Influence of storage conditions on survival and sowing value of seed of tropical pasture grasses. 2. Sowing value and storage strategies

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Abstract

Evaluation of effects of storage conditions of seed of 5 tropical pasture grass seeds (*Panicum maximum*, *Brachiaria decumbens*, *Brachiaria humidicola*, *Setaria sphacelata* and *Chloris gayana*) was extended from laboratory tests (Part 1) to seedling emergence and establishment tests in greenhouse and field in north Queensland. Seed cool-stored in woven bags at 10°C and 50% RH mostly had higher field sowing value than comparable open-stored seed, because the superior preservation of viability and vigour tended to outweigh the disadvantages of dormancy retention. Exceptions occurred when dormancy persisted, as it did inconsistently across seed lots, even within a single cultivar. Reduction in storage moisture content of seed sealed in moisture-proof packs helped to preserve viability and vigour, particularly with seed stored at ambient temperature. However, very low moisture content (7.2%) prolonged dormancy, with adverse effects on sowing value. Dormancy delayed germination even when not wholly preventing it. The benefits of retained vigour and the restrictions of dormancy were displayed in the field, but were masked in the more benign environment of the greenhouse. Cold storage at −12°C intensified dormancy of Gatton panic, delaying germination of seed in the greenhouse until the second and third seasons after sowing.

The shortcomings of conventional storage and means of mitigating them are discussed, with emphasis on the need to vary strategies depending on the duration of storage required.

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Introduction

Little is known about the deterioration of tropical pasture grass seed in storage, particularly as it affects sowing value. The present series of 2 papers reports an investigation of the influence of the storage environment on seed quality through experimental comparisons of the behaviour of sown seed after storage in different conditions. Part 1 (Hopkinson and English 2005) explained the reasons for the investigation, outlined its course, and covered the loss of viability and dormancy of stored seed as measured by laboratory tests. This paper reports the results of seedling emergence tests, and combines them with laboratory records to enable overall conclusions to be reached about storage strategies.

The aim of these tests was to extend knowledge of behaviour of stored seed of differing histories from viability and dormancy to seedling emergence from soil, vigour and (as the summation of all properties) sowing value. While field tests were necessary, they entailed high risks of failure through adverse weather. Therefore, greenhouse tests were carried out to provide weather-proof back-up, and to permit some measurements not possible in the field.

The scope and scale of the work was tailored each season to available resources, which varied unforeseeably over the 8 years of the investigation.

Materials and methods

Design of experiments

Three experiments, described in greater detail in Part 1 (Hopkinson and English 2005) were undertaken. In all, treatments consisted of the imposition of different storage conditions and their effects were measured in terms of seedling emergence in field and greenhouse from a succession of sowings as well as from laboratory tests.

Experiment 1. This exploratory experiment was designed primarily to check the appropriateness of choice of storage treatments, and seed was not field-tested. Seed of *Panicum maximum* cv. Gatton (Gatton panic) was used. Three treatments were applied: open storage in woven bags at ambient temperature; cool-room storage in woven bags at 10°C and 50% relative humidity; and cold storage at −12°C in a sealed packet for 1 year only. After treatment, seed was sown into soil in 2 series of greenhouse tests.

In Series 1, all seed was sown in the first season after harvest in 2 successive sowings using a total of 20 replicates sown on 3 occasions. Germination events were induced immediately after sowing and at about the same time of year for 4 subsequent years. Values presented are composite means of records of all sowings, graphed as cumulative totals over successive seasons up to and including the season shown (Figures 1a and 1c).

In Series 2, seed was taken out of cool and open storage during the 1st, 2nd and 3rd seasons after harvest, and each time sown in fresh tests (2 successive tests in the first season using 21 replicates; 1 in each of the second and third seasons, each using 5 replicates). Germination events were induced immediately after sowing and in subsequent seasons until all tests were ended 4 years after harvest. Records of each sowing are cumulative totals over all years (Figures 1b and 1d).

Experiment 2. The same open- and cool-room storage treatments as in Experiment 1 were employed, but with 5 seed lots: Gatton panic; *Setaria sphacelata* cv. Solander; *Brachiaria decumbens* (signal grass); *Brachiaria humidicola* cv. Tully; and *Chloris gayana* cv. Callide. Seed of both treatments of all species was sown in greenhouse and field tests for as long as open-stored seed survived in sufficient numbers for useful comparisons — for 2 seasons with Gatton panic, signal grass and Callide; and 1 season with Tully and Solander. Three successive greenhouse tests were run in the first season comprising 5 replicates in each of the first 2 tests and 3 replicates in the third test; and 1 test in the second season comprising 6 replicates. Germination events in the greenhouse were induced upon sowing and in a further 3 (first season sowing) and 2 (second season sowing) seasons.

Three field sowings were made in the first season and 2 in the second season (Tables 1 and 2). At times, reliable counting at the necessary time was impossible, *e.g.* when many very similar weed-grass seedlings also emerged or when protracted rainfall occurred. At such times, 2 improvised methods of measuring establishment success were substituted. One relied on a later-measured linear estimate of percentage sown row occupation, any space within 10 cm of an identified plant being deemed to be occupied. The other used a rating assessment in which, at the end of the growing season, success of establishment of each replicate plot was assessed visually in terms of sward depth and ground cover and allocated a rating (whole number) between 0 (total failure) and 8 (complete success).

