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THE
REGENERATION OF
Eucalyptus pauciflora Sieb. ex Spreng.
FROM SEED

by

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A thesis submitted for the degree
of Doctor of Philosophy of the
Australian National University

February 1985



CHAPTER 8

GENERAL DISCUSSION

CHAPTER 8

Studies in the previous chapters have examined the variation in the dormancy and germination behaviour of seeds and the emergence of seedlings of Eucalyptus pauciflora from a range of altitudes. The differences in the response of seed from different altitudes, which is primarily mediated by seed dormancy, provides a basis for understanding the regeneration of the species.

The mechanism of dormancy has not been considered in the studies reported in this thesis because the main concern was the influence of dormancy on the timing of germination and emergence. A precise understanding of the mechanism of dormancy would not achieve this objective. A study which investigates mechanism requires an understanding of the behaviour of the whole process to ensure that the mechanism which is eventually proposed is not an artefact of the laboratory but is relevant to the behaviour of the seed in the field. The studies in this thesis have contributed to the understanding of the response of the dormancy to environmental factors, in particular temperature.

The first section of this chapter evaluates the statistical techniques which were used to test differences in the germination capacity and times-to-germination. The second section of this chapter discusses the results from previous chapters in terms of the overall process of the regeneration of Eucalyptus pauciflora. The final two sections discuss the results in terms of the mechanism of dormancy and the regeneration of E. pauciflora.

8.1 Evaluation of statistical techniques

The analysis and interpretation of the data from germination tests was discussed in Chapter 2; particular attention was paid to the use of Generalized Linear Models in the analysis of germination capacity, and to the use of Cox models in the analysis of germination curves. This section reviews the usefulness of these techniques together with their limitations.

(i) Germination Capacity

The use of Generalized Linear Models to analyse germination capacity has permitted not only the elucidation of the effects of experimental treatments but also the investigation of the mathematical form of the responses to temperature in a similar manner to regression analysis. The main advantage of using Generalized Linear Models (with a Logit link function and Binomial errors), instead of angular transformation and analysis of variance, is their statistical validity (Section 2.4.1).

(ii) Times-to-germination

Previous approaches to the analysis of the times-to-germination have relied on invalid assumptions, mainly related to the treatment of Binomial data as if it were Normal (by using techniques which rely on least squares criteria for fitting various regressions to germination curves) or, in the case of Hunter *et al.* (1983), by assuming that the times-to-germination of a seed sample have a Normal or log-Normal distribution (Section 2.2).

Constraints imposed by field programs meant that very few of the experiments in the present studies had records of germination which were collected on a strict daily basis. This detracted from the analyses using the Cox model in many cases, particularly when the germination treatments began on different days in various parts of the experiment. The use of the Cox model would be more powerful where records could be kept on a strict daily basis.

The Cox model has much wider application in the analysis of the effects of experimental treatments on data such as the mortality or changes in life stage of individuals in a population over time. Weiss (1982) used a similar model to examine the mortality of Chrysanthemoides monilifera seedlings under a range of treatments in the field.

Whilst the Cox model permits the analysis of the times-to-germination it does not generate a measure which can be used to compare the rate of germination between experiments. This deficiency stems from the absence of an assumption about the theoretical form of the distribution of the times-to-germination which is part of the strength of the analysis. The rate of germination could be compared in different experiments either by combining the experiments in the same Cox model or deriving some other measure of the rate of germination, such as the time to 50% germination, from the germination curves predicted by the Cox models fitted to the experiments separately.

8.2 Synthesis

The studies in this thesis have concentrated on the influence of environmental factors on the regeneration of E. pauciflora from seed. This section discusses the influence of the timing of germination and emergence in increasing the chances of survival of seedlings at a range of altitudes.

The size and dispersal of Eucalyptus pauciflora seed

Examination of the physical characteristics of seed collected from a range of altitudes (960 m to 1910 m) showed that the size of viable seed decreases as the altitude of seed source increases. The reduction in the size of the seed could be associated with a restricted period of seed filling due to slightly later flowering and the reduction in the length of the growing season as altitude increases. Seed size is also likely to be under some degree of genetic control: this was not investigated in the present study.

