

Dormancy patterns in accessions of caryopses from savanna grass species in South Eastern Botswana

E. M. VEENENDAAL*† and W. H. O. ERNST*

**Department of Ecology and Ecotoxicology, Faculty of Biology, Free University, Amsterdam, The Netherlands* and †*National Institute for Development Research and Documentation, University of Botswana, Gaborone, Botswana*

SUMMARY

Caryopsis dormancy patterns of indigenous grass species from South Eastern Botswana were studied. Observed dormancy patterns in accessions from *Aristida congesta*, *Aristida stipitata*, *Chloris virgata*, *Eragrostis superba*, *Eragrostis rigidior*, *Heteropogon contortus*, *Rhyncelytrium repens*, *Schmidtia pappophoroides*, and *Tragus berteronianus*, indicated a drought avoidance dormancy syndrome while caryopses from *Cynodon dactylon* did not show dormancy. Under room storage conditions, most accessions lost at least part of their dormancy within 6 to 12 months. For some species differences in dormancy pattern were observed between accessions from the same season, as well as for accessions from different seasons. As the type of dispersal unit of the plant may influence its dormancy mechanisms, it is argued, that studies of dormancy patterns and mechanisms of indigenous grass species should include information on the seed dispersal strategy of the species and be based on the comparison of more than one accession.

Key-words: caryopsis, dispersal unit, dormancy, drought avoidance syndrome, savanna grasses.

INTRODUCTION

The savanna ecosystem in South Eastern Botswana is subject to range degradation processes, the result of heavy grazing by livestock and recurrent droughts (Van Vegten 1983; Arntzen & Veenendaal 1986; Tolsma 1989). An understanding of the adaptations of indigenous savanna grasses occurring in such an environment would enhance possibilities of natural and/or induced restoration of the range (Tietema *et al.* 1991). If reseedling is considered, then it is necessary to study the dormancy patterns of seeds (dispersal units and caryopses) of such grasses in greater detail.

The rainfall pattern of South Eastern Botswana can be characterized as a semi-arid (average 500 mm p.a.) summer rainfall, with a large variation among years and within seasons (Vossen 1988). If rains occur early in the season (September or October) germination of indigenous grasses in the field is spread out over several rainfall events,

Correspondence: Dr E. M. Veenendaal, Department of Ecology and Ecotoxicology, Faculty of Biology, Free University, De Boelelaan 1087, 1081 HV Amsterdam, The Netherlands.

while if the rainfall season starts late (November), field germination appears to be concentrated (Veenendaal 1991).

Angevine & Chabot (1979) have described a drought avoidance syndrome for species from semi-arid regions. This syndrome includes a high innate dormancy and an after-ripening period for seeds, so that germination before the next wet season can be avoided. Hypotheses can be put forward, that seeds from indigenous grasses in South Eastern Botswana have: (i) a high innate dormancy in order to avoid germination during the season in which they are produced; (ii) a high heterogeneity for dormancy, which ensures that dormancy is released in such a way, that the seed population produced by each plant is able to utilize several germination opportunities.

Seeds need to be exposed to moisture for a certain time, before the germination process becomes irreversible (Bewley & Black 1978). The induction time of seeds in semi-arid areas has been shown to influence their emergence in wet-dry cycles (Elberse & Breman 1989, 1990; Frasier *et al.* 1984, 1985, 1987). Field germination in semi-arid areas is triggered by a minimum amount of rainfall (Ernst & Tolsma 1988) which, in Botswana amounts to *circa* 20 mm (Veenendaal 1991). This quantity probably increases the soil moisture sufficiently for seeds to overcome their induction time. Subsequently it may also ensure a sufficient amount of soil moisture for the survival of the seedlings. The induction time of seeds thus functions as an adaptation to semi-arid conditions. In South Eastern Botswana, rainfall is particularly variable early in the season with showers often followed by long dry spells (Vossen 1988). Seeds of indigenous grass species from South Eastern Botswana should have an induction time of sufficient length to prevent them from germinating after small rainfall events.

The dispersal strategy of the plant may influence its dormancy pattern. In theory, plants which disperse their seeds over a larger distance could show a lower degree of dormancy, than those of which the seeds remain closer to the parent plant (Venable & Brown 1988) as they are less prone to intraspecific competition. Seeds are dispersed from the plant either as naked caryopses or with a surrounding dispersal structure (W. H. O. Ernst *et al.* submitted). Dormancy may either be regulated through the caryopsis itself or through the surrounding structure (Nikolaeva 1977; Simpson 1990) which may modify the quality and quantity of penetrating irradiation, the uptake of water, the gas exchange, or the effect of chemical inhibitors (Bewley & Black 1982; Tolsma 1989). The dispersal strategy of the species may therefore also influence its dormancy mechanism.

