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# VEGETATION DYNAMICS IN AN EXTREME DESERT WADI UNDER THE INFLUENCE OF EPISODIC RAINFALL

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**Abstract**. In an extreme desert stream channel (Wadi Aggag near Aswan, Egypt, precipitation 1 mm per year), vegetation structure and soil water content were investigated over a period of 13 years (one downstream site) or parts of this period (two upstream sites). Three large precipitation events were observed in that time (1987, 1990, 1996). After each storm, densities of 10–15 individual plants per $m^2$ were produced within a few weeks. This number decreased to almost zero during the following years before the next rain destroyed the surviving individuals. The stands of vegetation that developed subsequently after the floods contained mostly *Zilla spinosa, Morettia philaeana, Fagonia indica* or *Salsola imbricata* as frequent species. All stands showed a similar shift from short-lived to longer-lived species. Spatial differences were found between the wadi beds, terraces and slopes. Very rarely, single specimens of perennial woody species (*Acacia ehrenbergiana*, *Tamarix nilotica*) were found in only some parts of the wadi beds. The remaining parts of the wadi beds, terraces and adjacent lower slopes developed only accidental vegetation; the upper slopes remained barren.

**Key words**: *Zilla spinosa, Salsola imbricata, Acacia ehrenbergiana,* Aswan region (Egypt), desert floods, soil water content, vegetation periods

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## INTRODUCTION

In arid lands, water is the predominant ecological factor for vegetation growth. Rainfall in deserts occurs with high intensity but in low amounts. Rainfall is sporadic, coming in irregular intervals and with very large inter-annual variability (Thornes 1994). Under extreme arid conditions, the number of rainless years is higher than the number of rainy years. Here the mode of rainwater distribution is more important than the amount of water (Shmida *et al.* 1986). Lower ground may receive amounts of water (runoff) several times the amount of the actual rainfall there. In channels, sudden and intense precipitation results in flash floods with often catastrophic consequences (Shmida *et al.* 1986); this has been investigated many times (Fisher & Minckley 1978; Thornes 1994; Reid & Frostick 1997; Schick 1997; Jacobson *et al.* 2000).

Plant growth in extreme deserts is triggered by rain, and thus is as scarce and unpredictable as the precipitation itself. Vegetation develops in 'contracted mode' (Monod 1954) only in habitats receiving runoff water, such as depressions and channels (contracted desert, Shmida 1985). This highly dynamic vegetation is neither permanent nor seasonal, but is accidental *sensu* Kassas (1952, 1966), Bornkamm (1987, 2001) and Bullard (1997). This is because the storms do not follow an annual pattern. Extreme desert vegetation has been described worldwide (Evenari *et al.* 1985, 1986), but the data on vegetation dynamics after a flash flood in an extreme desert channel remain limited.

To fill this gap, we carried out a study in the southern part of the Eastern Desert of Egypt (Aswan region). Here the mean annual precipitation is close to zero, with great temporal gaps between the rare rain events. Nevertheless, the presence of deep wadis with highly variable surface conditions allows a particular type of vegetation to form (Springuel *et al.* 1986, 1991; Springuel & Sheded 1991). The aim of the investigation was to describe the spatial and temporal performance of the vegetation in three different stream sections. This was done over a time span of 13 years. The first reports on the early part of the study were given by Springuel *et al.* (1990) and Springuel (1997).

## AREA OF INVESTIGATION

Wadi Aggag, 30 km long and comprising a catchment area of *ca* 300 km$^2$, drains into the Nile in Nubia (Fig. 1). It rises in granite hills (*ca* 350 m a.s.l.), cuts through igneous and metamorphic rock, carves its main channel through the lower Nubia sandstone series (Timsah Formation and Abu Aggag Formation, Klitzsch *et al.* 1987), and reaches the Nile Valley 5 km north of Aswan at 100 m a.s.l. (Springuel *et al.* 1990). Pleistocene gravel and alluvial deposits, and in places also aeolian deposits (mostly sand), cover the wadi. Its gradient decreases from *ca* 4 m/km in the middle section to 1 m/km farther downstream.

The climatic conditions of Aswan are among the most arid in the world. The mean annual temperature is 25.9ºC, and mean annual precipitation (PRE) amounts to 1.2 mm (Vose *et al.* 1992). From the values of mean annual precipitation and potential evapotranspiration (ETP = 2066 mm/yr) presented from Ayyad and Ghabbour (1986) for Aswan, the Aridity Index (AI = PRE/ETP) is considerably lower than the threshold AI = 0.03 for classifying a climate as hyperarid (Ayyad & Ghabbour 1986). Precipitation events are very rare, but can happen without any clear seasonality. In the last 50 years, traces of rain have been observed at least once a month, with the exception of June and July (Vose *et al.* 1992; Springuel *et al.* 1991;

