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Germination characteristics of tropical and sub-tropical rangeland species

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Abstract. A study was made of the germination characteristics of a broad spectrum of rangeland species by studying their behaviour under different conditions. Seeds of common species (both native and exotic) were collected from tropical (north-east Queensland) (36 species) and sub-tropical areas (south-east Queensland) (47 species). The seeds were exposed to three storage treatments: in a shade-house for 60 months, in a seed store (tropical collection) or freezer (sub-tropical collection) for 60 months, or in an oven with fluctuating temperatures (25/60°C) for 3 (tropical collection) or 4 (sub-tropical collection) months. Germination was tested during and after storage under standard conditions of 30/25°C (tropical collection) or 30/20°C (sub-tropical collection) with light during the 12-h period of higher temperature. In addition, germination of the sub-tropical collection was tested in the dark and at lower temperature (20/10°C). The species were divided into groups on the basis of changes in germination during storage in a shade-house or in a seed store or freezer. The species showed a wide range of germination behaviour, changes during storage, and responses to germination conditions. Differences in the responses of seed lots of the same species in the two collections show that care is needed when extrapolating results from one experiment to other collections and regions.

Additional keywords: botanical groups, exotic, native, storage, viability.

Introduction

Germination is a critical phase in the life cycle of plants and needs to be timed so that the probability of seedlings encountering poor growing conditions in the period after germination is reduced (Angevine and Chabot 1979). In tropical rangelands this period is during the summer growing season and the optimum time for seeds to germinate is early in the growing season to gain resources for growth and reproduction but not so early that survival is unlikely (Rathcke and Lacey 1985). The situation is similar in the sub-tropics but these areas have greater amounts of winter rain and there may be opportunities for successful establishment at other times, at least in some years.

Timing of germination is influenced by the germination and dormancy characteristics of seeds but there is little or no information on these characteristics for many rangeland species. Comparative studies (e.g. Grime *et al*. 1981; Morgan 1998; Clarke *et al*. 2000) using a small number of treatments are an economical means of obtaining such information and there have been some studies of species from Australian rangelands (Silcock *et al*. 1990; Jurado and Westoby 1992; McIvor and Howden 2000). Although these studies do not replicate the sometimes complex environmental fluctuations that a germinating seed would experience in the field, they provide useful generalisations for a large number of species without the cost of more detailed studies which of necessity are limited to a smaller number of species (e.g. Grime *et al*. 1981).

The past comparative studies were extended to a larger number of species in this study where we examined seed of native and exotic species that are common in semiarid rangelands. Seed was collected from tropical (Townsville-Charters Towers) and sub-tropical (south-east Queensland) regions with 36 and 47 species in the respective collections of which 12 species were common to both collections. The species were mainly herbaceous but included two common woody shrubs. The overall aim was to determine the germination characteristics of a broad spectrum of species by studying their behaviour under different conditions. Specific objectives were to measure:

(1) Changes in germination over 60 months under different storage conditions. Seeds live longer when stored under low temperature and low humidity so storage under these conditions was used to assess potential longevity. Seeds were also stored under ambient conditions to obtain a guide to likely longevity under natural conditions – these are not equivalent to field conditions but enabled a comparison of species.
(2) Impacts of short periods of high and fluctuating temperatures. Surface soils can reach high temperatures and likely impacts

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of such temperatures were examined by storing seeds in an oven with a daily temperature range of 25/60°C.

(3) Germination in the dark and at low temperatures.

Materials and methods

Species and collection sites

Seeds were collected in two regions; a tropical collection from the Townsville-Charters Towers district in north-east Queensland, and a sub-tropical collection from the Brisbane, Crows Nest and Mundubbera districts of south-east Queensland.

The Townsville-Charters Towers district is typical of the seasonally dry tropics, which are characterised by a hot 'wet' season and a warm 'dry' season. Average annual rainfall is 1160 mm at Townsville and 660 mm at Charters Towers with 84% falling during the summer wet season (December–April). The average maximum temperature during January is 31°C and average minimum during July is 14°C at Townsville; the equivalent values at Charters Towers are 34 and 11°C. The tropical collection consisted of seeds of 36 species (one seed lot per species) collected between April 1987 and November 1988 (Table 1).

The Brisbane, Crows Nest and Mundubbera districts are typical of the moist coastal and drier sub-coastal areas of the sub-tropics. Average annual rainfall is 1150 mm at Brisbane, 850 mm at Crows Nest and 720 mm at Mundubbera with from 51% (Crows Nest) to 60% (Brisbane) falling during December–April. Average maximum temperatures in January range from 28°C at Crows Nest to 32°C at Mundubbera. The average minimum during July is 10°C in Brisbane but values are much lower in the two inland districts (4°C at Crows Nest and 6°C at Mundubbera) and frosts are common in both districts. Seeds of 47 species were collected between January 1998 and March 2000. Two independent samples were collected for four species giving a total of 51 seed lots.

Seed collection and preparation

In both regions, fully mature dispersal units (hereafter referred to as seeds) were collected directly by hand from at least 10 plants and usually from more than 50 plants. All seeds in a seed lot were collected on the same day. After collection, the seeds were air-dried, cleaned and where necessary the awns removed (*Heteropogon contortus*, *Heteropogon triticeus*, *Themeda triandra*). Botanical nomenclature is according to Henderson (2002). Abnormal and empty seeds were discarded and multiple samples of 50 apparently sound seeds were counted and placed in individual packets. Seed weights were measured for four (tropical collection) or six (sub-tropical collection) of these samples of 50 seeds.

Storage treatments

Although these species grow together in mixed swards they flower and set seed at different times during the year. Comparing species that mature at different times poses some problems with storage treatments. If all seed lots are assembled before commencing the storage treatments then the seeds are of variable age at commencement and this can impact on the results. Alternatively, if seeds are placed in the storage conditions immediately after collection they will be of similar physiological age but they may be exposed to different conditions during storage – this will be particularly so for storage under ambient conditions but could even occur under controlled conditions. We chose to commence storage immediately after collection because any differences in storage conditions are likely to have a smaller impact on results than variable seed ages at commencement.

Seeds packets were allocated to one of three storage treatments – shade-house, seed store or oven for the tropical collection; shade-house, freezer or oven for the sub-tropical collection. The seeds were placed in their respective storage treatments within 2 weeks of collection. For each storage treatment there were four replicates of each seed lot with all four replicates of a storage treatment stored in one location. As Morrison and Morris (2000) have pointed out it would have been more appropriate if the replicates had been stored in separate locations. The number of packets of each seed lot placed in each storage treatment depended on the various research questions being investigated.

Seeds in the tropical collection were stored at the CSIRO Davies Laboratory, Townsville, and for the sub-tropical collection at Indooroopilly, Brisbane. Average temperatures at Townsville (maximum/minimum) range from 31/24°C in January to 25/14°C in July, and average relative humidity (3 p.m.) from 51% in July to 68% in February. Average temperatures in Brisbane (maximum/minimum) range from 29/21°C in January to 20/10°C in July, and average relative humidity (3 p.m.) from 45% in August to 61% in February. Conditions in the shade-houses were close to ambient. The seed store for the tropical collection was maintained at 5°C and a relative humidity of 35%. Seeds of the sub-tropical collection allocated to freezer storage were placed in a desiccator containing ~10 g of P_2O_5 on a watch glass for 3 h to reduce moisture contents to ~5%, then transferred to sealed McCartney bottles and stored in a domestic freezer at –18 to −20°C. Seeds allocated to oven storage were stored in an oven with a diurnal temperature fluctuation of 25/60°C. Apart from the freezer treatment for the sub-tropical collection all seed was stored in paper envelopes.

Seed tests for germinability and viability

Each germination test consisted of four replicate seed packets (each with 50 seeds) for a total of 200 seeds except for a few occasions when there were only sufficient seeds for three replicates. At the time of placement, only packets of seeds from the shade-house were tested. Three (tropical collection) or 4 (sub-tropical collection), 12, 24, 36, 48 and 60 months after placement, replicate seed packets of each seed lot were retrieved from the shade-house (both collections), seed store (tropical collection) and freezer (sub-tropical collection) and tested for germination. The seeds stored in the oven were tested after 3 (tropical collection) or 4 (sub-tropical collection) months only.