Eucalyptus pauciflora does not have a long-lived soil seed bank but holds a store of seed in capsules in the canopy. The dispersal of the seed from the canopy may occur at any time of the year but studies on other eucalypt species in southern Australia show that it is likely to be concentrated in summer and autumn (Christensen 1971, Cremer 1965b). The variability in the timing of dispersal means that the conditions to which seed may be exposed after dispersal may vary widely, and the response of the seed to these conditions determines the timing of germination.

The dormancy of E. pauciflora seed

A variable proportion of Eucalyptus pauciflora seed is dormant at dispersal. The degree of innate dormancy was found to be similar for populations from a range of altitudes from 960 m to 1730 m but was greater in seed from populations near treeline (1910 m, 2000 m). The strength of dormancy increases with altitude but there is no difference in the form of the temperature response for breaking dormancy for seed from different altitudes. The increase in the strength of dormancy with altitude leads to an increase in the duration of cold conditions necessary to break dormancy; this effectively delays the onset of germination of the seed from higher altitudes compared to that from lower altitudes when they are exposed to similar conditions.

There was a large amount of variation in the strength of dormancy of seeds collected from trees growing in close proximity at the same altitude. The extent of this variation in the strength of dormancy has been demonstrated in Section 4.2.2 which showed that, as the duration of stratification was increased, the dormancy of an increasing proportion of the seeds was broken. Variation in strength of seed dormancy provides a basis for variation in the timing of germination which may be important for spreading and reducing the risk of mortality of the total seed population due to infrequent events, such as severe frosts.

The effectiveness of variation in the strength of dormancy of a seed sample in promoting the survival of at least some of the seedlings is indicated by the emergence of some seedlings from all seed sources in reciprocal transplant experiments at altitudes ranging from 960 m to 1740 m (Section 7.2).

Changes in dormancy of the seed during dispersal

Temperature conditions determine whether dormancy is broken or enhanced, and the moisture conditions appear to influence the rate at which changes in dormancy occur in response to the temperature conditions. The dormancy of the seed reaching the ground is largely determined prior to the shedding of the seed, however the strength of dormancy of the seed which is dispersed may be increased by conditions during the shedding of the seed from the capsule. Exposure to temperatures of 5°C and 40°C during seed shedding leads to slight increases in the strength of dormancy. However, the small degree of influence exerted by temperatures within the normal range suggests that the season of dispersal is unlikely to have a large influence on the dormancy of the dispersed seed. Changes in the dormancy of the seed whilst it remains in the capsule also seems unlikely since breaking of dormancy would be expected to occur over winter when temperatures are low. Seed shed from capsules collected in both June and September was found to have a low germination capacity immediately after shedding.

Preliminary evidence indicates that the strength of dormancy of seed dispersed from the canopy following a fire may be greater than that dispersed under normal conditions. However, this assertion is based on an incomplete knowledge of the temperatures to which capsules are exposed during a fire. Further studies are required to check whether the dormancy of seed dispersing following a fire is greater than the dormancy of seed shed under normal conditions.

In summary, the dormancy of the seed reaching the ground is unlikely to be influenced by the conditions around the time of seed shedding, although there is a chance that some of the seed dispersed

after a fire may be more strongly dormant.

The induction of dormancy

The conditions to which the seed is exposed prior to germination will vary widely depending on the timing of seed dispersal and the weather. It is likely that a large proportion of the seed will be dispersed before late February and will therefore be exposed to temperatures and moisture conditions which are conducive to the induction of dormancy.

The present studies have shown that dormancy is induced in moist seed exposed to temperatures above 9°C and broken at temperatures below 6°C (Section 4.2.2.1). Exposure to temperatures in the range 6°C to 9°C may lead to the breaking of dormancy of some of the seed in a population; however, there is evidence from Grose's (1963) studies of E. delegatensis that dormancy is induced after prolonged exposure to these temperatures. The precise response of the induction of dormancy to temperature has not been determined, but there is evidence that the rate at which dormancy is induced may vary with temperature (Section 4.2.2.1, Section 5.2).

