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Tropical pasture establishment.
2. Seed characteristics and field establishment

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Abstract

The relationships between measured properties of tropical pasture seeds and their ability to produce emerged seedling populations in different seedbed environments are reviewed. Experimental records of the behaviour of the grasses, green and Gatton panic (*Panicum maximum*), and the legume, Seca stylo (*Stylosanthes scabra*), are then examined in attempts to elucidate further the principal interrelationships among seed properties and seedbed factors that influence seedling emergence.

Critical seed characteristics were perceived to be vital quality, measured satisfactorily as viability, and the impediments to germination imposed primarily by dormancy in tight-husked panicoid grass seeds and hardseededness in legumes. Experimentally, survival of seeds and seedlings in soil was closely related to vital quality. Dormancy in grass seeds, however, led to complications that hampered prediction of field emergence. Inconsistencies arose because: dormancy diminished with age; threshing damage of variable severity had opposing effects of breaking dormancy but shortening life expectancy; and a level of dormancy existed that failed to prevent germination but prejudiced seedling survival in conditions of stress in the field. A further variable was imposed by differences in the course of germination of seed populations, patterns of which tended to be species-specific and led to widely differing risks of seedling death from desiccation during a field germination event.

Seedling emergence from Seca seed-in-hull had a close, positive, linear relationship with laboratory germination in conditions that precluded further seed softening. Scarified, naked seed had high absolute emergence levels but relatively high seedling mortality in soil, apparently from pathogen invasion of tissue damaged by scarification. The course of germination of populations of soft seeds depended on the route of water penetration, either immediate through fractures, or slow and staggered through the strophiole. By inference, scarified and strophiole-softened seed would have markedly different survival patterns under different sequences of available soil moisture.

Introduction

Establishment outcomes from pasture sowings are strongly influenced by numerous interrelationships among seed biological and seedbed physical and biological properties. In practice, the primary need is to identify the principal components of these relationships that affect the success of establishment and can be managed to improve it.

Previous systematic study of seed and seedbed interrelationships for tropical pasture plants has focussed on establishment of grasses in problem clay soils (Leslie 1965, 1968, 1984; Watt 1972). The new information reported here was derived from seed production research aimed at improving seed quality, and conducted in north Queensland where the relevant soils have coarser-textured, rapidly drying surface layers that introduce different problems. It has provided an opportunity to gain some insights into the relationships between seed and seedling emergence characteristics of grasses (particularly of the tight-husked panicoid species typified by *Panicum maximum*) and legumes (notably Seca stylo, *Stylosanthes scabra*). The emphasis on quality has focussed attention on the period from

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sowing to seedling emergence. Subsequent seedling survival, the other major component of establishment, is less directly connected with seed quality and has received less attention. Its consideration is best left until the present approach can be wedded to that based on rainfall probabilities and related subjects.

Properties of seed

The properties of seed that affect establishment can be divided into 2 categories:

1. The attributes that collectively constitute vital quality ; and
2. The built-in impediments to germination of viable seed, i.e. dormancy and seed coat impermeability to water.

The quality attributes are subject to processes that are universal and can be described in general terms that apply equally to grasses and legumes. However, the impediments are closely linked to seed structural characteristics and differ along taxonomic lines, making separate treatment of grasses and legumes necessary.

Vital quality

Description. Vital quality is the sum of the attributes that enable a seed to produce a successful seedling once the opportunity arises — viability, life expectancy, health, vigour, etc. The quality of any individual seed deteriorates progressively throughout its existence. Low vigour, non-viability and death are simply late stages or points in this progression. Deterioration may occur through curtailment of initial development, damage, pathogen invasion and aging. Aging is the progressive disruption of macromolecules that leads to impairment or loss of function and organisation of subcellular structures (Villiers and Edgcumbe 1975). To a degree it is reversible by repair mechanisms acting during periods of hydration, but, in general, its effects are simply cumulative with advancing time.

Individual seeds in a population may be at all stages of deterioration, and may have been subjected, in different degrees, to the effects of the various agents of deterioration. However, for a single population of common history, these agents may be treated as acting cumulatively. Loss of viability thus occurs as a single progression in the population, integrating the effect of deterioration processes. It is therefore legitimate to measure the quality of a population of seeds in terms of the proportion of its members that are viable.

This may seem oversimplified in view of the range of properties it is intended to represent, and is inadequate for some types of crop seeds, for which separate vigour tests are needed. Over the range of viabilities normal for tropical pasture seeds (much wider than for most crop seeds), however, quality attributes tend to vary together and in the same direction. In particular, vigour and life expectancy may safely be inferred to diminish as measured viability falls (Ellis and Roberts 1981).

Viability is preferably measured by germination tests under ideal conditions. Where barriers such as dormancy make this impossible, tetrazolium tests are used (Grabe 1970). Sometimes the best estimate of viability involves a combination of the two methods. The Queensland Seed Testing Laboratory, for example, provides a tetrazolium-based estimate of the number of live, ungerminated seeds on its test report which can be added to the germination value. With legumes, hard seeds can safely be considered viable.

Variation in quality. Since there are numerous causes of deterioration as well as numerous ways of minimising it, seed acquired for sowing may cover a very wide range of quality. At one extreme, occasional lines of seed of any species may approach 100% viability. A minimum limit is set for seed offered for retail sale in Queensland by the provisions of the Minimum Standards (Anon. 1984). However, seed may deteriorate after sale or for various reasons not be subject to the Standards, so the realistic low limit for sowing is totally dead seed.

The most common agents of deterioration are premature severance of the developing seed from the parent plant (mostly at harvest because ripening is never perfectly synchronised, but also sometimes through disease, etc.); threshing damage at harvest; mistreatment during post-harvest handling and drying; and storage deterioration.

Storage deterioration is usually the result of aging. Under constant conditions, percent viability over time follows a declining sigmoid curve. The relationship can be treated by the transformation of percentages to probits to produce a straight line (Roberts 1986). The slope then represents the rate of deterioration independently of the position. The rate depends primarily on the moisture content and temperature of stored seed, rising sharply with an increase in either, but especially an increase in moisture content. As a general rule, the extent of deterioration at any point in time is a consequence of the seed population's total history, whereas the rate at which it is proceeding at any time is governed by prevailing conditions.