Seeds were germinated on filter paper in Petri dishes in a germination cabinet with a diurnal temperature range of 30/25°C in Townsville and 30/20°C in Brisbane, both with a 12-h day. Optimal conditions for germination are not known for many species but these temperatures are in the optimum range for many tropical species (Ellis *et al*. 1985). Germinated seeds were counted and removed daily for 14 days. Any seeds which did not germinate during that period were dissected and classified as

Table 1. Collection site, dispersal unit weight, initial viability and germinability (as a percentage of total seeds) (mean ± s.e.) for seeds of 36 tropical herbaceous and woody species

Species	Collection site	Dispersal unit weight (mg)	Initial Viability (%)	Initial Germinability (%)
Native annual (or short-lived perennial) grass				
Dactyloctenium radulans (R. Br.) P. Beauv.	Charters Towers	0.3	99 ± 0.9	1 ± 0.5
Sporobolus australasicus Domin	Charters Towers	0.1	100 ± 0.0	1 ± 0.5
Tragus australianus S. T. Blake	Charters Towers	1.2	56 ± 2.7	0 ± 0.0
Exotic annual (or short-lived perennial) grass				
Dactyloctenium aegyptium (L.) Willd.	Townsville	0.2	100 ± 0.5	0 ± 0.0
Digitaria ciliaris (Retz.) Koeler	Charters Towers	0.9	95 ± 1.6	0 ± 0.0
Eleusine indica (L.) Gaertn.	Townsville	0.6	100 ± 0.0	1 ± 0.7
Urochloa panicoides P. Beauv.	Charters Towers	1.9	98 ± 1.2	0 ± 0.0
Native perennial grass				
Bothriochloa ewartiana (Domin) C. E. Hubb.	Charters Towers	0.7	78 ± 3.1	1 ± 0.7
Chrysopogon fallax S. T. Blake	Charters Towers	6.4	92 ± 2.0	56 ± 3.5
Heteropogon contortus (L.) P. Beauv. ex Roem. and Schult.	Charters Towers	3.9	65 ± 3.6	1 ± 0.7
Heteropogon triticeus (R. Br.) Stapf	Charters Towers	11.4	70 ± 3.4	1 ± 0.5
Sporobolus indicus (L.) R. Br.	Townsville	0.1	99 ± 0.7	8 ± 1.9
Exotic perennial grass				
Bothriochloa pertusa (L.) A. Camus	Charters Towers	0.7	90 ± 2.2	1 ± 0.5
Cenchrus ciliaris L.	Charters Towers	2.8	88 ± 2.4	0 ± 0.0
Melinis repens (Willd.) Zizka	Charters Towers	1.1	75 ± 3.2	37 ± 3.4
Urochloa mosambicensis (Hack.) Dandy	Townsville	1.7	97 ± 1.3	0 ± 0.0
Native annual (or short-lived perennial) legume				
Indigofera linifolia (L. f.) Retz.	Charters Towers	1.8	92 ± 2.0	3 ± 1.2
Indigofera linnaei Ali	Charters Towers	1.2	74 ± 3.3	16 ± 2.5
Sesbania cannabina (Retz.) Poir.	Charters Towers	7.4	100 ± 0.5	7 ± 1.7
Exotic annual (or short-lived perennial) legume				
Crotalaria goreensis Guill. and Perr.	Townsville	7.5	98 ± 1.1	16 ± 2.6
Crotalaria pallida var. *obovata* (G. Don) Polhill	Charters Towers	6.5	100 ± 0.0	58 ± 3.5
Macroptilium atropurpureum (DC.) Urb.	Townsville	16.6	96 ± 1.6	50 ± 3.5
Macroptilium lathyroides (L.) Urb.	Townsville	9.2	100 ± 0.0	3 ± 1.2
Stylosanthes hamata (L.) Taub.	Charters Towers	2.6	70 ± 3.4	1 ± 0.5
Stylosanthes scabra Vogel	Charters Towers	2.3	99 ± 0.9	2 ± 0.9
Native annual (or short-lived perennial) forb				
Abutilon fraseri (Hook.) Hook. ex Walp. subsp. *fraseri*	Charters Towers	2.6	91 ± 2.2	2 ± 1.0
Portulaca oleracea L.	Charters Towers	0.1	100 ± 0.0	0 ± 0.0
Exotic annual (or short-lived perennial) forb				
Amaranthus viridis L.	Townsville	0.5	100 ± 0.0	10 ± 2.7
Argemone mexicana L.	Charters Towers	2.3	100 ± 0.0	0 ± 0.0
Gomphrena celosioides Mart.	Townsville	3.5	100 ± 0.0	1 ± 0.7
Hyptis suaveolens (L.) Poit.	Townsville	5.7	100 ± 0.5	0 ± 0.0
Oxalis corniculata L.	Townsville	0.2	100 ± 0.0	0 ± 0.0
Sida acuta Burm. f.	Townsville	2.4	100 ± 0.0	5 ± 1.5
Sida spinosa L.	Charters Towers	2.3	96 ± 1.5	3 ± 1.1
Exotic woody perennial shrub				
Acacia farnesiana (L.) Willd.	Charters Towers	94.4	100 ± 0.5	7 ± 1.8
Parkinsonia aculeata L.	Charters Towers	51.2	46 ± 3.7	0 ± 0.0

dormant if the embryo and endosperm were firm and intact, or as dead if the tissues were pulpy and had begun to decay (Mott 1978). This gave three classes of seed: germinable, dormant and dead. For the legumes, hard seeds were counted separately but have been included in the dormant class. The number of viable seeds was determined as the sum of germinable and dormant seeds.

Additional tests to determine germination responses at low temperatures and in the dark were made on the sub-tropical collection using seed that had been stored in the shade-house for 12 months. For the low temperature tests, germination was measured at 20/10°C with a 12-h day. For germination in the dark the Petri dishes were kept in cardboard boxes at 30/20°C during the tests apart from the brief periods when seeds were counted in dim light. The Petri dishes were placed in the same germination cabinet as those under normal light conditions.

Data analysis

Species were classified into botanical groups [native and exotic annual grasses, perennial grasses, legumes and forbs; and exotic

Table 2. Collection site, dispersal unit weight, initial viability and germinability (as a percentage of total seeds) (mean ± s.e.) for seeds of 47 sub-tropical herbaceous species

Species	Collection site	Dispersal unit weight (mg)	Initial Viability (%)	Initial Germinability (%)
Native annual (or short-lived perennial) grass				
Chloris truncata R. Br.	Crows Nest	0.3	100 ± 0.0	28 ± 6.5
Eragrostis leptostachya (R. Br.) Steud.	Crows Nest	0.1	100 ± 0.0	32 ± 4.7
Eragrostis sororia Domin	Crows Nest	0.1	24 ± 3.0	9 ± 2.8
Exotic annual (or short-lived perennial) grass				
Bromus catharticus Vahl	Crows Nest	11.8	99 ± 0.7	0 ± 0.0
Digitaria ciliaris (Retz.) Koeler	Brisbane	0.5	76 ± 3.1	35 ± 4.9
Eleusine indica (L.) Gaertn.	Brisbane	0.6	100 ± 0.0	3 ± 1.7
Native perennial grass				
Chloris ventricosa R. Br.	Crows Nest	0.6	100 ± 0.0	32 ± 6.7
Cymbopogon refractus (R. Br.) A. Camus	Crows Nest	2.2	96 ± 1.5	54 ± 5.1
Dichanthium sericeum subsp. *sericeum* (R. Br.) A. Camus	Crows Nest	1.6	100 ± 0.0	27 ± 5.2
Heteropogon contortus (L.) P. Beauv. ex Roem. and Schult.	Mundubbera	1.8	99 ± 0.7	7 ± 2.6
Panicum effusum R. Br.	Crows Nest	0.5	100 ± 0.0	1 ± 0.8
Pennisetum alopecuroides (L.) Spreng.	Crows Nest	1.4	90 ± 3.0	43 ± 7.1
Sporobolus creber De Nardi	Crows Nest	0.1	88 ± 2.3	3 ± 1.7
Themeda triandra Forssk.	Brisbane	3.1	93 ± 1.3	39 ± 3.5
Exotic perennial grass				
Brachiaria decumbens Stapf	Brisbane	5.9	100 ± 0.0	0 ± 0.0
Eragrostis curvula (Schrad.) Nees	Crows Nest	0.3	100 ± 0.0	1 ± 0.7
Panicum maximum var. *maximum* Jacq.	Brisbane	1.2	100 ± 0.0	0 ± 0.0
Panicum maximum var. *trichoglume* Eyles ex Robyns	Crows Nest	1.0	100 ± 0.0	7 ± 2.1
Native annual (or short-lived perennial) legume				
Crotalaria linifolia L. f.	Brisbane	2.7	93 ± 1.8	8 ± 2.8
Glycine sp.	Crows Nest	4.1	94 ± 1.7	4 ± 1.9
Indigofera hirsuta L.	Brisbane	2.4	96 ± 1.6	21 ± 4.2
Indigofera linifolia (L. f.) Retz.	Mundubbera	1.3	89 ± 2.3	40 ± 5.0
Sesbania cannabina (Retz.) Poir.	Brisbane	8.8	53 ± 3.6	17 ± 3.8
Exotic annual (or short-lived perennial) legume				
Chamaecrista rotundifolia (Pers.) Greene	Brisbane	4.7	97 ± 1.1	12 ± 3.3
Crotalaria pallida var. *obovata* (G. Don) Polhill	Brisbane	6.0	95 ± 1.1	32 ± 3.4
Indigofera spicata Forssk.	Brisbane	1.3	87 ± 2.4	6 ± 2.5
Macroptilium atropurpureum (DC.) Urb.	Brisbane	13.0	92 ± 2.0	20 ± 4.1
Macroptilium lathyroides (L.) Urb.	Brisbane	6.3	68 ± 3.3	24 ± 4.3
Tephrosia glomeruliflora Meisn.	Brisbane	14.7	98 ± 1.0	33 ± 4.8
Trifolium repens L.	Crows Nest	1.0	92 ± 1.9	10 ± 3.0
Native annual (or short-lived perennial) forb				
Portulaca oleracea L.	Brisbane	0.1	100 ± 0.0	5 ± 2.2
Portulaca pilosa L.	Brisbane	0.1	99 ± 0.5	8 ± 2.7
Sida subspicata F. Muell. ex Benth.	Brisbane	2.6	100 ± 0.0	2 ± 1.4
Exotic annual (or short-lived perennial) forb				
Amaranthus viridis L.	Brisbane	0.5	100 ± 0.0	47 ± 5.0
Bidens pilosa L.	Brisbane	1.6	97 ± 1.1	93 ± 2.5
Chamaesyce hirta (L.) Millsp.	Brisbane	0.1	61 ± 3.6	57 ± 5.2
Chamaesyce hyssopifolia (L.) Small	Brisbane	0.2	59 ± 3.5	47 ± 5.1
Gomphrena celosioides Mart.	Brisbane	3.2	100 ± 0.0	5 ± 2.2
Lepidium bonariense L.	Crows Nest	0.4	100 ± 0.0	0 ± 0.0
Rapistrum rugosum (L.) All.	Crows Nest	4.8	100 ± 0.0	1 ± 0.7
Sida acuta Burm. f.	Brisbane	2.0	100 ± 0.0	7 ± 2.6
Solanum americanum Mill.	Brisbane	0.4	100 ± 0.0	92 ± 2.8
Tridax procumbens L.	Brisbane	0.8	99 ± 0.7	85 ± 3.7
Verbena bonariensis L.	Crows Nest	0.2	100 ± 0.0	98 ± 1.6
Verbena brasiliensis Vell.	Crows Nest	0.2	100 ± 0.0	64 ± 4.9
Verbena rigida Spreng.	Crows Nest	0.6	100 ± 0.0	5 ± 2.2
Exotic sedge				
Cyperus aggregatus (Willd.) Endl.	Crows Nest	0.6	100 ± 0.0	19 ± 4.0

