Germination physiology of seeds from New Zealand native plants

P. Bannister and P. E. Jameson[1]

Department of Botany, University of Otago, P.O. Box 56, Dunedin, New Zealand.
[1] Current address: Department of Plant Biology and Biotechnology, Massey University, Palmerston North, New Zealand.

Abstract

Published research on the germination of seeds of native New Zealand plants is reviewed and supplemented by recent unpublished investigations at the University of Otago. Germination is considered under the following headings: seeds which show no apparent dormancy; those which show dormancy induced by the outer coverings of fruit or seed; embryo dormancy which may be alleviated by after-ripening, light or chilling; and the effects of normal temperature and water potential on germination responses. It is suggested that systematic studies of large numbers of species are required to relate germination physiology to habitat and environment.

Additional key words: *dormancy, light, scarification, stratification, temperature.*

Introduction

Since Lloyd (1985) observed that there is no firm knowledge on the germination of New Zealand native species there have been a number of publications dealing with this topic (e.g., Conner, 1987; Haase, 1987; Court and Mitchell, 1988; Conner and Conner, 1988a,b; Burrows, 1989; Bannister, 1990; Partridge and Wilson, 1990; Bannister and Bridgman, 1991). Since the presentation of this paper (in August 1991) the germination requirements of New Zealand native plants have been reviewed by Fountain and Outred (1991) and information from this and other recent publications has been added to the following text where appropriate.

Seeds of New Zealand species often appear to germinate poorly, and while some of this may be due to poor viability (Table 1) it could also be a consequence of dormancy mechanisms, such as seed coat impermeability to water or gases; embryo dormancy due to immaturity of the embryo, inhibitors in the seed or fruit, or requirements for specific factors such as dry storage, light or chilling (Burrows, 1989). These dormancies can be broken by artificial scarification, removal of inhibitors, provision of dry storage, light or chilling and also may often be overcome by the application of gibberellic acid. Secondary dormancy may be induced by high light intensities, low temperature or desiccation.

There is much anecdotal knowledge on the germination requirements of New Zealand species to be found in books on gardening, in seed catalogues, in individual experience, and even in scientific papers which may lack adequate controls and confound the effects of various treatments. In this paper, we have included only information on species for which we had access to published or primary data. Most recommended horticultural treatments work in practice, but may not have been experimentally proven. For example, stratification is often recommended for seeds which are slow to germinate, but the resultant germination may be not a result of this treatment but merely the consequence of the passage of time. One catalogue recommends six weeks stratification for seed of *Pernettya macrostigma*, but experiment shows that this species still shows the same pattern of germination over the first six weeks, irrespective of whether the seed was stratified or not (Fig. 1).

Table 1. Germination percentages of some native species with low seed viability.

Celmisia spp.	<4%	Scott (1975)
Metrosideros umbellata	13%	Wardle (1971)
Leptopermum scoparium	<25%	Mohan *et al.* (1984)
Nothofagus menziesii	<40%	Allen (1987)
N. solandri	12-57%	Wardle (1970)

This paper reviews the published evidence for some of the germination requirements of seeds of native species, speculates on their ecological significance, and expands on recent and as yet unpublished work done in the Botany Department at Otago.

Germination and dormancy

In considering germination and dormancy, we have examined non-dormant seeds and then considered dormancy - separating dormancy which is a function of the seed coverings from that which is a function of the condition of the embryo (Villers, 1975). We have not followed Burrows' (1989) suggestion that the term "dormancy" should be restricted to biochemical blocking of germination and that other forms of dormancy should be classified as "delayed germination".

Apparent lack of dormancy

Some species may germinate directly without any special requirements except normal light and temperatures, e.g., *Weinmannia racemosa*, kamahi (Wardle, 1966), *Metrosideros umbellata*, southern rata (Wardle, 1971) and *Leptospermum scoparium*, manuka (Mohan *et al.*, 1984). However, many of these germinate better in light than in dark (Table 2), although others germinate equally well (e.g., *Dysoxylum spectabile*, kohekohe) in both light and dark (Court and Mitchell, 1988).