The aims of the present study were: (i) to study innate dormancy patterns and ripening of seeds (dispersal units and/or caryopses) of indigenous grass species from South Eastern Botswana and compare these patterns with the dormancy syndrome described for plants in semi-arid areas; (ii) to identify some of the mechanisms behind dormancy; particularly the possible role of the dispersal unit structure, and (iii) to study the induction time for germination of different species.

MATERIALS AND METHODS

Ripe dispersal units of a number of common indigenous grasses were collected directly from plants in a savanna area 45 km south east of Gaborone during the rainy seasons; 1987/1988, 1988/1989 and 1989/1990. Due to the occurrence of possibly independent seasonal populations within each grass species (cf. Ernst & Tolsma 1988) we have used the neutral term 'accession' instead of the well-defined term 'population'. The dispersal units were stored at room temperature in the laboratory in open plastic bags. Table 1 gives the

Table 1. Accessions of dispersal units and caryopses of different grass species from a savanna in South Eastern Botswana. (A = caryopsis surrounded by floret structures in small spikelet (1-2 florets); B = caryopsis within floret structures and part of a large spikelet; C = naked caryopsis)

Species	Collection date		annual/ perennial	type of dispersal unit	used in experiment	Relative habitat preference	
	month	year				light	moisture
<i>Aristida congesta</i> Roemer & Schultes	2	1988	annual/perennial	A	1	open	dry
	5	1988	annual/perennial	A	1	open	dry
	2	1989	annual/perennial	A	1	open	dry
	5	1989	annual/perennial	A	1	open	dry
	2	1990	annual/perennial	A	2	open	dry
<i>Aristida stipitata</i> Hackel	5	1989	perennial	A	1	open/shaded	moist
	2	1988	annual	A	1	open/shaded	moist
<i>Chloris virgata</i> S. w.	5	1988	annual	A	1	open/shaded	moist
	2	1989	annual	A	1	open/shaded	moist
<i>Cynodon dactylon</i> (L.) Pers.	2	1988	perennial	A	1	open	moist
	5	1988	perennial	A	1	open	moist
<i>Eragrostis rigidior</i> Pilger	2	1989	perennial	C	1	open	dry
	5	1989	perennial	C	1	open	dry
<i>Eragrostis superba</i> Peyr	4	1989	perennial	B	1	open	moist
	3	1990	perennial	B	2	open	moist
<i>Heteropogon contortus</i> (L.) Roemer & Schultes	4	1989	perennial	A	1	open	moist
	3	1989	perennial	A	1	open	dry
<i>Rhynclytarium repens</i> (Willd.) C.E. Hubb. <i>Schmidtia pappophoroides</i> Steudel	3	1989	perennial	A	1	open	moist/dry
	2	1990	perennial	A	2	open	moist/dry
<i>Tragus berteronianus</i> Schultes	12	1987	annual	A	1,3	open	dry
	2	1988	annual	A	1,3	open	dry
	1	1989	annual	A	1,3	open	dry
	3	1989	annual	A	1,3	open	dry
	2	1990	annual	A	2	open	dry

accessions of seeds of different species used in this study, together with information on their method of seed dispersal, life history and ecological requirements for light and moisture.

Experiment 1

Seeds (dispersal units and/or caryopses) of the collections of 1987/1988 and 1988/1989 of 10 species (Table 1) were regularly tested for dormancy under standard conditions in the climate chamber (12 h day/night light and 30/15°C day/night temperature regime). This treatment is not necessarily the optimum temperature and light regime for all species, but is in accordance with most reported optima for species from the drier parts of Southern Africa (e.g. Smith 1971; Van Niekerk & Wasserman 1976; Burger *et al.* 1979; Dannhauser 1982; Ernst & Tolsma 1988; Tolsma 1989). Dispersal units were tested in petri dishes on wet filter paper (three petri dishes per species and treatment, with between 25 and 100 seeds per petri dish depending on seed availability). Seeds were tested during June/July (midwinter) following the rainfall season and during December/February (midsummer) and in some cases June/July of following seasons. For each test new dispersal units were taken from the collections. Dispersal units were incubated for 3 weeks and were considered to have germinated, when the radicle and plumule were clearly visible. This may result in delay of up to a day in the registration of germination in those species in which the view of the caryopsis is obscured by thick or hairy surrounding structures (in this study: *Eragrostis superba*, *Heteropogon contortus*, *Rhyncelytrium repens* and *Schmidtia pappophoroides*). At the end of each experiment the remaining ungerminated dispersal units were checked for the presence of caryopses and visually inspected for viability. At this stage all caryopses attacked by fungi or affected by lysis were discarded as non-viable. Visually healthy caryopses were subsequently tested for viability with a standard tetrazolium chloride test (International Seed Testing Association 1985). Caryopses were considered viable, if the embryo was coloured bright red and the endosperm light pink to bright red. Uncoloured and purple coloured caryopses were discarded as dead or affected by bacteria or fungi. In cases where visual tests and tetrazolium tests gave the same results, only spot checks were taken during later trials.