The importance of the induction of dormancy as a mechanism for minimizing germination in autumn and winter depends on the conditions encountered by the seed after it reaches the ground. The high temperatures and moist conditions common in late summer prevented germination and led to the induction of dormancy in seed planted at that time; the dormancy of this seed was sufficiently strong at the beginning of winter to ensure that germination (Section 7.1) and emergence (Section 7.3) is delayed until spring.

As the time of planting becomes later in autumn the decrease in soil temperatures leads to an increase the chances that a proportion of the seed will germinate before dormancy is induced. Conditions which are suitable for the germination of a portion of the seed sample also result in an increase in the strength of dormancy of the seed which does not germinate, to the extent that further germination prior to winter is prevented (Section 5.2). As the time of planting is delayed further, the probability of the seed being exposed to conditions which induce dormancy is reduced, and there comes a point where the seed will be exposed to conditions which are wholly suitable for the breaking of dormancy. In this case the capacity of the environment to break dormancy may exceed the strength of dormancy of the seed (especially when it has not been incremented by induction) and the number of seedlings which emerge may be reduced by premature germination of seed during winter (Section 7.3).

The potential for the induction of dormancy in spring would seem to be limited to those seeds which have not received sufficient exposure to cold conditions to ensure germination at temperatures below 9°C. As the dormancy of a seed sample is broken by stratification the proportion of seed which germinates is increased and the strength of dormancy of the seeds which do not germinate is reduced (Section 5.2). It is conceivable that in years when an early snow melt is followed by dry, warm conditions, the capacity of the environment to break dormancy could be reduced to the extent that a proportion of the seed will not germinate at temperatures above 9°C: dormancy will thus be induced in that seed.

In summary, dormancy is induced in moist seed at temperatures

above 9°C and it would seem that the induction of dormancy effectively prevents the germination of a large proportion of the seed dispersed in summer and autumn. Seed dispersed later in autumn, which is not exposed to conditions which induce dormancy, may not have the strength of dormancy necessary to delay germination to a more favourable time in spring.

The breaking of dormancy

Laboratory studies have shown that, at constant temperatures, the breaking of seed dormancy occurs between 0°C and about 9°C, and that the rate at which dormancy is broken varies depending on the temperature within this range (Section 4.2.2). The effect of diurnal fluctuations in temperature on the breaking of dormancy was not investigated in the present study. It could be expected that temperature fluctuations within the range 0°C to 9°C might lead to a consistent breaking of dormancy; however, when the higher end of the temperature range exceeds 9°C, the nett effect on the dormancy of the seed could be expected to depend on any synergistic or antagonistic interactions between the induction and breaking of dormancy.

Soil temperatures decline to levels which are suitable for the breaking of dormancy during autumn but the effectiveness of the autumn and winter conditions for breaking dormancy in the field may vary depending on the temperature regime to which the seed is exposed. The variation in temperature with altitude will be particularly important in this respect. At low altitudes, which do not receive permanent snow cover, the breaking of dormancy will occur in a temperature regime which is fluctuating diurnally. At high altitudes, the period of snow cover will encompass a period of low, but relatively constant soil

temperatures at which the breaking of dormancy will proceed very slowly. The decline in temperature with altitude will mean that, in the first instance, the time when the temperature conditions change from nett induction of dormancy to nett breaking of dormancy will become earlier with increasing altitude and, in the second instance, that there will be a longer period when the rate of breaking dormancy is low at higher altitudes. The duration of snow cover increases with altitude (Slatyer et al. 1984) and the soil temperature conditions under snow (-0.5 to 0.5°C) will permit only very slow breaking of dormancy.

In summary, the induction of dormancy minimizes the germination of seed in autumn and preserves the seed for germination in spring. Survival of the seedling is dependent on the strength of dormancy being matched to the capacity of the environment to break dormancy at a time which is suitable for the germination and establishment of seedlings.

