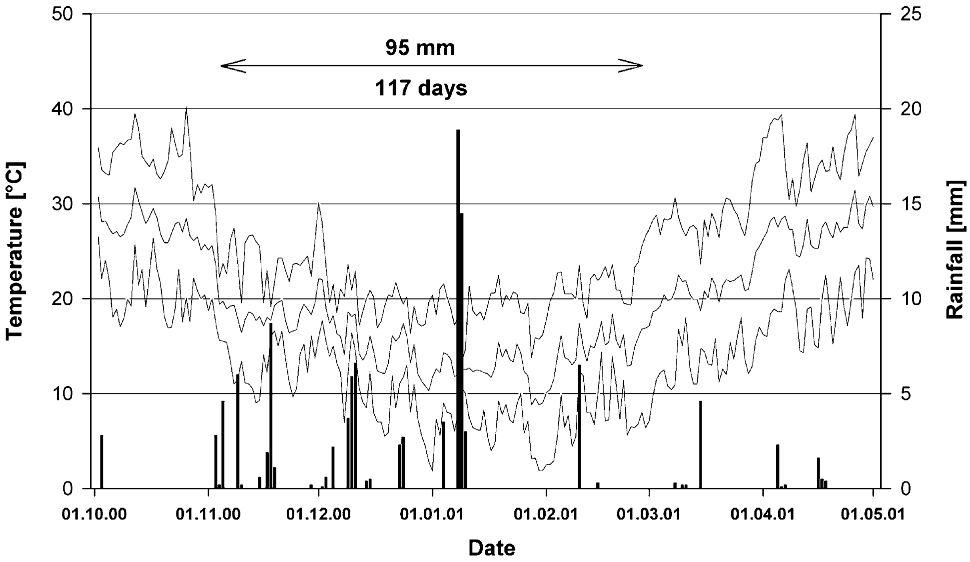

Fig. 2. Daily precipitation (vertical bars) and maximum and minimum temperatures (solid lines) for Kuwait International Airport (near Sulaibiya) from October 2000 to May 2001. The duration of the growth period is indicated by the horizontal arrow, which also gives the amount of rainfall during this period.

perennials), three 0.25 m^2 (0.5×0.5 m^2) quadrats were randomly selected within each block. In each quadrat, all species were identified and the number of individuals counted. To facilitate this process, the quadrat was divided up into 25 fields (subplots) of equal size (10×10 cm^2). In this study, abundances of species are given as subplot incidences (see Boeken and Shachak (1998)), i.e. the total number of subplots occupied by a species in each plot (multivariate analysis) or in all plots at each site (Appendix 1). This was done for two reasons. First, the number of individual plants would have been somewhat misleading, as some species (e.g. *Ifloga spicata*, *Loeflingia hispanica*, *Schismus barbatus*) are able to produce numerous but minute (<5 mm) individuals. Second, it allowed a comparison with data collected during the course of other studies in Kuwait in which the same procedure was adopted.

Multivariate procedures contained in the Cornell Ecology Package (Mohler, 1987) were used to compare species composition and abundance of the annual vegetation of the three sites. The data matrix was read into the program COMPOSE, whereby species recorded in fewer than three quadrats at all sites were excluded. Detrended correspondence analysis (DCA) was used for ordination of the data with the program DECORANA (Hill, 1979). Further statistical analysis of the data was carried out with the SPSS for Windows package. Significantly different means ($P < 0.05$) were identified by the Bonferroni procedure after the presence of significant effects ($P < 0.05$) had been confirmed by one-way ANOVA.

2.5. Biomass analysis of desert annuals

After vegetation analysis had been carried out in the three quadrats of each block, the aerial organs of the annual plants plus the few small perennials were harvested on a quadrat basis, transported back to the laboratory and dried in an oven for 5 days at 80 °C. Dry weight of aerial biomass was then determined. In total, 24 samples were analysed, eight for each site. One-way ANOVA was performed on the data to detect the presence of significantly different means and these were subsequently identified by the Bonferroni procedure ($P < 0.05$).