Other seeds, often those associated with large fleshy fruits, exhibit recalcitrance and show a loss of germinability when desiccated. Seeds of a number of New Zealand plants show characteristics which suggest recalcitrance (Fountain and Outred, 1991) but few have been experimentally tested. Seeds which have been experimentally demonstrated to show decreased germinability when desiccated include those of *Dacrycarpus dacrydiodes* (Fountain *et al.*, 1989), *Corynocarpus laevigatus*, and *Griselinia littoralis* (Bibby, 1992). Seeds of *Hoheria populnea*, listed as possibly recalcitrant by Fountain and Outred (1991), germinated after seven weeks of desiccation and showed enhanced rates of germination after either wet or dry storage, and

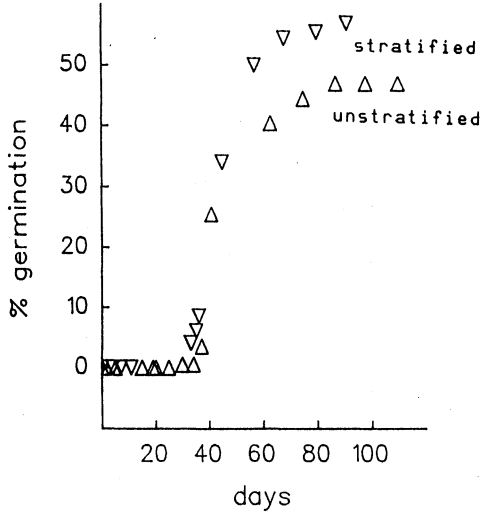

Figure 1. Germination of stratified and non-stratified seed of *Pernettya macrostigma* (data of Bannister, 1990). Upright triangles represent unstratified seed, and inverted triangles represent seed stratified for four weeks. The increase in percentage germination of stratified seed is not statistically significant ($p>0.05$).

Table 2. Light requirements of native seeds.

	No published records
Germinate better in dark	
Germinate better in light	
Acaena spp.	Conner (1987)
A. novae-zelandiae	Gynn & Richards (1985)
Celmisia spp.	Scott (1975)
Gaultheria antipoda	Bannister (1990)
G. depressa	
Leptospermum scoparium	Mohan *et al.* (1984)
Hebe elliptica	Simpson (1976)
H. salicifolia, H. stricta	
Pernettya macrostigma	Bannister (1990)
Plagianthus divaricatus	Partridge (1981)
Schoenus nitens	
Selliera radicans	
Spergularia marginata	
Triglochin striatum	
Germinate equally well in light and dark	
Arthropodium cirratum	Conner & Conner (1988a)
Atriplex novae-zelandiae	Partridge (1981)
Cotula coronopifolia	
Chordospartium stevensonii	Conner & Conner (1988b)
Dysoxylum spectabile	Court & Mitchell (1988)
Inhibition by high irradiance	
Arthropodium cirratum	Conner & Conner (1988a)

therefore cannot be considered as recalcitrant (Bibby, 1992).

Dormancy induced by seed coverings and fruit

Seeds of many native species may be retained on the plant for some time without being shed (e.g., Leptospermum scoparium, *Pittosporum eugenioides*) and do not germinate while in the fruit. This may be merely due to conditions for germination, such as moisture and light, not being met. However, even when the intact dry fruit is moistened, germination may not occur, e.g., in seed of matagouri, *Discaria toumatou*, (Keogh, 1990), whereas in *Pseudopanax* spp. germination occurs in intact fruit but takes longer and final germination percentages are less (Fig. 2). Removal of the outer covering of the achenes of *Celmisia* spp. increases germination and overcomes a light requirement (Scott, 1975).

Seeds do not usually germinate while still contained in fleshy fruits. For example, Roger James of the Botany Department of the University of Otago, has examined the germination of seeds in intact fruit of ngaio (*Myoporum laetum*), mahoe (*Melicytus ramiflorus*) and *Comprosma robusta* and compared them with artificially cleaned seed and seed that has passed through the gut of birds (Fig. 3). In all cases there was little or no germination in the intact fruit but enhanced germination in seed that had been cleaned or passed through birds. However, the germination of seeds of miro (*Prumnopitys ferruginea*) does not appear to be enhanced by passage through native pigeons (Clout and Tilley, 1992).

In some cases there is evidence that the fruit flesh itself may contain inhibitors: the fleshy mesocarp of fruits of *Pseudopanax crassifolius* and *P. ferox* reduces germination percentage and may delay germination, especially in *P. crassifolius* (Horrell *et al.*, 1990; Bannister and Bridgman, 1991). Inhibition by fruit flesh has also been reported for taraire (*Beilschmiedia tarairi*) (Myers, 1984). In mahoe, the seed itself has been shown to be the source of inhibition (Partridge and Wilson, 1990).