Experiment 3. Seed of Gatton panic each stored in sealed packets in cool-room and open storage at 5 different moisture contents (7.3, 8.7, 10.8, 12.2 and 12.9%) was used, though seed of the highest 2 moisture contents was omitted from second-season tests, as it was already largely dead. Seed was taken out of storage in the first and second seasons after harvest, sown in seedling compost in the greenhouse, and watered to induce a single germination event. Surviving seeds were then exhumed, separated out by standard seed-cleaning

Table 1. Details of field sowings in Experiments 2 and 3.

Experiment	2					3		
Sowing year	1995			1996		1998		1999
Sowing season	1st			2nd		1st		2nd
Sowing[1]	1st	2nd	3rd	1st	2nd	1st	2nd	1st
Sowing date	23/01	21/02	21/03	03/01	24/01	11/01	20/02	27/02
No. of replicates	4	4	4	4	3	5	5	4
Plot lengths (m)	7.0	7.0	6.2	8.0	8.0	10.0	10.0	1.0
No. of rows	6	6	6	6	6	4	4	1
Total row length (m)	42.0	42.0	37.2	48.0	48.0	40.0	40.0	1.0

[1] Within season.

techniques, de-husked and tetrazolium-tested [see Part 1 (Hopkinson and English 2005) for method] to provide a record of surviving dormant seed. One sowing per season was made, with 6 replicates in the first and 4 in the second season.

Table 2. Sowing rates and numbers of viable seeds sown per running metre in field tests in Experiment 2.

Season		1st		2nd
Sowing		1 & 2	3	1 & 2
Crop[1]	Storage	Sowing rate (kg/ha of product)		
Gatton panic	Open	2.0	2.3	5.4
	Cool	2.0	2.3	4.7
Signal grass	Open	4.0	4.5	9.5
	Cool	4.0	4.5	7.8
Tully	Open	4.0	4.5	
	Cool	4.0	4.5	
Solander	Open	2.0	2.3	
	Cool	2.0	2.3	
Callide	Open	1.0	1.1	2.7
	Cool	1.0	1.1	2.4
		Approximate number of viable seeds per running m		
Gatton panic	Open	58	65	104
	Cool	59	66	117
Signal grass	Open	16	18	31
	Cool	16	18	33
Tully	Open	14	16	
	Cool	21	24	
Solander	Open	7	8	
	Cool	43	49	
Callide	Open	25	28	88
	Cool	31	35	88

[1] Tully humidicola; Solander setaria; Callide rhodes.

Seed taken out of storage in the first season was also field tested in 2 sowings at rates shown in Table 3. Seed taken out in the second season was field tested in a single sowing on a much reduced scale. Seeds were counted out to provide 100 mature viable caryopses per 1 m row and were hand sown and covered.

Table 3. Approximate number of viable seeds of Gatton panic sown per running metre at a constant sowing rate of 2 kg/ha of product in field tests in the first season of Experiment 3.

Moisture content (%)	7.3	8.7	10.8	12.2	12.9
Ambient-stored	93	96	84	80	77
Cool-stored	92	98	99	91	94

The unexpected presence of strong field dormancy in the cool-stored seed of the first sowing in the first season caused a change of plan for the second sowing. A pre-sowing, dormancy-breaking treatment of all lines of cool-stored seed was applied to the seed prepared for 2 replicates. It consisted of rubbing seed between the ball of one thumb and the palm of the other hand until all membranous structures of the spikelets were detached. This was similar to a method reported by Smith (1979), and we had validated its usefulness in laboratory tests (J.M. Hopkinson and B.H. English unpublished records). In the second season, rubbed cool-stored seed was incorporated into the design of the field test to provide a statistically more satisfactory comparison with untreated seed.

Test procedures

All tests were carried out on the Atherton Tableland during the customary sowing period, the December–March summer wet season. Multiple tests per season and successive tests annually were conducted whenever possible.

Greenhouse tests. The greenhouse used was at Walkamin Research Station (17°08′S, 145°26′E; 580 m elevation). It was roofed with corrugated translucent plastic sheets of a type used in horticulture and had sides of fly-wire to allow free ventilation. Seed was sown into seedling trays on benches. Experimental and statistical units of replication were single compartments (25 cm^2 surface area) of trays filled with soil or seedling compost and sown with 100 pure seeds (that is, seed structures that included a caryopsis). In Experiments 1 and 2, soil, similar to that of the field tests, but steam-sterilised, was used. Later a proprietary peat- and sand-based seedling compost was used. The change to compost was made after comparative tests had shown that it produced more consistent and higher values of emergence than soil, apparently through reducing localised dormancy.

Seed was sown in the tray compartments and lightly covered to about 1 mm depth. Trays were then watered to induce a germination event. Frequent prior tests had shown that such events were invariably of limited duration, and that several months had to elapse after they ended before more seeds would germinate. During each event, the soil was kept moist and emerged seedlings were counted daily. When seedling emergence had ceased after 2–6 weeks, events were deemed to have ended and the soil was allowed to dry out. Subsequent germination events were induced by watering 1 or more years later, with soil remaining completely dry in the interim.

Maximum and minimum daily air temperatures at bench level were recorded during each event. Average bench-level air temperatures over an event ranged between 22.3°C and 28.4°C, with an overall average of 25.9°C.

Field tests. To have any practical relevance, field tests to determine grass seed sowing value have to be made against the background of a stated sward use within a defined production system, in this case, the establishment of the grass ley in the rotational cropping system practised on the Atherton Tableland. Seed is sown into a fully prepared seedbed on well structured arable krasnozems at a time of year of warm temperatures and a high probability of adequate rainfall. The expectations placed on the seed are high, since rapid and complete establishment is essential to the economic success of the ley.

