Aspects of the germination of some New Zealand Ericaceae

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Abstract

Seeds of Northern Hemisphere ericoid species are light-sensitive, long-lived, form seed banks, and may be stimulated by short periods of high temperature, but are usually unaffected or show reduced germination in response to low temperature stratification. Comparative study of the germination responses of five New Zealand species of *Gaultheria* (*G. antipoda*, *G. crassa*, *G. depressa*, *G. macrostigma*, *G. parvula*), two hybrids (*G. macrostima* x *crassa*, *G. macrostigma* × *depressa*) and one introduced European species (*Erica lusitanica)* showed that light stimulated germination of all species, while germination was not stimulated in dry seed subjected to short periods of high temperature but viability was little affected. Germination of imbibed seed of two other European species (*Erica ciliaris*, *E. erigena*) was stimulated by short exposures to high temperature, and germination in *E. erigena* was inhibited by low temperature stratification. Germination of some New Zealand seed lots was stimulated by low temperature stratification, particularly in collections from high altitude (*G. depressa*) and in some collections of *G. macrostigma* and its hybrid with *G. depressa*. Seeds were largely unaffected by up to ten successive periods of hydration and desiccation, and remained viable after 16 months of dry storage and 12 months of moist storage. There was evidence of after-ripening in seed of *G. depressa* and *G. macrostigma* × *depressa*. Seed lots collected from the same sites in different years showed variable germination responses. Seed germination in New Zealand Ericaceae is perhaps more similar to Northern Hemisphere Ericaceae than it is to other native woody plants.

Additional key words: Erica, Gaultheria, Pernettya, *after-ripening, desiccation, heat shock, light/dark, low temperature, stratification*

Introduction

Ericaceous plants have been widely studied in northern and western Europe, largely because of interest in heathland, initially as a wasteland that could be made more productive and more recently as a disappearing habitat that needs to be preserved (Gimingham, 1992). Consequently the biology and ecology of British and European heath species has been well studied and the germination characteristics of European ericaceous heath plants are reasonably well known, particularly for ericoid species such as heather (*Calluna vulgaris*) and common species of *Erica* (*E. cinerea, E. tetralix).*

These species have small (< 1 mm in length), long-lived seed that forms persistent seed banks. Afforestation of heathland in Britain leads to the elimination of heathland species, such as *Calluna vulgaris* and *Erica tetralix,* but there is significant regeneration of these species when trees are felled after 40 years or more (Hill and Stevens, 1981). As with many species that form seed banks, seeds do not germinate in the dark but are stimulated by exposure to light, do not appear to require low temperature stratification and germination may be stimulated by short periods of exposure to high temperatures (Whittaker and Gimingham, 1962; Bannister, 1965; Mallik and Gimingham, 1985) and diurnal fluctuations in temperature (Gimingham, 1960).

In New Zealand, native ericaceous species are confined to species of *Gaultheria* and *Pernettya*. These two genera are differentiated on the basis of fruit characters: in *Gaultheria* a dry capsule is surrounded by a fleshy calyx, whereas in *Pernettya* the true fruit is a berry with a persistent calyx which may also be succulent. Seeds are numerous and small, and of a similar size to those of European ericoid species (Moore, 1996). Intergeneric hybrids producing fertile seed occur and, consequently, we have followed Middleton (1991) in this paper and included all *Pernettya* species within *Gaultheria*. Written information on the germination requirements of *Gaultheria* species native to New Zealand appears to be limited to the unpublished work of Armstrong (1964), a short paper by Bannister (1990) and brief mentions elsewhere (e.g., Fountain and Outred, 1991; Bannister and Jameson, 1994). *Gaultheria* species

show no or minimal germination in the dark but germination is stimulated by exposure to light and (in *G. macrostigma*) may be enhanced by low temperature stratification (Bannister, 1990; Bannister and Jameson, 1994). Germination of the South American *G. mucronata* appears to respond to low temperature stratification (Arena *et al.*, 1994). The germination ecology of *Erica lusitanica*, a European ericoid species naturalised in New Zealand, has been investigated by Mather and Williams (1990). This paper also presents data for seeds of two other European species, *Erica erigena* and *E. ciliaris,* collected in the British Isles and germinated in New Zealand. The data for *E. ciliaris* have been published elsewhere (Rose *et al.*, 1996).