Seeds themselves may have hard impermeable coats which prevent imbibition of water or the diffusion of gases. This is frequent in leguminous seed (e.g., kowhai) and documented for *Chordospartium stevensonii* (Conner and Conner, 1988b). It also occurs in matagouri seed (Keogh, 1990) where there is a double dormancy involving seed coat impermeability and a chilling requirement (Fig. 4). In the rock lily, *Arthropodium cirratum*, the coat appears to be a mechanical barrier to embryo expansion (Conner and Conner, 1988a).

Embryo Dormancy

After ripening and storage: Some seeds may only germinate after a period of dry or moist storage. The rock lily (*Arthropodium cirratum* requires up to six

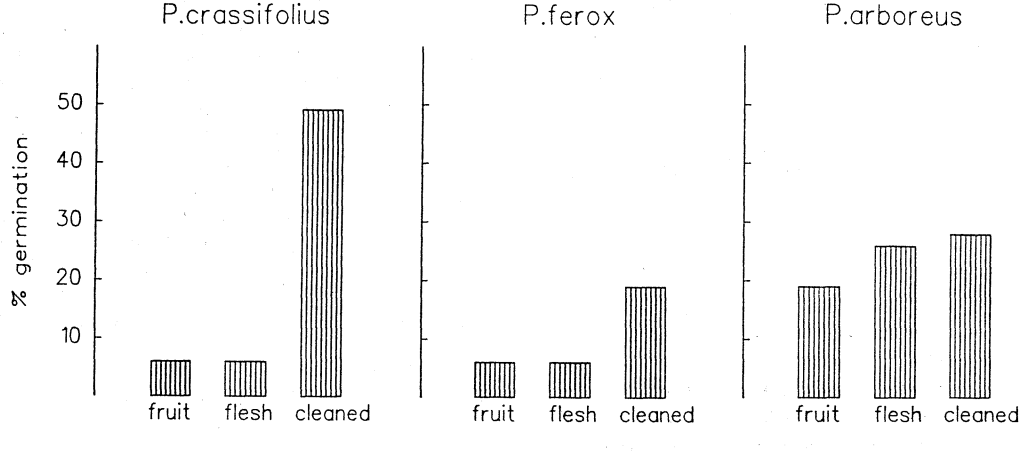

Figure 2. Final germination of seed of *Pseudopanax crassifolius, P. ferox,* and *P. arboreus* contained within the whole fruit, in contact with fruit flesh, or cleaned of all traces of fruit (data of Bannister and Bridgman, 1991).

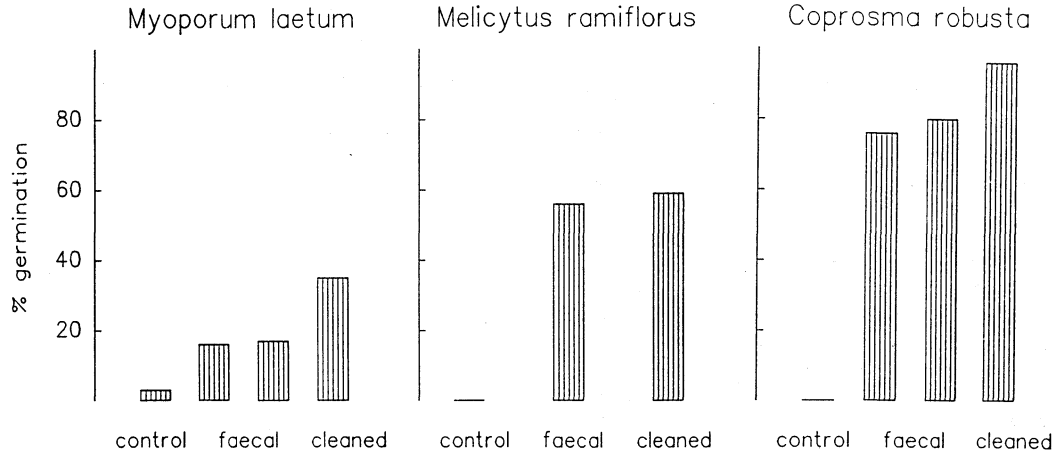

Figure 3. **Percentage germination of seed of *Myoporum laetum, Melicytus ramiflorus,* and *Coprosma robusta* within the fleshy fruit (control), from faeces of blackbirds (*Coprosma* only) or native pigeons (all species), or cleaned of all traces of fruit. The second faecal sample of *Myoporum* was washed and cleaned, and the two faecal samples for *Coprosma* were from blackbirds and pigeons respectively (Roger James, unpublished data).**