The germination of seed

Moist seed may respond to the temperature environment in three ways; germination, changing the strength of dormancy, or death. The response of the seed to temperature (in particular the proportion of seed germinating) changes as the dormancy of the seed sample is broken. As the duration of the stratification treatment is increased, the range of temperatures which are suitable for germination also increases and a larger proportion of the seed germinates (Section 6.1).

The advantages of seed dormancy as a mechanism for limiting germination to the more favourable spring season have already been discussed. The more precise control of the timing of germination

during spring may be equally critical for the subsequent survival of the seedlings. As the winter progresses and dormancy is broken, the range of temperatures which are suitable for germination increases and the seed is more likely to germinate at low temperatures.

Field germination of seed occurred over a period of 30 days, when soil temperatures were below 9°C. It could be expected that if soil temperatures had been depressed later into the spring, for example by persistent snow cover, then the seed would be likely to germinate at a later time and even lower temperatures. On the other hand, if soil temperatures had risen earlier, then the seed might have germinated earlier.

The strength of dormancy appears to be the critical attribute leading to variation in the germination response of seed from different altitudes to temperature and is sufficient to explain the differences observed in the emergence of seedlings in the field.

Emergence of seedlings

The field studies of Section 7.2 showed that seed from all sources was capable of producing some seedlings at all altitudes despite the wide differences in environmental conditions; this suggests that the variation within a population of seed was sufficient to include seeds which could produce seedlings in widely different conditions. Seed from higher altitudes was found to produce a lower proportion of seedlings when planted at low altitudes than seed collected and planted at low altitudes and vice versa (Section 7.2). When planted at high altitudes the weaker dormancy of seed from low altitudes means that this seed is likely to germinate earlier, thus exposing the seedling to

more severe conditions either under the snow or soon after the snow melts. When planted at low altitudes, the stronger dormancy of seed from higher altitudes may delay germination of a proportion of the seed population beyond the time of favourable conditions in spring.

In seed from a particular source, the decrease in the strength of dormancy with increasing seed size (Section 3.2) may permit a test of the importance of the strength of dormancy in relation to the capacity of the environment to break dormancy. Große (1963) has shown that the area of the cotyledons in E. delegatensis seed is related to the seed size. The results of the studies of Section 3.2 would suggest that it was likely to be the smaller seed from low altitudes which emerged at high altitudes and the larger, less dormant seed from high altitudes which emerged at low altitudes. A comparison of areas of cotyledons of seedlings emerging at different altitudes of planting may provide a simple field test of the basis for the differences in the proportion of the seed emerging.

The studies in Sections 7.1 and 7.2 show that there was a delay of 30 days between the germination of seed and emergence of the seedlings. It is presumed that the growth of the seedling between germination and emergence is also influenced by temperature, with low temperatures effectively delaying the emergence of the seedling and high temperatures hastening emergence. An advantage of the delay in emergence caused by low temperatures may lie in the avoidance of damage to the expanded cotyledons by needle ice or severe frosts. Similarly, the more rapid emergence at higher temperatures would be an advantage because the soil moisture will decline more rapidly at those temperatures.

Footnote to Section 8.2.

The influence of environmental factors before, during and after the dispersal of seed from the capsules has been summarized. The fate of seed depends on these processes together with the timing of the shedding of seed from the capsule. The following decision tree is included to clarify the discussion.

Seed shed from the capsule in the canopy?

YES

NO

Viable free seed *1

Seed shed from capsule after
dispersal? *2

YES

No

Viable free seed *3

Dead seed *4

*1 Seed is shed following desiccation of the capsule. Seed could be shed in this manner at any time of year and its fate will depend on the sequence of conditions that it encounters following dispersal.

*2 The liberation of seed from the capsule after dispersal depends on the desiccation of the capsule to release the seed and the action of gravity or some other agent to cause shedding of the seed (Cremer 1965a). Weather conditions and the microenvironment of the capsule will be the primary determinants of the rate of desiccation of the capsule. For example, the chances of desiccation are increased if the capsules are attached to branches or twigs which can hold the capsule away from the soil surface. The shedding of the seed will also be favoured if the capsule is suspended so the seed can fall out.