sedges (sub-tropical) or exotic woody perennial shrubs (tropical)] as given in Table 1 (tropical) and Table 2 (sub-tropical).

Initial viability and germinability

Initial (at placement) percentages of viable and germinable seed of species within botanical groups were modelled by fitting a generalised linear model (GLM) with binomial error and logit link function to the number of viable and germinable seeds relative to the total number of seeds assessed.

Effects of storage in a shade-house and seed store or freezer

The long-term effects of storage in a shade-house or storage in a seed store (tropical collection) or freezer (sub-tropical collection) of species in the botanical groups were modelled by a GLM with binomial error and logit link function to counts of germinable and viable seed over the seven times (0, 3/4, 12, 24, 36, 48 and 60 months) relative to the total number of seeds assessed. Given the lack of replication at the storage stratum, the storage methods within a collection were treated separately.

The species were divided into groups based on changes in germination over 60 months. Each species was allocated to the appropriate group for seeds stored in the shade-house and seed store or freezer. Two criteria were used – germination increased during storage, and germination occurred after 60 months of storage? Germination was considered to increase during storage if the confidence interval of at least one subsequent germination test was larger than, and did not include, the initial mean value. Germination was considered to occur after 60 months of storage if the confidence interval of the final germination test did not include zero. This generated four germination groups:

A – No subsequent germination exceeded the initial value; and final germination = 0.
B – No subsequent germination exceeded the initial value; and final germination >0.
C – At least one subsequent germination value exceeded the initial value; and final germination = 0.
D – At least one subsequent germination value exceeded the initial value; and final germination >0.

Effects of oven storage

Germinability of seeds stored in the oven was compared with germinability of seeds stored in the shade-house and the seed store (tropical) or the freezer (sub-tropical) for the same period. Seeds in the tropical collection were stored for 3 months and those in the sub-tropical collection for 4 months. Percentage germination of species within botanical groups was modelled by fitting a GLM with binomial error and logit link function to the number of germinable seeds relative to the total number of seeds assessed. Given the lack of replication at the storage stratum, the storage methods within a collection were treated separately.

Effects of dark (sub-tropical collection only)

The effect of dark on germination at 30/20°C was assessed by comparing germination of similarly stored seeds (12 months in the shade-house) but germinated at 30/20°C under light or dark conditions. Germinability of species within botanical groups were modelled by fitting a GLM with binomial error and logit link function to counts relative to the total number of seeds assessed. As seeds in the light and dark conditions were germinated in the same cabinet, models included an effect for light/dark germination.

Effects of low temperatures (sub-tropical collection only)

The effect of low temperatures on germination was assessed by comparing germination at 20/10°C with that at 30/20°C for similarly stored seeds (12 months in the shade-house). Germinability of species within botanical groups were modelled by fitting a GLM with binomial error and logit link function to counts relative to the total number of seeds assessed. As seeds germinated at different temperatures were in different cabinets, separate GLM models were fitted for low and high temperatures.

Results

The effect of species within botanical groups was significant in all analyses; however, it was always dominated by the main botanical group effect. Therefore, for simplicity of presentation, only results pertaining to the botanical groups have been presented.

Initial viability and germinability

Tropical collection

Viability of the tropical species ranged from 46 to 100% (Table 1). There were 13 species with less than 95% viable seed. These were mainly perennial grasses with 7 of the 9 native and exotic perennial grasses in this category. In contrast, only 4 of the 18 annual legumes and forbs had viability levels below 95%. Germinability varied from 0 to 58% in the tropical collection with only 10 species having more than 5% germinability and 20 species having 0 or 1% germinable seeds (Table 1). Among the botanical groups, the perennial grasses and annual legumes (both native and exotic) had more than 5% germinability but all other groups were below this level (Table 3).

Sub-tropical collection

Viability of the sub-tropical species varied from 24 to 100% (Table 2) with 15 species from several plant groups having less than 95% viable seed. Exotic perennial grasses and sedge, and native annual forbs had the highest viability, and the native annual grasses had the lowest (Table 3). In general, germinability levels were higher in the sub-tropical collection than in the tropical collection with 33 of the 47 species having more than 5% germinable seeds (Table 2). Apart from the exotic perennial grasses and native annual forbs, all botanical groups had more than 5% germinable seeds (Table 3).

Changes in proportions of viable and germinable seeds with time during storage in shade-house and seed store or freezer

Tropical collection

Viability of seed stored in a shade-house generally declined gradually over time for most botanical groups (Fig. 1*a*). Exceptions to this were the native annual legumes and forbs, and exotic woody shrubs. Germinability was generally low (<20%), especially after 12 months storage (Fig. 1*b*), although

Table 3. Initial (mean ± s.e.) seed viability and germinability (as a percentage of the total seeds) of botanical groups in the tropical and sub-tropical collections

Means followed by the same letter did not differ significantly ($P = 0.05$)

Botanical group	Tropical collection			Sub-tropical collection		
	No. sp.	Viability (%)	Germinability (%)	No. sp.	Viability (%)	Germinability (%)
Native annual (or short-lived perennial) grass	3	78 ± 1.3d	0 ± 0.2e	3	69 ± 1.2f	22 ± 2.6bc
Exotic annual (or short-lived perennial) grass	4	98 ± 0.5a	0 ± 0.2e	3	92 ± 1.0cd	12 ± 1.7d
Native perennial grass	5	81 ± 1.3d	13 ± 0.8b	8	96 ± 0.5b	24 ± 1.3b
Exotic perennial grass	4	88 ± 1.2c	9 ± 0.9c	4	100 ± 0.0a	2 ± 0.7e
Native annual (or short-lived perennial) legume	3	89 ± 1.3c	8 ± 1.1c	5	85 ± 1.0e	18 ± 1.7c
Exotic annual (or short-lived perennial) legume	6	94 ± 0.7b	21 ± 1.0a	7	91 ± 0.7d	21 ± 1.4bc
Native annual (or short-lived perennial) forb	2	95 ± 1.1b	1 ± 0.5e	3	100 ± 0.2a	5 ± 1.3e
Exotic annual (or short-lived perennial) forb	7	99 ± 0.2a	4 ± 0.5d	13	94 ± 0.4c	46 ± 0.9a
Exotic woody perennial shrub	2	73 ± 1.9e	4 ± 0.9d	–	–	–
Exotic sedge	–	–	–	1	100 ± 0.5a	19 ± 4.0bcd