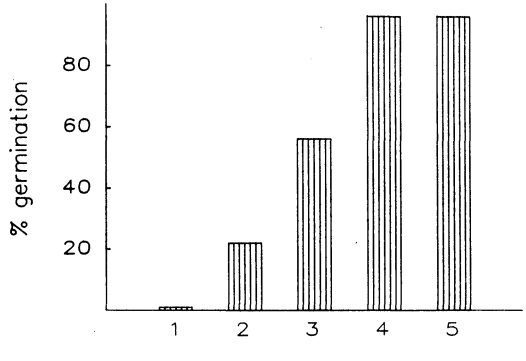

Figure 4. **Percentage germination of seeds of *Discaria toumatou* after about six weeks at 20°C. Treatments: (1) untreated control, (2) scarified seed, (3) unscarified seed stratified at 4°C for 24 weeks, (4) fully imbibed seed stratified for 8 weeks, and (5) scarified seed treated with 10^{-4}M gibberellic acid (data of Keogh, 1990).**

months of dry storage (Conner and Conner, 1988a). On the other hand, seeds may lose their viability during dry storage - complete loss of seed viability occurred after 10 months' dry storage in seeds of *Acaena* spp. (Conner, 1987), after 20-30 months in *Hebe* spp. (Simpson, 1976), and after 5-7 years in *Arthropodium cirratum* (Conner and Conner, 1988a). Hard-seeded species are considered to remain viable for long periods, e.g., seeds of *Discaria toumatou* showed no loss of viability after four years of dry storage (Keogh, 1990), but seed of *Chordospartium stevensonii* lost viability after 2-3 years (Conner and Conner, 1988b). Furthermore, the requirement for dry storage may often be alleviated by other treatments, such as light, chilling, alternating temperature, or scarification (Villiers, 1975). In *Arthropodium cirratum* the requirement for dry storage is overcome and other forms of dormancy are broken when the testa is nicked in the region of radicle emergence (Conner and Conner, 1988a).

The effects of light: Traditionally, seeds have been classified as positively photoblastic, where they germinate more readily in the light, or negatively photoblastic, where they germinate less well in the light, or merely indifferent. Some of the published work on native species has examined this (Table 2), but

germination in the light and dark has not always been a component of germination studies. The role of phytochrome in these light responses is well known and will not be repeated here. The ecological consequences are that seeds with a light requirement "detect gaps" by responding to the high proportion of red light when seeds are exposed by disturbance of the soil or canopy, while inhibition by far-red light prevents seeds germinating under a vegetation canopy. The high irradiance reaction prevents shade plants germinating in the open, or ensures that seeds of species of open habitats only germinate in more shaded (and moister) locations. A high irradiance response has been demonstrated for the rock lily, *Arthropodium cirratum* (Conner and Conner, 1988a), a species of open habitats. Furthermore far-red light and high irradiance may induce secondary dormancies (Górski *et al.*, 1977; Górski and Górska, 1979), and in European ericaceous species a period in darkness reduces the intensity of light needed for subsequent germination (Pons, 1989). Apart from Conner and Conner (1988a), information on the effects of irradiance and spectral composition on germination of native species is lacking, and would repay further study.

The effects of chilling and high temperature: Chilling, or stratification, often breaks dormancy, but is effective only on imbibed seed. In matagouri seed, chilling is much more effective and the response more rapid if all seeds are imbibed before chilling. When dry seeds are used, the protracted response to chilling is a function of rate at which increased permeability of seed coats allows seeds to become imbibed (Keogh, 1990). Native species for which there is good documented evidence of a chilling requirement for germination include those of cold habitats at high altitude e.g., Hebe spp. (Simpson, 1976), *Gentiana* spp. (Simpson and Webb, 1980), *Hoheria glabrata* (Haase, 1987) or from more continental areas, e.g., Discaria toumatou (Keogh, 1990), although montane species of *Celmisia* have no chilling requirement (Scott, 1975). Lowland species, such as *Pittosporum* spp., may also respond to chilling and even germinate during chilling (Fig. 5). Chilled seed often show an increased rate of germination at higher temperatures, even if the percentage germination is unaffected (e.g., in *Pseudopanax* spp., Bannister and Bridgeman, 1991).