The object of this work was to examine the germination responses of native *Gaultheria* species in more detail and compare them with what is known for Northern Hemisphere Ericaceae. The principal factors examined in this paper are responses to high and low temperature, desiccation, after-ripening and longevity.

Materials and Methods

Species and sites of seed collection

Seed of *Erica lusitanica* was collected from the Silverpeaks, near Dunedin, in April 1992 and April 1993, that of *E. ciliaris* from Dorset, England, in October 1994 and that of *E. erigena* from Errisbeg, Co. Galway, and Mallaranny and Furnace Lough, Co. Mayo, Ireland, in August 1994. Seeds of native New Zealand species were collected from a variety of sites in the southern South Island of New Zealand (site details are given by Moore 1996). In April 1992 and 1993 collections of seed were made from Leith Valley, Dunedin (*Gaultheria antipoda*) and the Hawkdun Range, near Undaunted Creek and on Otematata Station (*G. crassa*, *G. depressa* from 775 m, 1280 m, 1580 m, *G. macrostigma* (=*Pernettya macrostigma*) and *G. parvula* (=*Pernettya nana*)). Seeds of *G. macrostigma* and its hybrids were collected from Flagstaff, Dunedin, in April 1992 and March 1993 (*G. macrostigma*, *G. macrostigma* × *depressa*, *G. macrostigma x crassa*) with additional collections of *G. macrostigma* in December 1992 and May 1993.

Mature fruits were collected from several plants within each site. The fleshy fruits of the *Gaultheria* species were placed in petri-dishes and allowed to dry in the sun. Dried fruits were broken open to release the seeds which were separated from any extraneous material and stored in light-proof canisters at room temperature until used. The fruits of the *Erica* species were already air-dry on collection and further drying caused their capsules to open and shed their seed. The separated seeds were stored either in light-proof canisters (*E. lustitanica*) or in transparent containers (*E. ciliaris*, *E. erigena*) at room temperature.

Seed germination

Seeds were plated out on two layers of Whatman No 29 filter paper placed over a layer of absorbent cotton wool in glass petri dishes. Paper and cotton wool were kept moist with distilled water during the course of the experiments. Only apparently filled seeds were used in the experiments and typically two replicates of 100 seeds were used for each treatment. In experiments with *E. erigena*, only 50 seeds were used in each replicate and only 25 seeds were used in hydration-dehydration experiments.

Seeds of the *Gaultheria* species and *Erica lusitanica* were kept in an illuminated cabinet (50 $\mu mol/m^2/s$) with a twelve hour alternation of light at 22°C and dark at 12°C. Petri dishes were laid out in a randomised block design within the cabinets. Some treatments were started in, or transferred to, an unheated, shaded (c. 56 % of ambient) glasshouse. Seeds of *Erica* species were germinated at ambient laboratory temperatures and light. Radicle emergence was taken as evidence of germination and experiments were terminated after about 270 d when germination had usually ceased, although some experiments with *Erica erigena* were terminated after one year. The final germination percentage was the main statistical parameter used in analyses of variance. The inverse of the time taken for 50 % of final germination was also used as a function of germination rate, but is referred to in the text only if there is a particular point to be made.

Experimental treatments

Seeds were stratified at 4°C for four weeks, although a 12 week period was also used for *Gaultheria macrostigma* and *G. macrostigma* × *depressa,* and additional periods of 8 and 12 weeks for *E. ciliaris* and *E. erigena*. Heat treatments of 30 sec and 2 min at 100°C were used on dry seeds of the *Gaultheria* species and *E. lusitanica*, whereas imbibed seeds of the *Erica ciliaris* and *E. erigena* were soaked in water at 20, 50, and 80°C for five min and at 100°C for one and five min.