Experiment 2

The effect on dormancy of the surrounding dispersal structure versus the naked caryopsis and pre-exposure of the dispersal unit/caryopsis to imbibition and high temperature was tested for accessions of four species (*Aristida congesta*, *Eragrostis superba*, *Schmidtia pappophoroides* and *Tragus berteronianus*) with different dispersal unit types (Table 1). Caryopses were separated by gently rubbing the dispersal units between two layers of fine sandpaper. Dispersal units and caryopses were pre-treated by either (a) exposing them to 50°C for 72 h, (b) imbibition in H₂O for 24 h and left to dry for at least 3 days, or (c) no pre-treatment (control). Afterwards the dispersal units and caryopses were exposed to the same germination test conditions as described in experiment 1.

Experiment 3

Dormancy release of dispersal units and caryopses were compared within *T. berteronianus*, a species with a zoochoric dispersal pattern (due to the structure of the surrounding spikelet, Ernst & Tolsma 1988) and a high initial seed dormancy. Caryopses of four accessions of different ages were separated as in experiment 2, and the testing procedure was the same as in experiment 1.

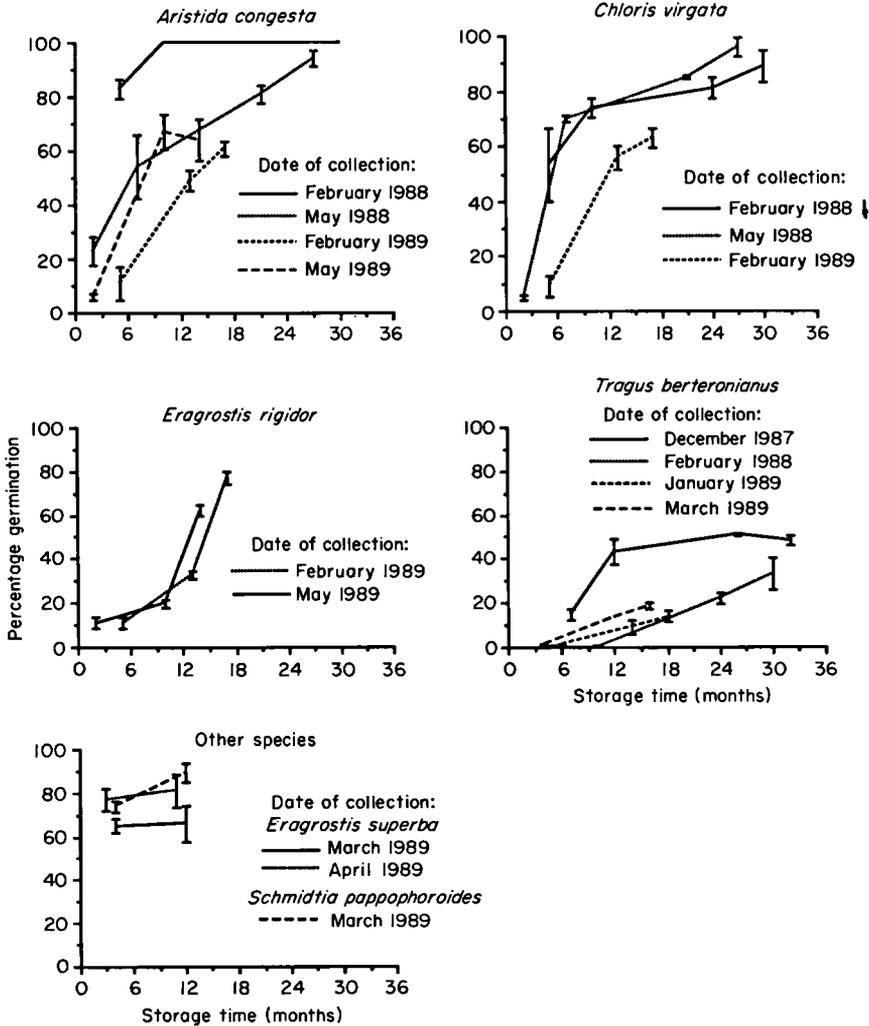


Fig. 1. Germination percentage of dispersal units stored under laboratory conditions for various lengths of storage time (error bar = ± 1 SE, n = 3).