Access to land on Kairi Research Station (17°13′S, 145°34′E; 680 m elevation; annual average rainfall about 1270 mm of which 70% falls in December–March) enabled us to reproduce the relevant conditions. Seed samples for sowing were weighed out to allow calculation of numbers of pure and viable seeds sown from contemporary records (See Tables 1 and 2 for full details of all sowings). Weighed amounts of seed were sown into firm, fine, level seedbeds through a tractor-drawn precision planter of 2 m width set to deliver and lightly cover seed uniformly along a chosen number of rows (4 or 6) over a predetermined distance for each replicate plot. On completion of sowing, each whole test area was rolled with a Cambridge roller. Sowing rates were chosen to reflect customary commercial practice. Sowing dates and numbers of tests in any season were governed by rainfall and its effect on preparatory tasks. Circumstances forced a major reduction in scale for the second sowing season of seed of Experiment 3.

The primary field measurement was the number of emerged seedlings per replicate over the first germination event, which was induced by the first penetrating rainfall after sowing. Seedling counts could be made only from first emergence to the start of tillering, after which individuality became unrecognisable. Earlier work had demonstrated that successful establishment in the relevant time frame depended almost entirely on the first flush of emergence in the season of sowing (Hopkinson 1993). In 2 sowings of Experiment 2, prevailing conditions prevented counting of seedlings and alternative, improvised methods of measuring establishment success, described later, were devised.

Analyses of records. All tests, whether greenhouse or field, were laid out as individual complete randomised block experiments and results were analysed accordingly by conventional analysis of variance. When records from several greenhouse tests were used to provide quoted means, variances were pooled across tests to obtain relevant LSDs.

Results

Experiment 1

Results of the 3 first-year greenhouse sowings are combined for presentation as they followed similar patterns. Seedling emergence from cool-stored seed sown in the first season after harvest was clearly greater than from open-stored seed, while freezer-stored seed produced very few seedlings (Figure 1). Emergence from seed open-stored for a further 1 and 2 seasons before being sown (Series 2) declined sharply with age at sowing while cool-stored seed remained unchanged. These records are broadly consistent with those of Part 1, and reflect relatively rapid loss of viability in open storage and the persistence of dormancy in the freezer. They leave little reason to invoke other properties such as vigour.

Experiment 2

Seedling emergence data for the 5 lines of seed from Experiment 2 sown in the greenhouse (Table 4) refer to separate sowings in the first and second seasons after harvest and to emergence only during the first germination event, as further emergence in subsequent seasons was negligible. The results show the general superiority of cool-stored seed over ambient-stored seed, sometimes (particularly in the second season) extreme, though in 2 first-season comparisons, Gatton panic and Tully, there was no detectable difference. With the exception of second-season Tully, differences were due to the numbers of viable seeds sown. These results broadly confirmed the expectations from the viability records, and (as