3. Results

3.1. Cover by perennial shrubs and graminoids

Fig. 3 indicates that there were no significant differences in cover of dwarf shrubs between Sulaibiya and Sabriya-IN, but shrub cover in Sabriya-OUT was substantially and significantly lower. *R. epapposum* was the predominant shrub at all three sites, with *F. aegyptia* being restricted to Sulaibiya, where it was very scarce. *H. salicornicum* was absent not only from Sulaibiya, but also from the two

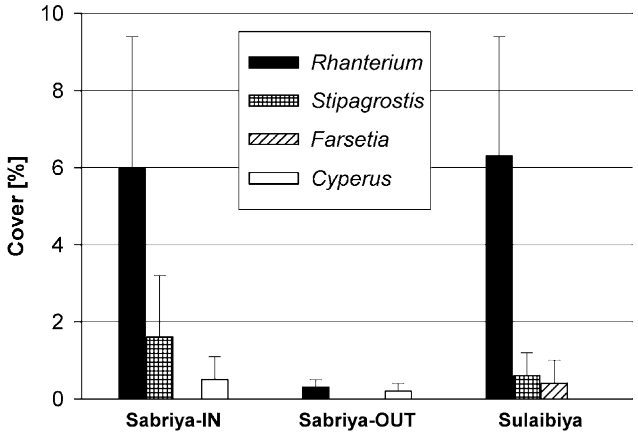

Fig. 3. Mean percentage cover of perennials (excluding seedlings) in blocks at the three study sites. *Rhanterium* = *Rhanterium epapposum*; *Stipagrostis* = *Stipagrostis plumosa*; *Farsetia* = *Farsetia aegyptia*; *Cyperus* = *Cyperus conglomeratus*. Error bars give SD.

Sabriya sites, despite the fact that it occurred sporadically on more consolidated ground in the immediate vicinity of the latter. *C. conglomeratus* was absent in blocks at Sulaibiya, although it did occur abundantly in grazed areas outside the enclosure. No significant differences were detected in *Cyperus* cover between Sabriya-IN and Sabriya-OUT blocks, and in both cases it was extremely low (<0.5%). The grass *S. plumosa* was virtually absent at the heavily grazed Sabriya-OUT site, but occurred regularly in Sabriya-IN as well as at Sulaibiya.

Regarding size structure of *Rhanterium* shrubs, there is a conspicuous similarity between that of Sabriya-IN and Sulaibiya (Fig. 4), with less than 50% of shrubs belonging to the smallest size class, whereas at Sabriya-OUT, 96% of shrubs belonged to this group. However, there was no significant ($P < 0.05$) difference in shrub density among the three sites, with values ranging from 3 to 13 shrubs per 20 m^2, and means of 7.0 ± 2.7 (SD) for Sulaibiya, 8.8 ± 1.9 for Sabriya-IN and 4.8 ± 3.4 for Sabriya-OUT.

3.2. Regeneration of perennial shrubs and graminoids

Numerous *R. epapposum* seedlings were registered in the blocks at Sulaibiya, but none in the other two sites (Table 1). Plants closely resembling seedlings in Sabriya-OUT (but not in Sabriya-IN) turned out to be fresh shoots that had emanated from underground woody stumps (see Fig. 5). These had been chewed back to such an extent that they were not visible above the surface. In total, 252 *R. epapposum* seedlings were recorded in the blocks at Sulaibiya, and 10 in the quadrats. Bearing in mind that these randomly selected quadrats accounted for only 3.75% of the entire area of the blocks, simple extrapolation would give a total of 267 seedlings over the area, a figure that

