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Seed bank dynamics — longevity, viability and predation of seeds of serotinous plants in the central Namib Desert

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Longevity, viability and predation of seeds were studied over 2 years in *Aptosimum spinescens* (Scrophulariaceae), *Blepharis grossa* (Acanthaceae), *Geigeria alata*, *G. ornativa* (Asteraceae), *Petalidium setosum* and *P. variabile* (Acanthaceae). The majority of seeds were stored on parent plants of the study species, apart from *G. alata* which showed a dimorphic seed dispersal mode. A decline in viability was found in two species (*G. alata* and *G. ornativa*) during the study period. Seed losses to Coleoptera and Diptera larvae ranged on average from 16% (*P. setosum*) to 25% (*B. grossa*). In this study the degree of serotiny was related to life form. Seed viability was related to seed characteristics rather than to the method of seed storage.

Keywords: desert plants; Namib Desert; seed dispersal; seed stores; serotiny

Introduction

Seed bank dynamics are regulated by factors such as seed dispersal, longevity and germination of seeds (Harper, 1977; Cook, 1980; Hassan & West, 1986; Thompson, 1987; Simpson *et al.*, 1989). In deserts, plants have developed various mechanisms to ensure that seed release and germination are coupled with sufficient moisture supply. Most seeds are dormant during the dry periods and require complex combinations of appropriate conditions for germination (Freas & Kemp, 1983; Gutterman, 1983). The unability to predict the environment reduces establishment of seedlings and was suggested to favour seed dormancy in arid regions (Templeton & Levin, 1979; Cook, 1980; Westoby, 1981).

Dormancy is one way to deal with uncertainties of the environment, delay in seed release is an additional option (Venable & Lawlor, 1980). Retention of seeds on the parent plant, i.e. serotiny (Lamont, 1991), is often coupled with seed release triggered by an environmental factor. Serotiny is a common phenomenon in fire-controlled and desert systems (Stopp, 1958; Evenari *et al.*, 1982; Zedler, 1986), but its evolutionary significance has not been satisfactorily explained in arid regions. Nothing is known about seed bank dynamics of serotinous plants in deserts (Grime, 1989), and questions related to this aspect might help to understand the evolutionary significance of serotiny.

The regulation of germination and permanent occupation of a favourable site had been suggested as advantages of serotiny in desert regions (Zohary, 1962; Evenari *et al.*, 1982). Also protection against seed predators was suggested (Ellner & Shmida, 1981; Gutterman,

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1990), but no empirical evidence exists for any possible advantages of serotiny. Seeds of serotinous plants are stored in seed containers that are often equipped with spines, thorns and hairs making it difficult for predators to harvest or eat the seeds. Nevertheless, in early stages of seed maturation, insect larvae can damage the seeds (pers. obs.).

At the edge of the Namib Desert serotinous plants are an important component of the vegetation, yet nothing is known about the life history of these plants and their contribution to seed bank dynamics. On a regional scale a rainfall regime between 50 and 100 mm and habitats related to runoff conditions favour serotinous plants in the central Namib (Günster, 1992). Yet, factors related to the persistence of seeds in the seed bank and prevention of seed loss to predators might be as important in explaining their distribution.

This study was based on two major questions: (a) does serotiny guarantee longer high levels of seed viability? and (b) is serotiny an adaptation to reduce seed predation? The persistence and viability of seeds on the parent plant and seed loss to invertebrate predators were investigated over a 2-year period.