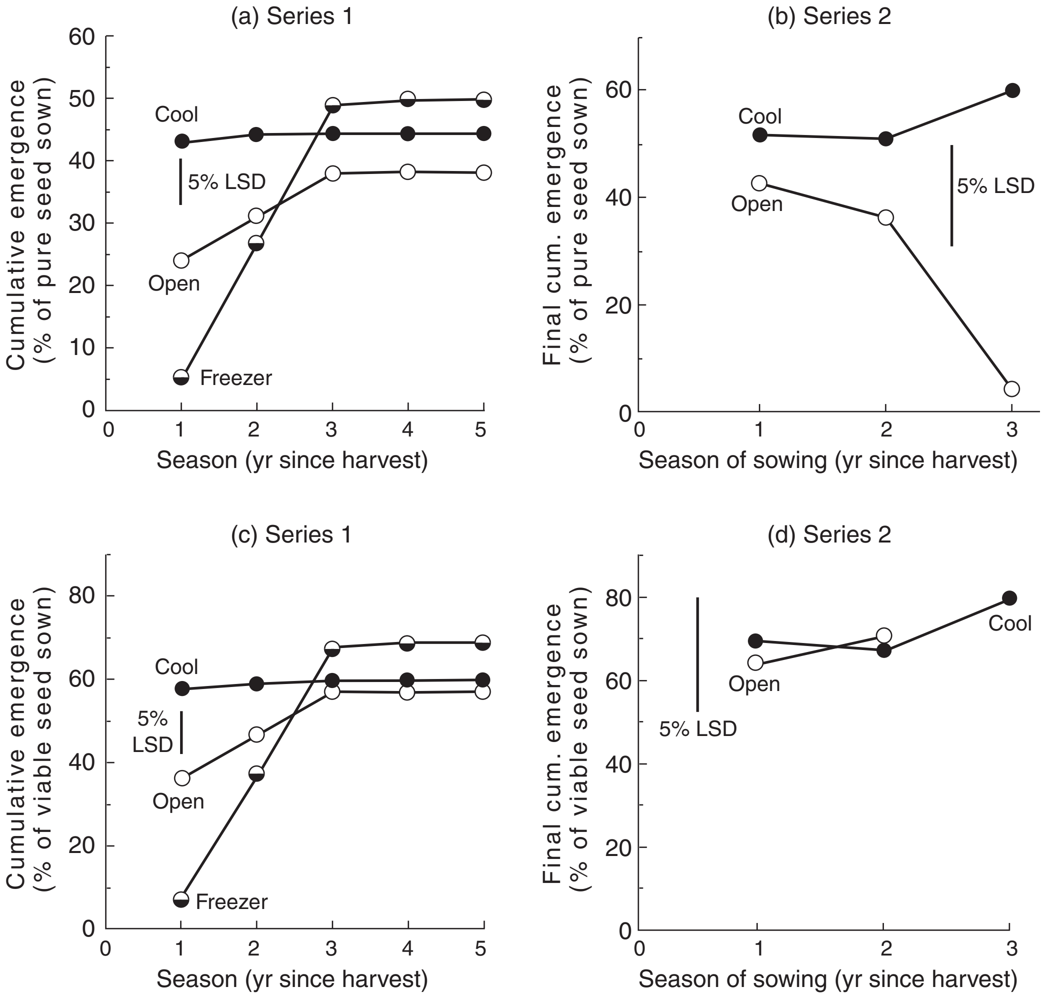

Figure 1. Seedling emergence of Gatton panic seed in the greenhouse as a percentage of pure and viable seed sown after open, cool-room and freezer storage in Experiment 1. In Series 1, all seed was sown in the first season after harvest, and germination events induced in each of 4 subsequent seasons. In Series 2, different samples were removed from storage and sown in each of 3 seasons following harvest.

in Experiment 1) demonstrated that success or failure was determined by the number of viable seeds sown.

Field establishment tests of Experiment 2 in the first season after harvest were beset with difficulties of measurement. The first sowing was followed by 3 weeks of hot, dry weather that prevented any germination. This was succeeded by a very wet, humid, overcast period that stimulated germination of not only sown seed but also weed grasses. These could not be distinguished so counting of most sown seedlings was impossible. After the second sowing, wet but unseasonally cool weather extended the period of emergence, so that tillering of early seedlings had begun before emergence of others was complete. Both sets of circumstances prompted adoption of the improvisations described earlier (estimates of percentage row occupation and success rating methods), neither of which allowed direct measurement of sowing value or survival index. The third sowing was followed by dry weather unfavourable to establishment, resulting in relatively few seedlings and high experimental variation.

However, trends were discernible (Table 5). Cool-stored seed of Gatton panic was vastly superior to ambient-stored seed in all 3 sowings, though any statistical support for it in the third sowing was prevented by the level of variability. Solander showed similar differences in all 3 sowings. Callide produced a similar difference with the first sowing only. Cool-stored seed of signal grass had consistently better establishment than ambient-stored seed, but not significantly so, while Tully produced so few seedlings overall that no useful conclusions could be drawn. Records of emergent seedlings as a percentage of viable seeds sown add nothing, and are omitted.

The final success ratings do more to emphasise the differences in conditions for establishment

Table 4. Emergence of seedlings from soil in the greenhouse after sowing in each of the 2 seasons following harvest in Experiment 2.

	No. of emergent seedlings														
Crop	Gatton			Tully			Signal			Solander			Callide		
Storage[1]	A		C	A		C	A		C	A		C	A		C
(% of pure seed sown)															
1st season	55.0		55.2	43.3		39.9	22.4	***	40.8[2]	14.6	***	36.8	48.4	*	59.7
2nd season	19.0	*	28.0	8.0	**	20.8	0.6	***	21.6	0	***	39.6	7.0	***	33.6
(% of viable seed sown)															
1st season	68.4		73.0	54.2		51.2	45.7		56.4	NA[3]		50.4	88.6		87.5
2nd season	40.0		45.5	13.2	**	26.5	NA		30.1	NA		76.9	NA		42.5

[1] Seed stored in open storage (A) or cool-room (C).
[2] Asterisks denote significant differences due to storage type.
[3] Viability of seed lots too low to provide reliable results.

Table 5. Records of success of field establishment in the first and second seasons after harvest of seed of 5 grass crops kept until sowing in open (A) and cool-room (C) storage in Experiment 2.

Crop[1]	Gatton			Tully			Signal			Solander			Callide		
Storage	A		C	A		C	A		C	A		C	A		C
First season															
Row occupation (%)															
Sowing 1	25	***[2]	80	—		—	83		90	50	***	95	60	**	75
Sowing 2	20	***	78	—		—	80		88	22	***	94	—		—
Emergent seedlings (% of pure seed sown)															
Sowing 1	—		—	4.5		3.4	—		—	—		—	—		—
Sowing 2	—		—	5.8		7.4	—		—	—		—	6.1		5.6
Sowing 3	0.27		0.68	0.68		0.57	21.2		26.7	0.32	***	14.8	1.20		0.41
End-of-season average success rating[3]															
Sowing 1	4	*	8	3		3	8		8	5	*	8	8		8
Sowing 2	1	*	6	4		4	8		8	3	***	8	4		4
Sowing 3	0		0	0		0	3		3	0	*	2	0		0
Second season															
Emergent seedlings (% of pure seed sown)															
Sowing 1	2.4	**	13.9	—		—	19.7	**	42.0	—		—	0.20	*	0.72
Sowing 2	18.7	**	38.5	—		—	23.6	**	53.3	—		—	2.9	**	14.0
Emergent seedlings (% of viable seed sown)															
Sowing 1	5.1	**	22.6	—		—	32.5	**	53.6	—		—	0.33	*	1.06
Sowing 2	39.4	**	62.7	—		—	32.5	**	67.9	—		—	4.8	**	20.7

[1] Gatton panic; Tully humidicola; Signal grass; Solander setaria; Callide rhodes.
[2] Asterisks denote significant differences due to storage type.
[3] Range of 0 = total failure to 8 = complete success.

than the differences in performance between seed pairs. The superiority of the cool-stored seed was clear with Gatton panic and Solander, but recovery by stolon spread in Tully and Callide and by vigorous tussock growth in the signal grass evened out differences that may otherwise have been present.

