PATTERNS OF DELAYED GERMINATION IN SEEDS

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ABSTRACT

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Patterns of delayed germination in seeds of wild angiosperms are classified according to their observed manifestation in the field and in laboratory experiments simulating natural conditions. Appropriate terms for the various phenomena are proposed. Seeds of a few species may germinate on the parent, or soon after being shed, but for most species there is a delay in germination ranging from a few weeks to at least several decades, depending on the species and the circumstances. These seeds form short or long term "seed banks", in some species retained on the parent plant in dry fruit, in other species lying on, or within the soil. The causes of delayed germination appear to fall into four main classes: (1) Thick seed coats or plugs in the micropyle which prevent ingress of water and oxygen (*physical constraint*); (2) Requirements for particular sets of environmental conditions for germination which are not met in the prevailing circumstances (*environmental constraint*); (3) Immature embryos (*immaturity*); (4) Biochemical blocking factors which reside in seed coats, embryos or other parts of the seed contents, or sometimes in the perianth or other organs that invest the fruit (*dormancy*). These latter causes of delay are complex in their manifestations (*primary* and *secondary*, *complete* and *incomplete* dormancy; polymorphisms or dormancy developed to varying degrees in cohorts of seeds). Their ultimate causes are also complex. Satisfactory explanatory models for their controlling mechanisms are not yet available.

KEYWORDS: Seeds - delayed germination - classes of delay - seed banks.

INTRODUCTION

This paper discusses the range of delayed germination phenomena which can be recognized in the seeds of wild angiosperms by field observations and from simple manipulative experiments on their germination requirements (simulating the environmental conditions which they would experience in nature). Examples from the New Zealand native and introduced flora are used to illustrate the various patterns.

A few plant species have seeds which germinate on the parent. In other species seeds are ready to germinate as soon as they are shed. The seeds of most plant species, however, delay their germination for periods ranging from a few weeks to many years, depending on the species and also on the circumstances. Although the causes of delay are straightforward in some instances, in others both the causes and the resultant germination patterns are complex, as will be outlined later.

Delays in seed germination, and the particular means for overcoming these delays are ecologically important because they enable seeds, interacting with whatever factors overcome these delays, to exert some control over the time of their germination. In this way seeds can be dispersed in time, as well as in space. The populations of seeds waiting to germinate form "seed banks", which may in some species be retained on the parent plants, and in other species lie on, or within, the soil. This enables the seeds to survive unfavourable periods for as long as their viability lasts. If the delay is for several growing seasons, more than one cohort of seeds may be present in seed banks. The selection of future generations will thus be from a wider range of genotypes than would be the case if only one cohort was present in the seed bank population. Of course there is attrition of these seed populations by animal predation, microbial attack, climatic hazards and loss of viability (as well as removal by germination of some of the seeds).

The ecological success of many "weedy" species is due to their ability to form seed banks. Delayed germination is a critical factor in the survival of many annual species, including desert ephemerals, and is often very important for perennial species too. It may be a vital factor in the survival of some rare perennial plant species.

There is an extensive literature on delayed seed germination, which is usually discussed under the heading of *seed dormancy* (cf., e.g., Nikolaeva 1969, 1977, Harper 1957, Khan 1977, Mayer & Poljakoff-Mayber 1975, Cook 1980, Bewley & Black 1982, Baskin & Baskin 1985). Nevertheless there is no generally agreed conceptual system which describes the complex array of delayed germination phenomena and expresses them in a way which would be helpful to ecologists. In this paper delayed germination phenomena are classified, and a functional system of terminology is developed. It is hoped that this classification will provide a comprehensive means for considering the ecological implications of these phenomena. Examples from the New Zealand native flora are drawn from Mohan *et al.* (1984) (*Leptospermum*), Conner & Conner (1988) (*Arthropodium*) and otherwise from my unpublished experimental results. Examples from the introduced flora come from Mayer & Poljakoff-Mayber (1982) or Bewley & Black (1982), or in a few cases (*Dactylis*, *Hakea*) from my own observations.

THE RANGE OF DELAYED GERMINATION PHENOMENA

Refer to Fig. 1 for the outline classification. The seeds being considered are those in which fertilization of ovules has occurred (i.e., non apomictic), which are potentially viable and which escape predation on the parent plant.