Grass and legume seeds are both subject to the full range of forces of deterioration. They differ, however, in the impact on the final product, so that legume seed is generally of much higher quality at sowing than is grass seed. There are two main reasons for this: it is generally much more difficult to eliminate physically inferior seed during cleaning in grasses than in legumes, and grass seed lots mostly contain substantial proportions of prematurely detached and therefore immature seeds; and legume seed tends to be stored at a lower moisture content than grass. This is partly because it is harvested and dried at a time of year when the air humidity is low, and partly because its mechanisms preventing re-entry of moisture as water vapour are much more effective. Legume seed is mostly stored at 5-9% moisture, and grass seed at 10-14%. Legume seed for sowing is seldom below 60% viability, whereas grass seed may often be as low as 40%.

Impediments to germination

Grass seed dormancy. Grass and legume seeds both show dormancy, but in legumes it is of short duration and has little or no relevance to conventional establishment (Gardener 1975; Argel and Humphreys 1983). Grass seed dormancy, on the other hand, may persist for years and has to be taken into account in sown seed.

In the simplest view, grass seed dormancy is caused by an inhibitor of metabolic activity present in the embryo. Its influence is strongest in fresh seed and wanes with age (Harty *et al.* 1983). In germination tests, it can be reduced by various chemical treatments often involving oxidising agents; temperature fluctuation (Goedert and Roberts 1986); and removal or disruption of covering structures that may limit gaseous diffusion between embryo and external atmosphere (Renard and Capelle 1976; Whiteman and Mendra 1982; Hacker 1984; West and Marousky 1989). Usual treatments are irrigation with potassium nitrate solution; acid scarification; and choice of appropriate temperatures in the germinator. Dormancy can be prolonged by cool (Hacker 1984) or cold (Harty *et al.* 1983) storage of dry seed. It is reduced unwittingly by threshing damage at harvest and later by processing actions that cause some attrition of husks — e.g. repeated passage through augers during blending.

The extent of dormancy in seed lots is highly variable. Besides changing with age, it differs between species, ecotypes and cultivars (Hacker 1984; Hacker *et al.* 1984) . The greatest differences appear to be linked with the nature of the caryopsis coverings. The most intransigent dormancy occurs in that group of the *Paniceae* with the characteristic, hard protective husk formed by the lemma and palea of the fertile floret (e.g. *Panicum, Brachiaria, Setaria, Urochloa*). Seed of most sown species within this group is too dormant to use for most purposes for at least 3 months after harvest, and dormancy is commonly still evident at planting time in the following season. It is less important with the relevant members of the *Andropogoneae*, which have less tightly protected caryopses, or with seeds that have only very flimsy coverings like *Chloris gayana* and the group of the *Paniceae* that contains *Cenchrus* and *Pennisetum*. It is sometimes considered a testing problem in these groups, but seldom a field establishment barrier.

Legume seed coat impermeability. All tropical pasture legumes but no grasses produce seeds with prolonged impermeability to water (hardseededness). It is caused by external structures that almost all the papilionaceous pasture legume species share (Quinlivan 1971; Ballard 1973; Rolston 1978). The seedcoat or testa, when mature and intact, is watertight over most of its surface. The only exception is the strophiole, a small protuberance in which the columnar cells of the testa are elongated and under apparent physical tension. They are apt to split to produce a cleft that allows water to penetrate. This is the "natural" route of entry of water. The strophiole may be induced to cleave if further stresses are imposed on the testa through sudden physical shocks or temperature changes, or it may do so over time without detectable cause. Another structure, the hilum or stalk scar, acts as a one-way hygroscopic valve, allowing water vapour to pass out but not in (Hyde 1954). It thus allows the seed to reach and maintain the low moisture content which is necessary for the full development of hardseededness.

The *Mimosaceae* and *Caesalpiniaceae* have different seed structures (Corner 1951). The hilum is less distinct and appears to be a less important, and not the only, route of late moisture loss (Tran and Cavanagh 1984). The strophiole erupts rather than cleaving, and a plug of tissue is ejected (Dell 1980). This can easily be seen in seeds of *Leucaena leucocephala, Desmanthus virgatus* and *Cassia rotundifolia* under magnification after hot water treatment (J.M. Hopkinson, unpublished data).

Rupture of the strophiole to reduce hardseededness is not always easy, and scarification is often preferred. It simply involves fracturing of the testa to allow penetration of water to the embryo.

Sown seed may thus be impermeable (hard); permeable (soft) because of fractures to the testa; or permeable because of cleaving of the strophiole. The relative proportions of the three states vary with the history of the seed and change with time as strophioles cleave or as soft seeds leave the system by germination or death. Species differ in their normal levels of hardseededness. Seeds that are shed naked tend to be softened to some degree by abrasion and impact at or after harvest, while seeds that remain protected by pod structures tend to retain high levels of hard seed. The strophioles of some cleave readily and early in life (e.g. lablab) while those of others remain impermeable for long periods. Cultivars of *Stylosanthes scabra* and *S. hamata* produce seeds well protected by pod structures and with very high levels of hardness. When young, well dried and untreated, well formed seeds are often hard, and the only ones that germinate then are defective ones — usually prematurely harvested individuals, present in very small proportions.

The significance of hardseededness to establishment is purely as a timing device governing when germination may occur. It spreads over time the risks that accompany germination, but this spread may be too protracted for rapid establishment from sowings.

Protective structures

The dual role of some structures covering seeds should be emphasised. Their damage or removal creates opportunities to germinate but increases vulnerability to pathogens. Experience of exhumation suggests that only physically perfect seeds with intact protective structures have any prospect of long-term survival in soil.

Imperfectly protected caryopses of tight-husked grasses have a very short life expectancy. Immature seeds have a slack seal between palea and lemma which often allows fungi to penetrate and infect the caryopsis even before post-harvest drying is complete. Husks visibly damaged by threshing seldom contain a live caryopsis, and naked caryopses found sometimes in seed lots are invariably non-viable. Caryopses of grasses with poorly protective surrounding structures are much less vulnerable. They appear to have more robust pericarps, which is perhaps why they survive readily (and may even be marketed) in the naked state.