In the second season, when Tully and Solander had been omitted because of the death of the open-stored seed, conditions for both establishment and counting were far better and the results were much more clear-cut (Table 5). In every measured detail, the cool-stored seed performed substantially better than the ambient-stored seed, with clear indications that not only its higher viability but also the superior emergence of its viable seed (taken as evidence of better preserved vigour) contributed to the result. This applied even with Callide, despite very low overall survival rates. Visible differences reflecting the seedling emergence records were conspicuous throughout the rest of the growing season.

Experiment 3.

In the greenhouse, patterns of emergence as a percentage of pure seed sown showed poorer performance in seed stored at high moisture contents (Figure 2), though most differences were

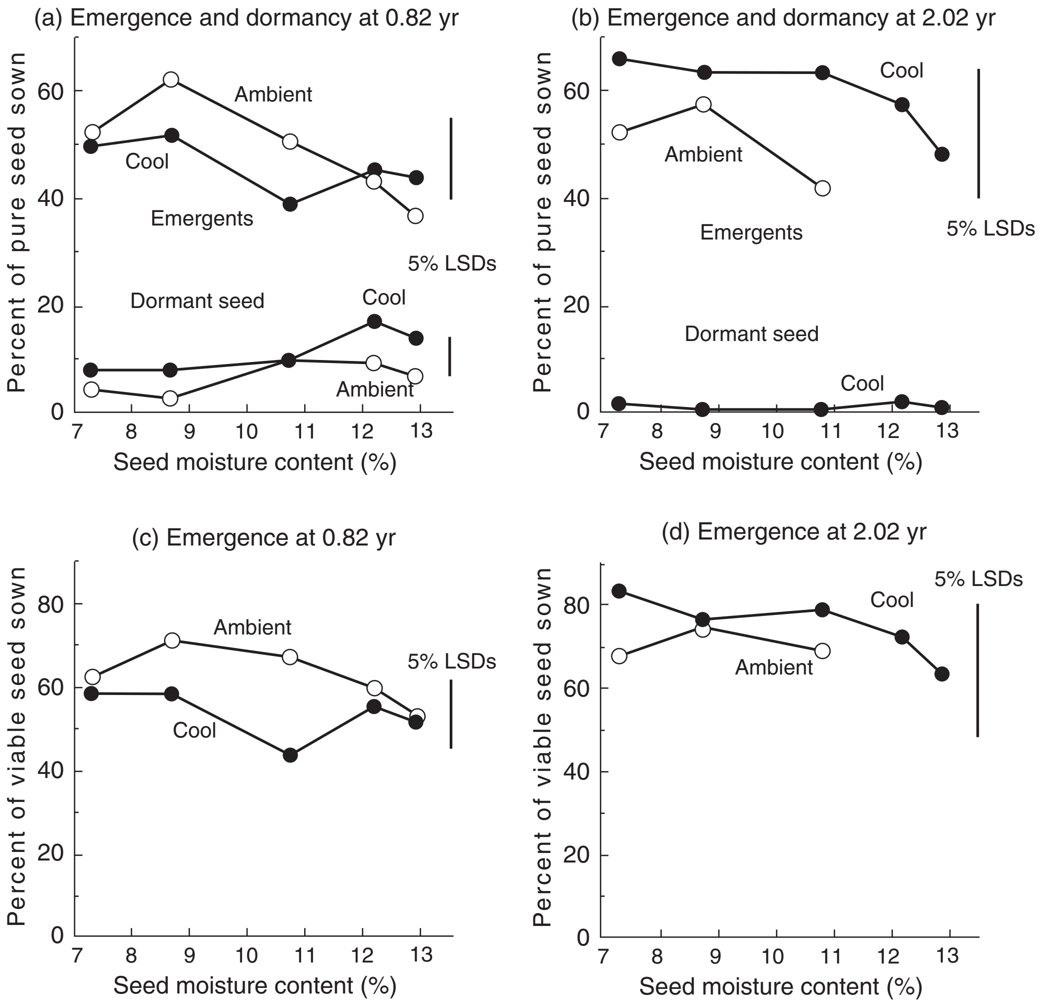

Figure 2. Seedling emergence of Gatton panic seed in the greenhouse and dormancy after ambient and cool-room storage at 5 different moisture contents in Experiment 3. Of the dormant seed at 2.02 years, none of the ambient-stored, and too few of the cool-stored for useful analysis, survived.

not significant. A similar tendency may also have been present with emergence as a percentage of viable seed, but its reality is less certain.

Ambient-stored seed generally produced more emergent seedlings than cool-stored seed in the first season but fewer in the second, an effect most readily attributable to its more rapid loss of both dormancy and viability. No ambient-stored seed, and very little cool-stored seed, survived in the dormant state into the second season. The numbers of unaccountable seeds [the discrepancy between viable on the one hand (Hopkinson and English 2005) and the sum of emergent and dormant on the other; data not presented] averaged about 23%. They were distinctly fewer in the cool-stored seed in the second season than the first, perhaps a reflection of a decline in the numbers of partially as well as fully dormant seeds. Partially dormant seeds, being slow to germinate (Part 1), are exposed to hazards for longer than non-dormant seeds while attempting to germinate, and possibly therefore suffer more frequent deaths.