RESULTS

Experiment 1: comparison of accessions within and between seasons

In Figure 1 germination percentages at the end of the test after 3 weeks incubation are given for the dispersal units of different accessions of seven species. Most accessions show a low germination percentage for fresh dispersal units, often less than 10%, while dormancy is released to a significant extent after 6–12 months of storage. Within species comparison shows that differences in dormancy release can be observed between accessions from within the same season. Differences within the same season can be very high as in *Aristida congesta* with 83% and 44% germination after 5 months of storage for the accessions of February and May 1988, respectively. This difference may last for more

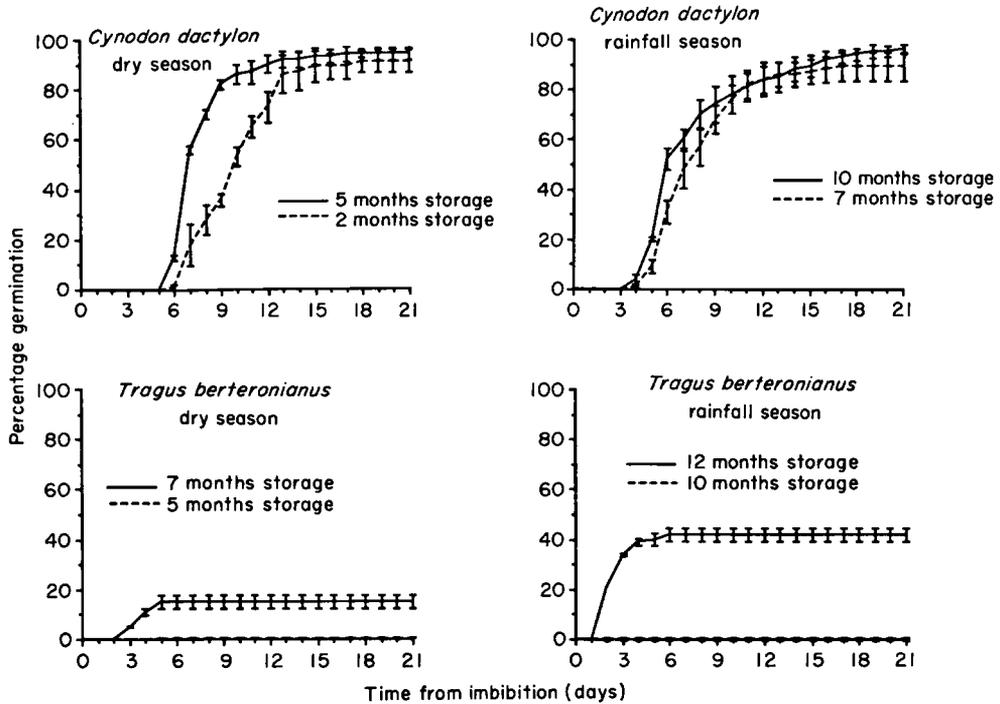


Fig. 2. Part 1

than 2 years, as demonstrated for *Tragus berteronianus*, where the release of dormancy was zero for the accession of February 1988 and 30% for the accession of December 1987 for 10 months and remained still different after 30 months of storage. Such variation in release of dormancy, however, was also very species specific, with no significant difference in *Chloris virgata* for the accessions of February and May 1988 and small differences in *Eragrostis superba*, in contrast to the great differences in *A. congesta* and *T. berteronianus*.

Release of dormancy between accessions from different seasons can be pretty high as in *A. congesta*, where the accession of February 1988 had no dormancy after 9 months of storage, while the accession of February 1989 had still a dormancy of 60%. In contrast, the accessions of May 1988 and May 1989 did not show any difference after 9 months. In *C. virgata* the between-years difference was highest after 5 months (50%) and diminished to 18% after 12 months of storage.

Particularly high germination percentages were found for dispersal units of *Cynodon dactylon* (accessions Feb '88, 95%; May '88, 93%; April '89, 89%; results not shown in Figure 1), when tested during the first dry season after collection. This was also the case for naked caryopses of *E. superba* and *S. pappophoroides* (both more than 70%). Field observations of seed dispersal and germinating seedlings indicated however, that caryopses of the latter two species are dispersed within the spikelet and are not released separately. Dispersal units of single accessions of *Aristida stipitata* and *Heteropogon contortus*, showed 100% dormancy shortly after collection, but lost their dormancy almost completely within 6 months.