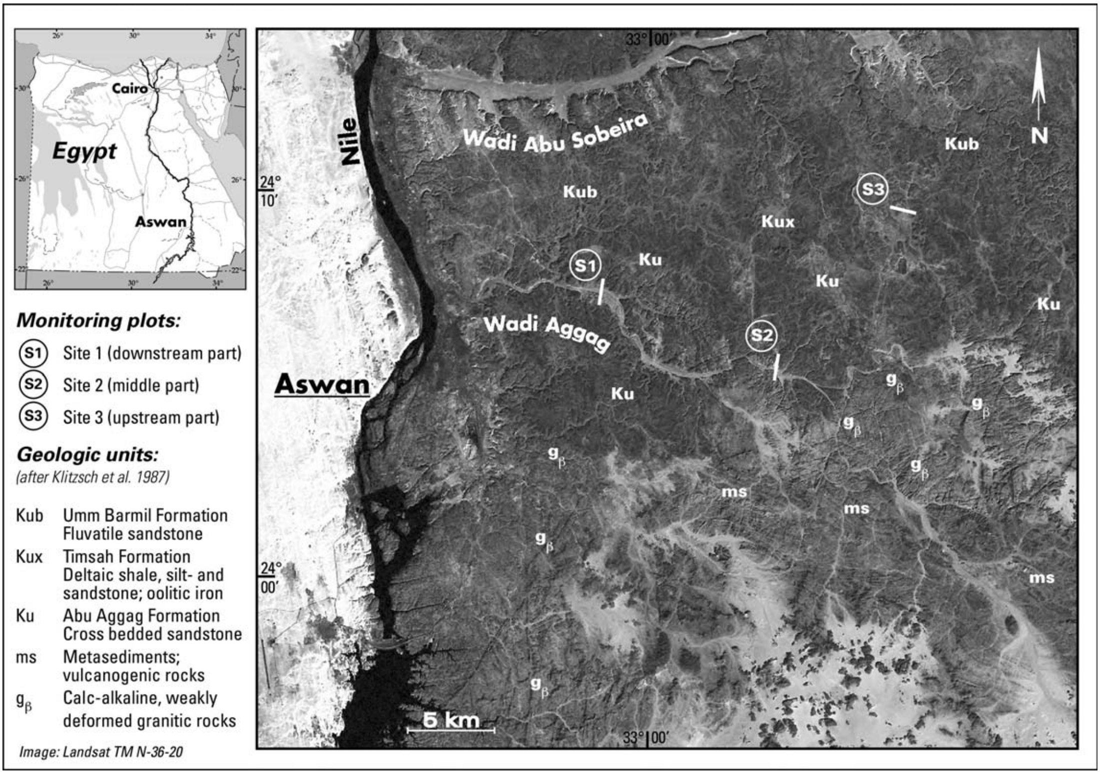

**Fig. 1**. Map of the Aswan region showing Wadi Aggag, transect locations and other features mentioned in the text.

**Table 1**. Reported rainfall during the observation period. Numbers – rain (mm), . – no rain, t – trace at Aswan (NOAA 2001); * – rain at Wadi Aggag (own observations).

| Year | J | F | M | A | M | J | J | A | S | O | N | D | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1987 | . | . | . | . | . | . | . | . | . | 0* | . | . | 0 |
| 1988 | . | . | . | . | 0* | . | . | 0* | . | . | . | . | 0 |
| 1989 | . | . | . | . | . | . | . | . | . | . | . | . | 0 |
| 1990 | . | . | . | . | . | . | . | . | . | . | . | 0* | 0 |
| 1991 | . | . | . | . | . | . | . | . | . | . | . | . | 0 |
| 1992 | . | . | . | . | . | . | . | . | . | 0* | . | . | 0 |
| 1993 | . | . | . | . | t* | . | . | . | . | . | t | . | 1 |
| 1994 | t | . | . | . | . | . | . | . | . | 7* | . | . | 8 |
| 1995 | . | t | . | . | . | . | . | . | . | . | . | . | 0 |
| 1996 | . | . | 1 | . | . | . | . | . | . | . | t* | . | 1 |
| 1997 | . | . | 1 | . | . | . | . | . | . | 1* | . | . | 2 |
| 1998 | . | . | . | . | 2 | . | . | . | . | . | . | . | 2 |
| 1999 | . | . | . | . | . | . | . | . | . | . | . | . | 0 |
| 2000 | . | t | . | . | . | . | . | . | . | . | . | . | 0 |

Table 1). This means that Aswan is located exactly in the transition zone between winter and summer rain.

The possibility of violent floods is a typical feature of the Eastern Desert of Egypt. Cloudbursts in the Red Sea mountains may cause flash floods at its western slopes every four to five years on average (Labib 1981). Our observations on plant growth in that area started after a storm on October 16, 1987. Earlier there was an exceptional torrential flood in 1980. The frequency of rain during the present study period (1987–2000) is given in Table 1. At the Aswan meteorological station, 11 precipitation events were recorded (annual average 1 mm). In Wadi Aggag no measurements were made, but we observed 9 events, some of them very weak and strictly local. Rain occurred simultaneously in two places (25 km apart) only 4 times. This is not surprising because the diameter of storm cells in deserts usually does not exceed 10–14 km (Reid & Frostick 1997: 207). The storms of October 1987 and November 1996 were the strongest and were followed by a torrential flood in Wadi Aggag. The latter, originating from an interseasonal convective rain in the Red Sea area (Geb 2000), caused a flood 2 m high, as indicated by litter in the branches of an *Acacia tortilis* ssp. *raddiana* tree in the downstream section. Another storm took place in Aggag on the last day of 1990. During all those strong storms the flooded Wadi Aggag reached the Nile River.

## METHODS

Three sites within the Wadi Aggag were chosen to represent most of the physiographic variations in the study area (Fig. 1). At site 1 (S1) in the downstream part (10 km E of the Nile; 24°7.2′N/32°58.5′E) the wadi is 300 m wide and is bounded by slopes 50 m high. At Site 2 (S2) in the middle reaches (20 km E of the Nile; 24°05.1′N/33°3.5′E) the wadi is 200 m wide, and otherwise is geomorphologically similar to S1.

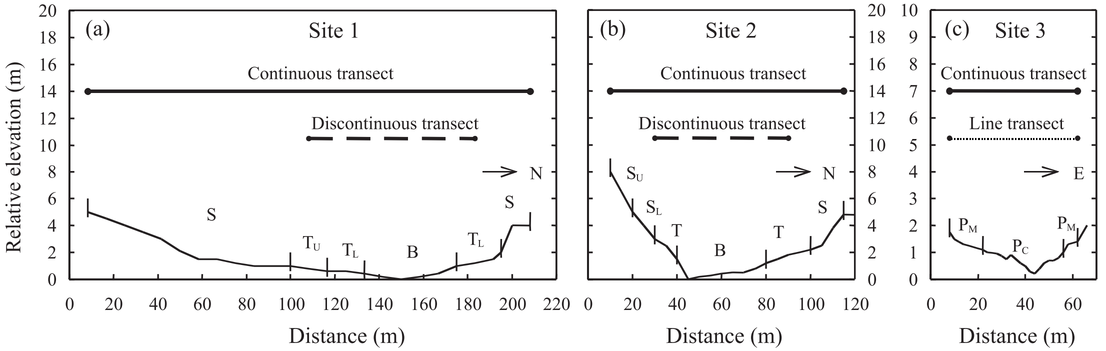

**Fig. 2**. Cross sections, transect positions, and selected habitats of (a) S1, downstream part, (b) S2, middle part, and (c) S3, upstream part of Wadi Aggag; S – slope, T – terrace, B – bed with runnels, P – playa; subscripts: U – upper, L – lower, M – margin, and C – center.