In the field in both sowings of the first season, the diminishing success of open-stored seed with increasing storage moisture content was conspicuous, whether emerged seedling numbers were expressed as a percentage of pure or viable seed sown (Figure 3). Poorer emergence per unit of viable seed is again taken as evidence

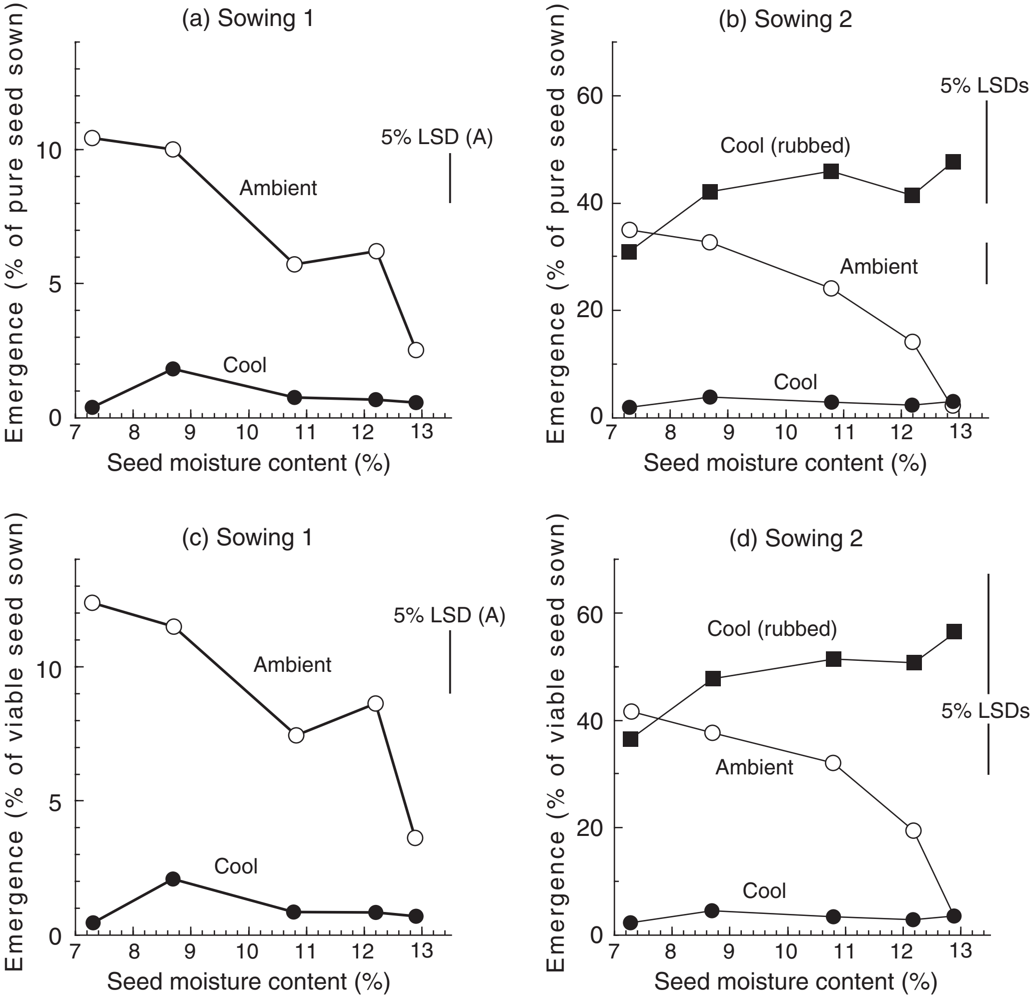

Figure 3. Seedling emergence of Gatton panic seed in the field from 2 sowings made in the first season after harvest following ambient and cool-room storage at 5 different moisture contents in Experiment 3. Cool-stored seed of Sowing 2 included a hand-rubbed treatment to break dormancy.

of lost vigour. Cool-stored seed behaved entirely differently. Untreated, it was so dormant that it was incapable of showing up any other effect. When the extent of its dormancy had been realised and the rubbing treatment applied before the second sowing, there was a massive increase in the number of emerging seedlings (Figures 3b and 3d). The results show a curious trend with respect to the relationship between storage moisture content and seedling numbers, which went in the opposite direction from that of the ambient-stored seed. The limited replication of the revised layout reduced the prospects for statistical support: only the driest seed differed from the rest with an acceptable level of probability, and linear regression analysis of the full data set provided unconvincing support for the trend. Nevertheless, when reinforced by contemporary records of viability and speed of germination (Part 1, Figure 3d), the effect seems real and a function of the greater retention of dormancy at lower storage moisture contents.