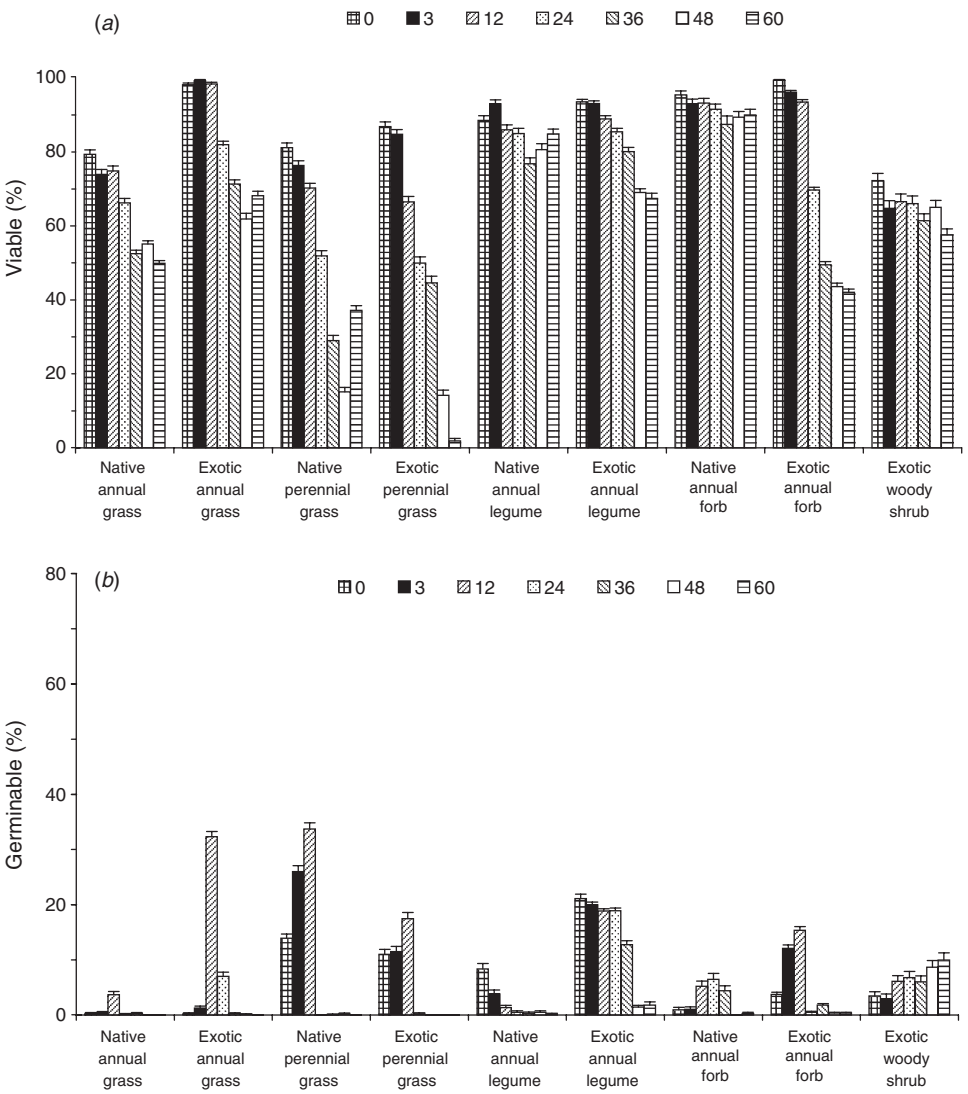

Fig. 1. Changes in (*a*) viability and (*b*) germinability of seeds of botanical groups stored in a shade-house (tropical collection). Standard errors are indicated by error bars.

germinability of exotic annual legumes remained at ~20% for 24 months before declining. When seed was stored in a seed store, viability was maintained over time for legumes, forbs and shrubs but declined gradually for grasses (Fig. 2*a*). Germinability for native annual grasses and forbs was low regardless of time seeds were stored (Fig. 2*b*) but increased for the other grasses.

Sub-tropical collection

Over the first 12 months there was little reduction in viability of seed stored in a shade-house for all botanical groups (Fig. 3*a*). Viability then declined for all groups except the sedge. Germinability was greatest for most botanical groups after 12 months storage (Fig. 3*b*) but fell to zero after 60 months for all groups except the legumes and native annual forbs. For the legumes, forbs and sedge, viability was maintained during storage in a freezer (Fig. 4*a*) but viability of the grasses declined, although the decline was small for the exotic perennial grasses and only occurred after 48 months of storage. Apart from the sedge, germinability was maintained or increased by freezer storage (Fig. 4*b*).

Patterns of germinability change during storage

Average values for changes in the proportions of germinable, dormant and dead seeds for the four groups over the 60 months' storage are shown in Fig. 5.

The numbers of species from each botanical group allocated to the germination groups A–D are shown in Table 4 and the relevant germination group for each species is given in Table 5. In both collections, species from a botanical group were often placed in more than one germination group. There was a significant ($P < 0.001$) relationship between storage regime and germination group for both tropical and sub-tropical collections ($\chi^2 = 20.7$ and 37.9, respectively; 3 d.f.). In the tropical collection fewer species for seeds stored in the shade-house and more species for seeds stored in the seed store were in germination group D than expected. In the sub-tropical collection more species

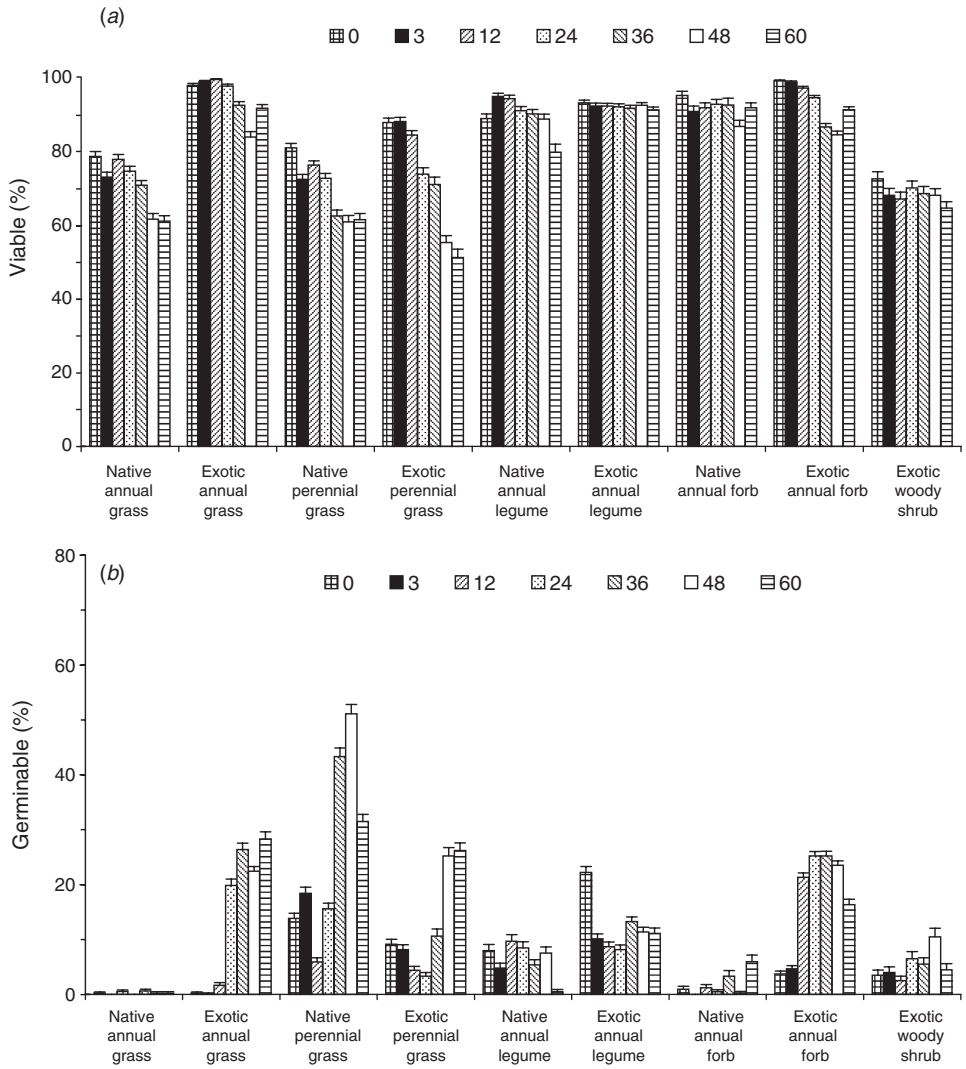

Fig. 2. Changes in (*a*) viability and (*b*) germinability of seeds of botanical groups stored in a seed store (tropical collection). Standard errors are indicated by error bars.