Site 3 (S3) is situated upstream (30 km E of the Nile; 24°9.2′N/33°7.0′E) on the plateau of the Timsah Formation (Klitzsch *et al.* 1987). It is a playa (*sensu* Briere 2000) with southerly outflow.

Immediately after the rain in October 1987, 20 permanent quadrats (1 $m^2$ each) were established at S1 and S2 arranged in a discontinuous transect 60 m long which covered the wadi bed and the two terraces on both sides of the bed (Fig. 2a, b). At the beginning of the growth period, the vegetation at S1 comprised only a few desiccated specimens of *Salsola imbricata* and *Aerva javanica*, and one small living shrub of *Acacia ehrenbergiana* (not in any of the quadrats), whereas S2 showed only one dry shrub of *Salsola imbricata.* Outside the transects the area was barren. At the beginning of the experiment the number of species and distribution of individuals were recorded weekly, then at about monthly intervals over a 3-year period until December 1990, when a torrential rain flooded S2. From that time on, only the species composition and number of individuals were monitored at S1 until October 2000. At S3 (Fig. 2c) a transect covering the margins and center of the playa was used for vegetation analysis from November 1987 until May 1989, when all plants had died.

After a very heavy storm in November 1996, continuous transects were established at all three sites. These provided for a more comprehensive inventory of the wadi vegetation and allowed detection of their spatial change within the wadi channel. At S1 the continuous transect was set out in parallel to the already existing discontinuous transect. We expanded it to 25 plots (size 3.1 × 8 m = 25 $m^2$ each). It covered a wider range and extended from the north-facing slope of the wadi northward over terraces and the wadi bed to south-facing rocky outcrops (Fig. 2a; see also Fig. 3 in Bornkamm 2001). A similar transect was set up at S2 next to the place where the old discontinuous transect had been (23 plots of 5 × 5 m). This transect covered part of the rocky north-facing upper slope, the lower slope with sand cover, ending in a narrow terrace, the gravelly wadi bed and a broad sandy terrace at a road embankment (Fig. 2b). The continuous transects were sampled in 1997, 1998 and 2000 (at S3 only in 1997 and 1998) for cover and abundance of each species. Only plants with at least some green parts were included. However, in 1997 both dead and living plants were recorded. Here the number of dead plants was used as an approximation to the vegetation developed after the devastating floods at the end of 1996, when no measurements were made.

In S1, the half-life values and mean lifetime of the populations of the most frequent species were calculated from the exponential depletion curves. Since the individuals in the subplots were counted but not marked, the age of the single plants generally could not be calculated, but the last survivors in a subplot could be spotted.

Soil samples for texture analyses were initially taken once from pits reaching down to weathered bedrock or boulders (depth: S1, 60 cm; S2, 50 cm; S3, 30 cm) at 10 cm intervals. Subsequent samples were taken together with the floristic sampling (44 dates at S1, 15 dates at S2 and S3) in the wadi-fill deposits in both the active channel and the left terrace at three different depths (0–10, 10–20 and 40–50 cm at S1, S2; 0–15 and 15–30 cm at S3). The samples were stored in plastic bags, and water content was determined by oven drying and calculated as % d.w.

Ordination was carried out to find the low-dimensional representation of the temporal change in population structure using non-metric multidimensional scaling (NMDS) (Legendre & Legendre 1998). The algorithm for calculating the stress values as well as the default procedure and parameter settings followed McCune & Mefford (1999). The lowest final stress value in the presented ordination was 7.442 for the 3-dimensional solution with a stability criterion of $<10^{-5}$. All abundance values were log-transformed. The similarity matrix was based on calculation of the Steinhaus coefficient (i.e., Bray-Curtis distance; Legendre & Legendre 1998).

Nomenclature follows Boulos (1995).

## RESULTS

### SOIL MOISTURE

At the downstream site (S1) the observed rainfalls in the Aggag area and the soil water content in the wadi bed are shown in Figure 3 (a, b) for two depths. The occurrences of rain in October 1987 and spring 1988 resulted in a double peak of water content. Taking into account the time span between rainfall and first sample (1987, 14 days; 1990, 3 days; 1996, 30 days), these events and the precipitation in December 1990 and November 1996 (Table 1 and Fig. 3a) had the strongest impact on soil water content and vegetation growth. Two four-year periods (1991–1994, 1997–2000) were almost rainless. In spite of this, enhanced water content was observed at the end of 1994. In most cases the water content in the deeper subsoil was higher than in the upper layer. This

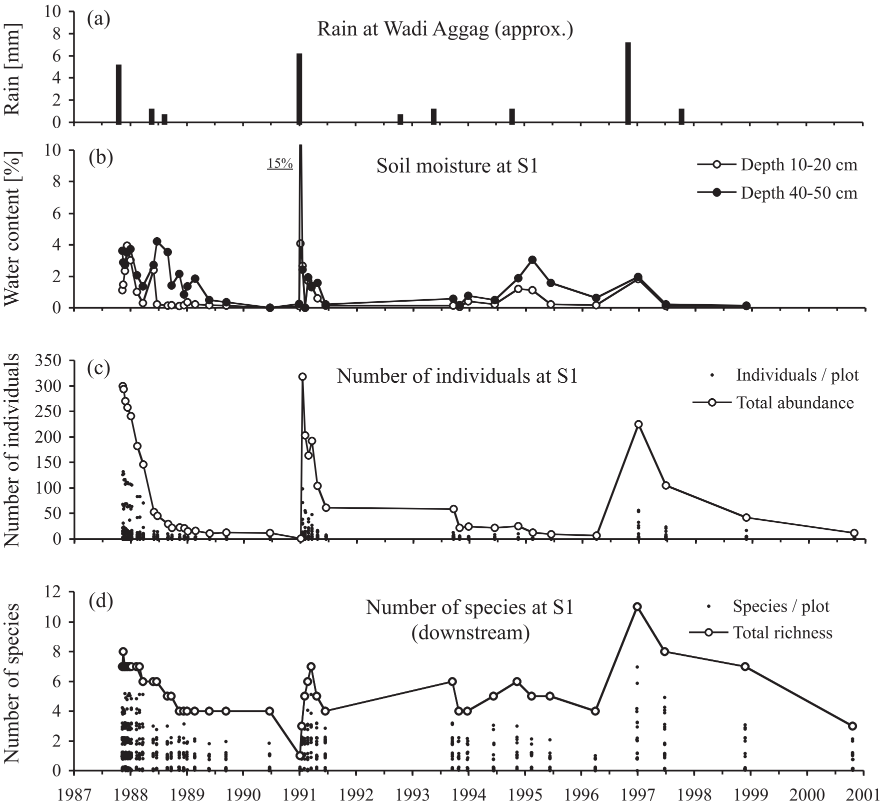

**Fig. 3**. Variations in (a) precipitation input, (b) soil moisture (%) at 10–20 cm and 40–50 cm depths, (c) number of plant individuals, and (d) number of species during the observation period (1987–2000) at Wadi Aggag, downstream site S1.