The single set of small-scale field tests of the second sowing season was subjected to severe soil disturbance by small nocturnal animals soon after sowing, despite netting protection. Although conditions for establishment were favourable, this inflated experimental error to the point where records of numbers of emergent seedlings from individual storage treatments became meaningless. The only useful records that could be salvaged were of overall patterns of emergence in comparisons between rubbed and untreated cool-stored seed, and of mean emergence times (which, being independent of numbers of seed lost by the disturbance, retained normal levels of variability). Overall, similar numbers of seedlings emerged with either treatment (averages of 36.3% and 35.4% of pure seeds sown for untreated and rubbed, respectively, and of 58.3% and 57.1% of mature viable seed sown). Mean emergence time was shortened by the rubbing treatment [9.1 *vs* 10.2 days; LSD ($P < 0.05$) of 0.9 days], but the difference was most conspicuous in seed kept at the lowest 2 moisture contents, where it was extended to about 2.3 days [LSD ($P < 0.05$) of 1.4 days]. This seems to provide clear evidence that, while residual dormancy was no longer strong enough to prejudice overall emergence of any seed line in the benign establishment conditions that prevailed, it still had sufficient influence to delay the course of germination of the cool-stored seed.

Discussion

From the results of the 3 experiments, a reasonably clear picture can be constructed of the behaviour during and after storage of Gatton panic and, with minor qualifications, the other types of seed used. We discussed the influence of decline of viability in Part 1 (Hopkinson and English 2005) and shall now consider changes in dormancy and vigour and their impact on sowing value, before recommending storage strategies.

Dormancy

Fresh seed of most tropical pasture grasses, especially of firm-husked species, is usually dormant, but the dormancy disappears over time. This is well known from long commercial experience and its course has been documented to some extent (Harty *et al.* 1983). However, the extent of early dormancy varies, even within a species or cultivar (Whiteman and Mendra 1982), and is clearly apparent in the behaviour of the different Gatton panic seed lots in the present investigation. In their first seasons after harvest (the critical period from most points of view), 2 lots of cool-stored seed showed relatively little dormancy. However, strong dormancy in the third lot greatly reduced sowing value of untreated seed, and persisted, albeit only in very dry cool-stored seed, a year later. The extent of early dormancy is unpredictable. In the present comparison, the 3 seed lots were all derived from the same sward, where crop management and seed treatment were similar and only seasonal conditions differed. Since dormancy is unpredictable, the only safe policy is to anticipate the worst and plan storage strategies in expectation of its being present.

Despite variation in the extent of early dormancy, trends in the general patterns of its loss during storage are evident. Rates of loss in Gatton panic seed clearly increased with rising seed storage temperature. At −12°C, dormancy remained and even appeared to intensify. At +10°C, it declined over time, but appreciably more slowly than in open storage at +22.5°C. Loss was retarded at low storage moisture contents as well as by low temperatures. In looking for patterns, we conclude that extinction of viability and disappearance of dormancy are influenced similarly by changes to the storage environment. Though doubtless an oversimplification, it is tempting to view both as manifestations of a common aging process.

The persistence and apparent intensification of dormancy of freezer-stored seed supported the inference of this drawn in Part 1 (Hopkinson and English 2005) from the slow germination of naked caryopses. The high ultimate success rate of freezer-stored seed, and the curious survival of more open- than cool-stored seed to produce seedlings in seasons beyond the first, are noteworthy. To attempt explanations, however, is pointless: too little is known about too many influences potentially acting in either direction — delay in aging through reduction of seed moisture content in dry soil or its acceleration due to elevated temperatures; action of aging-repair mechanisms under wetting-drying cycles (Villiers and Edgcumbe 1975); death from pathogens; etc. While we have experience of cold storage of only a single seed lot for 1 year, its effects on dormancy were distinct enough to raise serious implications for long-term germplasm maintenance.

Dormancy is undesirable for establishment of a ley in rotation farming. Fully dormant seed can make no contribution to the sward within the required time frame, while partial persistence of dormancy compromises seedling establishment in the field, probably by retarding germination. This effect could be more severe in the field because of fluctuating soil moisture conditions than in the greenhouse. This, at least, provides the simplest (and only credible) explanation for the extraordinary differences in the numbers of seedlings produced by cool-stored seed in the field and greenhouse in Experiment 3 (*cf.* Figures 2 and 3). However, with permanent pasture establishment, where the environment is frequently harsher, the time frame longer, and the circumstances closer to those in which the relevant grasses originated, dormancy probably has advantages.

Beyond the foregoing, almost any conclusion about dormancy is premature: there is simply too little known about a subject of great complexity. Understanding of the background mechanisms (Adkins *et al.* 2002) is still too crude to offer much promise of control or prediction in the field.

Vigour

There were substantial differences in seedling emergence as a percentage of viable seed sown. They showed up clearly in the field but hardly at all in the less rigorous conditions of the greenhouse. Where uncomplicated by dormancy effects, they can be attributed only to differences in vigour. While vigour of tropical pasture grass seeds has hardly been considered in the past, and its variation has not been demonstrated before to our knowledge, its decline with aging must be postulated from general principles. Arguably, vigour would strongly influence establishment success through its effect on seedling survival (Heydecker 1972; Perry 1976; Powell 1988), especially in a hazardous environment. The extent of the hazards may be gauged from the fact that customary sowing rates allow for failure of over 95% of sown viable seeds. The links that lead to conviction of the importance of vigour in field establishment are thus essentially in place.

Wherever prevailing conditions allowed field-sown seed to produce useful results, the results emphasised the superior sowing value of cool-stored seed. Where satisfactorily measurable, success as a percentage of viable seed was as conspicuous as success as a percentage of pure seed. Clearly the advantage of cool storage extended beyond mere survival and produced a result that is explicable in terms of conservation of vigour.