The chilling requirement has been substituted by the application of gibberellic acid in matagouri seed (Fig. 4; Keogh and Bannister, 1992) and in *Pittosporum obcordatum* (Simon Moore, unpublished). Low temperatures may induce a secondary dormancy, as in the rock lily *Arthropodium cirratum* (Conner and Conner, 1988a).

High temperature shock may also break dormancy. There is some evidence for this occurring in seeds of matagouri (Keogh, 1990) but high temperature treatment failed to break dormancy in seed of *Acaena inermis* (Conner, 1987).

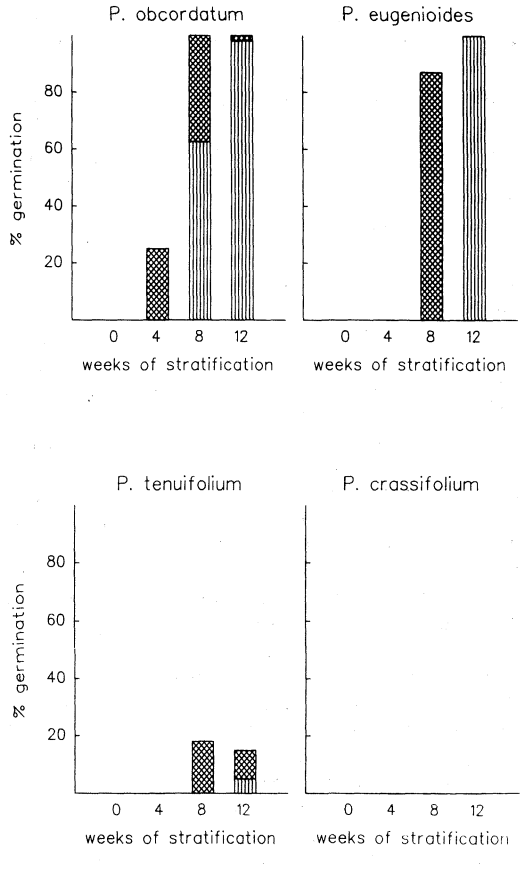

Figure 5. Percentage germination of seed of *Pittosporum obcordatum, P. eugenioides* and *P. tenuifolium* after 0, 4, 8 and 12 weeks of moist stratification at 4°C. Seed of *P. crassifolium* failed to germinate. Crosshatching indicates germination after stratification, vertical ruling indicates germination during stratification (Simon Moore, unpublished data).

Effects of other factors on germination:

Temperature: There are some studies on the effects of temperature on germination. The percentage germination of seed of *Leptospermum scoparium* (Mohan *et al.*, 1984) and *Dysoxylum spectabile* (Court and Mitchell, 1988) is little affected by temperature in the range 12-25°C (*Leptospermum*) or 6-16°C (*Dysoxylum*) but rates increase with temperature. Optimum temperatures for germination in subalpine species of *Acaena* are from 17-21°C (Conner, 1987) and from 10-20°C in *Celmisia* spp. (Scott, 1975), about 15°C in *Arthropodium cirratum* (Conner and Conner, 1988a) and 20-25° in *Chordospartium stevensonnii* (Conner and Conner, 1988b). The range of temperatures may be related to the season or seasons of the year when the seeds germinate. Seeds of plants from warmer habitats may show peak germination in winter and spring whereas those from seasonally cold habitats may show peak germination in late spring and early summer.

Water relations: Seeds of manuka (*Leptospermum scoparium*) survive 30 days of cycles of drying and rehydration without loss of germination potential, although with longer periods of desiccation the onset of germination may be delayed by as much as 30 days (Mohan *et al.*, 1984). In salt marshes, the mucilaginous seed of *Selliera radicans* is less affected by desiccation than the non-mucilaginous seed of *Spergularia media* (Partridge, 1981). Water potentials may also affect germination, the germination of seeds of *Acaena* spp are severely affected by water potentials as high as -0.2 MPa (Conner, 1987) although seeds of *Arthropodium cirratum* and *Chordospartium stevensonii* may eventually germinate in water potentials as low as -1.5 MPa (Conner and Conner, 1988a,b).