Methods

Study area and study species

The study area is located in the eastern part of the central Namib (23° 17′S and 15° 30′E). A mean annual temperature of 21·5°C and mean annual rainfall of 68 mm characterize the climate in the study area (Weather Bureau, Windhoek). During the study period (June 1989 – August 1991) rainfall totalled 54·7 mm in 1989, 48·4 mm in 1990 and 32·7 mm in 1991. Rain falls most commonly in late summer and autumn (January – April) and the length of the vegetation period can vary between 1 to 5 months depending on the timing and amount of rainfall. Gravel plains intersected by drainage lines characterize the study area. The vegetation mainly consists of dwarf shrubs confined to dry water courses. Within a shrub community dominated by *Petalidium setosum*, a number of serotinous species was chosen as study plants: *Aptosimum spinescens* (Thunb.) Weber (Scrophulariaceae), *Blepharis grossa* (Nees) T. Anderson (Acanthaceae), *Geigeria alata* (DC.) Benth & Hook fil. ex Oliver & Hiern, *G. ornativa* O. Hoffm. (Asteraceae), *Petalidium setosum* C. B. Clarke ex Schinz and *P. variabile* (Engler) C. B. Clarke (Acanthaceae). *Aptosimum spinescens* and *Petalidium setosum* are deciduous shrubs, *P. variabile* is an evergreen shrub and the remaining species are annuals. For simplicity seed-enclosing structures are referred to as seed containers in all study plants. These are seed capsules in *A. spinescens*, fruit capsules in the Acanthaceae, and capitula in the Asteraceae. They vary according to taxonomy in shape and position on the study species (Fig. 1).

Persistence of seed containers on parent plants

To determine whether seed containers were dispersed during the observation period, seed containers were marked with metal tags after the vegetation period (June 1989). One to 10 seed containers were tagged on five to 20 plants, in a total of 20 to 78 marked seed containers per species. The seed containers remaining on the plants were counted at monthly intervals. In *G. alata*, in addition to seed containers on branches, one seed container at the base of each plant was tagged.

Soil seed bank

Seed stores were selectively investigated around the study plants to find evidence whether seed dispersal occurred other than when triggered by rain. Soil samples were taken every
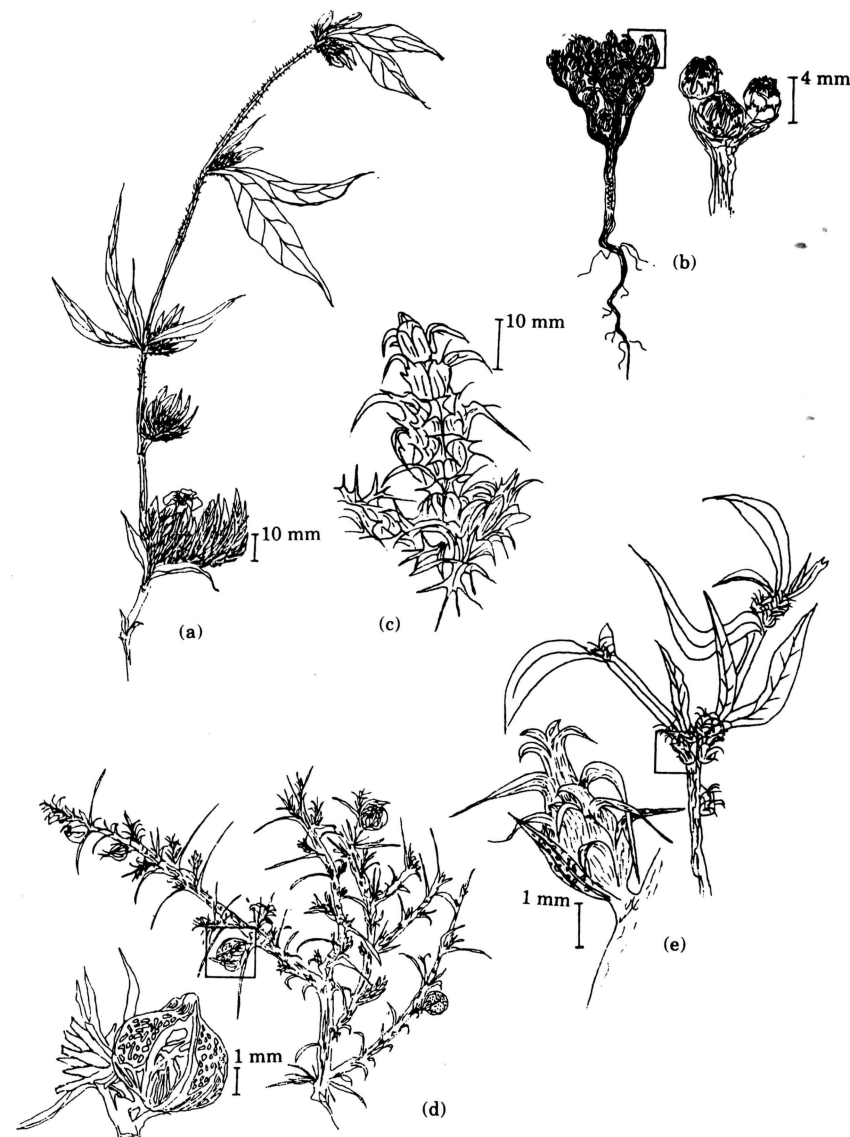
Figure 1. Habit and position of seed containers on the plants of (a) *Petalidium setosum* (Acanthaceae), (b) *Geigeria ornativa* (Asteraceae), (c) *Blepharis grossa* (Acanthaceae), (d) *Aptosimum spinescens* (Scrophulariaceae) and (e) *Geigeria alata* (Asteraceae) (after originals by M. Nel).