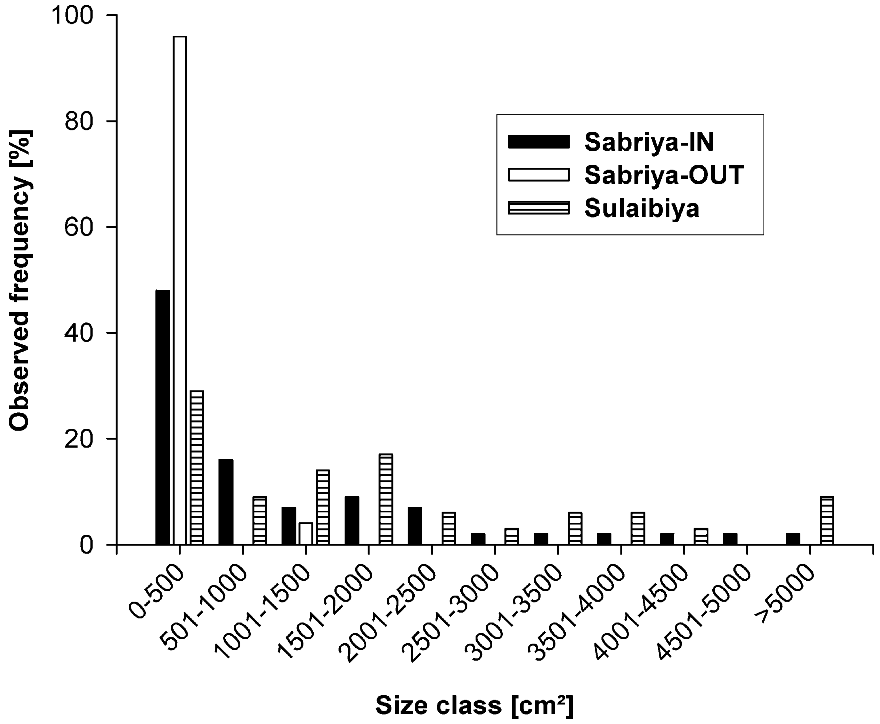

Fig. 4. Frequency diagram showing size structure of *Rhanterium epapposum* shrubs at the three study sites. Size classes are based on the area of individual shrubs.

corresponds very well to that actually counted in the blocks.

3.3. Desert annual vegetation

Mean cover by desert annuals was highest in Sabriya-IN (22.9%), but not significantly more so than at Sulaibiya (Table 2). Values were significantly lower at Sabriya-OUT than at the other two sites. Biomass values ranged from 164 kg/ha (Sabriya-OUT) to a maximum of 577 kg/ha at Sabriya-IN (Table 2).

In total, 41 species of desert annuals were found in the 0.25 m^2 plots, 32 at Sulaibiya, 26 at Sabriya-IN and 20 at Sabriya-OUT (Table 2, Appendix 1). Sabriya-OUT quadrats contained significantly fewer species per quadrat (5.5) than the two protected sites (Table 2).

Plant frequencies were high at both Sulaibiya and Sabriya-IN, but substantially lower at Sabriya-OUT. Based on subplot incidence, the most abundant species were *S. barbatus*, *I. spicata*, *Lotus halophilus*, *Picris babylonica*, *Plantago boissieri* and *Rostraria pumila*, as well as *S. plumosa* seedlings (Appendix 1).

However, there were certain differences among the sites. *S. barbatus*, *I. spicata*, *L. halophilus* and *P. babylonica* occurred at all three sites, but were most frequent at Sabriya-IN, with incidence values substantially higher than at the other two sites. Of the more common species, *Senecio glaucus* was restricted to Sulaibiya, and *P. boissieri* was conspicuously most frequent there. Whereas many species were more frequent at Sulaibiya than at Sabriya-OUT, there were some notable exceptions. For instance, *S. barbatus* was equally frequent at both sites, and *L. halophilus* and *Arnebia decumbens* were actually more frequent at Sabriya-OUT.