The critical protective structure of legume seeds is the testa. Damage to the testa exposes the flesh of the cotyledons to invasion by pathogens, and the entry of water vapour, which raises moisture content and reduces life expectancy. Where the pod segment persists it seems to protect the testa from impact or scarification, and prolong its impermeability. Strophiole breaching appears not to extend to the surface of the testa in general, and therefore not to impair the protective function.

Seedbed environment

In the Queensland tropics, the dominant seedbed variable is soil moisture. The most direct approach to simplifying the system is therefore to take account of soil moisture and to treat other variables as background noise. This approach is justified when a satisfactory interrelationship with seed properties can be obtained. However, common sense must be applied to other variables such as sowing time, seedbed preparation, etc. to minimise unnecessary variation.

The target soils of the northern tropics have predominantly poor moisture retention in the surface layers where seed is sown. At the relevant time of year they are subject to strong evaporative forces. The soil surrounding a seed typically dries out very quickly after rain, often passing from field capacity to wilting point in the course of a morning. It is a further acceptable simplification, therefore, to ignore continuous variation in soil water potential, and to think only in terms of how long the soil is wet or dry. The dimension of the dominant variable thus becomes time, and a particular period of time may be viewed as dry, intermittently wet, or continuously wet.

Dry conditions

In dry conditions there is obviously no germination and the only point to take into account is loss of live seed. Ultimately what matters is the amount and condition of seed when the opportunity to germinate arises. Losses unrelated to seed properties, such as through predation, are irrelevant in the present context though presumably their risk is more or less proportional to the duration of exposure. Losses due to deterioration of seed are more relevant, but are virtually impossible to quantify. They will depend on seed temperatures and moisture contents which are hard to predict and seldom measured. A few isolated records exist (e.g. Gardener 1975), but in general it is hard to do more than point to trends inferred from general principles. Time is a key variable, and the extent of deterioration increases as the interval between sowing and rainfall extends. It is likely too that seed buried or otherwise protected will have a longer life expectancy than exposed seed. However, if aging deterioration is at all significant, intact, high quality seed will have by far the best chance of leaving survivors capable of vigorous germination at the end of the dry period.

Wet conditions

Continuously wet conditions are generally regarded as allowing sown seed to realise its greatest potential, and with minor reservations this is correct. Its truth is reflected in the universal observation that there is no substitute for a week of "proper wet season weather" to obtain a good initial strike, and that neither irrigation nor intermittent storms provide a satisfactory alternative to continuously overcast, humid, wet weather in which the soil surface never dries out.

Intermittent wetting

Intermittent moisture availability is a normal state, and seeds possess mechanisms to cope with it. In general, if a seed imbibes but dries back before radicle emergence, it survives and can start again and germinate later. Indeed, it may even benefit from the experience. A brief period of tissue hydration promotes repair of subcellular aging damage and thus prolongs the subsequent life of a quiescent seed (Villiers and Edgcumbe 1975). This has been amply demonstrated with *Panicum maximum* in unpublished experiments by R. Medeiros at Walkamin. It is probably applicable to any non-hard pasture seeds lying for long periods in or on the soil. Its short-term benefits are less clear, though a reduction in the time taken to germinate at a second wetting ought to aid survival prospects.

Brief rehydration can be accompanied by changes to protective tissues, and this may increase vulnerability, even if it does prolong life expectancy in other respects. Pericarps of grass caryopses are ruptured by expansion of the plumule and coleorhiza. Hydrated legume testas develop cracks when dried back and remain permeable. Consequences of these changes remain supposition, however. In soil, they probably prejudice long-term survival but permit the exploitation of brief cycles of moisture availability.

Radicle emergence is believed to correspond to the start of cell division in the embryo of grasses, with prior changes no more than cell enlargement. It represents the point of no return simply because the radicle is intolerant of desiccation, and because few seedlings can survive death of the radicle. The plumule is more resistant to desiccation, though this varies with the type of seed. Of those we have observed, the plumule of tight-husked panicoid grasses is least resistant, and the entire embryo dies rapidly. That of andropogonoid grasses is highly resistant, and Susie McKeague, in a project at Walkamin, observed that rehydrated seedlings of *Andropogon gayanus* are quite capable of replacing a dead radicle with secondary roots arising from the plumular axis just above the scutellar node. Legume seeds seem unable to survive desiccation after radicle emergence, though in experiments with *Stylosanthes scabra* we have observed survival of the plumule, but with no secondary root development and therefore no future.

The state of partial germination before radicle emergence in grass seeds was described by Watt (1978), who called it hydropedesis because he associated it with the development of certain water potentials in soil. It was the most advanced stage that could be reached when water was not freely available. Seed could be dried back from it with impunity. Watt (1978; 1982) recorded it with *Dichanthium sericeum* and other subtropical grasses, and we have since observed the same thing in a wide range of grasses. The same state is reached by a proportion of seeds when dormancy prevents germination in routine tests. Staff of the Queensland Seed Testing Laboratory confirm that it is widespread and commonplace in grass seeds. In recent experiments with *Urochloa mosambicensis,* we obtained indirect evidence that arrival at the partially germinated state is under the influence of dormancy in a similar way to that of germination itself.

Interrelationships

Two kinds of record are available for deriving interrelationships. One is the comparative behaviour in laboratory, shadehouse or field of seed lots of widely differing properties. The other is the course of germination and seedling emergence from seeds with various characteristics, from which inferences about survival prospects can be drawn. We make use of both.

A preliminary to any measurement of seedling emergence is confidence that records cover the whole period of useful germination. Sown grass leys thicken up substantially into the second season, possibly from delayed germination of originally sown seed. Unthreshed Gatton panic seed showed this capability in the protected environment of a shadehouse (Figure 3). In 3 field experiments over successive seasons with green and Gatton panics, and with all alternative sources of seedlings and causes of concealment eliminated, very few seedlings ever emerged after the first wave following germinating rains. The start of this period may or may not be delayed, but it usually lasts a few weeks. The practical definition of its end is when it becomes impossible to identify new emergents without removal of earlier emerged grass and weeds. Only about 0.03% of 15 000 seeds sown provided seedlings after this initial period but still in the season of sowing; and fewer than 0.2% produced seedlings in the following season. We therefore concluded that the contribution of long dormant seed to establishment of the sward was negligible, and that the immediate emergence record adequately measured the sown seed's potential. None of this precludes recruitment in other circumstances, such as from dormant sown seed relocated by later soil disturbance.