After-ripening and longevity of seed was tested by germinating seed stored dry for 1, 3 and 16 months. The response of seeds to repeated desiccation and rehydration was tested for up to ten cycles where seeds were allowed to imbibe for a week and then desiccated for 24 h before being rehydrated.

The effects of time of harvest on seed of *G. macrostigma* collected from Flagstaff at various times

during summer and autumn (1992-1993) were also evaluated by both standard germination in the cabinet and by using seed that had been stratified at 4°C for 12 weeks. Ecotypic comparisons were also made on *G. macrostigma* from various sites and *G. depressa* from an altitudinal range. Comparisons were also made with hybrid seeds and their parents.

Results

Patterns of germination

Erica lusitanica showed only low germination in the cabinet (< 20 %) which was completed in about fifty days. However, after six months to a year, when petri-dishes from various completed experiments were transferred from the cabinet to the glasshouse, a secondary burst of germination occurred resulting in 70-90 % final germination (Moore 1996). Seed of *Erica ciliaris* and *E. erigena* was germinated in laboratory conditions with uncontrolled fluctuations in light and temperature and photoperiod. Germination was low in *E. ciliaris* (20-30 %) and more or less complete after 50 days. In *Erica erigena* germination commenced only after one month with a major spurt of germination around 100 days (autumn) and a secondary spurt around 200 days (midwinter). Maximum germination in untreated seed was 50-60 %.

In *Gaultheria antipoda*, *G. crassa* and *G. depressa*, there was an initial period of two to three weeks with no germination, followed by a period of rapid germination with germination more or less completed in 30 days (*G. crassa*), 40 days (*G. antipoda*) or 80 days (*G. depressa*). The high altitude collection of *G. depressa* (1580m) began to germinate after only four weeks and showed an initial phase of rapid germination which was completed after about 90 days and secondary burst of germination which commenced at 120 days and was more or less complete after about 290 days. Seed of *G. macrostigma* tended to show a more gradual increase of germination over a longer period with germination of control seed tailing off after 200 days. The seed collected from the Hawkdun Range showed poor germination (< 25 %) but that from Flagstaff showed > 60 % germination. The hybrid, *P. macrostigma* × *depressa*, showed some characteristics of its parents, and resembled *G. depressa* in completing most of its germination between day 20 and day 100, although its final germination was low (< 30 % in control seed). Germination percentages in *G. macrostigma*× *crassa* were similar to those of both its parents, although germination rates were intermediate between those of its parents. *G. parvula* showed very low germination (< 10 % in untreated seed) with continuous germination through the experimental period. Further details of germination patterns are given in Moore (1996).

Germination in the growth cabinet and in the glasshouse

In all species (including *Erica* spp.), germination was greatest in the light and, except for two collections of *G. macrostigma* where there was a minimal amount of germination, there was no germination in the dark (Moore, 1996). *E. lusitanica* showed low germination in the low illumination of the cabinet but germination was substantially enhanced in the glasshouse, particularly in seed that had had a pretreatment of 375 days of moist storage in the dark. Germination of *Gaultheria antipoda* and *G. depressa* was more or less unaffected by conditions; *G. crassa* showed poorer germination after the dark pretreatment, and *G. macrostigma* and *G. parvula* showed reduced germination in the cabinet (Table 1).

Germination in response to temperature pretreatments

In general, the species examined showed little or no response to low temperature stratification. In *Erica erigena*, stratification decreased germination below that of the controls and had no significant effect on the germination of *E. ciliaris*. However, *G. macrostigma, G. macrostigma* × *depressa* from Flagstaff, and the high altitude population of *G. depressa* showed a significant increase in percentage germination and germination rate when stratified (Fig. 1). Different collections of *G.*

Table 1. Percentage germination of untreated seed sown in the cabinet and in the glasshouse, and of seed pretreated with 375 days of dark, moist storage in the cabinet and then sown in the glasshouse.