The records are not direct or comprehensive enough to enable us to trace any clear pattern of loss of vigour in relation to loss of viability, but in view of the orthodox behaviour of these seeds, other indices of aging and loss of vigour over time should precede and be similar to loss of viability (Ellis and Roberts 1981). If so, then at some point there will be evidence of a decline in vigour before much loss of viability is detectable. An example of behaviour at this point seems to have been captured in the records of ambient-stored seed of Experiment 3 in the first season after harvest [compare Figure 3c (A) with Part 1 (Hopkinson and English 2005) Figure 3a (0.82 years)].

Sowing value

Sowing value, the synthesis of viability, dormancy and vigour characteristics, is obviously sensitive to variation in any of them. The differences in sowing value induced by the different storage treatments were often very great. These are easily explained once the influence of the component processes is known. The common pattern is for values of all 3 characteristics to diminish progressively. Since they do so at different rates in different circumstances, and 2 are advantageous and 1 disadvantageous, the timetable of change in the resultant sowing value is highly variable. Sowing value will presumably always peak at some point in the life of a seed lot, but when and at what height will depend on storage history.

The simplest general conclusion is that the greatest sowing value is obtained from the least physiologically aged seed, provided its storage conditions have allowed dormancy to break. If they have not, then dormancy overrides everything else. The surprising element of the results was the magnitude of the effect of the various influences in the field, and particularly the way they could arise so early in the storage life of seed as a result of quite small differences in moisture content.

Storage strategies

Obviously, storage conditions must be chosen to fit requirements, and will differ as targets and strictures vary. The defects of conventional open storage of seed in moisture-permeable bags emphasises the huge scope for improvement in commercial practices. Vast quantities of sown seed must have been, and still be, of unnecessarily low sowing value, leading to innumerable costly pasture establishment delays and failures. The route to immediate commercial improvement lies primarily through attention to seed moisture content, because seeds are sensitive to it, and because temperature control is impracticable in many circumstances. The key question is: what is the optimal moisture content? Two details complicate the otherwise simple and well established principle of aiming for the lowest possible value. One is the matter of determining a commercially attainable target minimum moisture content, the other the tendency for dormancy to persist in very dry seed. The compromise is to suggest a target of about 8–9% moisture content for routine bulk storage. This calls for careful drying, avoidance of moisture regain between drying and bagging, the use of adequately moisture-proof packaging material and the capacity to monitor moisture content conveniently at all stages. Fortunately, for all of these, simple, cheap, readily available technology exists. A level of 8–9% moisture is appropriate for the anticipated storage duration of most commercial seed, based on expected disposal before the seed is a year old, but with provision to hold it for up to 3 years. Given seed of 80% initial viability, an annual decline of about 5% would be expected over this period, which is an improvement on present expectations and an acceptable trade-off for the prospect of dormancy reduction. The benefits of such a practice would be felt along the entire supply chain. A lengthening of saleable life would reduce losses to the merchant, and establishment risks to the user would diminish through access to seed of improved sowing value.

As the anticipated storage life of seed extends and the concern over dormancy persistence declines, the attraction of lower temperature storage increases. Cool storage should be considered whenever seed must be kept for a second season or longer, and when high value and low volume warrant the extra cost. It has some, though limited, commercial application, mainly with valuable stocks that are expected to be slow to market. Its place seems to lie mainly with the storage of pedigree stocks destined for periodic re-multiplication or public release as part of cultivar maintenance schemes, and too bulky for cold storage. Here, the combination of cool temperatures (*e.g.* +10°C), coupled with the reduction in moisture content (*e.g.* to about 9%) that accompanies controlled low air relative humidity (*e.g.* 50%) and the use of open-weave bags, reduces aging to a point where the regeneration interval can be extended by many years, greatly reducing overall costs of cultivar maintenance. While the early death of comparable open-stored seed has prevented experimental comparisons, records of establishment of Gatton panic seed leave no doubt about the prolonged retention of high sowing values. For example, cool-stored seed from Experiments 1 and 2, harvested in 1992 and 1994, respectively, and sown with the seed of Experiment 3, was still capable in 1999 of 32 and 35% seedling emergence measured as a percentage of pure seed sown, or 49 and 59% as a percentage of mature viable seed. These values far exceed the levels needed at customary sowing rates to produce adequate swards.

The chief drawback of cool storage arises when seed is removed for sowing in the first (and, if seed is very dry, the second) season after harvest while the risk of dormancy retention remains. If seed is to be sown in the first season, storage at ambient temperature is appropriate (with, of course, due attention to ensuring a suitable moisture content) for the first year of the seed's life, after which it can be placed in cool storage if unused. The penalty in terms of reduction in viability after one year is the same as that quoted for commercial seed –about 5%.

Cold storage is the customary method of indefinitely maintaining germplasm. Such seed is stored presumably with the intention that it will eventually be sown. The main concern with cold storage of tropical pasture grasses is fear of the persistence and even deepening of dormancy, reducing the sowing value of the seed. The absence of information on effects of cold storage beyond the first year leaves uncertainty, and it is prudent to assume that dormancy will persist indefinitely at sub-zero temperatures. One obvious policy to counter this risk, suggested by the results of Experiment 1, is to remove seed from cold storage at least a year before its planned sowing.

We have not considered the wider use of pre-sowing dormancy-breaking treatments to overcome dormancy persistence, despite experimental success, as none is commercially available. The rubbing method we used is merely an experimental tool and will remain so until it can be reproduced on a scale of commercial automation; acid treatment for field sowing was wisely abandoned in Australia long ago; and all other methods are relevant only to laboratory testing.

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