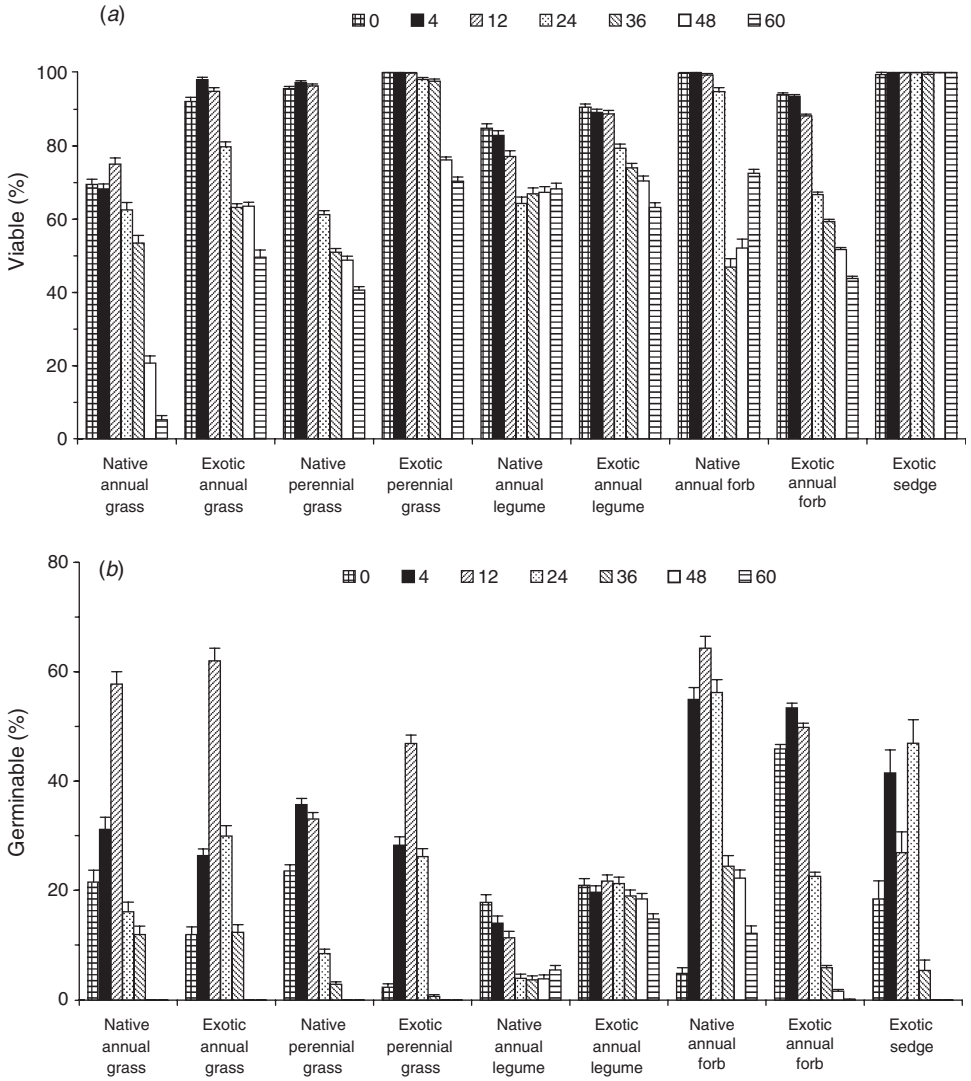

Fig. 3. Changes in (*a*) viability and (*b*) germinability of seeds of botanical groups stored in a shade-house (sub-tropical collection). Standard errors are indicated by error bars.

for seeds stored in the shade-house were in group C and fewer in group D and fewer species for seeds stored in the freezer were in group C and more in group D than expected.

In the tropical collection, most species in the shade-house were in groups A and C (i.e. the final germination = 0). When stored in the seed store, 10 species were in group A but the largest group (17 species) was in group D with another 5 species in group B (i.e. final germination >0). In the sub-tropical collection, most species (60%) were in group C when stored in the shade-house and in group D (51%) when stored in the freezer. Comparing the grasses, more were in group C after storage in the shade-house in the sub-tropical collection (89%) than in the tropical collection (56%).

Impact of oven storage on germination

For both collections, germination of all botanical groups except native annual and perennial grasses (tropical collection) and native annual forbs (sub-tropical collection) was higher after oven storage than after storage in a shade-house (Fig. 6). For the tropical collection, oven storage basically doubled germinability for exotic annual and perennial grasses, legumes and forbs (Fig. 6*a*). Germination was greatest for legumes and least for native annual grasses when seeds were stored in the oven. For the sub-tropical collection, oven storage approximately doubled germinability of grasses and legumes, but had little impact on germinability of exotic annual forbs (Fig. 6*b*). For seed stored in the oven, germination was greatest for exotic sedge, then annual grasses and least for annual legumes.

The response to oven storage by individual species was assessed using confidence intervals at $P = 0.05$. A species was considered to respond positively to oven storage if germination was higher after storage in the oven than in the shade-house, and its mean value for germination after oven storage was outside the confidence interval of germination after storage in a shade-house. In the tropical collection positive responses to oven storage were observed for 17 species – *Abutilon fraseri*, *Bothriochloa*

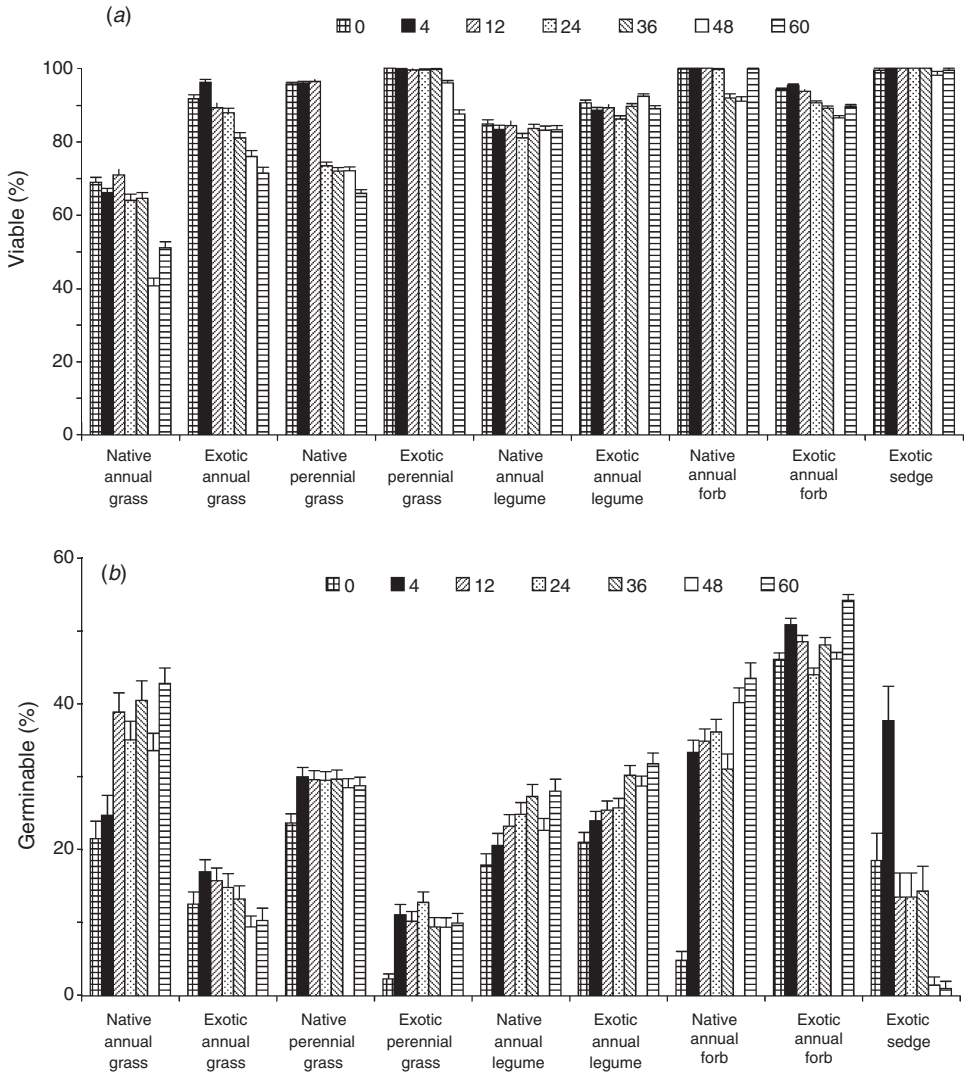

Fig. 4. Changes in (*a*) viability and (*b*) germinability of seeds of botanical groups stored in a freezer (sub-tropical collection). Standard errors are indicated by error bars.

ewartiana, *Bothriochloa pertusa*, *Cenchrus ciliaris*, *Crotalaria goreensis*, *Crotalaria pallida*, *Digitaria ciliaris*, *Gomphrena celosioides*, *Heteropogon contortus*, *Indigofera linnaei*, *Macroptilium lathyroides*, *Parkinsonia aculeata*, *Sesbania cannabina*, *Sida acuta*, *Sida spinosa*, *Stylosanthes hamata* and *Stylosanthes scabra*. For the sub-tropical collection 28 species gave a positive response – *Brachiaria decumbens*, *Bromus catharticus*, *Chamaesyce hirta*, *Chamaesyce hyssopifolia*, *Chamaecrista rotundifolia*, *Chloris truncata*, *Crotalaria linifolia*, *Cyperus aggregatus*, *Eleusine indica*, *Eragrostis curvula*, *Eragrostis leptostachya*, *Eragrostis sororia*, *Glycine* sp., *Gomphrena celosioides*, *Heteropogon contortus*, *Indigofera hirsuta*, *Indigofera spicata*, *Macroptilium atropurpureum*, *Macroptilium lathyroides*, *Panicum effusum*, *Panicum maximum* var. *trichoglume*, *Portulaca oleracea*, *Sporobolus creber*, *Sida acuta*, *Tridax procumbens*, *Themeda triandra* and *Tephrosia glomeruliflora*.

Impact of light and dark on germination

Germination of native perennial grasses and annual legumes were not impacted by light conditions while germination of annual grasses, annual forbs and exotic sedge increased by 10% or more under light (Fig. 7). The exotic sedge only germinated in the light.

Impact of low temperature on germination

Germination was lower at low temperature for all groups except native and exotic annual legumes (Fig. 8). For other botanical groups, low temperature generally reduced germination percentage by more than 20%. Only two species (*Bromus catharticus* and *Trifolium repens*) had a greater germination percentage at the low temperature. Germination for all botanical groups was slower at the low temperature than at the regular temperature requiring on average, 3 more days to achieve 50% of final germination (results are not presented).