We lack comparable records for legume seeds, and unambiguous direct evidence in the literature is scarce. However, it is widely and probably correctly believed that legume seeds, with their fundamentally different delay mechanisms and more effective protective coverings, retain the capability to survive within the soil layers from which they can then germinate after very long intervals.

Grasses

When seed of numerous lots of green panic (*Panicum maximum*) was sown into soil in trays, seedling emergence recorded until it ceased, and surviving seeds then exhumed, there was a clear, linear relationship between viability of the sown seed as measured by tetrazolium and total survivors in soil expressed as the sum of emergent seedlings plus surviving dormant seed (Figure 1a).

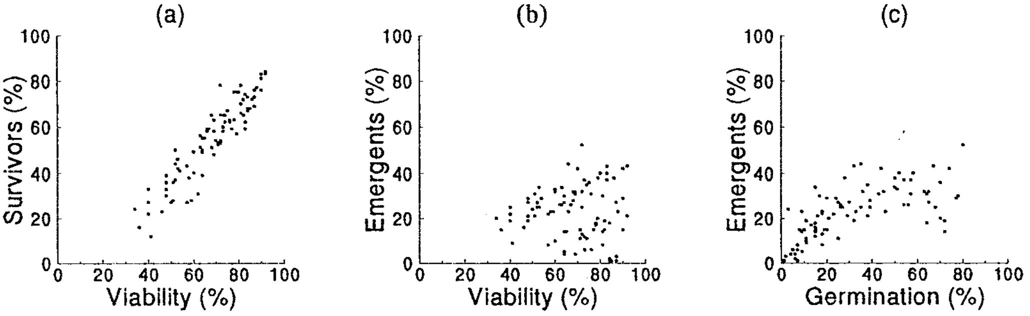

Figure 1. Survival in, and emergence from soil of seed and seedlings of 84 separate lines of green panic sown in a shadehouse in 1984. Survivors are the sum of emerging seedlings and later-exhumed live seeds.

The pattern was largely as might have been predicted: there was a certain level of unaccountable variation; some seeds deemed viable failed to survive, especially at the lower end of the quality range as if low vigour and short life expectancy prejudiced their prospects; but essentially there was a reassuringly simple linear relationship. However, emergence alone was much less closely related to "official" germination (the usually quoted test value, being the higher of the figures obtained in potassium nitrate and water tests); and it was largely unrelated to viability (Figures 1b and 1c). Emergence is what counts, and clearly it was dormancy that was preventing any close relationship with emergence.

The seed lots used, though all of the same chronological age, had been cold-stored for different lengths of time and effectively represented 3 different physiological age groups. Separation into age groups retained the previous relationship between survival and viability, the curves being displaced only in as much as viability fell with age (Figures 2a–2c). Although it reduced the scatter in the relationships between emergence and both viability and official germination, mainly by isolating the young dormant seed (Figures 2d–2i), some other factor involving dormancy was also at work.

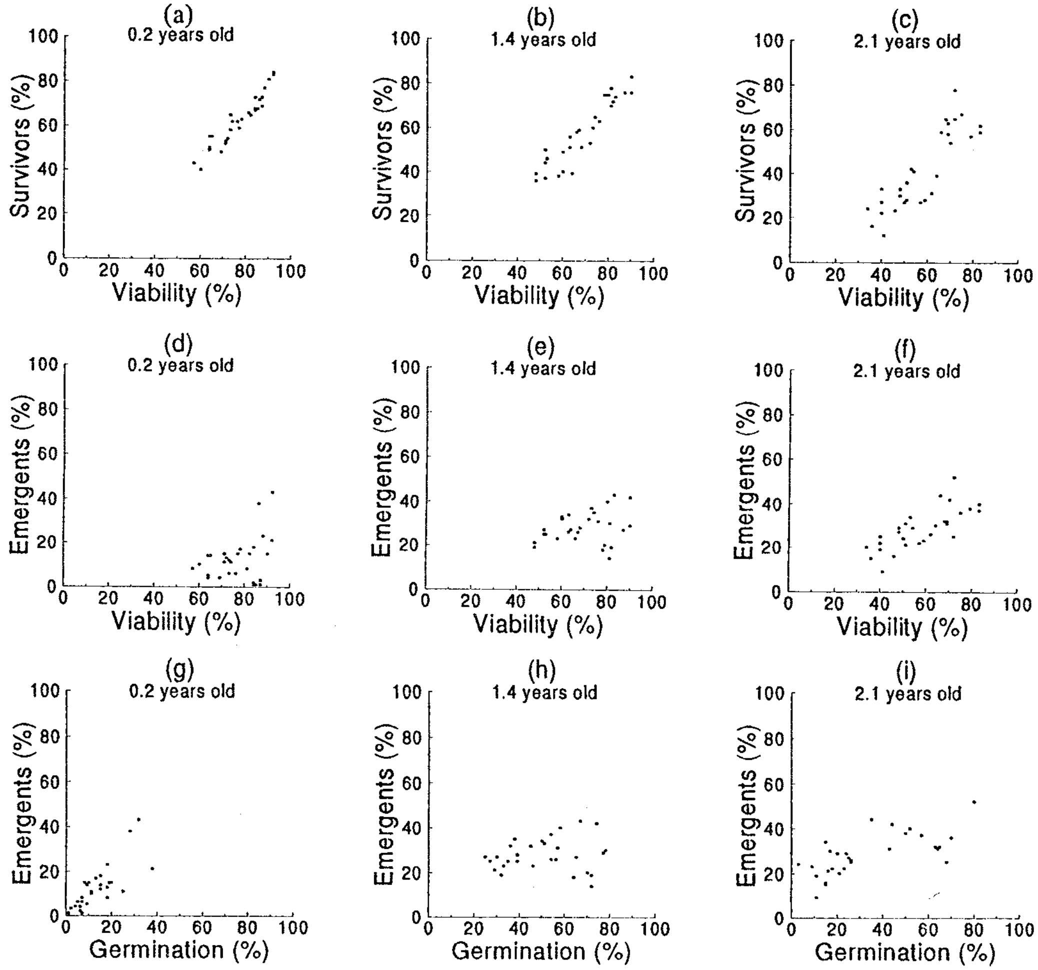

Figure 2. Survival in, and emergence from soil of seed and seedlings of 84 separate lines of green panic of 3 different physiological ages sown in a shadehouse in 1984. Survivors are the sum of emerging seedlings and later-exhumed live seeds.