3 months in the following fashion; three individuals of four species (*B. grossa*, *G. alata*, *G. ornativa*, and *P. setosum*) were randomly selected and a metal cylinder, 7 cm in diameter, was pressed 3 cm into the soil, to take one sample at 0, 50, and 100 cm from each plant in each of the four cardinal compass points. The soil samples were then air dried and sieved with a set of 500–2000 er Tyler sieves according to seed size. Seeds were extracted

by hand or under a microscope at 10 × magnification and identified by comparison with a reference collection.

Seed viability

To investigate whether there were any losses in seed viability, seeds were tested every 3 months. At each observation date seeds were collected on plants in the study area to guarantee natural storage conditions. Several plants were marked after the vegetation period 1989 to 1990 to ensure that samples were taken from plants that had germinated in the same vegetation period. Each time, 50 to 90 randomly collected seeds per species were tested for viability by staining with tetrazoliumchloride. Only seeds from the base of the plants were taken from *G. alata* since seeds on branches were dispersed after a few months. To activate the germination process, seeds were soaked for several hours in distilled water. Seeds and the embryos were cut in half and one half of the embryo placed in a 1%-Tetrazoliumchloride solution. They were stored in a dark cabinet for 8 h and staining of the embryos examined under a microscope. All embryos that stained purple to red were scored as viable (Barton 1961; Pili-Sevilla 1987).

Seed predation

Prior observations indicated that Coleoptera and Diptera larvae prey on seeds of the study plants. After the vegetation periods 1989 and 1990, three seed containers from 10 individuals from *B. grossa, G. alata, G. ornativa* and *P. setosum* were randomly collected every 3 months, and the number of damaged seeds and seed containers counted respectively. The number of damaged seeds was determined for *B. grossa* and *P. setosum*, but since in *G. alata* and *G. ornativa* seed predators usually consumed all the seeds in a seed container, the number of infected seed containers was counted instead.

Results

Persistence of seed containers on parent plants

The loss of marked seed containers during the study period indicated the persistence of seed containers on the parent plants and served as a measure for degree of serotiny. During the study period, the number of seed containers on the parent plants remained constant for *B. grossa, G. ornativa* and at the bases of *G. alata* (Fig. 2). The other study species lost marked containers during the 21-month period, either rapidly (branches in *G. alata*) or continuously (*A. spinescens, P. setosum* and *P. variabile*) (Fig. 2). *G. alata* showed a dimorphic dispersal strategy. All aerial branches were dispersed within 6 months, whereas all basal seed containers were still present after 21 months. About 50% *A. spinescens*, 20% *P. setosum* and 60% *P. variabile* seed containers were dispersed after 12 months. Among those three species, *A. spinescens* lost seed containers most rapidly and could be expected to lose the remaining marked containers within the next few months after the observation period.