allowed some water storage throughout the first year after the rain. The water content of the topsoil (0–10 cm) was always <0.5% (data not shown). In the second layer (10–20 cm) it rarely exceeded 2%; in the lower layer (40–50 cm), soil moisture of 4% remained after more than half a year.

The discharge pattern within the drainage system of Wadi Aggag is illustrated by comparing the soil water content of the three transects during the desiccation process after the 1987 storm (Fig. 4). Two weeks after the flood, the highest moisture values were found at the upstream playa (S3, Fig. 4c), where open water was visible for several weeks after the rain, followed by the wadi bed of the middle reaches (S2). One month later the downstream wadi bed (S1) had higher water content than the more upstream transects. The picture changed again after the short shower in May 1988, when the upstream playa was filled for a further month. After a year the downstream sediments still had more than 2% soil moisture in the deepest layer. At that time, S2 and S3 were already dry.

The available water in the soil profiles did not differ between the wadi bed and terrace at S1, where it decreased from 15 to 3 l/m$^2$ in one year (Fig. 4a). This was in contrast to S2, where the water content in the wadi bed reached >30 l/m$^2$. At the terrace, however, the stored amount did not exceed 8 l/m$^2$ and was exhausted within 2 months (Fig. 4b).

## VEGETATION AT SITE 1

Within four weeks after the first rainfall in 1987, the number of plant individuals in the discontin-

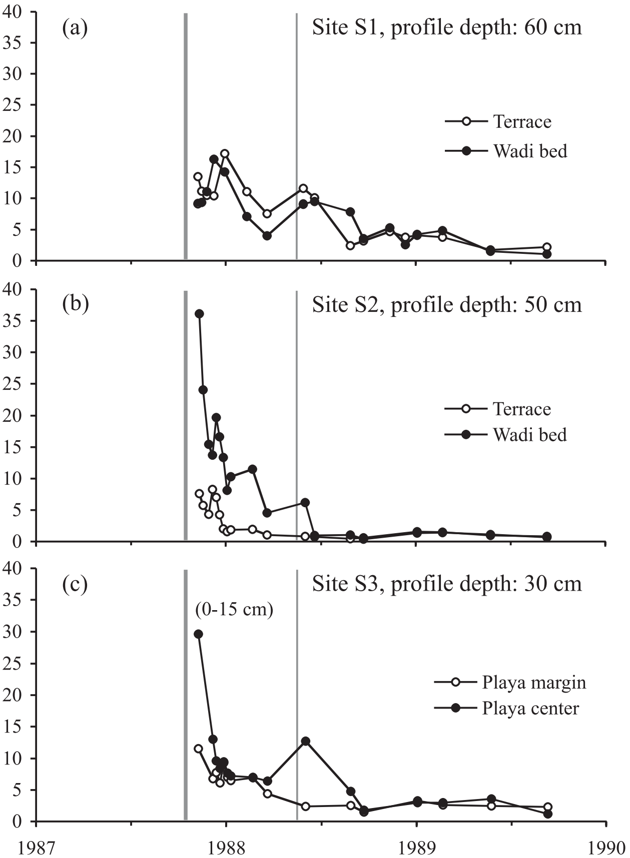

**Fig. 4**. Variations in the soil water content of two contrasting habitats during the first observation period (Nov. 1987 – Sept. 1989) for transect (a) S1, (b) S2, and (c) S3. Absolute water content (l/m$^2$) was calculated for the profiles down to weathered bedrock or boulders. Vertical lines indicate rainfall events.

uous transect at S1 reached a maximum of 300 (Fig. 3c). Within one year it dropped to about 20 individuals. The density of individuals did not differ between the wadi bed and lower wadi terrace, reaching a maximum mean 15 individuals per m$^2$ in each location. In the following years the other two main precipitation events resulted in almost the same amount of individuals per transect. The most frequent species (Fig. 5) was *Zilla spinosa* with up to 90% representation in the first vegetation period, *ca* 70% in the second and 55% in the third. *Morettia philaeana* contributed up to 18% of the individuals in the first period, up to 50% in the second and *ca* 30% in the third.

Six months before the end of the first period, 9 specimens of *Z. spinosa* and just one specimen each of *Fagonia indica, Crotalaria aegyptiaca* and *Senna italica* were still alive. These species (all perennials) survived 32 months (Table 2) and were killed by the flood. However, *M. philaeana* and *Fagonia bruguieri* were present for 8 months, and *Euphorbia granulata* for only 4 months. These species were probably killed by desiccation.

The new plant growth after the flood started with one specimen of *F. indica* (3 Jan. 1991) and subsequently other species elsewhere. In 1993 and 1994 there were small peaks of species diversity but not of number of individuals (Fig. 3d). At the last sampling date of the second period (2 Apr. 1996) 7 individuals – 4 *Z. spinosa*, 1 each of *F. indica*, *C. aegyptiaca* and *M. philaeana* – were recorded (6 of them in the wadi bed). The first two of these