It proved in part to be differences in the extent of threshing damage, which introduced inconsistencies through two opposing effects, breaking dormancy and shortening life expectancy. Further complications arise from each effect. The extent to which dormancy is broken varies with both seed age and the conditions for germination; and the degree to which life is shortened depends on both time elapsed and storage conditions. Two examples of these effects are given as comparisons between otherwise-identical unthreshed and header-harvested, threshed seed. One summarises comparative performances in a range of conditions (Table 1), and the other illustrates the course of events over time for a single comparison (Figure 3). Clearly every response is situation specific. Even with a thorough knowledge of seed history, it is difficult to predict the size or the time scale of the two effects. The severity of threshing damage is itself very variable. When the two main effects also act in different directions, a large measure of apparent inconsistency in seed-behaviour is inevitable.

Most of the foregoing records of emergence were made in benign conditions. They introduce consequences of interrelationships between different seed properties, but not interactions with different seedbed conditions. When variation in seedbed conditions (primarily in time of availability of soil moisture) is introduced, many other effects appear. Some, like survival of drying-back, are simply accounted for, whereas others, such as predation by soil fauna, are not interactive with seed properties. However, one has been detected with a strong bearing on dormancy.

It was frequently noticed that seed sown in the first season after harvest, often 6–10 months old, performed worse in the field than indicated in laboratory tests. The effect tended to be absent from sowings in trays, and most conspicuous when field seedbed conditions were dry. Our clearest records of this are illustrated in Figure 4, which shows that first-year seed had a very poor emergence record in 3 plantings with intermittent rainfall, but in a fourth planting with continuously available moisture over the critical period, emergence was consistent with quality.

A similar effect is evident in the records of Table 1, showing field emergence (in very dry conditions) of seed of the appropriate age (0.78 years). Unthreshed seed performed relatively poorly in spite of high viability, germination and emergence in trays.

The evidence points to the persistence of dormancy at a level that does not prevent germination in favourable conditions but prejudices its success under stress. This effect might be caused by the slowing down of the course of germination, either of individual seeds or of the population as a whole. There is ample evidence of slow population germination of fresh seed in *Panicum maximum* (Harty *et al.* 1983). Table 1 provides further evidence, together with significant occurrence of abnormal seedlings when dormancy is strong. Abnormalities are mostly in radicle emer-

Table 1. Behaviour of otherwise-identical threshed and unthreshed green panic seed of 3 different effective ages in viability, germination, soil-in-tray emergence and field emergence tests. Trays were dry between days 80–238. "Effective age" is chronological age minus time spent in cold storage.

	Unthreshed			Threshed		
Effective age at start of tests (years)	0.25	0.78	1.52	0.25	0.78	1.52
Laboratory:						
Viability (%)	93	83	80	86	75	60
Official germination (%)	58	77	69	48	49	24
Mean germination time (days)	17.0	7.5	7.3	12.8	10.0	9.1
Abnormal seedlings in germination test (%)	9.7	2.7	6.0	7.2	1.8	1.4
Soil-in-trays:						
Emergence (%)						
Days 0–79	2	27	36	23	16	6
Days 239–253	71	33	9	12	2	0
Mean emergence time (days)						
Days 0–79	11.5	7.2	7.5	10.6	9.7	8.0
Days 239–253	4.8	5.1	4.8	5.2	5.6	—
Field:						
Emergence (%)	0.3	2.6	9.8	0.5	6.6	11.3

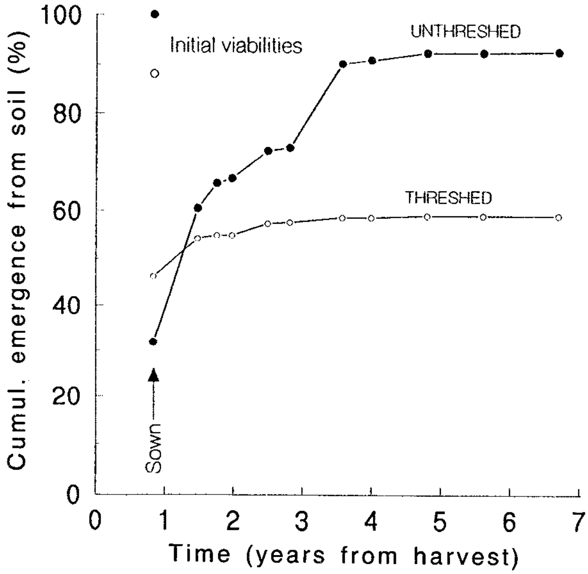

Figure 3. The course of emergence of otherwise-identical threshed and unthreshed Gatton panic seed from soil in a shadehouse with intermittent periods of watering over a 6-year period.