Comparisons between germination rate and induction time (from start of imbibition to germination) during dormancy release are shown in Figure 2. The germination characteristics are shown for early and late season accessions of five species, either from the season

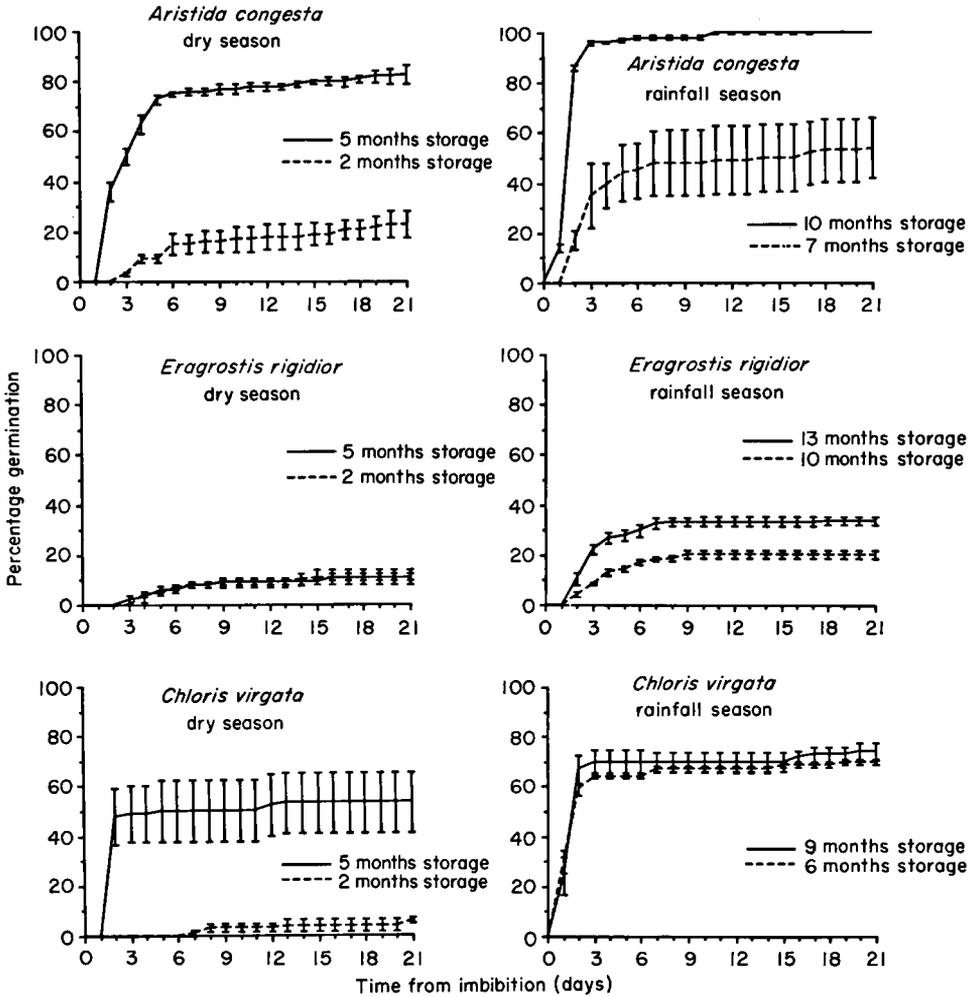


Fig. 2. Part 2

Fig. 2. Dormancy release of early and late accessions of caryopses (dispersal units) during the first dry and wet season after collection (error bar = ± 1 SE, $n=3$).

'87/'88 (*A. congesta*, *C. virgata*, *C. dactylon*, *T. berteronianus*) or '88/'89 (*E. rigidior*). Results from the dry season after collection and the subsequent rainfall season are compared. The induction time for germination varies among species and is dependent on the state of dormancy, generally decreasing with the length of storage. Accessions of *A. congesta* showed an induction time from 1 to 2 days during the dry season test, while in the test carried out during the rainfall season, this time decreased to 1 day or less. In *C. virgata* induction time varied initially between 1 and 6 days while in the rainfall season test it decreased to less than a day for both accessions. For *E. rigidior* induction time changed from between 2 and 3 days to 1 day but the percentage of germination did not achieve more than 35%. Dispersal units of the early accession of *T. berteronianus* showed a reduction of induction time by one day while the late accession remained dormant. *C.*