Species	cabinet	glass-house	dark/glass-house
E. lusitanica	17.0[a]	67.0[a]	93.5[a]
G. antipoda	78.0	63.0	77.0
G. depressa (775m)	78.0	90.0	50.5[a]
G depressa (1140m)	89.5	90.5	93.5
G. depressa (1580m)	78.5	82.0	82.5
G. macrostigma (Hawkdun)	9.0[a]	45.0	29.5
G. macrostigma × *depressa*	44.5	36.0[a]	59.0
G. parvula	0.5	12.5	3.0

[a] denotes values are significantly different (P < 0.05)

macrostigma and *G. macrostigma* × *depressa* showed a variable response so that there was no overall significant increase in germination percentage in stratified seed (Fig. 2), although there was a significant increase in germination rate (Moore, 1996).

Five minutes of moist heat pretreatment of imbibed seeds at 50°C (*E. ciliaris*) and 80°C (*E. erigena*) stimulated germination above that of controls and seeds were killed at 100°C (although some seeds of *E. ciliaris* germinated after treatment at 100°C for one minute). When dry seeds of *Gaultheria* spp. and *E. lusitanica* were exposed to two minutes or 30 seconds at 100°C there was generally no stimulation of germination. Germination percentages were depressed in low altitude *G. depressa* (100°C for 2 minutes) and in *G. parvula* (both treatments) (Fig. 3).

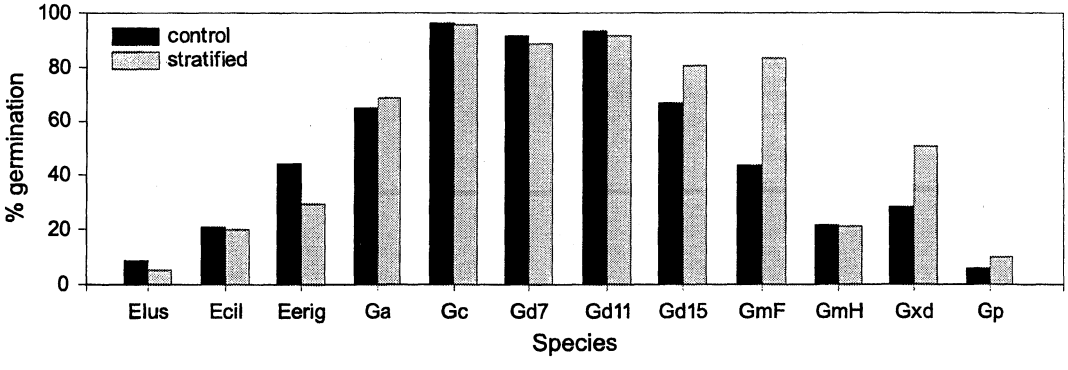

Figure 1. Percentage germination of control seeds and seeds stratified for four weeks at 4°C. Species: *Erica lusitanica* (Elus), *E. ciliaris* (Ecil), *E. erigena* (Eerig), *Gaultheria antipoda* (Ga), *G.crassa* (Gc), *G. depressa* from 775 m (Gd7), 1140m (Gd11) and 1580m (Gd15), *G. macrostigma* from Flagstaff (GmF) and Hawkdun Range (GmH), *G. macrostigma* × *depressa* (G×d), *G. parvula* (Gp).