Soil seed bank

Seeds of *G. alata* and seed containers of *G. alata, G. ornativa* and *A. spinescens* were found in the soil. Neither seeds nor seed containers of *B. grossa* and *P. setosum* were present (Fig. 3). Many soil samples contained capsules of *G. alata* at all observation dates and *G. alata*
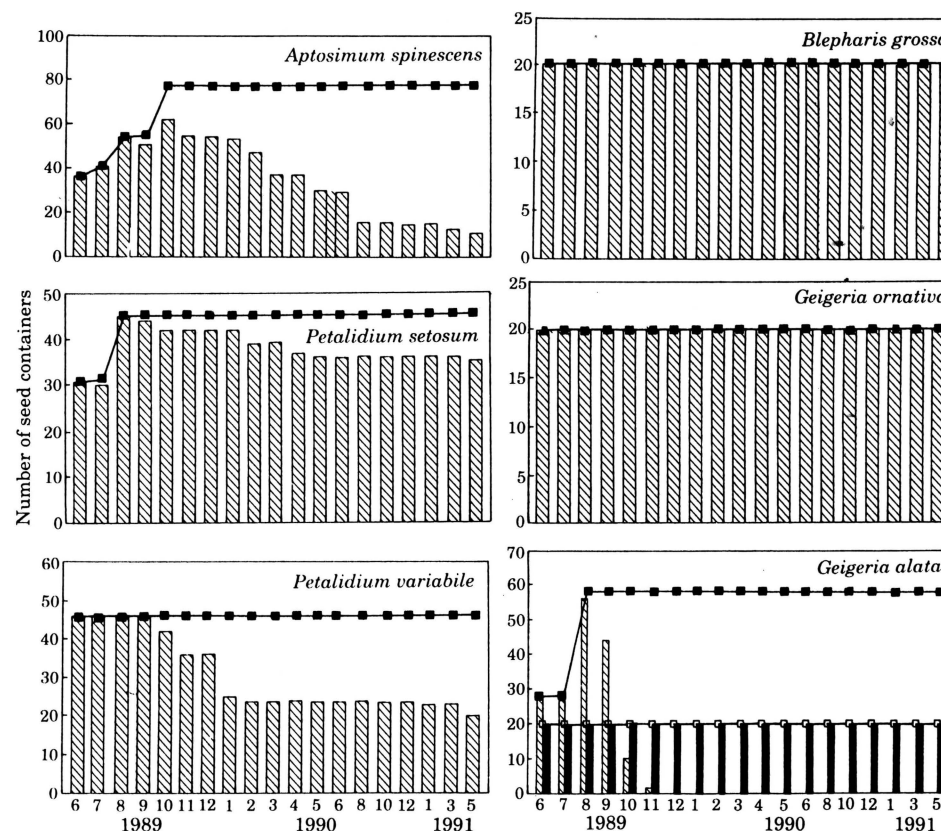
Figure 2. Number of initially marked (–■–) and counted (▨) seed containers at each observation date in the study plants. Seed containers of *Geigeria alata* were also marked initially (–□–) and counted (■) at the base separately. (In *Aptosimum spinescens*, n = 19 individuals/78 seed containers; in *Blepharis grossa*, n = 20 individuals/20 seed containers; in *Geigeria alata*, n = 20 individuals/78 seed containers; in *Gleigeria ornativa*, n = 20 individuals/20 seed containers; in *Petalidium setosum*, n = 15 individuals/43 seed containers; in *Petalidium variabile*, n = 6 individuals/46 seed containers).

seeds were found at three out of four observation dates. *A. spinescens* and *G. ornativa* seed containers were found only once.