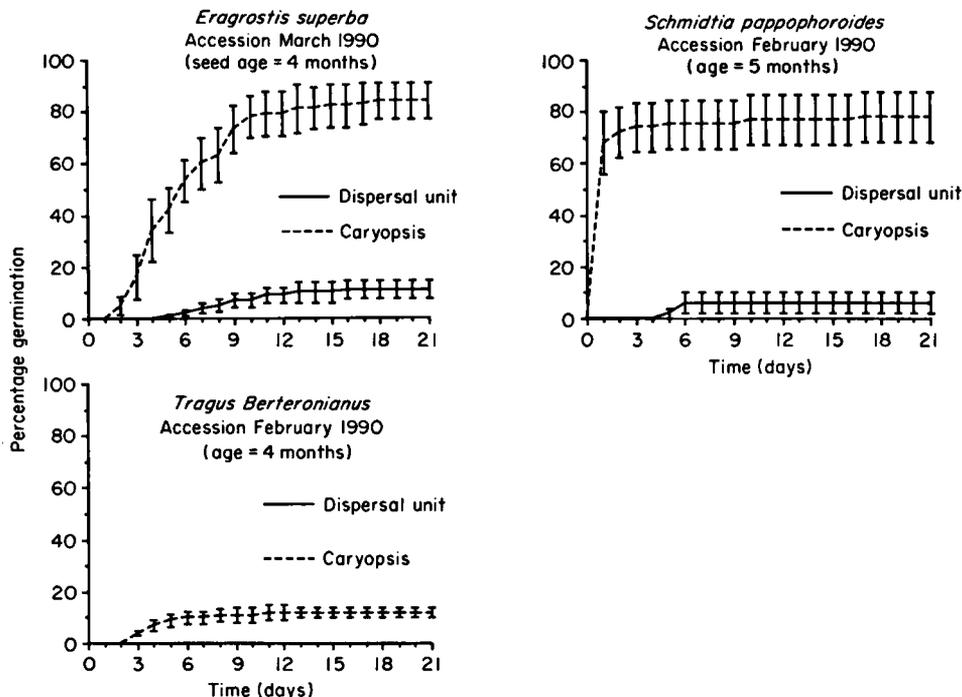


Fig. 3. Differences in germination between dispersal units and naked caryopses of three savanna grass species (error bar = ± 1 SE, $n=3$).

dactylon, which did not show dormancy, nevertheless showed a reduced induction time during the second test. During later trials induction time either remained the same (*A. congesta* and *C. virgata*) or reduced further (*E. rigidior*, to 1 day). The induction time of *T. berteronianus* remained variable between 1 and 2 days.

Experiment 2: comparison between dispersal units and naked caryopses

Imbibition or exposure to higher temperature did not influence the outcome of the germination tests of dispersal units and caryopses of the tested species, so that only the results from the control group are presented. Removal of the glumes from the caryopsis significantly increased germination in all species tested. The total dormancy of *A. congesta* caryopses could not be determined, as the removal of the glumes made caryopses of this species very vulnerable to fungal attack. Caryopses either germinated or decayed. Germination occurred in 20% of the dispersal units (accession February '90, tested after 4 months). Germination results for the other three species are shown in Figure 3. Naked caryopses germinated to an essentially higher level than complete dispersal units varying from 0, 6 and 18% in dispersal units of *T. berteronianus*, *S. pappophoroides* and *E. superba*, respectively to 12, 74 and 82% in naked caryopses. The dispersal structure influenced both the induction time and the overall germination percentage. Caryopses of *E. superba* and *S. pappophoroides* showed a low dormancy in this experiment, while caryopses of *T. berteronianus* still showed a high dormancy. Caryopses of *S. pappophoroides* from the accession in experiment 2, were also tested immediately after collection and then showed a high initial dormancy of 97%.