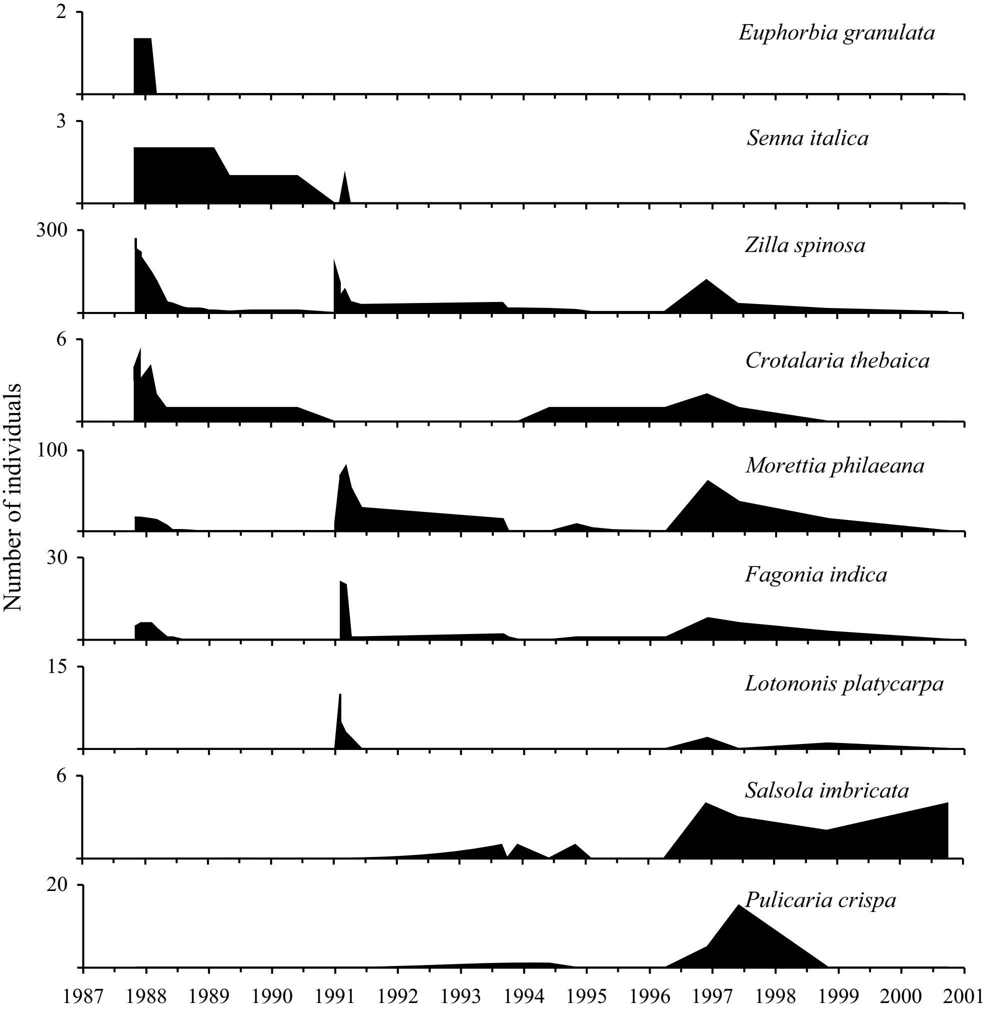

**Fig. 5**. Variation in abundance of nine species in the discontinuous transect at S1 during 13 years of observation.

species persisted for 41 months, and *C. aegyptiaca* (invaded in 1994) for only 17 months. They were probably killed by the flood.

In the third vegetation period (1996–2000) the sampling intervals were too large to track the vegetation dynamics in detail, but it can be stated that at the end (October 2000) 12 individuals – 4 *Z. spinosa*, 4 *F. indica*, 4 of other plants – (6 in the wadi bed, 6 on the terrace) survived. In the last two periods, other species including *Pulicaria crispa*, *Pulicaria incisa* and *Salsola imbricata* appeared. Consequently the number of species increased in the years before the final desiccation (Fig. 3d).

In Table 2 the half-life values of the most important species are presented. It becomes evident that the breakdown of the populations is faster with *M. philaeana*, *F. bruguieri* and *Z. spinosa* than with *F. indica* and *C. aegyptiaca*.

Altogether, 10 species were recorded in the continuous transect. With a maximum of 16 individuals in the wadi bed, the average number per m$^2$ was always less than one (Table 3). The plant density estimated for 1996 did not differ

**Table 2**. Age of the oldest individuals and half-life values of populations (in months) during the vegetation periods I (1987–1990), II (1991–1996) and III (1996–2000) at Site 1; x – presence without estimation of age.

| Species | Max. age (half-life), months | | | |
|---|---|---|---|---|
| | Period I | | Period II | Period III |
| *Crotalaria aegyptiaca* | 32 | (14) | x | x |
| *Fagonia indica* | 32 | (11) | 41 (26) | x |
| *Zilla spinosa* | 32 | (5) | 41 (14) | x |
| *Senna italica* | 32 | ( - ) | x | x |
| *Fagonia bruguieri* | 8 | (2.5) | x | x |
| *Morettia philaeana* | 8 | (2) | x | x |
| *Euphorbia granulata* | 4 | ( - ) | | |
| *Zygophyllum simplex* | x | | x | x |
| *Cistanche phelypaea* | x | | | |
| *Salsola imbricata* | | | x | x |
| *Polycarpaea robbairea* | | | x | x |
| *Pulicaria crispa* | | | x | x |
| *Astragaluis vogelii* | | | x | |
| *Lotononis platycarpa* | | | x | x |
| *Pulicaria incisa* | | | | x |

much between transect sections. In 1997 and 1998, population density was highest in the wadi bed (B), whereas the upper slope was devoid of living plants. In 2000 the last living individuals were found on the lower slope. *Z. spinosa* and *M. philaeana* attained the highest values, followed by *Fagonia* sp. The other species were of minor importance, but *Salsola imbricata* and *Acacia ehrenbergiana* persisted until 2000. The maximum number of individuals (as % of total individuals) shifted from *Zilla spinosa* and *Moretta philaeana* at the beginning, to *Fagonia indica*, *F. bruguieri*, *Pulicaria incisa*, *Zygophyllum simplex* and *Astragalus vogelii* in the middle, and to *Acacia ehrenbergiana* and especially *Salsola imbricata* at the end of the monitoring period in 2000.

Vegetation cover (Table 3) was less than 10%. At the beginning of the observation period, vegetation cover was highest on the right terrace below the rocky outcrops. Later on it was observed to be highest in the wadi bed. Comparing the values of numbers of individuals (% of total number) with the values for cover (% of total cover) of the species, it is evident that the individuals of *Morettia philaeana* were smaller than those of *Zilla spinosa*, *Salsola imbricata* and *Acacia ehrenbergiana*. The latter was one of five surviving specimens in 2000. It contributed two-thirds of the sparse vegetation cover.