Viability

A first peak in viability was reached about 8 months after the seeds were produced in all species of both seed generations (Fig. 4). Viability dropped to a low point simultaneously in all species in seeds from seed generation 1989, towards the end of the vegetation period (May 1989). In *B. grossa* and *P. setosum*, relatively high percentages of viability were then maintained. At the end of the observation period, viability of *Geigeria* seeds from seed generation 1989 was remarkably lower than that of *B. grossa* and *P. setosum* seeds. Both Acanthaceae (*B. grossa* and *P. setosum*) showed overall higher viability than the
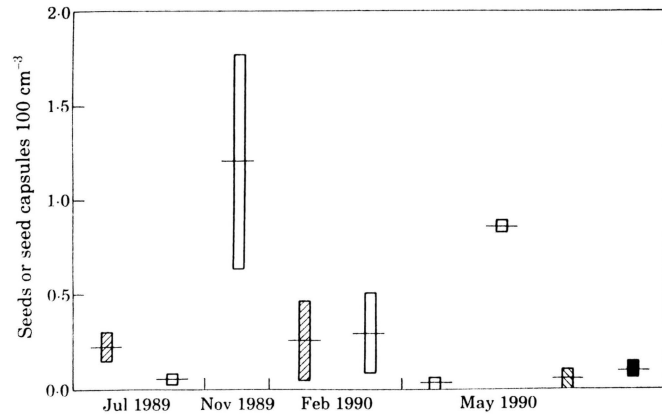
Figure 3. Seed stores in and on soil: means and standard errors of number of seeds and seed containers per 100 cm^{-3} after the vegetation period 1989 found in the study area (☐ = *Geigeria alata* capitula, ▨ = *Geigeria alata* seeds, ▧ = *Geigeria ornativa* capitula, ■ = *Aptosimum spinescens* capsules).
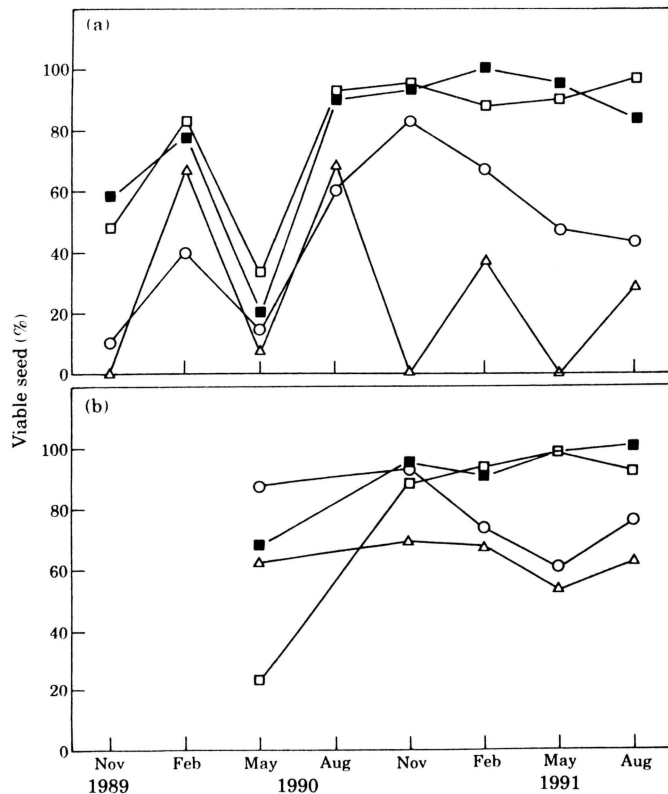

Figure 4. Viability of seeds from plants which germinated in the vegetation period 1989 (a) and 1990 (b). –■– = *Blepharis grossa*; –△– = *Geigeria alata*; –○– = *Geigeria ornativa*; –☐– = *Petalidium setosum*.

Asteraceae (*Geigeria* species). Seeds produced in the vegetation period 1990 indicated a similar trend.