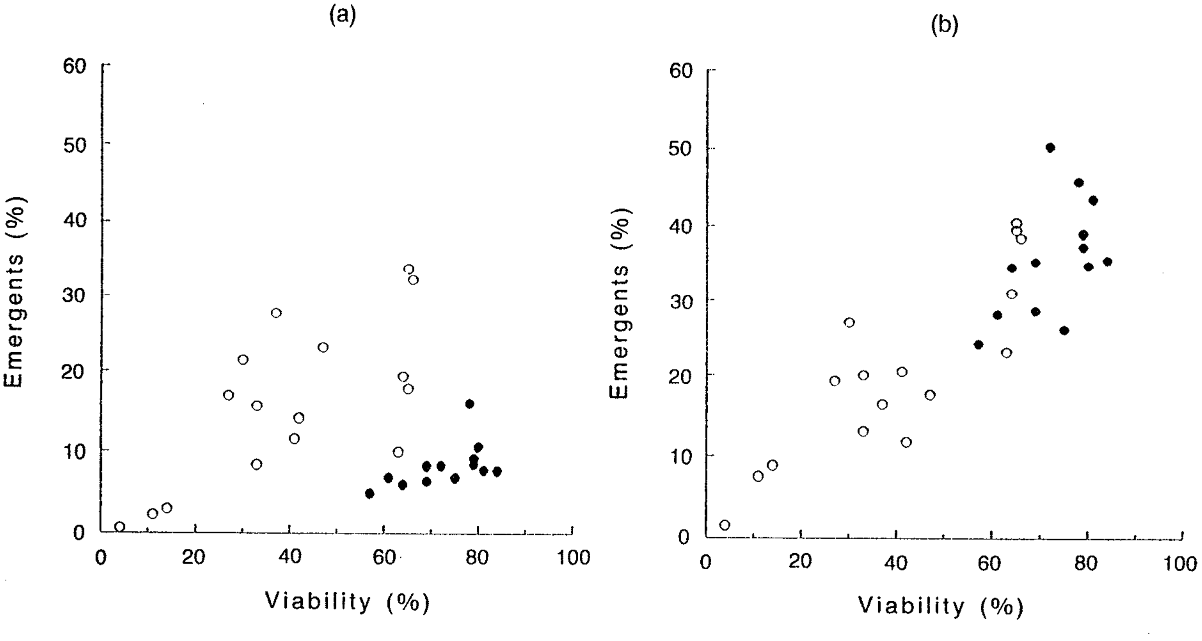

Figure 4. Field emergence of first-year (●) and 2- and 3-year-old (O) seed of Gatton panic in relation to viability, from (a) plantings 1–3 with intermittent soil moisture, and (b) planting 4 with continuously available soil moisture. Seed was cold-stored between plantings to prevent dormancy breaking.

gence, as if the disappearance of dormancy is spatially inconsistent in the embryo and latest to occur in the radicle. When vigorous root penetration is critical, as is assumed in conditions of rapid soil surface drying, delays of this kind are likely to be fatal.

In any single germination event in soil, for seedling emergence to succeed the time pattern of germination must match that of soil moisture availability. In the absence of experimental records of the consequences of matches or mismatches, we have drawn inferences from patterns of germination or emergence in conditions of freely available moisture. These provide useful lessons.

In the simplest seedbed situation, seed is sown into the dried surface layers of soil which has received enough rain to provide reserves of moisture at depth. Germination is stimulated by the next fall of rain. Moisture in the soil surface layers remains adequate for a finite period during which the seedling must get its root into a safer level of soil or perish. If the pattern of germination of the population is known, and some arbitrary time is chosen as the interval between germination of a seedling and its becoming temporarily "safe", it is possible to apply a form of risk analysis to the system and to depict how death risks may change with differing duration of moisture availability.

Different grasses have different characteristic patterns of emergence in conditions of continuously available moisture, which have been used to calculate death risk patterns. It is assumed that, before radicle emergence, a seed is under no death risk from soil drying because it can dry back with impunity; and that a germinating seedling which does not suffer desiccation before its root can reach a secure moisture supply is also safe. The root is assumed to reach a safe supply of moisture in 2 days. Although the time will vary, the patterns remain the same in general shape and relativity to one another over a wide range of chosen values.

Typically, in conditions of continuously available moisture and normal summer temperature ranges, grass seed lots have single-peak seedling emergence patterns that start at a time characteristic of the species and dwindle almost to an end by about the third week. In field conditions, the soil surrounding the seed usually dries out long before this. Death of newly-germinated seedlings follows. It is common, conspicuous, and perhaps even the cause of the most deaths overall. Figure 5 shows that Callide rhodes, beginning and completing its germination early,

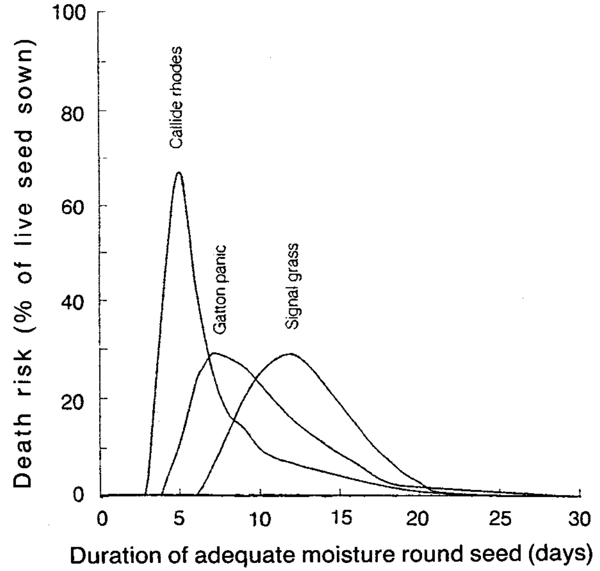

Figure 5. Smoothed eye-fitted curves, based on actual soil-emergence records of 3 grasses, relating death risks to time of soil drying.

has a brief, early period of high risk, whereas signal grass needs a longer period of wet soil to start but spreads its risks much more widely.

Obviously this is an over-simplification. It takes no account of intermittent moisture availability or of other, variable seed characters. Seed size for example, which affects both depth from which seed can germinate and probably rate of root penetration, must affect the pattern. Even so, it matches observed behaviour of establishment in prepared seedbeds. Callide rhodes normally establishes rapidly and readily, but occasional cases of otherwise-inexplicable total failure occur. Signal grass is slower but surer, and very seldom fails completely; and the behaviour of panics is intermediate.

Legumes

Recent emphasis on the problems of establishing stylos in the very harsh seedbed conditions where they are required to survive has provided much background information (McKeon and Mott 1984). Survival is apt to be dominated by the events that follow emergence, particularly hard seed breakdown in relation to soil surface conditions and death from soil drying while seedlings are trying to establish. This tends to obscure direct connections between seed properties and emergence, which belong to only the first of a succession of hazardous phases. Our experience with Seca stylo adds a little to the picture of these earliest events.

Measurements made on 18 separate lots of seed-in-hull showed a close relationship between laboratory and soil behaviour, both in numbers surviving and numbers germinating (Figure 6). Soil conditions favoured unimpaired germination of soft seed and were not conducive to further hard seed breakdown, so everything favoured a close relationship. Even so, the time scales of measurement differed greatly, which might have been expected to introduce inconsistencies.

The lowest quality seed lots performed poorly in soil relative to their laboratory record, as if again reflecting low vigour and survival capacity. These seeds had been subjected to heat treatment which appeared to have aged them. Emergence from soil was 54% of laboratory germination compared with 106% for comparable high quality seed. Soil survival as a percentage of laboratory viability was 49% compared with 81% for the high quality seed.