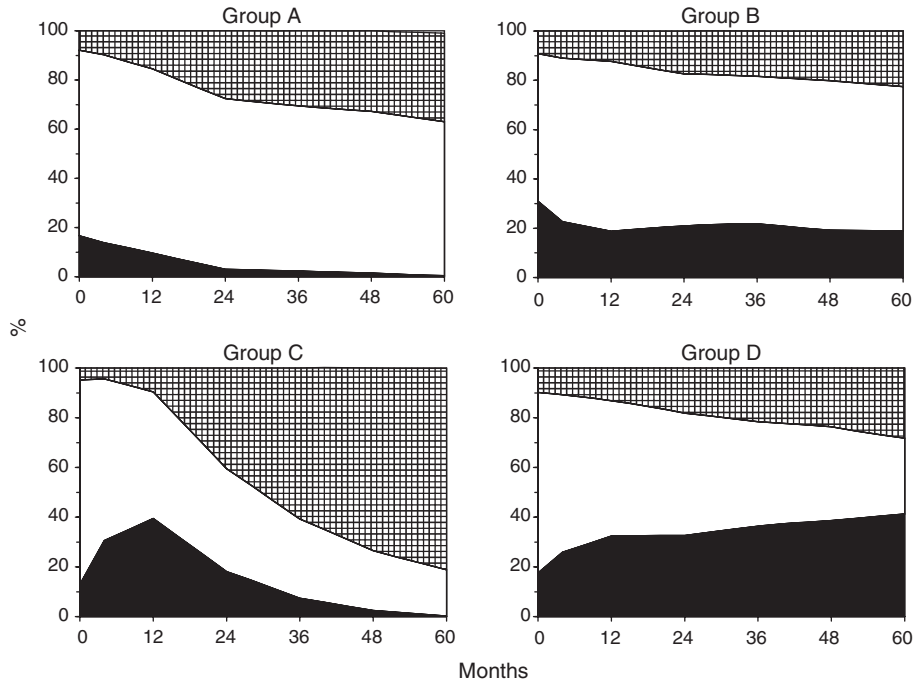

Fig. 5. Mean changes in the proportions of germinable (■), dormant (□) and dead (⌗) seeds over 60 months for four germination groups (A–D).

Table 4. Numbers of species within botanical groups allocated to germination groups based on germination patterns during storage (see text for definitions of groups A–D)

	Shade-house					Seed store/freezer				
	A	B	C	D	Total	A	B	C	D	Total
Tropical collection										
Native annual (or short-lived perennial) grass	2	–	1	–	3	3	–	–	–	3
Exotic annual (or short-lived perennial) grass	2	–	2	–	4	1	–	–	3	4
Native perennial grass	2	–	3	–	5	–	1	1	3	5
Exotic perennial grass	1	–	3	–	4	1	–	1	2	4
Native annual (or short-lived perennial) legume	3	–	–	–	3	3	–	–	–	3
Exotic annual (or short-lived perennial) legume	3	1	2	–	6	–	3	–	3	6
Native annual (or short-lived perennial) forb	1	–	1	–	2	1	–	–	1	2
Exotic annual (or short-lived perennial) forb	3	–	3	1	7	1	–	2	4	7
Exotic woody perennial shrub	–	–	–	2	2	–	1	–	1	2
Total	17	1	15	3	36	10	5	4	17	36
Sub-tropical collection										
Native annual (or short-lived perennial) grass	–	–	3	–	3	–	–	–	3	3
Exotic annual (or short-lived perennial) grass	–	–	3	–	3	1	–	–	2	3
Native perennial grass	1	–	7	–	8	3	2	–	3	8
Exotic perennial grass	1	–	3	–	4	1	–	1	2	4
Native annual (or short-lived perennial) legume	2	3	–	–	5	–	4	–	1	5
Exotic annual (or short-lived perennial) legume	1	1	1	4	7	–	3	–	4	7
Native annual (or short-lived perennial) forb	–	–	2	1	3	1	–	–	2	3
Exotic annual (or short-lived perennial) forb	5	–	8	–	13	1	4	1	7	13
Exotic sedge	–	–	1	–	1	–	–	1	–	1
Total	10	4	28	5	47	7	13	3	24	47

Discussion

Seeds of species in this experiment showed a wide range of viability levels and germination behaviour (changes in germination over time during storage and responses to germination conditions). Species with a range of germination responses co-exist as has been found in other environments (Angevine and Chabot 1979; Baskin and Baskin 1988) and in an

Table 5. Germination groups (A–D) for species stored in a shade-house or seed store (tropical collection) or freezer (sub-tropical collection)

Tropical collection	Shade-house	Seed store		Shade-house	Seed store		Shade-house	Seed store
Abution fraseri	A	A	*Digitaria ciliaris*	C	D	*Parkinsonia aculeata*	D	D
Acacia farnesiana	D	B	*Eleusine indica*	C	D	*Portulaca oleracea*	C	D
Amaranthus viridis	A	D	*Gomphrena celosioides*	C	D	*Sesbania cannabina*	A	A
Argemone mexicana	A	A	*Heteropogon contortus*	C	D	*Sida acuta*	C	D
Bothriochloa ewartiana	C	D	*Heteropogon triticeus*	A	D	*Sida spinosa*	D	C
Bothriochloa pertusa	C	D	*Hyptis suaveolens*	C	D	*Sporobolus australasicus*	A	A
Cenchrus ciliaris	C	D	*Indigofera linifolia*	A	A	*Sporobolus indicus*	C	C
Chrysopogon fallax	A	B	*Indigofera linnaei*	A	A	*Stylosanthes hamata*	C	D
Crotalaria goreensis	A	B	*Macroptilium atropurpureum*	B	B	*Stylosanthes scabra*	A	D
Crotalaria pallida	A	B	*Macroptilium lathyroides*	C	D	*Tragus australiana*	C	A
Dactyloctenium aegytium	A	A	*Melinis repens*	A	A	*Urochloa mosambicensis*	C	C
Dactyloctenium radulans	A	A	*Oxalis corniculata*	A	C	*Urochloa panicoides*	A	D
Sub-tropical collection	**Shade-house**	**Freezer**		**Shade-house**	**Freezer**		**Shade-house**	**Freezer**
Amaranthus viridis	C	D	*Eragrostis curvula*	C	D	*Portulaca oleracea*	D	D
Bidens pilosa	A	D	*Eragrostis leptostachya*	C	D	*Portulaca pilosa*	C	D
Brachiaria decumbens	A	A	*Eragrostis sororia*	C	D	*Rapistrum rugosum*	A	A
Bromus catharticus	C	A	*Glycine* sp.	B	D	*Sesbania cannabina*	B	B
Chamaecrista rotundifolia	D	B	*Gomphrena celosioides*	C	B	*Sida acuta*	C	B
Chamaesyce hirta	C	D	*Heteropogon contortus*	C	A	*Sida subspicata*	C	A
Chamaesyce hyssopifolia	A	B	*Indigofera hirsuta*	B	D	*Solanum americanum*	A	B
Chloris truncata	C	D	*Indigofera linifolia*	A	B	*Sporobolus creber*	C	A
Chloris ventricosa	C	D	*Indigofera spicata*	C	D	*Tephrosia glomerulifera*	B	D
Crotalaria linifolia	A	B	*Lepidium bonariense*	C	C	*Themeda triandra*	C	B
Crotalaria pallida	A	B	*Macroptilium atropurpureum*	D	B	*Tridax procumbens*	A	D
Cymbopogon refractus	A	B	*Macroptilium lathyroides*	D	D	*Trifolium repens*	D	D
Cyperus aggregatus	C	C	*Panicum effusum*	C	A	*Verbena bonariense*	C	D
Dichanthium sericeum	C	D	*Panicum maximum*	C	C	*Verbena brasiliensis*	C	D
Digitaria ciliaris	C	D	*Panicum maximum* var. *trichoglume*	C	D	*Verbena rigida*	C	D
Eleusine indica	C	D	*Pennisetum alopecuroides*	C	D	–	–	–

earlier shorter-term study of some of these species in the same tropical region (McIvor and Howden 2000). This current study extends those conclusions to a greater number of species and over a longer time period. There appeared to be little difference in germination changes during storage between the native and exotic species. Chi-square tests showed no significant relationship ($P > 0.05$) between origin (native or exotic) and germination group for both tropical and sub-tropical collections.

There were some species (*Argemone mexicana*, *Dactyloctenium aegyptium*, *Dactyloctenium radulans* and *Sporobolus australasicus* in the tropical collection, and *Rapistrum rugosum* in the sub-tropical collection) that had low germination (<2%) under all storage regimes despite the seed appearing to be sound. This could be a result of the conditions being unsuitable for germination of these species but it more likely reflects a high level of dormancy. Silcock and Williams (1975) reported frequent low germination values for *Dactyloctenium radulans* but germination was increased by mechanical scarification, treatment with concentrated sulfuric acid, and potassium nitrate. All five species are good colonisers and need some mechanism to survive until suitable conditions arise for germination.