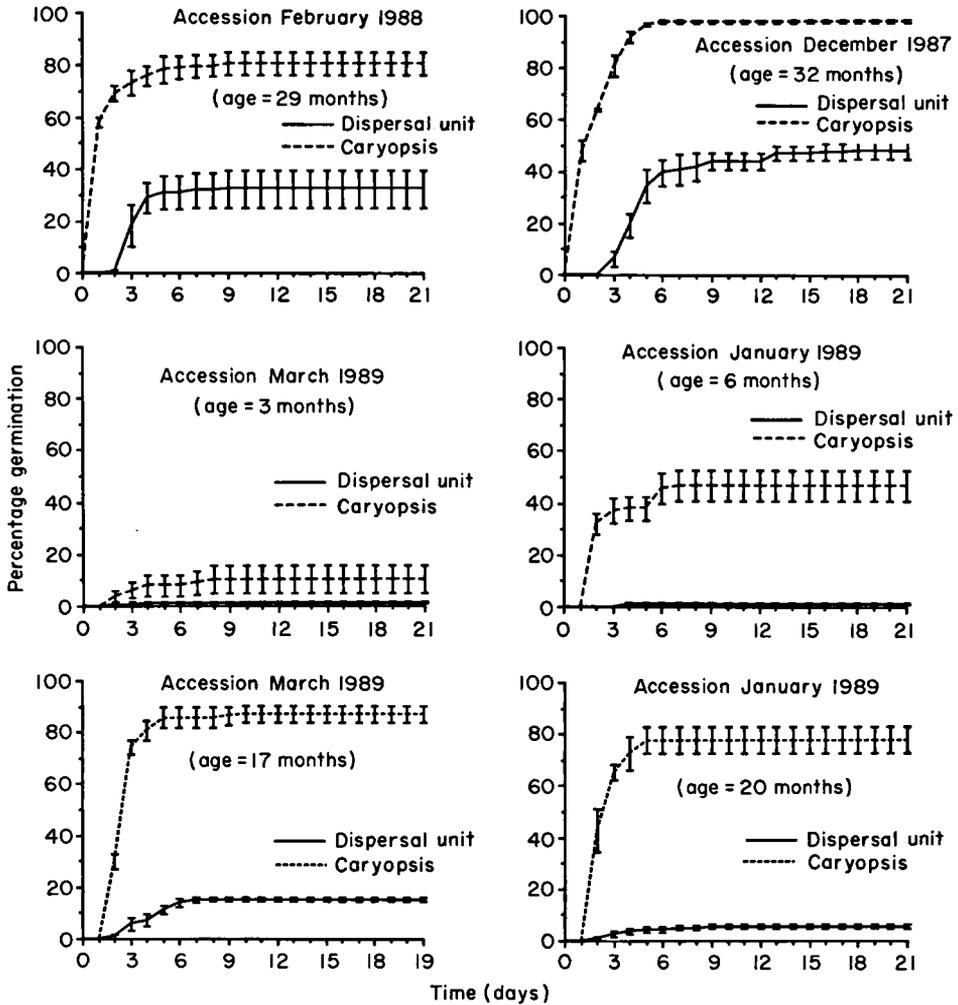


Fig. 4. Differences in dormancy release between dispersal units and naked caryopses of *Tragus berteronianus* (error bar = ± 1 SE, $n=3$).

Experiment 3

The dispersal unit and caryopsis of *T. berteronianus*, a species with a zoochoric dispersal pattern, showed a decreasing dormancy of the caryopsis over time. Caryopses from 3-month-old dispersal units germinated to 10%, while caryopses from 32-month-old dispersal units germinated to almost 100% (Fig. 4). After 32 months complete dispersal units still showed a dormancy of 60%. Caryopses dormancy was thus released much quicker than the dormancy effect caused by the surrounding floret/spikelet structures, if the seeds are stored under room conditions.

DISCUSSION

Initial dormancy appears to be a general feature of grass seeds of different species in semi-arid ecosystems, for example the Sahel (Elberse & Breman 1989) and Northern Australia

(Mott 1978). In this study dispersal units of most accessions showed an initial innate dormancy and a subsequent release of dormancy over time and are thus also characterized by the drought avoidance syndrome as described by Angevine & Chabot (1979). Exceptions were dispersal units of *C. dactylon* and naked caryopses of *E. superba* and *S. pappophoroides*. Dispersal units of *C. dactylon* remained attached to the inflorescence well into the dry season (personal observation by the authors) which in itself may be enough to avoid untimely germination. For *E. superba* and *S. pappophoroides* only naked caryopses were tested in experiment 1 because it was thought, that these would be released by the spikelet. This however was found not to be the case under field conditions. Whole dispersal units of both species showed a higher initial dormancy (Fig. 3) and in this respect, appeared to be not different from other species. The variation in level of dormancy between different accessions within one species is often considerable. Seed quality could be a cause of such a variation. Seed accessions collected from different periods during the year may differ in their average weight. Ernst & Tolsma (1988) reported smaller average weight for seeds from later accessions of *Cenchrus ciliaris*, *Chloris virgata* and *Tragus berteronianus*. Smaller caryopses showed a tendency towards higher dormancy. Environmental factors during the seed development on the parent plant can cause differences in dormancy patterns of different accessions from the same plants/populations (van der Vegte 1978). Late accessions of caryopses of the savanna grasses are exposed to different rainfall and temperature regimes during their ripening process on the plant, compared to early accessions; also subsequent storage may influence dormancy patterns. Exposure of dormant seeds to moisture may increase dormancy (Groves *et al.* 1982; Elberse & Breman 1989; Ernst & Tolsma 1988). Seeds thus show a considerable phenotypic plasticity.

Seed accessions of the same species, but of different geographical regions can have different germination characteristics in relation to their environment (Groves *et al.* 1982; Hacker & Ratcliff 1989). This could also result in genetic differentiation. Within populations from the same area genetic differentiation could also occur in relation to microsite adaptation and flowering time. Variation in the local redistribution of rainfall could easily induce flowering differences and subsequently introduce genetic differences in seed accessions from different time periods. In other words, different accessions could have been sampled from different genetic pools.