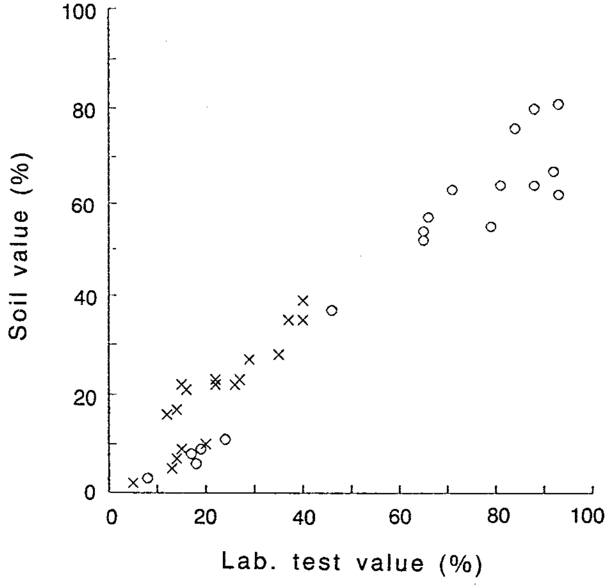

Figure 6. Relationships between laboratory test values and behaviour in soil of Seca stylo seed-in-hull from 18 separate seed lots. Crosses relate laboratory germination (germinating plus live imbibed seeds after 10 days at 20/35 °) to cumulative soil emergence (in 3 sequences of alternating wet and dry periods over 3 months). Circles relate laboratory viability (germination plus hard seed) to numbers of survivors in soil (emergents plus exhumed live seeds) in the same conditions.

In other words, in the absence of seedbed irregularities, seed-in-hull behaved as expected. Naked, partly scarified seed did not conform to this pattern, however, with relatively poor soil performance for seed of high viability and germination (69% and 61% respectively, for the criteria quoted above). Invasion by fungal pathogens was conspicuous in sowings of scarified seed, leading to damping off not observed otherwise. The high mortality may be due to the ease of penetration of pathogens to the embryo through fractures of the testa.

Simple timetables of germination or soil emergence can add to McKeon and Mott's (1984) conclusions on effects of speed of germination if seed in different imbibition categories is considered separately. There are 3 categories to consider — scarified seed, strophiole-breached or breaching seed and hard seed. Scarified seed imbibes rapidly and virtually immediately on contact with free water. Water penetration through the strophiole is much slower even after it has begun. This can readily be seen if seed is soaked in ferrous ammonium sulphate solution (Ballard 1973), which blackens the testa wherever moisture penetrates. Also the start of penetration through the strophiole is greatly staggered in time among seeds of a population. This happens even when there is no obvious continuing hard seed-breaking influence. It is as if earlier events predispose the strophiole to rupture rather than cause it to do so at the time. Figure 7 shows emergence of seed that was exposed to direct sunshine intermittently for a week before being buried in soil in a shadehouse which experienced neither high temperature nor rapid temperature fluctuations.

The course of germination of a population of seeds in continuously favourable conditions depends a little on the presence of the hull, which briefly delays water entry (Gardener 1984); and a little on variation in the interval between water entry and radicle emergence (we have measured it as averaging 2 days, with the range 1–3 days taking in more than 98% of all live seeds). However it is dominated by the time of first entry and hence by the route of penetration-fracture or strophiole. Penetration via the strophiole, and hence germination and emergence, may continue for a very long time, the 3 months of Figure 7 being common.

Smoothed curves derived from actual records and representing typical emergence patterns of seed in 3 conditions are shown in Figure 8a and used to produce the death risk patterns of Figure 8b in the same way as was done earlier for 3

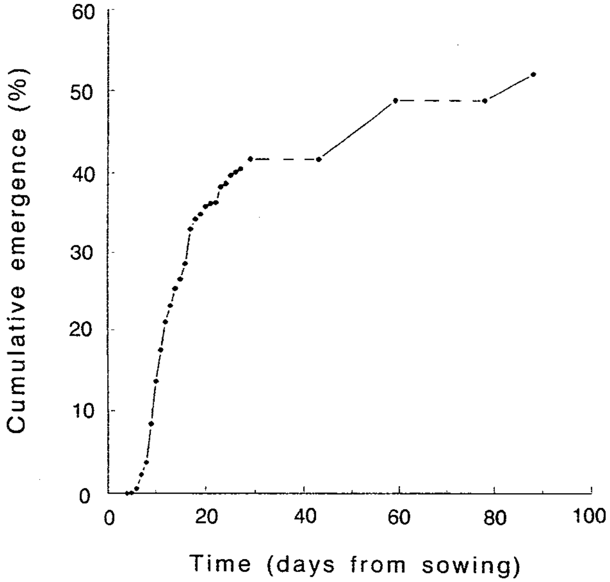

Figure 7. Cumulative emergence of seed-in-hull of Seca stylo buried in soil in a shadehouse (average temperature of about 25 °C). Seed had been exposed to direct summer sunlight intermittently for a week before sowing. Soil was dried out over periods shown by dotted lines.