Storing seeds under ambient conditions for 60 months provided some useful guidelines for how species perform. Some of these species are used for land rehabilitation (e.g. native perennial grasses) and seed is stored for lengthy periods. For species in germination group C (e.g. *Bothriochloa ewartiana*, *Cymbopogon refractus*, *Dichanthium sericeum*, *Heteropogon contortus* and *Themeda triandra*), germination declined after 12 months and storage for longer periods would lead to low germination. Several studies (Grime *et al*. 1981; Baskin and Baskin 1988; Elberse and Breman 1989; Washitani and Masuda 1990) have concluded that field behaviour can be related to laboratory germination and response to storage conditions, but how useful are the current results for predicting the behaviour of seeds in the field? Species with the highest germination after being stored for 60 months in a shade-house were in germination groups B and D. All species in these groups were annual legumes and forbs or woody shrubs. All these species are pioneer plants, and apart from the two woody shrubs, most live for only short periods. Their long-term survival depends on frequent re-establishment, and long-lived seeds enable these species to maintain a seed presence in the soil to take advantage of suitable establishment gaps whenever they are created in the vegetation. In contrast, all grasses were in germination groups A and C (no germination after 60 months). Perennial grass species depend on long-lived plants for their long-term survival and are not as dependent on frequent re-establishment. However, annual grasses (like the annual legumes and forbs) do depend on frequent re-establishment and the absence of any germinable seeds after 60 months was

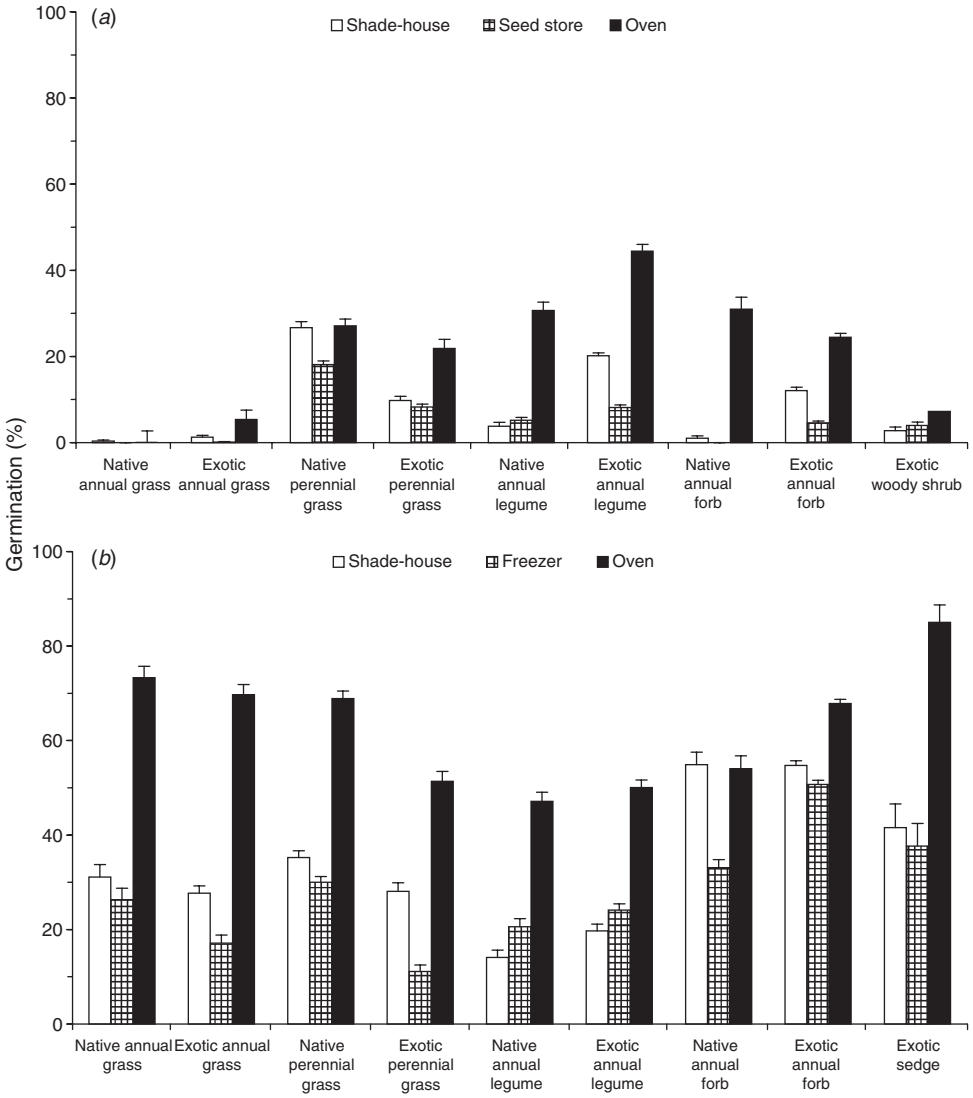

Fig. 6. Impact of oven storage on germinability of botanical groups in the (*a*) tropical and (*b*) sub-tropical collections. Standard errors are indicated by error bars.

surprising. Thus the results for some, but not all, groups show useful relationships with field behaviour and the results are consistent the conclusion of McIvor and Howden (2000) that storage conditions that are as similar as possible to the conditions actually experienced by seeds in the field will be the most useful for predicting field behaviour.

Surface soil temperatures frequently exceed 50°C during the dry season in tropical and sub-tropical areas (Mott 1978; Mott *et al*. 1981; McKeon *et al*. 1985) and exposure to such high temperatures is an important dormancy-breaking mechanism in some tropical species (Mott 1978; Mott *et al*. 1981; Hacker and Ratcliff 1989). Previous studies using similar techniques to those in this study (Mott 1980; McKeon and Mott 1982; Hacker and Ratcliff 1989; McDonald 2000; McIvor and Howden 2000) have shown that *Cenchrus ciliaris*, *Chamaecrista rotundifolia*, *Digitaria ciliaris*, *Macroptilium atropurpureum*, *Sida acuta*, *Stylosanthes hamata* and *Stylosanthes scabra* can all respond to large diurnal temperature fluctuations during oven storage. In this study, 17 species (from all botanical groups except native annual grasses) in the tropical collection and 28 species (from all botanical groups) in the sub-tropical collection responded (significantly higher germination) to storage in an oven with fluctuating temperatures simulating temperatures on the soil surface. However, some of the statistically significant responses were small (e.g. germination of *Tragus australianus* increased from 0 to 0.5%) and likely to be of little biological significance. Considering an increase in germination of 20% as representing a biologically important increase then this study extends the list of responsive species to include *Abutilon fraseri*, *Bothriochloa ewartiana*, *Bromus catharticus*, *Chamaesyce hirta*, *Chloris truncata*, *Crotalaria goreensis*, *Crotalaria linifolia*, *Crotalaria pallida*, *Cyperus aggregatus*, *Eleusine indica*, *Eragrostis curvula*, *Eragrostis leptostachya*, *Eragrostis sororia*, *Glycine* sp., *Gomphrena celosioides*,

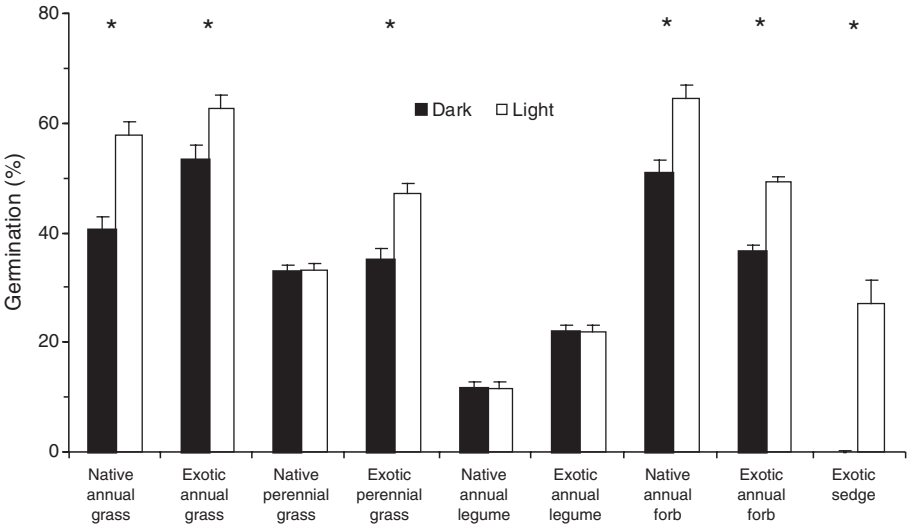

Fig. 7. Impact of light and dark at 30/20°C on germinability of botanical groups for species in the sub-tropical collection stored for 12 months in the shade-house. Standard errors are indicated by error bars. Asterisks indicate differences ($P < 0.05$) between light and dark treatments within botanical groups.