A. Relatively few plant species exhibit *vivipary*, where seeds germinate on the parent. A local example where seeds habitually sprout on the parent and the seedlings fall, ready to take root, is the mangrove (*Avicennia resinifera*) a shrub or small tree of northern tidal estuaries. Some monocotyledon species (e.g., sea rush *(Juncus maritimus* - another salt-marsh plant), and some grasses, (e.g., cocksfoot (*Dactylis glomerata*)) also have seeds that sometimes germinate in the inflorescence. It is not absolutely certain whether the viviparous seedlings of these species establish in the wild, but they probably do, as they are easily cultured artificially.

B. Most seed species do not germinate on the parent plant.

(I) In some instances much of a season's crop of apparently mature and viable seeds is retained in dry fruit on the parent, for periods varying from a few months to a year, or possibly more. Examples are manuka (*Leptospermum scoparium*) and kowhai (*Sophora microphylla*). The fleshy fruits of the cabbage tree (*Cordyline australis*) and the drier fruits of the lemonwood (*Pittosporum eugenioides*), if not removed by birds, become fully dry and some of the seeds are retained in them on the parent. The seeds of these species are shed as a result of wear and tear of the fruit by wind buffeting, or in the case of *Leptospermum*, by high temperature shock (including fire) and possibly other kinds of climatic shock. Species of introduced Australian shrubs in the genus *Hakea* have woody fruit containing seeds which appear to remain viable for several years at least. They are released by fire.

(II) The seeds of most species are shed from the parent in various ways as soon as they are apparently mature. Most of these seeds reach the ground and some of them become buried through natural processes.

(a) In many species the seed water content is low (usually $< 15\%$ by weight) when they are shed. All of these seeds require water before they will germinate, but they fall into two classes:

(i) Those species (relatively few) which germinate within a week or two of being moistened. Examples are: some *Celmisia* species, willows (*Salix* spp.) and poplars (*Populus* spp.).

(ii) Those species which do not germinate immediately when they are moistened. Seeds of renga lily (*Arthropodium cirratum*), kohuhu (*Pittosporum tenuifolium*), and snow tussocks (*Chionochloa* spp.) are in this category. All of the seeds in category B(I) which I have examined also behave in this way. I will consider the range of causes for delayed germination in such seeds later.

(b) In a wide range of species, seed water

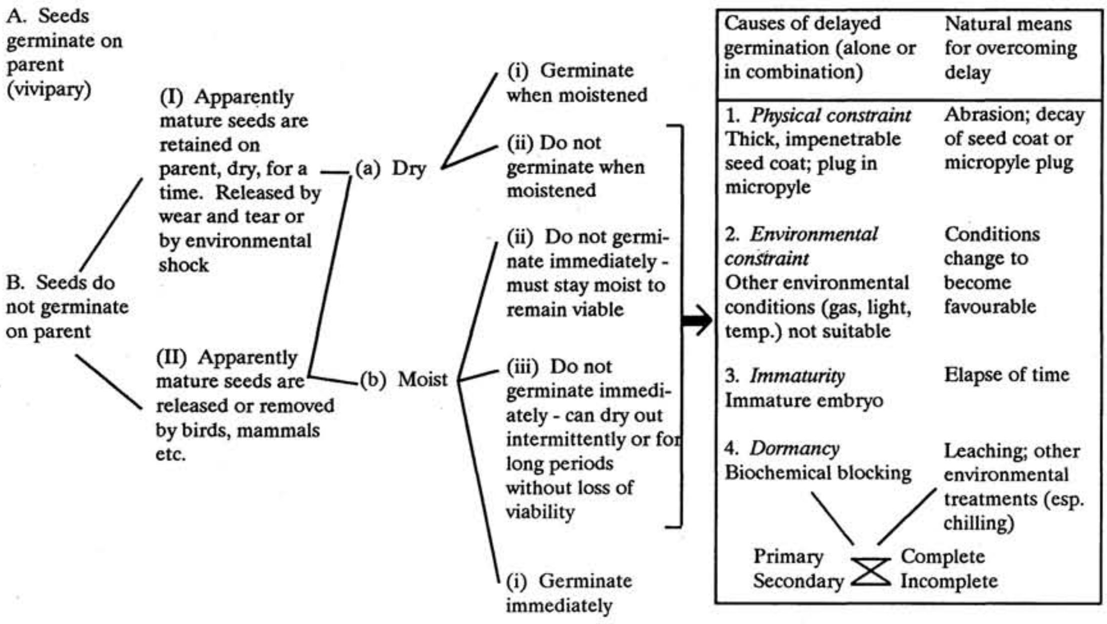

Figure 1. Non-delayed versus delayed germination: the behaviour of seeds of different plant species under natural conditions.