### VEGETATION AT SITE 2

On a small scale, the vegetation in the discontinuous transect at S2 was very heterogeneous. Plant growth was recorded only on 5 of the 20 plots (3 on terrace, 2 in wadi bed). The transect was uniform in terms of species diversity: *Zilla spinosa* was the only colonizing species! The number of individuals (Fig. 6) reached a peak of 136 individuals and sharply dropped afterwards to *ca* 50 within 2 months. The half-life value was reached after 4.5 months, a slightly faster popu-

**Table 3**. Structural data for Site S1, continuous transect. Ind. – number of individuals; $T_U$ – upper terrace, $T_L$ – lower terrace, B – wadi bed; ZIL – *Zilla spinosa*, MOR – *Morettia philaeana,* FAG – *Fagonia indica + F. bruguieri,* SAL – *Salsola imbricata,* PUL – *Pulicaria incisa + P. crispa,* ZYG – *Zygophyllum simplex,* ACA – *Acacia ehrenbergiana.*

| Measure | Year | Left | | | Right | | | ZIL | MOR | FAG | SAL | PUL | ZYG | ACA |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | $T_U$ | $T_L$ | B | $T_L$ | Mean | | | | | | | | |
| Ind. | 1996 | 15 | 23 | 16 | 14 | 16 | Ind. | 38 | 32 | 14 | 4 | 7 | 4 | 1 |
| per plot | 1997 | 0 | 2 | 8 | 3 | 4 | (% total) | 38 | 0 | 35 | 10 | 15 | 0 | 2 |
| (25 m$^2$) | 1998 | 0 | 0 | 4 | 3 | 2 | | 21 | 0 | 43 | 29 | 4 | 0 | 4 |
| | 2000 | 0 | 1 | 0 | 0 | 0 | | 0 | 0 | 0 | 75 | 0 | 0 | 25 |
| Cover | 1996 | 1.2 | 3.5 | 8.2 | 9.6 | 6.6 | Cover | 48 | 13 | 14 | 5 | 7 | 6 | 6 |
| (% area) | 1997 | 0.0 | 0.5 | 6.3 | 5.0 | 4.0 | (% total) | 56 | 0 | 19 | 5 | 9 | 0 | 11 |
| | 1998 | 0.0 | 0.0 | 2.6 | 1.1 | 1.3 | | 40 | 0 | 20 | 14 | 0 | 0 | 25 |
| | 2000 | 0.0 | 0.1 | 2.4 | 1.0 | 1.3 | | 0 | 0 | 0 | 34 | 0 | 0 | 66 |

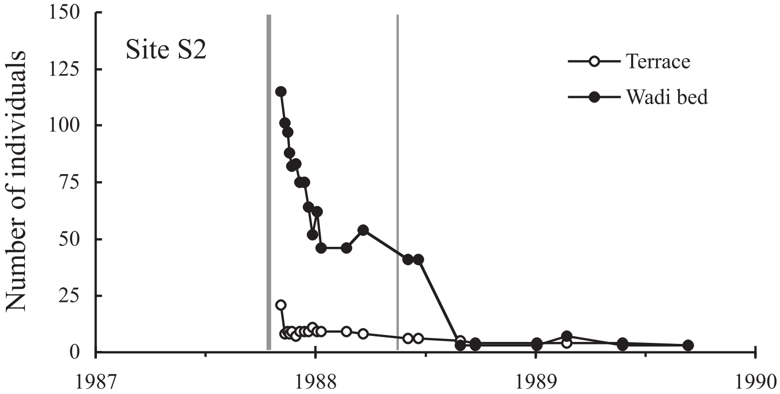

**Fig. 6**. Number of individuals of *Zilla spinosa* (as the only species present) at the terrace and the wadi bed of S2 (discontinuous transect); total area 20 m$^2$. Vertical lines indicate rainfall events.

lation breakdown than at S1 (Table 2). Then the number of plants remained stable for half a year but finally decreased to 6 survivors 11 months after the rain. The plant density on the terrace at peak time amounted only to 2.6 individuals per m$^2$ (average of all 8 plots) and 7.0 respectively (average of the vegetated plots only). It then dropped rapidly to less than one. In contrast, the population density in the bed started with 9.6 (all 12 plots) or 57.5 (vegetated plots only), but in the end also reached the same low level as on the terrace.

After the rain in 1996, plant density in the continuous transect was much higher at S2 than in the discontinuous transect during 1987–1989 (Table 4). The upper slope always remained barren (not shown in Table 4); the lower slope and the left terrace showed large numbers of individuals, which, however, had very little cover. In contrast to this, in the bed and on the terrace to the right, fewer individuals were recorded but with distinctly higher cover. In 1997 and also in the following years, only plant densities of less than one individual per m$^2$ were found. *Salsola imbricata* held the highest number of individuals, almost equalled by *Morettia philaeana* in 1996 and by *Zilla spinosa* in 1997 (Table 4). Regarding relative cover, *Z. spinosa* dominated in 1996 and 1997, and *Salsola imbricata* did so in 1998 and 2000. It should be mentioned that *Acacia* sp. was not present as a shrub. Only a seedling of *Acacia* sp. appeared after 1998 in the wadi bed, but dried up in 2000.