Seed predation

Seed loss to invertebrates was highly variable between observation dates except in *P. setosum* (Fig. 5). An average loss of 15% was found in the *P. setosum* seeds produced in the vegetation period 1989. The other species showed 0–80% seed loss. Although overall variation was high, more variation was found between observation dates than between species. Apart from *P. setosum*, the study species showed corresponding trends in six out of eight observation dates in plants during 1989 (Fig. 5). A similar trend was also indicated in plants from the vegetation period 1990. Overall (means of observation dates in 1989), seed loss averaged at 15% in *P. setosum*, 35% in *B. grossa*, 34% in *G. alata* and 32% in *G. ornativa*.
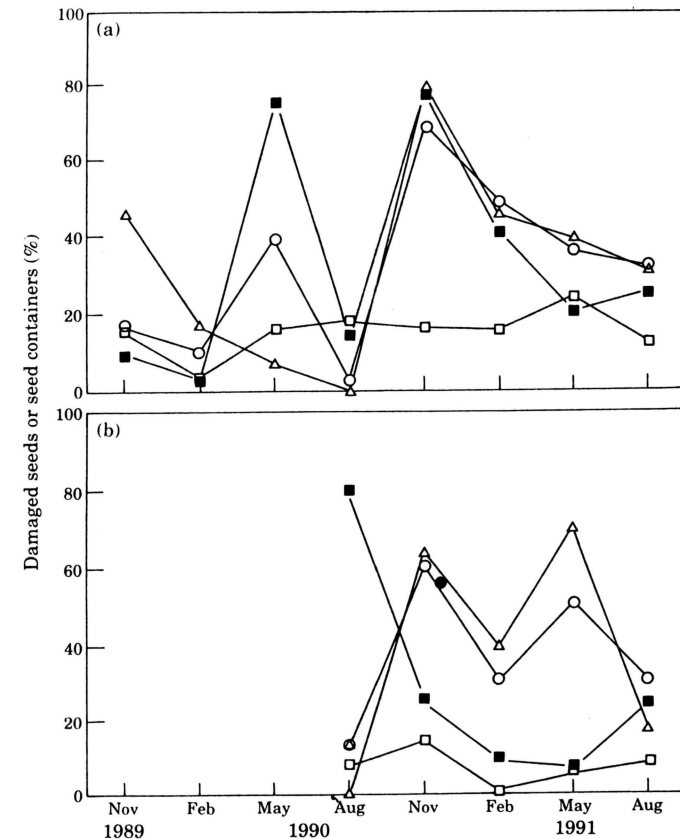

Figure 5. Percentage of seed containers damaged by insect larvae of plants which germinated in the vegetation period 1989 (a) and 1990 (b). The figures refer to capitula in the *Geigeria* species and fruits in *Blepharis grossa* and *Petalidium setosum*. (Symbols as for Fig. 4).

Discussion

In summary, varying degrees of serotiny (i.e. persistence of seed containers on the parent plant) occurred in the study species. A decline in viability of seeds was found in two species (*G. alata* and *G. ornativa*) after 2 years. Invertebrate seed predators depleted the seed stores partially (16–35%).

Varying degrees of serotiny

Serotiny is defined as delay of seed release at least until a new generation of seeds matured (Le Maitre, 1984; Lamont, 1991). According to this definition, all study species showed some degree of serotiny (Fig. 2). In general, the annual study species were serotinuously stronger than the perennials in this study.

B. grossa and *G. ornativa*, which are annuals, showed no loss of seed containers. *P. setosum* and *P. variabile* lost a few and *A. spinescens* lost about 80% of the seed containers during the study period. This suggests that *A. spinescens* is serotinously weaker than the other species. Ungulates, such as springbok (*Antidorcas marsupialis*) and gemsbok (*Oryx gazella*), and ostriches (*Struthio camelus*) are common in the study area (Stuart, 1975). They were often observed to break branches and seed containers of *A. spinescens*.

Seeds remained in the seed containers during the dry periods. This was supported by investigations of the seed containers to assess seed loss and by the findings in relation to the soil seed bank (Fig. 3). There were some seeds in all seed containers that had been investigated to determine seed loss to predators, except those that had been emptied entirely by predators. In addition, only a few seeds and seed containers were found in the soil samples. During each rain event, a few seeds were dispersed (pers. obs.) and the remaining seeds were stored on the parent plant.

G. alata showed a dimorphic dispersal mode. Here, branches weathered after the vegetation period and were broken off by animals and the wind. The branches act as tumble weeds which have often been observed in semi-arid regions (Zohary, 1962; Rabinowitz & Rapp, 1979; Van der Pijl, 1982). Basal seed containers of *G. alata* remained at the location of the parent plant (Fig. 2). Seeds and seed containers of *G. alata* in soil samples might have originated from the broken branches, and may support the observation of the dual dispersal mode (Fig. 3). Alternative methods of seed dispersal were suggested to be advantageous in arid regions (Comins *et al.*, 1980; Levin *et al.*, 1984) and are commonly found in the Asteraceae (Sorensen, 1978; Venable, 1985; Plitmann, 1986).