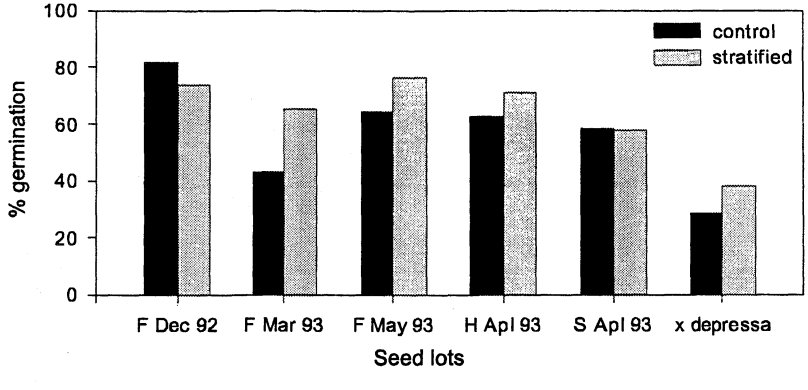

Figure 2. Percentage germination of control seeds of *Gaultheria macrostigma* and *G. macrostigma* × *depressa* and of seeds stratified for four weeks at 4°C. Seeds collected on different dates from Flagstaff (F), Hawkdun Range (H), and Silverpeaks (S).

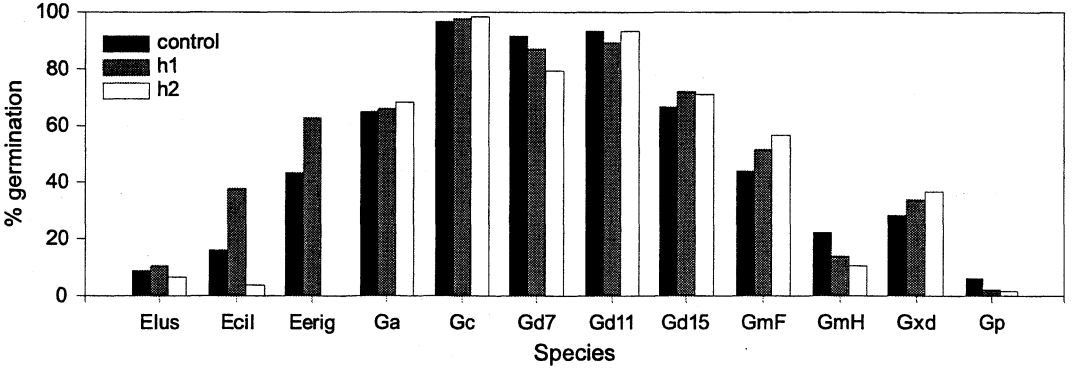

Figure 3. Percentage germination of control seeds and dry seeds subjected to 30 sec (h1) and two min (h2) at 100°C or imbibed seeds subjected to 5 min at either 60°C (h1, Ecil) or 80°C (h1, Eerig) and one minute at 100°C (h2, Ecil,Eerig). Species: *Erica lusitanica* (Elus), *E. ciliaris* (Ecil), *E. erigena* (Eerig), *Gaultheria antipoda* (Ga), *G. crassa* (Gc), *G. depressa* from 775 m (Gd7), 1140m (Gd11) and 1580m (Gd15), *G. macrostigma* from Flagstaff (GmF) and Hawkdun Range (GmH), *G. macrostigma* × *depressa* (G×d), *G. parvula* (Gp).

After-ripening, longevity, and seasonal variation

Dry seed of *E. lusitanica* and *Gaultheria* spp. was stored for 1, 3, and 16 months and germinated in the cabinet (Table 2). Germination of most species was unaffected by 16 months of dry storage; only seed of *G. crassa* showed reduced germination. However all collections of *G. depressa* and *G. depressa x macrostigma* showed evidence of after-ripening as germination of seeds stored for only one month was significantly less than that stored for longer periods.

Seed collected in different years (Table 3) did not always show the same percentage germination. Germination was significantly greater in seed collected in 1993 for *G. antipoda*, *G. depressa* (775 m), *G. macrostigma* (Hawkdun) and *G. macrostigma* × *depressa*, while seed of *G. macrostigma* from Flagstaff showed

Table 2. Percentage germination of untreated seed following dry storage of one, three and sixteen months in standard conditions in the growth cabinet.