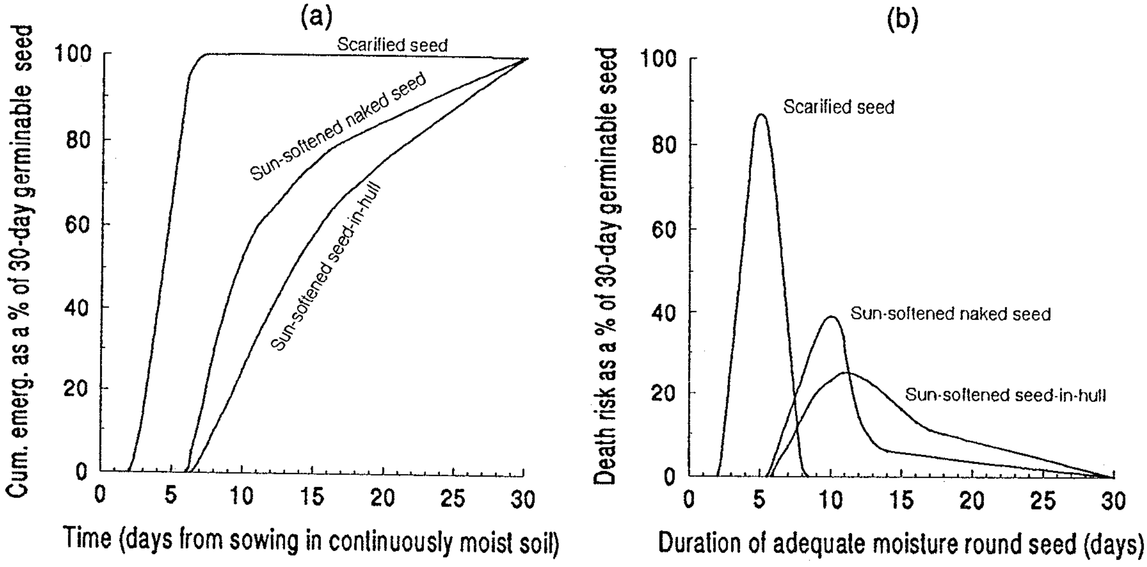

Figure 8. Smoothed eye-drawn curves based on (a) actual records of seedling emergence of 3 classes of Seca seed, and (b) patterns of death risk derived from (a) in relation to time of soil drying out.

grasses. They illustrate the very different advantages and risks attached to using seed softened by the 2 different routes.

The routine recommendation for Seca in north Queensland is to use untreated seed for early sowings (i.e. about October, in expectation of at least 2 months before rain). D. Gramshaw (personal communication) obtained far greater success with strophiole-softened than with scarified seed of Fitzroy stylo in central Queensland under conditions in which brief rainfall events occurred. Explanations of these findings in terms of risk patterns and of vulnerability arising from testa fractures is obvious.

Discussion

The interrelationships described provide explanations of observed behaviour. Do they allow the user of seed to make useful predictive judgements — to choose the most suitable seed for a particular use, or to estimate the relative chances of success from seeds of differing properties?

Up to a point, they do. So long as vital quality is the main variable to consider, the position is straightforward. Seed of the highest vital quality offers the greatest likelihood of successful seedling emergence, other things being equal. The high quality seed not only contains more live seeds, but those live seeds also have greater vigour and longevity, reinforcing the relationship between quality and success. However, once the impediments to germination start to influence events, such simple conclusions need substantial qualification.

Grasses

The tight-husked grasses introduce the complication of dormancy. The occurrence of opposing effects, dormancy breaking and reduced life expectancy, dependent on the same causal factors of husk damage and the passage of time, is confusing enough. However, it is compounded by the persistence of levels of dormancy that do not prevent germination, are not readily detectable in tests, and cause inconsistency in field emergence. Moreover, these complications are greatest at the time when seed is most likely to be sown, in the first season after harvest. At this time, emergence cannot be predicted with any accuracy. At other times, with either fresh, deeply dormant seed on the one hand, or much older seed with little dormancy left on the other, prediction is more reliable.

The subject of dormancy warrants attention. Although dormancy prevents premature germination of young seed and is sometimes usefully exploited, as when perennial grasses are undersown with winter forages, it persists too long for our convenience. In conventional summer sowings, long-dormant seed contributes little to the sward and partially dormant seed establishes unreliably. We should, therefore, investigate ways of shortening the duration of dormancy. In the long term, selection or breeding might offer a route, since the extent of dormancy is a genetically variable attribute (Hacker 1984). However, in the short term, the improvement of valuable existing cultivars depends on some form of seed treatment.

Manipulation of storage environment offers little promise. Although loss of dormancy is delayed by storage at low temperature, the limited evidence available (Harty *et al.* 1983) shows it is not materially hastened by higher-than-normal storage temperature. The other obvious route is through deliberate, controlled husk damage, preferably carried out at the end rather than the beginning of the seed's storage life in order to reduce the accompanying shortening of life expectancy. We found acid treatment unsatisfactory, as it is dangerous and difficult and produced no net improvement in establishment of seed of *Brachiaria decumbens* of normal sowing age. Less damaging forms of husk attrition could perhaps usefully be developed.

Legumes

Experience of Seca stylo, though more limited, appears to indicate an essentially simpler situation than that applying to the husked grasses. Seed coat impermeability involves less fickle mechanisms than dormancy. In the absence of further softening and in benign conditions, laboratory germination reasonably predicts soil emergence. Further softening is best viewed purely as a consequence of seedbed conditions and not something dependent on seed properties that are measurable before sowing. Viability and current hard seed status provide most of the necessary information about the characteristics of seed for sowing. Only the condition of the soft seed fraction warrants consideration also.

Tests do not normally discriminate between scarified and strophiole-softened seeds. Yet it is important to know in which category the soft seed falls, in view of the very different time course of germination that each follows. Fortunately, it is usually possible to infer the form of the seed from the physical condition of a sample: seed-in-hull, for example, cannot possibly have been effectively scarified and, if soft, must be strophiole-softened; and naked seeds, regardless of the state of the strophiole, will almost certainly have undergone some testa damage.

With respect to seed softening, two matters warrant further investigation. One is to check the inferred advantages of the use of strophiole-softened seed over scarified in conditions of low expectation of either imminent rainfall or further natural softening. The other is to seek to understand the time course of strophiole opening after seed has been subjected to strophiole-breaching treatment. As shown (Figure 7) there is a variable, and in many seeds prolonged, lapse of time between treatment and effect. This is a major component of the spread of germinability that is so important for survival. The reasons for it are not understood, and ignorance of them prevents any purposeful attempt to manipulate the course of strophiole opening to our advantage.

Establishment

The work described aimed to establish relationships between seed properties and seedling *emergence*. To pass beyond emergence to *establishment* introduces a different set of issues. While failure to emerge guarantees failure to establish, good emergence does not guarantee establishment.

In one instance the step from emergence to sward establishment was measured with panic seed in prepared seedbeds sown at different times in the wet season on the Atherton Tableland. Under these benign conditions, a close relationship was found between seedling numbers and sward development up to the point where seedlings exceeded the necessary minimum density for complete cover.

Establishment of stylo sown on to unprepared surfaces in conditions of low fertility, variable rainfall, or uncontrolled competition from grasses is very different. Emergence is only one in a chain of extremely hazardous events. A combination of knowledge of seed behaviour, soil characteristics, rainfall probabilities and plant ecology is necessary to obtain a connection between seed properties and establishment, and to derive expectations of success.

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