content is relatively high at the time of shedding (> 15% by weight). A further complicating factor is that many such seeds in the New Zealand native flora are surrounded by fleshy fruit tissue. Most of these are either swallowed by birds and later voided, or the fleshy coverings are removed by birds and the seeds discarded. Assuming that seeds had no fleshy fruit surrounding them, or that frugivorous birds have cleaned the fleshy fruit from most seeds (some drop to the ground still in the fruit), the seeds fall into three classes:

(i) Those species which germinate within a week or two of being shed. Examples are tree tutu (*Coriaria arborea*) and broadleaf (*Griselinia littoralis*).

(ii) Those species which do not germinate immediately after shedding but in which the seeds must stay moist to remain viable. Examples are tawa (*Beilschmiedia tawa*), oak (*Quercus robur*) and supplejack (*Ripogonum scandens*).

(iii) Those species which do not germinate immediately after shedding and in which the seeds may dry out for a period, while still remaining viable. Examples are tree fuchsia (*Fuchsia excorticata*), mahoe (*Melicytus ramiflorus*) and wineberry (*Aristotelia serrata*).

Considering the seed species in categories B(I)(a)(ii), B(II)(a)(ii), B(II)(b)(ii) and (iii) (i.e., where there are delays in germination), based on both local and overseas experience (e.g., Nikolaeva 1969, 1977, Mayer & Poljakoff-Mayber 1975, Bewley & Black 1982) the delays appear to be due to four general causes.

1. The presence of a thick, impenetrable seed coat, and at least in some, a plug of tough tissue in the micropyle which prevents the entry of water. Before the seeds can germinate these physical barriers must be removed (e.g., by abrasion or puncturing or cracking of coats, which occurs naturally by tumbling in streams; or by microbial decay of the coat or plug. Examples in the native flora are *Sophora microphylla* and convolvulus (*Calystegia tuguriorum*). It is possible that these seeds could remain in dry soil for several to many years before the conditions required for their germination are met; we do not know the full extent of their longevity. The persistence in seed banks for many years of similar introduced species such as gorse (*Ulex europaeus*) and fathen (*Chenopodium album*) are well known. Seed tissues impervious to gases have been cited as a cause of delayed germination (Nikolaeva

1969) but there appears to be little available information about this.

2. Other environmental conditions are not suitable for germination (e.g., the proportions of oxygen and carbon dioxide; light intensity or quality; day length; or temperature range). Often the unsuitable conditions are imposed through shading by a leafy canopy (light quality), by burial of the seeds in plant litter, or in the soil (gases, light intensity), or by the particular season (day length, temperature). As soon as the conditions change (through the occurrence of a canopy gap, the unearthing of buried seed, or by a change in the season), the seeds begin to germinate. Examples are broad-leaved plantain (*Plantago major*) and *Chenopodium album* which are inhibited by far-red light such as that found beneath a forest canopy; groundsel (*Senecio vulgaris*) and shepherd's purse (*Capsella bursa-pastoris*), which are inhibited by high CO_2 concentrations (and lack of light) when buried in the soil. In the case of shade inhibition of germination by a leafy canopy, mediation by the phytochrome system appears to be involved (Mancinelli & Rabino 1976).

3. The seeds have immature embryos which must mature before they can germinate. This requires time. Examples are *Ripogonum scandens*, pepperleaf (*Pseudowintera colorata*) and kawakawa (*Macropiper excelsum*).

4. Biochemical blocks are present in seed coats, in the embryo, or in some other part of the seed contents. Before the seeds can germinate these blocks must be removed in some way, often by particular environmental treatments. Examples are wild oats (*Avena fatua*), dock (*Rumex crispus*), feathery tutu (*Coriaria angustissima*) and *Aristotelia serrata*.

In almost every instance that I have investigated, where seeds fall to the ground still contained in fleshy fruits, there is a delay imposed, compared with the germination time for cleaned seed of the same species. The delay varies from a few weeks to several months. Examples are: *Cordyline australis*, *Melicytus ramiflorus* and *Aristotelia serrata*. Experiments on some species with seeds that exist in dry fruit show that the fruit walls, also, may prolong the period of germination delay (e.g., *Pittosporum tenuifolium*).