Species	1 month	3 months	16 months
E. lusitanica	14.5	10.0	17.0
G. antipoda	60.5	64.0	78.0
G. crassa	85.5	96.5[a]	78.0
G. depressa (775m)	65.0[a]	92.5	89.5
G depressa (1140m)	76.5	94.5	89.5
G. depressa (1580m)	55.5[a]	80.0	78.5
G. macrostigma (Hawkdun)	15.5	24.0	9.0
G. macrostigma × *depressa*	9.5[a]	28.5	44.5
G. parvula	5.5	7.0	0.5

[a] denotes values are significantly different ($P < 0.05$)

Table 3. Percentage germination of untreated seed collected in autumn 1992 and autumn 1993 and germinated in standard conditions in the growth cabinet.

	1992	1993
E. lusitanica	14.5	7.0
G. antipoda	60.5	84.0[a]
G. crassa	85.5	77.5
G. depressa (775m)	65.0	91.0[a]
G depressa (1140m)	76.5	87.0
G. depressa (1580m)	55.5	75.5
G. macrostigma (Flagstaff)	77.5[a]	43.0
G. macrostigma (Hawkdun)	15.5	62.5[a]
G. macrostigma × *depressa*	9.5	28.5[a]
G. parvula	5.5	1.5

[a] denotes values are significantly different ($P < 0.05$)

Table 4. Percentage germination after 0, 1, 3 and 10 cycles of hydration and dehydration.

	Number of dehydration cycles			
	0	1	3	10
E.lusitanica	7	2	4	8
G. antipoda	84	72	82	84
G. crassa	78	78	76	66
G. depressa - 1140m	87	88	82	80
G. macrostigma (Flagstaff)	43	38	42	50
G. macrostigma ×*depressa*	29	28	14	32
G. parvula	2	0	0	0

significantly higher germination in the 1992 collection. *G. macrostigma x crassa* showed no difference between years of collection (Moore, 1996).

All species, except perhaps *G. parvula* which showed no germination in any dehydration treatment but only 2 % germination in the untreated controls, were unaffected by up to ten repeated cycles of hydration and dehydration (Table 4).

Discussion

Stimulation of germination by light is a common characteristic of plants that form seed banks (Pons, 1991) and is found in many ericaceous seeds such as *Calluna vulgaris* (Gimingham, 1960; Pons, 1989a), *Erica ciliaris* (Rose *et al.*, 1996), *E.cinerea* (Bannister, 1965), *E. tetralix* (Bannister, 1966; Pons, 1989), *Pernettya mucronata* (Arena *et al.*, 1994), and *Vaccinium myrtillus* (Grime *et al.*, 1981) and the species examined in this paper. Low temperatures may substitute for the light requirement in some ericaceous seeds such as *Arbutus unedo* (Ricardo and Veloso, 1987) and *E. lusitanica* (Mather and Williams, 1990).

Ericaceous seeds do not necessarily show increased germination after low temperature stratification. *Calluna vulgaris*, *Erica tetralix* (Mallik and Gimingham, 1985), *E. cinerea* (Bannister, 1995), *E. ciliaris* (Rose *et al.*, 1996) and *E.lusitanica* (Fig. 1) show no response to low temperature stratification, whilst germination of *E. erigena* is depressed by it (Fig. 1). However, overwintered seed of *E.lusitanica* showed higher germination than fresh seed (Mather and Williams, 1990), germination in *Pernettya* (*Gaultheria*) *mucronata* was stimulated by 300 hours of chilling (Arena *et al.*, 1994) and dormancy in seed of *Vaccinium vitis-idaea* was broken by low temperature stratification (Mallik and Gimingham, 1985). In this paper, germination in some seed lots of *Gaultheria* species (e.g., *G. macrostigma*, *G. depressa* and *G. macrostigma* × *depressa*) was stimulated by low temperature stratification whereas that of others (including *G. antipoda* and *G. crassa*) was not. In *G. macrostigma* the responses were variable, apparently depending on both location and season of collection (Fig 2). Chilling requirements are often inferred from observations of enhanced germination after over-wintering (Fountain and Outred, 1991) but only experiment with adequate controls will establish a chilling requirement. Other factors such as prolonged moist storage, after-ripening, scarification of the seed coat by microbial or other agencies, and increased temperatures in spring could account for increased germination after overwintering. Burrows (1994a,b) suggests that few native New Zealand woody species have a chilling requirement, reflecting their tropical origins. Some of the native *Gaultheria* species, however, go against this trend and their variability of response reflects that found in ericaceous species from the Northern Hemisphere.