Regarding the overall characteristics of the desert annual flora, taking not only species composition but also species abundance into account, Fig. 6 shows that despite the much higher number of species and higher cover values in Sabriya-IN than Sabriya-OUT, floristic features (i.e. proportional frequency of species) were very similar, as indicated by the overlap of quadrat scores on the first two axes of the DECORANA ordination. Quadrats of the Sulaibiya sites, though, are clearly set apart from those of Sabriya-OUT and -IN, suggesting marked differences in species composition and relative abundance, as also indicated in Appendix 1.

Table 1
Number of *Rhanterium epapposum* seedlings per 20 m^2 block at Sulaibiya. Values in parentheses give the number from the three 0.25 m^2 quadrats per block

	Sulaibiya	Sabriya-IN	Sabriya-OUT
Block 1	62 (1, 1, 3)	0	0
Block 2	59 (2, 0, 1)	0	0
Block 3	66 (1, 1, 0)	0	0
Block 4	43 (0, 0, 0)	0	0
Block 5	22 (0, 0, 0)	0	0

Fig. 5. Photograph showing a fresh shoot of *Rhanterium epapposum* appearing above the surface from an old underground stump (partly visible immediately in front of the shoot) in Sabriya-OUT.

4. Discussion

Deserts are generally regarded as fragile ecosystems that are highly susceptible to anthropogenic disruption (Evenari et al., 1982). Overgrazing has been cited as the primary cause of desertification in Kuwait (Khalaf, 1989), and this has led to a complete destruction of the dwarf shrub vegetation in many areas (Brown, 2003). Several vegetation studies in northern Arabia have also briefly mentioned the potential for vegetation recovery in degraded areas (Thalen, 1979; Omar, 1991; Zaman, 1997), and the results have been somewhat contradictory. However, these studies have largely ignored the nature of the substrate, which has important consequences for the regeneration process. Both Knapp (1991) and Webb and Wilshire (1980) have found the degree of soil compaction to be a major determinant of the rate of plant recovery in semi-arid landscapes in the USA dominated by *Larrea tridentata*, with compacted soils showing the slowest recovery rates.

In the present study, vegetation recovery has been impressive in depressions protected from grazing where the loose, sandy substrate has not been lost to deflation to any great degree (Fig. 7). This is in marked contrast to the situation on adjacent sealed crusts, where no distinct

Table 2
Important characteristics of the annual flora at the three study sites. Means with SE are given where appropriate. Significantly different means ($P < 0.05$) were identified by the Bonferroni procedure after the presence of significant effects ($P < 0.05$) had been confirmed by one-way ANOVA and are indicated by different letters in parentheses

	Sulaibiya	Sabriya-IN	Sabriya-OUT
Cover of annuals (%)	16.7 ± 1.78 (a)	22.9 ± 2.50 (a)	6.1 ± 1.33 (b)
Estimated biomass (kg/ha)	421 ± 45 (a)	577 ± 63 (a)	164 ± 34 (b)
Mean species no. per quadrat	12.4 ± 0.65 (a)	10.9 ± 0.81 (a)	5.5 ± 0.52 (b)
Total number of annuals	32	26	20

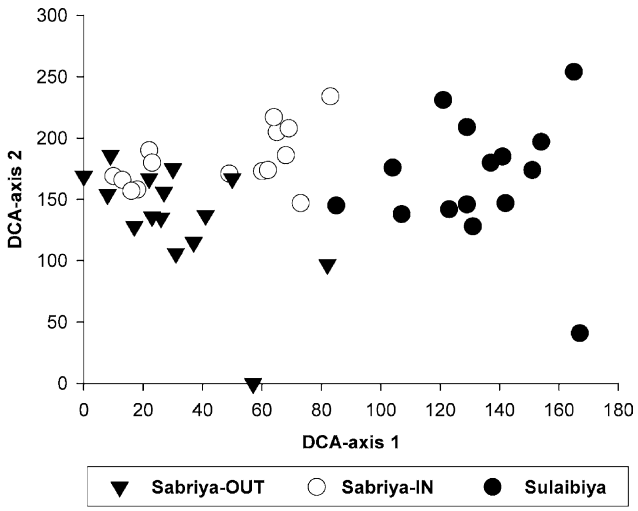

Fig. 6. Quadrat scores of annual vegetation on the first two axes of DECANORA ordination.