A DISCUSSION OF APPROPRIATE TERMINOLOGY FOR THE VARIOUS KINDS OF DELAYED GERMINATION

I propose that the term *delayed germination* should be the general one which we use for all of the phenomena where a delay is imposed, whatever its cause. In some seed species germination delays may have more than one cause (cf., Nikolaeva 1969). Furthermore, polymorphisms for biochemically imposed types of delayed germination are known in some seed species (e.g., in various species of Asteraceae, Brassicaceae and Chenopodiaceae) (Bewley & Black 1982). In seeds which have not been well-investigated, the unravelling of the complexities of delayed germination may require elaborate experimentation. In this discussion I will not be concerned much with the release of seeds from germination delay, although some modes of release are briefly indicated in Fig. 1.

Some authors (e.g., Nikolaeva 1969 and Conner & Conner 1988) have suggested that mechanical strength of seed coats (which prevents expansion of embryos of imbibed seeds) causes delayed germination, but Bewley & Black (1982) say that there is little evidence in favour of this view. The condition where seed coats prevent access of water or gases (or where there is resistance to embryo expansion, should it exist) may be called *physical constraint*.

Where delay is imposed by unsuitable environmental conditions alone, an appropriate term is *environmental constraint*. Other terms have been used for this phenomenon (e.g., "quiescence", by Bewley & Black 1982; "enforced dormancy", by Harper 1957). No special term seems to be needed for a delay caused by dryness of seeds; this is simply another environmental constraint.

Delay caused by immaturity of the embryo may simply be termed *immaturity*. *After-ripening* would be an appropriate term for the release from this kind of delay, implying maturation of the embryo tissues. As we will see later, however, this term has been used in a different way by some authors.

The term *dormancy* has been in the literature for a long time and I suggest that it be retained, but confined to the biochemical blocking type of delay. The rationale for this is that biochemical blocking which maintains seeds in a dormant state resembles the other plant dormancy phenomena, such as leaf bud dormancy or the dormancy of bulbs or corms, during unfavourable seasons. In spite of the extensive literature describing literally thousands of experiments on the proximate causes of biochemical blocking (some are outlined in Khan 1977, Heydecker 1973, Mayer & Poljakoff-Mayber 1982, and Bewley & Black 1982) there are no general agreements on the nature of the causal mechanisms. Several kinds of mechanism may occur.

In nature various kinds of environmental treatment are required to release seeds of different species from dormancy. Perhaps the commonest, in temperate regions, is a period of winter chilling, but others such as prolonged leaching of seeds, or particular light regimens, or high temperature treatments are known to be effective, suggesting that there is considerable diversity in the specific causes.

Experiments involving excision of various parts of seeds of different species show that the factors inhibiting germination may reside in one or more of: the seed coats; embryos; or other parts of the seed contents. As noted above, factors in the perianth or other tissues investing the ovary may also be involved.

Appropriate models to explain biochemical blocking must account for the known facts, which include: localization of the causes of blocking in seed coats, embryos etc.; development of blocking to differing degrees in a cohort of seeds; dormancy polymorphisms in seeds derived from particular individuals; the ability to remove blocks using environmental treatments such as chilling or leaching; rather abrupt changes in the dormancy status of seeds; release from dormancy of a cohort of seeds, then its re-establishment in those individuals which, for various reasons, have not germinated.

I do not intend to describe in detail the various models which have been proposed, except to note that they fall into several broad classes.

1. Blocking (and release from blocking) are determined by the particular balance of growth promoters (gibberellic acids, cytokinins) versus inhibitors (abscissic acid, coumarin etc.) (Nutile 1945, Wareing 1965, Hamilton & Carpenter 1976). Bewley & Black (1982) indicate that the investigators who invoke such causes have often confused the two separate phenomena (a) control of *germination* (which *is* effected by balance of inhibitors and promoters) and (b) control of *dormancy* (where the evidence for inhibitor influence is equivocal). Whether or not inhibitors are involved remains an open question, although there is some circumstantial evidence that they do play a role.

2. Blocking is caused by the inhibitors of a biochemical process believed to be essential for the initiation of germination, namely the operation of the oxidative pentose phosphate pathway (Roberts & Smith 1977). The interference may consist of insufficient oxygen reaching key enzymes. Experimental results, however, are not all in agreement, and Roberts & Smith themselves say that the role of the pentose phosphate pathway remains enigmatic.