High temperature responses have generally been examined in species that inhabit fire-prone communities. Whittaker and Gimingham (1961) showed that short exposures to temperatures between 40 and 80°C stimulated germination in imbibed seeds of *Calluna vulgaris*. Similar results were found for *Erica cinerea* (Bannister, 1965), *E. ciliaris* (Rose *et al.*, 1996) and *E. erigena* (Fig. 3). Mallik and Gimingham (1985) treated dry seed and found that germination of *Vaccinium myrtillus* and *V. vitis-idaea* was stimulated by heat shock (30 seconds at 100°C) but not by longer periods of exposure. None of the dry seeds treated in this study (Fig. 3) showed any stimulation of germination after similar periods of heat shock and any significant diminution of germination was only slight. In the field, germination of *E. lusitanica* is stimulated by fire (Mather and Williams, 1990) but it is difficult to determine whether this is due to heat stimulation or other factors such as removal of litter and disturbance exposing the buried seeds to light.

All seeds that were subjected to hydration and dehydration were unaffected by up to ten such cycles. Seed of *Calluna vulgaris* and *Erica tetralix* (Pons, 1989) and of *Leptospermum scoparium* (Mohan *et al.*, 1984) was similarly unaffected. Seeds often show enhanced germination after a period of dry storage (after-ripening). Grime *et al.* (1981) found such enhancement in the majority of 403 species examined, particularly in small-seeded species, but in this study only *G. depressa* and *G.*

macrostigma × *depressa* showed any evidence of after-ripening. All species showed substantial germination after 16 months of dry storage, and only *G. crassa* showed significantly reduced germination. Comparative data are hard to find. Dry seed of *Erica lusitanica* did not lose viability when stored for five months in the dark (Mather and Williams, 1990) and that of *Leptospermum scoparium* retained viability for one year (Mohan *et al.*, 1984). Substantial germination occurred after two years' storage in *Erica cinerea* (Chippendale and Milton, 1934) and after four and a half years in *E. tetralix* (Bannister, 1966). Different collections of seed from the same source may show differences in germination with respect to season and year. These doubtless reflect differences in maturation and seasonal climate.

There are many similarities between the germination of Northern Hemisphere Ericaceae and the Southern Hemisphere species of *Gaultheria* examined here. All germinate best in the light and germination in most species is usually completely inhibited in the dark. Viability is not lost to any great degree in either dry or moist storage, and imbibed seeds are unaffected by short periods of dehydration. These characteristics favour persistence in a seed bank until disturbance exposes the seed to light which in turn stimulates germination. Although there is some evidence that low temperature stratification enhances germination in some seed collections, substantial germination occurs in most species in its absence. While germination of dry seed is not stimulated by heat shock, there is little loss of viability in dry seed subjected to two minutes at 100°C, suggesting tolerance to fire, which is not an uncommon feature of scrubland. These seeds differ from those of other woody plants in the New Zealand flora - the selection of which has been described as "...affected neither by dark/light differences or by winter cold...." (Burrows, 1994a). The similarities in germination between European and antipodean Ericaceae suggest that taxonomic affinities have overridden any such adaptation to local climates.

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