The germination of native salt marsh species may be completely inhibited by 1.5% - 3.5% salinity (-1.1 to -2.6 MPa), but recovers when seeds are transferred from 3.5% salinity (seawater) to freshwater. The germination of seeds of *Spergularia media*, *Atriplex prostrata* and *Cotula coronopifolia* are least affected by salinity, whereas *Schoenus nitens*, *Triglochin striatum*, *Selliera radicans* and *Plagianthus divaricatus* are increasingly more sensitive, indicating a correlation with position on the marsh. *Cotula coronopifolia* shows a similar response to salinity and equivalent concentrations of mannitol, suggesting that the effect is one of reduced water potential rather than salt content (Partridge and Wilson, 1987).

Discussion

This review is almost certainly incomplete, but it appears that seeds of New Zealand plants show patterns of germination behaviour similar to those from elsewhere. Some show no dormancy, e.g., *Dysoxylum spectabile* (Court and Mitchell, 1988), whereas others remain dormant because of the presence of the fruit, or because of an impermeable seed coat which prevents the uptake of water, e.g., *Chordospartium stevensonii*, (Conner and Conner, 1988b) or gases. Others show embryo dormancy which may be alleviated by maturation of the embryo during dry storage, e.g., *Arthropodium cirratum*, (Conner and Connor, 1988a) or by light, e.g., *Celmisia* spp. (Scott, 1975), or by low temperature stratification, e.g., *Hoheria glabrata*, (Haase, 1987). Other species may even have a "double dormancy" involving both seed coat and embryo dormancy, e.g., *Discaria toumatou* (Keogh, 1990; Keogh and Bannister, 1992). These patterns of behaviour result in most seeds germinating in the best possible conditions for survival, but non-uniform responses within a cohort of seeds ensures that not all seeds germinate at the same time. For example, in *Discaria toumatou*, some seeds germinate without scarification or stratification, some with scarification only and others only when they receive both. This ensures germination over a protracted period (Keogh, 1990).

Research on the germination of seeds of native plants is unlikely to reveal new patterns of behaviour or new mechanisms of dormancy. What is needed are precise comparative studies of broad ranges of species with respect to their ecology. For example, we know little of how light requirements for germination relate to open and shaded habitats; or how chilling or other temperature responses relate to latitudinal and altitudinal distribution or the biogeography of species; or whether native and introduced species show similar responses when growing together. There is a wealth of interesting research still to be done.

Acknowledgements

We particularly wish to thank Roger James and Simon Moore, students from the Botany Department at the University of Otago, for free access for their unpublished primary data on seed germination.

References

Allen, R.B. 1987. Ecology of *Northofagus menziesii* in the Catlins Ecological District, South-East Otago New Zealand (I) Seed production, viability and dispersal. *New Zealand Journal of Botany* **25**, 5-10.

Bannister, P. 1990. Seed germination in *Gaultheria antipoda, G. depressa* and *Pernettya macrostigma. New Zealand Journal of Botany* **28**, 357-358.

Bannister, P. and Bridgman J. 1991. Responses of three species of *Pseudopanax* to low temperature stratification, removal of fruit flesh and application of gibberellic acid. *New Zealand Journal of Botany* **29**, 213-216.

Bibby, T. 1992. A study of recalcitrance in the seeds of three New Zealand native species: *Corynocarpus laevigatus, Griselinia littoralis, Hoheria populnea.* B.Sc. Honours thesis, University of Otago.

Burrows, C.J. 1989. Patterns of delayed germination in seeds. *New Zealand Natural Sciences* **16**, 13-19.

Clout, M.N. and Tilley, J.A.V. 1992. Germination of miro (*Prumnopitys ferruginea*) seeds after consumption by New zealand pigeons (*Hemiphaga novaeseelandiae*). *New Zealand Journal of Botany* **30**, 25-28.

Conner, A.J. and Conner, L.N. 1988a. Germination and dormancy of *Arthropodium cirratum* seeds. *New Zealand Natural Sciences* **15**, 1-10.

Conner, L.N. 1987. Seed germination in five subalpine *Acaena* species. *New Zealand Journal of Botany* **25**, 1-4.

Conner, L.N. and Conner, A.J. 1988b. Seed biology of *Chordospartium stevensonii. New Zealand Journal of Botany* **26**, 473-475.