3. Blocking (and release from blocking) have been linked to cell membrane properties, in particular, to changes in physical properties of membrane lipids, or to inhibitory effects of short chain fatty acids (Raison 1972, Wood & Paleg 1974, Hendricks & Taylorson 1976, Stewart & Berrie 1979). Again it is uncertain whether these kinds of mechanism really are involved (Bewley & Black 1982).

We must hope that eventually the plant physiologists and biochemists will resolve the riddles of proximate causes for dormancy. Meanwhile, in the seeds of many wild plants, we can regard dormancy (in the strict sense as outlined above) as being a kind of "black box", with particular ecological repercussions, linked, for example, to the specific conditions required to overcome the dormant state and the time spans of delays in relation to favourable growing seasons.

Baskin & Baskin (1985) point out that the expression of dormancy in some seeds may be very complex. If it occurs in new seeds while they are retained on parents, or when they are first shed, it is known as *primary dormancy*. *Secondary dormancy* is the phenomenon where seeds which were able to germinate when first released from their parent acquire a biochemical block later (Bewley & Black 1982). Also included under this heading is the situation where seeds which were primarily dormant emerge from the biochemical blocking, but do not germinate (through environmental constraint), then return to the dormant state. Primary dormancy was called "innate dormancy" by Harper (1957), but that term is etymologically inappropriate. Harper's term for secondary dormancy was "induced dormancy"; again, secondary is more apt.

A further complication is that dormancy is imposed to varying degrees on seeds from the same population (even on seeds from the same individual parent). In some species, seeds will not germinate whatever treatments the seeds experience. I suggest that this phenomenon be called *complete dormancy*. Baskin & Baskin (1985) use the term "innate" for it, a different meaning from that of Harper. In some other species biochemical blocking is *incomplete* and the seeds will germinate over a narrow range of environmental conditions. This pattern is called "conditional dormancy" by Baskin & Baskin (1985) and "relative dormancy" by Bewley & Black (1982). To confuse matters further, Nikolaeva (1969, 1977) and other authors noted by Bewley & Black, use other sets of terms for various delayed germination phenomena, but they are not so widely known and I will not outline them here. It may seem undesirable to promote yet another set of terminology, but none of the other authors, except perhaps Nikolaeva, has outlined the full range of phenomena which must be considered, and then presented a comprehensive and etymologically satisfactory terminological framework.

Other terms in use in the literature include *after-ripening*, which I believe to be appropriate for the period required for immature embryos to mature prior to seed germination. Baskin & Baskin (1985) and others use the same term for the sequence of biochemical changes causing seeds to go from a state of innate (i.e., *primary*) dormancy to non-dormancy. The straightforward expression "release from dormancy" seems more appropriate for this latter phenomenon, and also covers the change from dormancy to non-dormancy in secondarily dormant seeds.

Seed testing laboratories often use the term "hard-seededness" to describe the impermeable seed coat condition (i.e., *physical constraint*): similarly "recalcitrant seeds" are those which must retain high moisture content to remain viable. They are generally short-lived. The term refers to the difficulty of storing these seeds. Again, neither of these terms is very apt.

A concomitant set of unsolved problems concerns the causes of different viability retention periods by different seed species. Loss of viability is thought to be caused by accumulated molecular and cellular organelle damage (which is rapid in short-lived seeds, and gradual in longer-lived seeds). Villiers (1973) proposed that long-lived seeds, which in nature are usually buried in the soil or beneath plant litter, retain viability by being continually imbibed, or at least by occasional wetting and imbibition. Imbibed seeds, he suggests, are able to carry out restorative metabolic processes to repair the damage. This cannot be the case for all seeds, as some desert species are dry for very long periods while remaining viable. In addition, some physically constrained seeds, lying in the soil in temperate climates, do not seem to be imbibed.

In conclusion it may be said that the complexities of delayed germination phenomena provide a fascinating area of study for ecologists, physiologists and biochemists. There is also scope for microbiological research into the reasons why some seeds go mouldy while others do not. Until we understand the various causes of delays in seed germination we will remain uncertain about other ecological phenomena such as the causes of specific regeneration patterns, and the potentialities for vegetation change. One thing which has emerged from experiments on the germination requirements of various native plant species is that experimental programmes must begin as soon as seeds are ripe. Storage, even for a few weeks, can alter the subsequent germination behaviour of the seeds. Research on such matters requires long-term continuity, but can be effectively subdivided into smaller studies on particular species or problems suitable for masters or doctoral projects, which can be integrated into a wider programme.

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