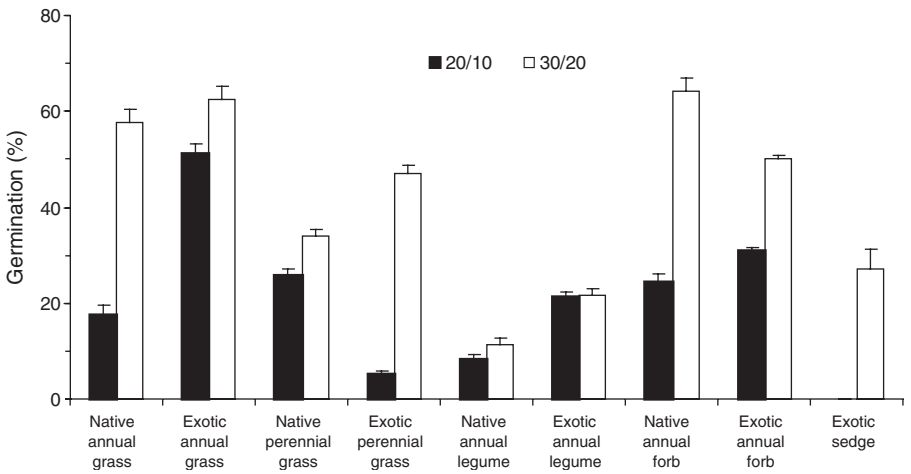

Fig. 8. Impact of regular (30/20°C) and low (20/10°C) temperature on germinability of botanical groups for species in the sub-tropical collection stored for 12 months in the shade-house. Standard errors are indicated by error bars.

Heteropogon contortus, *Macroptilium lathyroides*, *Panicum effusum*, *Portulaca oleracea*, *Sesbania cannabina*, *Sporobolus creber* and *Tephrosia glomerulifera.*

The often slower and sometimes lower germination at the low temperature was expected for seeds collected from a sub-tropical area. *Bromus catharticus* and *Trifolium repens* were the only two species that had a germination percentage more than 10% higher at the lower temperature. These occur in sub-tropical areas but they are both common temperate species. Although the average germination of most botanical groups were significantly higher in the light than in the dark, *Cyperus aggregatus* was the only species that had no germination in the dark and significantly higher germination in the light. Two other species (*Verbena bonariense* and *Verbena brasiliensis*) had markedly higher germination in light than in the dark. Overall the results show that a light requirement for germination is not widespread in these species.

Most species on both collections were represented by only one seed lot. However, there were four species in the sub-tropical collection with two seed lots, and there were 12 species represented in both collections. These allow some consideration of within-species differences in response to storage and germination conditions. For the four species with duplicate seed lots in the sub-tropical collection (*Crotalaria pallida*, *Panicum effusum*, *Panicum maximum* var. *trichoglume* and *Themeda triandra*), the duplicate seed lots of all species were placed in the same germination groups. However, for the 12 species included in both collections, some species performed similarly in both

collections but others performed differently. Three of the 12 species (*Crotalaria pallida*, *Digitaria ciliaris*, *Eleusine indica*) were placed in the same germination group after storage in both the shade-house and the seed store/freezer. However, for the other nine species, the tropical and sub-tropical seed lots were placed in different groups for at least one storage regime (*Amaranthus viridis*, *Gomphrena celosioides*, *Heteropogon contortus*, *Indigofera linifolia*, *Macroptilium atropurpureum*, *Macroptilium lathyroides*, *Portulaca oleracea* and *Sida acuta*) and for both regimes for *Sesbania cannabina*. Both genetic differences and environmental influences (including carbon dioxide levels, daylength, light quality, mineral nutrition, soil moisture, solar radiation, light quality, temperature) on the mother plant during seed development and maturation influence germination behaviour (Baskin and Baskin 1998). It is impossible to separate the two sources of variation in these data but the results show that care is needed when extrapolating results from one experiment to other collections and regions.

Conclusions

We draw two conclusions about studies of seed germination and storage from these results. First, changes in viability and germination under different storage conditions provide useful practical information on survival of seeds during storage but may provide only limited ability to predict the field behaviour of seeds. Second, differences in the responses of multiple seed lots from the same species show that care is needed when extrapolating the results from one seed lot to the behaviour of the species. The study identified species which can be stored under ambient conditions for varying periods, and also additional species where germination of fresh seed is increased by exposure to fluctuating temperatures in an oven for 3 or 4 months.

Acknowledgements

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References

Angevine, M. W., and Chabot, B. F. (1979). Seed germination syndromes in higher plants. In 'Topics in Plant Population Biology'. (Eds O. T. Solbrig, S. Jain, G. B. Johnson and P. H. Raven.) pp. 188–206. (Columbia University Press: New York.)

Baskin, C. C., and Baskin, J. M. (1988). Germination ecophysiology of herbaceous plant species in a temperate region. *American Journal of Botany* **75**, 286–305. doi:10.2307/2443896

Baskin, C. C., and Baskin, J. M. (1998). 'Seeds. Ecology, Biogeography and Evolution of Dormancy and Germination.' (Academic Press: San Diego.)

Clarke, P. J., Davison, E. A., and Fulloon, L. (2000). Germination and dormancy of grassy woodland and forest species: effects of smoke, heat, darkness and cold. *Australian Journal of Botany* **48**, 687–699. doi:10.1071/BT99077

Elberse, W. Th., and Breman, H. (1989). Germination and establishment of Sahelian rangeland species. I. Seed properties. *Oecologia* **80**, 477–484. doi:10.1007/BF00380069

Ellis, R. H., Hong, T. D., and Roberts, E. H. (1985). 'Handbook of Seed Technology for Genebanks 2. Compendium of Specific Germination Information and Test Recommendations.' (International Board for Plant Genetic Resources: Rome.)

Grime, J. P., Mason, G., Curtis, A. V., Rodman, J., Band, S. R., Mowforth, M. A. G., Neal, A. M., and Shaw, S. (1981). A comparative study of germination characteristics in a local flora. *Journal of Ecology* **69**, 1017–1059. doi:10.2307/2259651

Hacker, J. B., and Ratcliff, D. (1989). Seed dormancy and factors controlling dormancy in buffel grass accessions from contrasting provenances. *Journal of Applied Ecology* **26**, 201–212. doi:10.2307/2403661

Henderson, R. J. F. (2002). 'Names and Distribution of Queensland Plants, Algae and Lichens.' (Environmental Protection Agency: Brisbane.)

Jurado, E., and Westoby, M. (1992). Germination biology of selected central Australian plants. *Australian Journal of Ecology* **17**, 341–348. doi:10.1111/j.1442-9993.1992.tb00816.x

McDonald, C. K. (2000). Variation in the rate of hard seed breakdown of twelve tropical legumes in response to two temperature regimes in the laboratory. *Australian Journal of Experimental Agriculture* **40**, 387–396. doi:10.1071/EA99099

McIvor, J. G., and Howden, S. M. (2000). Dormancy and germination characteristics of herbaceous species in the seasonally dry tropics of northern Australia. *Austral Ecology* **25**, 213–222. doi:10.1046/j.1442-9993.2000.01026.x

McKeon, G. M., and Mott, J. J. (1982). The effect of temperature on the field softening of hard seed of *Stylosanthes humilis* and *S. hamata* in a dry monsoonal climate. *Australian Journal of Agricultural Research* **33**, 75–85. doi:10.1071/AR9820075

McKeon, G. M., Rose, C. W., Kalma, J. D., and Torssell, B. W. R. (1985). Pasture seed dynamics in a dry monsoonal climate. 1. Germination and seedbed environment of *Stylosanthes humilis* and *Digitaria ciliaris*. *Australian Journal of Ecology* **10**, 135–147. doi:10.1111/j.1442-9993.1985.tb00875.x

Morgan, J. W. (1998). Comparative germination responses of 28 temperate grassland species. *Australian Journal of Botany* **46**, 209–219. doi:10.1071/BT96117

Morrison, D. A., and Morris, E. C. (2000). Pseudoreplication in experimental designs for the manipulation of seed germination treatments. *Austral Ecology* **25**, 292–296. doi:10.1046/j.1442-9993.2000.01025.x

Mott, J. J. (1978). Dormancy and germination in five native grass species from savannah woodland communities of the Northern Territory. *Australian Journal of Botany* **26**, 621–631. doi:10.1071/BT9780621

Mott, J. J. (1980). Germination and establishment of the weeds *Sida acuta* and *Pennisetum pedicellatum* in the Northern Territory. *Australian Journal of Experimental Agriculture* **20**, 463–469. doi:10.1071/EA9800463

Mott, J. J., McKeon, G. M., Gardener, C. J., and 't Mannetje, L. (1981). Geographic variation in the reduction of hard seed content of *Stylosanthes* seeds in the tropics and subtropics of northern Australia. *Australian Journal of Agricultural Research* **32**, 861–869. doi:10.1071/AR9810861

Rathcke, B., and Lacey, E. P. (1985). Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* **16**, 179–214. doi:10.1146/annurev.es.16.110185.001143

Silcock, R. G., and Williams, L. M. (1975). Methods for improving the laboratory germination of *Dactyloctenium radulans* seed. *Australian Seed Science Newsletter* **1**, 59–61.

Silcock, R. G., Williams, L. M., and Smith, F. T. (1990). Quality and storage characteristics of the seeds of important native pasture species in south-west Queensland. *Australian Rangeland Journal* **12**, 14–20. doi:10.1071/RJ9900014

Washitani, I., and Masuda, M. (1990). A comparative study of the germination characteristics of seeds from a moist tall grassland community. *Functional Ecology* **4**, 543–557. doi:10.2307/2389322

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