Court, A.N. and Mitchell, N.D. 1988. The germination ecology of *Dysoxylum spectabile* (Meliaceae). *New Zealand Journal of Botany* **26**, 1-6.

Fountain, D.W. and Outred, H.A. 1991. Germination requirements of New Zealand native plants: a review. *New Zealand Journal of Botany* **29**, 311-316.

Fountain, D.W., Holdsworth, J.M. and Outred, H.A. 1989. The dispersal unit of *Dacrycarpus dacrydiodes* (A. Rich) de Laubenfels (Podocarpaceae) and the significance of the fleshy receptacle. *Botanical Journal of the Linnean Society* **99**, 197-207.

Górski, T. and Górska, K. 1979. Inhibitory effects of full daylight on the germination of *Lactuca sativa* L. *Planta* **144**, 121-124.

Górski, T, Górska, K. and Nowicki, J. 1977. Germination of seeds of various herbaceous species under leaf canopy. *Flora* **166**, 249-259.

Gynn, E.G. and Richards, A.J. 1985. Biological Flora of the British Isles - *Acaena novae-zelandiae*, T. Kirk. *Journal of Ecology* **73**, 1055-1063.

Haase, P. 1987. Ecological studies on *Hoheria glabrata* Malvaceae) at Arthur's Pass, South Island, New Zealand. *New Zealand of Botany* **25**, 401-409.

Horrell, B.A., Jameson, P.E. and Bannister, P. 1990. Propagation and regulation of phase change in some heteroblastic species. *Combined Proceedings of the International Plant Propagators' Society* **25**, 268-274.

Keogh J.A. 1990. The ecology and seed biology of wild Irishman, *Discaria toumatou* Raoul, an endemic woody weed. Ph.D. Thesis, University of Otago.

Keogh, J.A. and Bannister, P. 1992. A method for inducing rapid germination in seeds of *Discaria toumatou* Raoul. *New Zealand Journal of Botany* **30**, 113-116.

Lloyd, D.G. 1985. Progress in understanding the natural history of New Zealand plants. *New Zealand Journal of Botany* **23**, 707-722.

Mohan, E., Mitchell, N. and Lovell, P. 1984. Environmental factors controlling seed germination of *Leptospermum scoparium* (manuka). *New Zealand Journal of Botany* **23**, 95-101.

Myers, S.C. 1984. Factors affecting the germination of *Beilschmiedia tarairi* seeds. *New Zealand Journal of Ecology* **7**, 205.

Partridge, T.R. 1981. The halophytic vegetation of Otago. Ph.D. Thesis, University of Otago.

Partridge, T.R. and Wilson, J.B. 1987. Germination in relation to salinity in some plants of salt marshes in Otago, New Zealand. *New Zealand Journal of Botany* **25**, 255-261.

Partridge, T.R. and Wilson M.D. 1990. A germination inhibitor in the seeds of mahoe (*Melicytus ramiflorus*). *New Zealand Journal of Botany* **28**, 475-478.

Pons, T.L. 1989. Dormancy and germination of *Calluna vulgaris* (L.) and *Erica tetralix* L. seed. *Acta Oecologica/Oecologia Plantarum* **10**, 35-43.

Scott, D. 1975. Some germination requirements of *Celmisia* species. *New Zealand Journal of Botany* **13**, 653-64.

Simpson, M.J.A. 1976. Seeds, seed ripening, germination and viability in some species of *Hebe. Proceedings of the New Zealand Ecological Society* **23**, 99-108.

Simpson, M.J.A. and Webb, C.J. 1980. Germination in some New Zealand species of *Gentiana*: a preliminary report. *New Zealand Journal of Botany* **18**, 495-501.

Villiers, T.A. 1975. *Dormancy and Survival of Plants.* Edward Arnold, London.

Wardle, J. 1970. The ecology of *Nothofagus solandri.* 3. Regeneration. *New Zealand Journal of Botany* **8**, 571-608.

Wardle, P. 1966. Biological flora of New Zealand 1. *Weinmannia racemosa* Linn. f. (Cunoniaceae) Kamahi. *New Zealand Journal of Botany* **4**, 114-131.

Wardle, P. 1971. Biological flora of New Zealand 6. *Metrosideros umbellata* Cav. (Myrtaceae) southern rata. *New Zealand Journal of Botany* **9**, 645-671.