Fig. 7. Typical view of a sandy depression inside the protected enclosure (Sabriya-IN) after 4 years of protection, with *Rhanterium epapposum* as the predominant dwarf shrub and lush growth of the annual *Picris babylonica*. Compare with Fig. 1.

recovery was observed (unpublished results). This rapid recovery can be attributed to several important factors, apart from the direct effects of soil compaction and deflation. First, in arid and semi-arid regions, coarse, sandy substrates are usually favourable for plant growth due to the fact that water percolates through the surface layers quite rapidly. These dry out quickly, but the moisture is held in subsurface layers where it is protected from evaporation, thus remaining available to plants for long periods of time. This has been referred to as the 'inverse-texture hypothesis' (Noy-Meir, 1973). However, it should be added that such sandy substrates are only favourable for plant growth when they are reasonably stable, unlike mobile barchan dunes, for instance.

Second, rainfall characteristics are central to processes in desert ecosystems (Noy-Meir, 1973), and since the enclosure was established at Sabriya, rainfall in Kuwait has been quite high, especially in 1998 (240 mm), when it was about twice the annual mean (Brown and Schoknecht, 2001). Le Houérou (1986) reports that vegetation recovery was generally positive (although rather slow) on sandy substrates and in depressions in an enclosure at Nefta (Tunisia) whenever there was a series of rainy years. In fact the photos provided by this author (his p. 129) reveal that vegetation structure both inside and outside the enclosure (after 70 years of protection) was very similar to that of the present study.

Third, in deep sandy substrates, seeds can accumulate and be retained. It is generally accepted that many desert plants build up substantial inter-annual seedbanks with which they buffer the negative effects of adverse years for plant growth and reproduction (Gutterman, 1993; Pake and Venable, 1996). With seedbank analyses carried out on soil samples collected from an area immediately adjacent to the current study site at Sabriya, Brown and Schoknecht (2001) found that the number of seedlings emerging from crusted soils was significantly lower than in samples from favourable microsites with a looser, coarser substrate. Brown and Schoknecht attributed this to the fact that many species produce minute, dust-like seeds that are blown off crusted surfaces, but become lodged between the coarser grains of sandier substrates.

Fourth, and perhaps most importantly in the context of the present study, there is the enormous vegetative regeneration potential of *Rhanterium* shrubs that have survived for long periods as subterranean woody stumps. Initially, it came as a surprise to observe that *Rhanterium* was the main perennial species to recover in the depressions, as according to vegetation maps (Halwagy et al., 1982), the area is largely dominated by *H. salicornicum*. This latter species was completely lacking from the study sites, although it still occurs in adjacent areas. Its absence was something of a mystery, as it produces numerous mobile diaspores that germinate readily (Brown and Al-Mazrooei, 2001), in contrast to the rather specialised requirements exhibited by *Rhanterium* (see Thalen (1979) and Brown (2001)). Own detailed observations indicate that *Rhanterium* germinates almost exclusively in years with large individual rainfall events (in excess of about 30 mm). However, despite the occurrence of heavy rainfall in 1998, the facts that no significant difference in shrub density was detected between Sabriya-IN and Sulaibiya, that the size structure of Sabriya-IN shrubs was very similar to that of Sulaibiya ones, and that shrub density was only marginally lower in the heavily grazed Sabriya-OUT site strongly suggest that shrub recovery in Sabriya-IN has taken place from stumps that have been buried in the sand, rather than from seed. Clearly, stumps in some heavily grazed, sandy areas still manage to produce a sufficient quantity of fresh shoots each year to prevent the shrub from dying away completely. As serious overgrazing has been a major problem for at least the past two to three decades, these stumps at Sabriya may have survived for that amount of time in the soil. Although 2001 was a very favourable year for *Rhanterium* germination, as indicated by the large number of seedlings at Sulaibiya, the fact that no seedlings were registered at Sabriya could have been due either to the lack of rainfall, which on the basis of annual vegetation cover seems unlikely, or to the absence of diaspores from the soil. This is a more plausible explanation, as it is only in the past 2 years that the shrubs inside the newly formed enclosure could have recovered sufficiently in order to flower. Flowering was profuse in Sabriya-IN in 2001, with some flowering in 2000, but no flowering shrubs were observed during the previous 5 years in this part of northern Kuwait due to heavy grazing (own observations). Own preliminary studies suggest that *Rhanterium* is able to build up a long-term seedbank (heads that have been stored for up to 4 years at room temperature still germinate well), but whether heads could have survived predation in the soil for decades and then be located in the upright position necessary for germination seems highly doubtful. In addition, the rather large size of many Sabriya-IN plants shows that they have not been recently recruited from seed.