One entire plant of *G. ornativa* was present in the soil samples and was probably uprooted by animals and dispersed by wind. The two Acanthaceae, *B. grossa* and *P. setosum* have a ballistic mode of seed dispersal triggered by rain (Bremekamp, 1926; Gutterman *et al.*, 1967). Neither their seeds nor fruits were found in the soil and all seeds were stored on the parent plant.

Seed storage times of several to 20 years have been reported in fire-controlled ecosystems (McMaster & Zedler, 1986; Bond, 1984; 1985; Zedler, 1986). No exact data for storage times of seeds on desert plants are known, but decades rather than years have been suggested (Friedman & Stein, 1980). Longer observation periods than used in this study are required to support or reject the hypothesis.

Decline in seed viability in some species

Even if seeds of serotinous desert plants were assumed to remain viable for long periods of time (Friedman & Stein, 1980) and, in comparison, the study plants were only investigated over a short time span, a decline in viability was indicated in the *Geigeria* species after 2 years. This suggests that viability in desert serotinous plants might not be as long lasting

as it had been assumed previously. In comparison, *Euphorbia* seeds in the North American deserts were viable for more than 20 years (Went, 1957). Nothing is known about longevity of seeds in other deserts but similar figures can be expected.

However, one trend appeared in both seed generations: the two large-seeded species *B. grossa* and *P. setosum* maintained longer durations of increased viability than the small-seeded *Geigeria* species. This suggests that seed characteristics related to taxonomic differences might be more important to viability than the way of seed storage.

Seed loss to insect predators

Seed containers damaged by Coleoptera and Diptera larvae (Anobiidae, Pentatomidea and Tephrititae were identified) were common in all study species. The extent of damage varied considerably between species, individuals and dates, which coincides with similar studies (Klinkhamer *et al.*, 1988). *P. setosum* was the only species showing relatively constant seed loss over time. This might be explained by a more regular distribution of *P. setosum* in the study area. The other species occurred in clumps and were less common. Insects might have invaded only a few clumps here. The fact that overall variation was higher between observation dates than between species also supports the idea that insects invaded certain patches more than others.

Seed losses ranged overall from 16 to 35% but seed losses to invertebrates might be underestimated if not studied by an insect exclusion experiment (Andersen, 1988). However, seed loss is low compared to other desert regions where it ranged between 30 and 80% (Nelson & Chew, 1977; Brown *et al.*, 1979; Reichman, 1979; Davidson *et al.*, 1984). Seed loss to vertebrate seed predators was not quantified in this study but vertebrates contribute to seed loss in the Namib also. Ostriches were observed to swallow entire *B. grossa* plants (S. Milton, pers. comm.), irrespective of their prickly habit, and *B. grossa* seeds were found in caches collected by gerbils (*Gerbillurus setzeri*) (Downs & Perrin, 1989). Other granivorous vertebrates, such as birds, might also contribute to the depletion of the above-ground seed bank.

Conclusion

Combining the effects of seed persistence on the parent plant, seed viability over time and seed loss to predators, suggested that among the study species viable seed stores could be available for the longest time on the parent plants of *B. grossa* (Table 1). This might explain its abundance in parts of the central Namib (pers. obs.).

With respect to the initial questions: (a) Does serotiny guarantee longer high levels of seed viability? In this study seed size rather than serotiny determined longevity of seeds. However, viability should be observed over longer periods and should be compared with

Table 1. *General trends of degree of serotiny, viability of seeds and seed loss*

Species	Persistence/ degree of serotiny	Viability	Seed loss
Aptosimum spinescens	Weak	—	—
Petalidium variabile	Intermediate	—	—
Petalidium setosum	Intermediate	High + long	Low
Blepharis grossa	Strong	High + long	Intermediate
Geigeria alata	Strong	Intermediate + decline	Intermediate
Geigeria ornativa	Strong	Intermediate + decline	Intermediate

non-serotinous species. (b) Is serotiny an adaptation to reduce seed predation? Seed loss to invertebrates was comparatively low but vertebrates should be included and overall seed loss compared to non-serotinous plants to draw a general conclusion.

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