**Table 4**. Structural data for Site S2, continuous transect. Ind. – number of individuals; SL – lower slope, T – terrace, B – wadi bed; ZIL – *Zilla spinosa*, MOR – *Morettia philaeana*, CRO – *Crotalaria aegyptiaca*, FAI – *Fagonia indica*, SAL – *Salsola imbricata*, PUC – *Pulicaria crispa*, ZYG – *Zygophyllum simplex*.

| Measure | Year | Left | | | Right | | | ZIL | MOR | FAI | CRO | SAL | PUC | ZYG |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | $S_L$ | T | B | T | Mean | | | | | | | | |
| Ind. | 1996 | 462 | 193 | 12 | 65 | 98 | Ind. | 19 | 26 | 5 | 0 | 30 | 18 | 1 |
| per plot | 1997 | 0 | 13 | 5 | 17 | 9 | (% total) | 40 | 0 | 14 | 3 | 44 | 0 | 0 |
| (25 m$^2$) | 1998 | 0 | 9 | 2 | 11 | 6 | | 12 | 0 | 5 | 2 | 80 | 2 | 0 |
| | 2000 | 0 | 5 | 1 | 6 | 3 | | 5 | 0 | 0 | 9 | 82 | 4 | 0 |
| Cover | 1996 | 16 | 25 | 13 | 62 | 32.7 | Cover | 48 | 13 | 10 | 0 | 15 | 11 | 1 |
| (% area) | 1997 | 0 | 4 | 7 | 28 | 13.7 | (% total) | 54 | 0 | 13 | 0 | 33 | 0 | 0 |
| | 1998 | 0 | 6 | 2 | 12 | 6.0 | | 20 | 0 | 7 | 0 | 72 | 2 | 0 |
| | 2000 | 0 | 4 | 0 | 6 | 2.5 | | 6 | 0 | 0 | 1 | 87 | 6 | 0 |

### VEGETATION AT SITE 3

At the end of November 1987, vegetation development started with two therophytes (*Sonchus oleraceus* and *Astragalus vogelii*) and one short-lived perennial (*Morettia philaeana*; Table 5). Later the two perennials *Pulicaria crispa* and *Salsola imbricata* showed up, but all plants died by May 1989. *P. crispa* was the first perennial species to appear. Almost a decade after the beginning of the experiment, *Tamarix nilotica* and *Glinus lotoides* colonized this area. All three species, which were almost completely lacking at S1 and S2, are known as pioneer colonizers in depressions with good water supply (Abd El-Ghani 2000), larger wadis (Ali *et al.* 1997), in ecotones at the shore of Lake Nasser (Springuel 1996) and margins of oases (Bornkamm & Kehl 1990), where intermittent inundation is possible.

### ORDINATION OF VEGETATION CHANGE AT SITE 1

The change of the community over the observation time at S1 (wadi bed and lower terrace) is illustrated in Figure 7. The first two axes of the NMDS ordination represent different aspects of the temporal dynamic: following 36 time steps of sampling from 9 Nov. 1987 to 26 Oct. 2000, axis 1 clearly depicts the change of the community after every main rainfall, whereas axis 2 separates successive development stages from event to event. Some irregular changes can be recognized in 1993 and 1994 (census dates 24–28).

The centroids of the species give their relative performance within the ordination space. *Euphorbia granulata* and *Zygophyllum simplex* show up on the lower left of the graph, indicating preference for the early stages of development after a rain event. *Pulicaria* sp. and *Salsola imbricata*, on the other hand, are placed near the upper right, showing their increasing performance in later stages of the community. All the other species are between these extremes, with *Zilla spinosa*, *Morettia philaeana* and *Fagonia* spp. in the very center, indicating their dominant position within the communities.

## DISCUSSION

At all three sites (S1–S3), both the number of individuals and the maximum soil water content

**Table 5**. Two periods (1987–89 and 1996–98) of vegetation development at site S3 (line transect). MOR – *Morettia philaeana*, SON – *Sonchus oleraceus*, AST – *Astragalus vogelii*, PUC – *Pulicaria crispa*, SAL – *Salsola imbricata*, PUI – *Pulicaria incisa*, TAM – *Tamarix nilotica*, GLI – *Glinum lotoides*, ZYG – *Zygophyllum simplex*.

| Measure | Date | MOR | SON | AST | PUC | SAL | PUI | TAM | GLI | ZYG |
|---|---|---|---|---|---|---|---|---|---|---|
| Transect marks (see Methods for details) | 11/09/87 | | | | | waterlogged | | | | |
| | 11/30/87 | 1 | 1 | 1 | | | | | | |
| | 12/21/87 | 2 | 1 | 1 | | | | | | |
| | 12/28/87 | 2 | 1 | 1 | | | | | | |
| | 1/04/88 | 2 | 1 | 1 | 1 | | | | | |
| | 2/22/88 | 3 | 1 | 1 | 1 | | | | | |
| | 3/21/88 | 6 | 1 | 1 | 1 | | | | | |
| | 8/28/88 | 4 | | | 3 | 3 | | | | |
| | 1/03/89 | 3 | | | 3 | 2 | | | | |
| | 2/21/89 | 2 | | | 3 | 2 | | | | |
| | 5/25/89 | | | | | | | | | |
| Cover (% area) | 1996 | 8 | 0 | 0 | 3 | 26 | 1 | 0 | 1 | 0 |
| | 1997 | 14 | 0 | 0 | 13 | 19 | 13 | 10 | 5 | 1 |
| | 1998 | 0 | 0 | 0 | 2 | 36 | 0 | 16 | 1 | 0 |
| Cover (% total) | 1996 | 20 | 0 | 0 | 7 | 68 | 2 | 0 | 3 | 0 |
| | 1997 | 19 | 0 | 0 | 17 | 26 | 17 | 13 | 7 | 1 |
| | 1998 | 0 | 0 | 0 | 4 | 65 | 0 | 29 | 2 | 0 |