Almost all accessions, irrespective of their life history have a remaining percentage of dormant caryopses, which may ensure survival especially for annuals, in years of extremely low or variable rainfall. The annual *T. berteronianus* has a particularly high proportion of dormant caryopses. The species is characteristic of drier, more exposed areas and most of its caryopses remain at the site of dispersal, resulting in a seedbank with high densities of seeds (despite its zoochoric dispersal mechanism; W. H. O. Ernst *et al.* submitted). In such a situation a dormancy pattern enabling the formation of a long-term seedbank is expected (Grime 1979; Venable & Brown 1988). Field observations at the research site over a period of four rainfall seasons indicate a much larger fluctuation in the populations of this species than that of annuals from more shaded moister habitats such as *Chloris virgata*. This species is dispersed by wind and shows a low long-term dormancy. However the differences in dormancy between species of drier and wetter habitats do not always contrast. For instance, dispersal units of *C. virgata* germinate at the same rate as those of *A. congesta*, an annual/perennial species of open drier habitats. In this case both species are wind dispersers and may have seedbanks with a lesser seed density; in years of normal rainfall a large proportion of plants of *A. congesta* survives till the next season (E. M. Veenendaal & Modise, unpublished results). In addition it should be taken into

account in the assessment of habitat conditions that, due to differences in physiological adaptation of species, for instance different soil moisture and temperature regimes are experienced as similar by these species.

The induction time of germination of dispersal units is not a fixed character but changes both among accessions of the same species, as with ripening of the seeds. Studies by Elberse & Breman (1989; 1990) and Frasier *et al.* (1987) indicate a relative advantage of slower germination under less reliable rainfall. Early season rainfall conditions in Botswana may favour seeds with a longer induction time. Later in the season when rainfall is more reliable, a faster germination will give the seedling an advantage in inter- and intraspecific competition (Kadmon & Shmida 1990). The changes in germination patterns found among seeds of different species in this study show, when they are stored under laboratory conditions, a reduction in induction period over time. It can be expected that similar patterns will occur in seeds that lose their dormancy under natural conditions.

In relation to the seed dispersal strategy, different mechanisms behind dormancy can be identified. *Eragrostis rigidior*, which releases most of its seeds as caryopses shows a dormancy pattern completely controlled by the caryopsis. In other studied species which release their dispersal units as spikelet or enclosed by palea and lemma, the outer hull plays a role in the dormancy pattern. This can be either physical or chemical. For Australian *Aristida* species, the importance of the outer hull as a physical barrier has been shown (Mott 1974; Mott & Tynan 1974; Brown 1982). Although leachates have been considered, Tolsma (1989) has shown, for *Cenchrus ciliaris*, *Panicum maximum*, *Tragus berteronianus* and *Urochloa trichopus*, that concentrations of water soluble phenolics are low and that the leachate does not affect germination in these species. Also in *C. ciliaris* the importance of the fascicle in dormancy has been shown (Hacker 1989) and the intact connection between the caryopsis and scutellum appears to play a role in the dormancy of the dispersal unit (observations by the authors). The example of *T. berteronianus* in this study shows, that more than one dormancy mechanism can be involved in the dormancy pattern. In this case, the effect of the caryopsis-related dormancy is more quickly reduced over time, than the effect of the dormancy induced by the surrounding structure.

In early accessions of dispersal units from indigenous species in this study, when stored under room temperature conditions, there is generally a sufficient reduction of dormancy over time for these accessions to be used in reseeded experiments during the next season. The species tested in this study can also be stored for longer periods, without losing viability, in the case of *E. rigidior* and *T. berteronianus* for more than 10 years (W. H. O. Ernst, personal observation). Caryopses of many grasses from semi-arid areas will normally survive storage for several years (Silcock *et al.* 1990; Tolsma 1989). Removing the caryopsis from the dispersal unit, will in most species increase germination, but is not recommended for *Aristida* species because of the damage to the caryopsis. It should be clear from the effects of the surrounding structures of the caryopses on the dormancy of the dispersal unit, that information on the dispersal strategy of the species is an important aspect of the study of ecological aspects of seed dormancy. The differences in dormancy between different accessions show, that conclusions on seed dormancy strategies of species cannot be based on single accessions only.

ACKNOWLEDGEMENTS

Dr J. M. Dangerfield and Dr B. Riddoch made useful comments on an earlier draft of this paper. Mr G. S. Modise is kindly acknowledged for his assistance with the collection of the

seeds, while Mr M. M. Kebakile, M. Mpho, and M. Molale assisted with the germination experiments. This research was funded by The Free University of Amsterdam, The University of Botswana and the Swedish Assistance for Co-operation in Research Organization.

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