The effects of grazing on cover of the annual vegetation is quite striking, as shown by the comparison between Sabriya-OUT and Sabriya-IN. After 4 years of protection, mean cover values for annuals were at least as high in Sabriya-IN as at Sulaibiya. Intensive grazing can be expected to lead to a substantial decrease in seed production, although this decrease is difficult to quantify precisely. The differences in annual species composition and relative abundance between Sabriya-IN and Sulaibiya as revealed by DCA could simply be due to geographical factors (the two sites are located about 65 km apart), and therefore possibly to site factors. An alternative explanation might be that there has been a loss in the seedbank of certain species at Sabriya-IN, or at least it has become seriously depleted, particularly regarding more sensitive species. Only longer-term monitoring studies would be able to provide reliable indications as to the answer.

The results of this study appear at first sight to contradict the findings of de Soyza et al. (2000) that, at an advanced stage of deterioration, merely removing the anthropogenic stressors is usually insufficient to halt or even slow the continuing processes of degradation. However, it is important to define what is actually meant by vegetation recovery. In this study, recovery refers to a notable increase in shrub cover, as well as an increase in annual species number and cover. But the central question is what actually constitutes the climax vegetation in this part of Kuwait. Due to the relatively high mean annual rainfall, it is possible that the vegetation was once dominated by a savanna-like open *Acacia* woodland in which perennial grasses (e.g. *Stipagrostis* spp.) formed a thin but ± continuous ground-layer, and in which dwarf shrubs were very localised. A similar type of vegetation has been described in detail by Le Houérou (1986) for northern Africa, more or less on the same latitude as Kuwait, but with a slightly lower mean annual rainfall. Evidence for the presence of such arid woodlands in Kuwait is forthcoming from the fact that trees can survive in the Kuwait desert without irrigation once they have reached a certain size, as demonstrated by a lone extant specimen of the native tree *Acacia gerardii*, as well as numerous individuals of the introduced *Prosopis juliflora*. It can also be assumed that natural regeneration of the *Acacia* vegetation in protected areas can be ruled out for a number of reasons: (1) the nutrient-rich surface layer, formed and held together by the dense roots of the perennial grasses, has been destroyed, and (2) the soil seedbank has been lost. Furthermore, even if seeds of the tree species were present, they would need one to several seasons of extremely favourable climatic conditions in order to germinate and for the seedlings to become established, an event that is likely to be very rare.