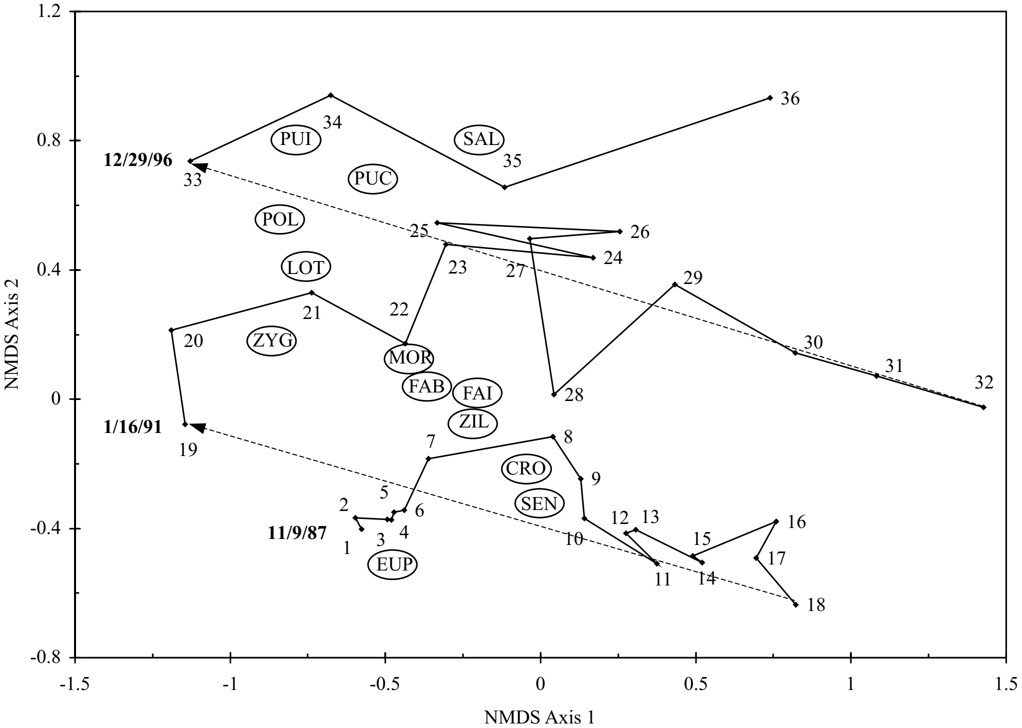

**Fig. 7**. Ordination (NMDS) diagram showing the temporal variation of species composition at site S1. Census dates are numbered 1–36; species names are placed at their centroids in the ordination space. CRO – *Crotalaria aegyptiaca*, EUP – *Euphorbia granulata*, FAB – *Fagonia bruguieri*, FAI – *Fagonia indica*, LOT – *Lotononis platycarpa*, MOR – *Morettia philaeana*, POL – *Polycarpaea robbairea*, PUC – *Pulicaria crispa*, PUI – *Pulicaria incisa*, SAL – *Salsola imbricata*, SEN – *Senna italica*, ZIL – *Zilla spinosa*, ZYG – *Zygophyllum simplex*. The first census following a main rainfall is indicated by its date.

coincide very well with the occurrence of the main storms (1987, 1990, 1996). The higher water content observed in 1993/94 at S1 was accompanied by some vegetation change (as indicated by higher species numbers) but the number of individuals remained very low. This phenomenon of seemingly minor importance may have been caused by rain events we missed, by strictly local showers, or by rainfall farther upstream in the Wadi Aggag.

During long intervals of the vegetation periods the water content of the soil was <4%. However, since it is known that the fill deposits in Wadi Aggag contain 91% gravel + sand and only 9% silt + clay in the topsoil and 87% gravel + sand and only 13% silt + clay in the deeper soil (Springuel *et al.* 1990), even at 2% water content there is still water available to plants. Furthermore, the roots of larger plants reach the bedrock and boulders and branch off on the surface of the Nubian sandstone, which is able to store water (Springuel *et al.* 1990).

To understand the changes in the vegetation one has to take into account the twofold action of water flow:

1. The flash flood itself destroys vegetation, removes large portions of sediments including seed banks, and also moves large boulders.

2. A less violent discharge beneficially infiltrates the soil layers and introduces fine sediments together with diaspores from other vegetated areas. At S1 and S2 the floods of 1987 and 1990 destroyed the existing vegetation completely with the exception of *Acacia ehrenbergiana* in S1, which was thrown down and continued to grow with lateral branches. In 1996, when the sampling was not as frequent as in the first years, the species in the

new vegetation period were observed to settle at locations (subplots) where they had not been before. This supports the assumption of discontinuity in vegetation development.

It can be assumed that the main source of diaspores is import with flowing water. *Zilla spinosa* floats for a long time (Montasir 1951; Danin 1983). Species with plumose (*Pulicaria* spp.) or soft hairs (*Tamarix nilotica*) can be transported by wind. Other species with stellate hairs (*Morettia philaeana*) and spiny structures (fruit beaks of *Zilla spinosa*) or which are browsed by camels and gazelles (*Acacia* fruits; van Rheede van Oudshoorn & van Rooyen 1999) can be distributed by animals. Groups of camels occasionally pass by Wadi Aggag, and gazelles live there. *Crotalaria aegyptiaca* in particular is browsed heavily.

In the different vegetation flushes, plant life forms (following Boulos 1999, 2000, 2002) show a characteristic distribution. True annuals (e.g., *Astragalus vogelii*, *Euphorbia granulata*, *Glinus lotoides*, *Astragalus vogelii*) occurred mainly in the first part of the flush. Most other species proceed through therophytic, short-lived perennial (*Lotononis platycarpa*, *Morettia philaeana*, *Pulicaria incisa*, *Zygophyllum simplex*) or even long-lived perennial life cycles (*Crotalaria aegyptiaca*, *Fagonia* spp., *Pulicaria crispa*, *Polycarpaea robbairea*, *Salsola imbricata*, *Zilla spinosa*) 'depending on moisture regime' (Danin 1983 for *Zilla spinosa*; see also Kassas & Girgis 1970: 69). These species with life cycles determined not by an internal but by an external factor are called poikilorhythmic species (Bornkamm 2001). They are the characteristic life form of accidental vegetation *sensu* Kassas (1952).

Among the plant species in our study there were only two woody perennials, *Acacia ehrenbergiana* and *Tamarix nilotica*. In suitable habitats, plant communities with dominating *A. ehrenbergiana* or *T. nilotica* are widespread in the Aswan region (Springuel *et al.* 1991; Kassas 1973). In Wadi Aggag they occur as single trees or shrubs in the most favorable parts of the wadi bed only. They need a permanent source of water. The large distances (5–10 km or even more) between the trees imply that the water source consists in local groundwater pockets rather than a persistent groundwater stream along the wadi. The two species are endangered by both lack of water and by water excess, that is, destruction by floods.

The occurrence of woody species such as *A. ehrenbergiana* is a sign that desert shrub vegetation in a wadi bed could transform to *Acacia* scrub under favorable conditions. This change would be a one-step succession (telescope succession *sensu* Whittaker 1974) proceeding in steep and narrow tributaries of Wadi Aggag close to S2 and S3. However, the terraces and slopes of the wadi, with too little storage capacity, produce only accidental and never longer lasting vegetation. Here the absence of succession can be confirmed, and the pioneering accidental vegetation is identical to the climax vegetation (Barbour *et al.* 1999: 301).

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