It therefore seems likely that the predominance of dwarf shrub communities is a response to long-term moderate grazing, as shown by Le Houérou (1986) for north Africa, and that this stage may be quite resilient. This author also reported that when chamaephytic steppes dominated by dwarf shrubs such as *Rhanterium suaveolens* (very similar to *R. epapposum* in Kuwait) are protected long enough, a graminaceous steppe characterised by palatable perennial grasses tends to develop. Some of the main grass species listed by this author also occur in Kuwait, including *S. plumosa* (locally common), *S. ciliata*, *S. obtusa* and *Cenchrus ciliaris*, but after over 20 years of protection, this successional pathway is not immediately obvious at Sulaibiya, where *Rhanterium* still predominates.

This study has given an insight into the speed of recovery of the dwarf shrub vegetation under reasonable climatic conditions in north-eastern Arabia, and the results agree well with those presented by Le Houérou (2000) for arid and semi-arid Mediterranean ecosystems. Depressions with sandy substrate varying considerably in size occur sporadically through most of northern Kuwait, and are probably an important prerequisite for dwarf shrub regeneration. These 'islands' represent nuclei for larger-scale vegetation regeneration in an otherwise hostile matrix, and are therefore important sites in the fight against desertification when protected from overgrazing. In this context, Le Houérou (2002) emphasises that enclosures can be a cheap and efficient tool for restoring arid lands. Finally, although the vegetation of transitional areas between semi-arid and arid ecosystems deteriorates rapidly as a result of detrimental human practices, as underlined by Schlesinger et al. (1990), this study shows that it can also possess considerable powers of regeneration.

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Appendix A

Appendix A1
List of species occurring at the three sites with subplot incidence as a measure of species abundance. 'sldg' = seedling

		Subplot incidence		
		Sulaibiya	Sabriya-IN	Sabriya-OUT
1	*Anisosciadium lanatum*	0	3	1
2	*Anthemis deserti*	0	1	0
3	*Arnebia decumbens*	3	25	14
4	*Asphodelus viscidulus*	12	0	0
5	*Astragalus annularis*	0	7	4
6	*Astragalus hauarensis*	1	2	1
7	*Astragalus schimperi*	32	4	1
8	*Atractylis carduus*	2	0	1
9	*Brassica tournefortii*	3	0	0
10	*Cakile arabica*	1	0	0
11	*Cornulaca monacantha*	1	0	0
12	*Cutandia memphitica*	9	9	4
13	*Cyperus conglomeratus* (sdlg)	0	0	2
14	*Dipcadi erythraeum*	1	0	0
15	*Gypsophila capillaris*	0	4	1
16	*Herniaria hirsuta*	0	1	0
17	*Hippocrepis areolata*	26	5	0
18	*Ifloga spicata*	101	201	32
19	*Koelpinia linearis*	8	7	0
20	*Launaea capitata*	2	2	0
21	*Launaea mucronata*	11	12	0
22	*Loeflingia hispanica*	23	22	4

Appendix A1 (*continued*)

		Subplot incidence		
		Sulaibiya	Sabriya-IN	Sabriya-OUT
23	*Lotus halophilus*	27	146	51
24	*Moltkiopsis ciliata*	0	0	1
25	*Neurada procumbens*	9	1	0
26	*Ogastemma pusillum*	2	0	0
27	*Ononis serrata*	3	5	5
28	*Picris babylonica*	32	146	15
29	*Plantago boissieri*	113	39	3
30	*Plantago ciliata*	0	10	0
31	*Polycarpea repens*	1	0	0
32	*Reseda arabica*	3	0	0
33	*Rhanterium epapposum* (sdlg)	10	0	0
34	*Rostraria pumila*	26	51	17
35	*Savignya parviflora*	4	0	0
36	*Schismus arabicus*	0	0	2
37	*Schismus barbatus*	163	252	162
38	*Schimpera arabica*	10	2	0
39	*Senecio glaucus*	45	0	0
40	*Silene arabica*	27	4	0
41	*Stipagrostis plumosa*	2	5	0
	Stipagrostis plumosa (sdlg)	18	33	1
	Species number	32	26	20

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