*3 The dormancy of seed released from capsules after dispersal could be expected to be strengthened but not reduced as a result of the conditions after dispersal. Grose (1960) noted that the dormancy of seed extracted from E. delegatensis capsules which had been held under cold, moist conditions was similar to seed from untreated capsules. The desiccation of the capsule prior to seed release may also result in the induction of dormancy in the seed (Section 5.3).

*4 As the capsule decomposes the chance of the seed being released becomes more remote due to hardening of the valves (Grose 1960). If the seed is not released from the capsule it will eventually become non-viable.

The discussion above has proposed two pathways by which viable seed may be dispersed. Differences in the timing of germination of seed dispersed in these two ways (*1, *3) are most likely to be observed when dispersal occurs during winter since seed dispersed in the capsule will not begin to break dormancy until it is released from the capsule and desiccation will be delayed by wet, cold conditions. Seed or capsules may fall onto snow and will melt their way down through the snowpack to arrive at the soil surface. At this stage free seed (1) will have imbibed and begun to break dormancy whereas seed in the capsule (3) must be released from the capsule before dormancy can be broken. Germination of seed (1) in the snowpack is unlikely because the rate of breaking dormancy and the rate of germination are very slow at the prevailing temperatures (-0.5-0.5 C). Desiccation and release of seed from the capsule (3) will occur after the snow has melted and the breaking of dormancy and germination of this seed will depend on the sequence of conditions after seed release. If the thaw occurred in early spring the chances of the seed (3) becoming seedlings is greater

than if the snow persisted until early summer. At this stage the soil temperatures will be too high to break dormancy and may be high enough to induce dormancy - the seed may not germinate until the following spring and is unlikely to produce seedlings (Section 7.2).

8.3 Mechanism of dormancy

This section reviews the evidence for the mechanism of dormancy of E. pauciflora seed. The basic cause of dormancy is the inability of the embryonic axis to overcome the constraints against growth which are acting upon it (Bewley & Black 1982). The restraint of the embryo may be achieved by constraints on the potential for growth of the embryo or by the strength of the covering structures of the seed or both. Three aspects of seed dormancy are commonly studied which seek either to find experimental treatments which can break dormancy, or to associate dormancy with particular structures (seed coat, cotyledons), or to elucidate the biochemical events, and thereby the mechanism, which governs the breaking of dormancy.

Bewley & Black (1982) reviewed many studies which have searched for the mechanisms controlling seed dormancy in a range of species and have concluded that

it is apparent that many of the changes [in metabolism] which have been described are non-specific either to conditions of cold temperatures or to dormant seeds. The true nature of the effects of cold stratification on dormancy breaking remains to be elucidated.

There are no reports in the literature of studies on the mechanism of the dormancy of E. pauciflora or of any other eucalypt species; however, several studies have examined the conditions necessary for, and the structures involved in, the breaking of dormancy in E. pauciflora and E. delegatensis.

The embryo of E. pauciflora is able to grow when the seed coat has been removed (Boden 1957, Bachelard 1967). The group of eucalypts

which includes E. pauciflora (Subgenus Monocalyptus, Section Renantheria, Series Obliquae) has a seed coat which has an inner integument with a distinctive structure which was described by Gauba & Pryor (1958)

[the inner integument] occurs immediately below the outer integument. In ripe seeds the median cuticle delimiting the two integuments is resorbed. In the genuine Renantherae the inner integument is two-layered, being formed of both epidermal layers alone. The cells are tabular and without intercellular spaces.... [the inner integument] is suberized throughout, the walls not merely being impregnated with fatty substances..... the walls are in addition more or less impregnated with tannin-like material.

Pryor (1954), Boden (1957) and Bachelard (1967) noted that most of the eucalypts of the colder areas (E. delegatensis, E. pauciflora, E. stellulata, to name a few, see Table 8.1), which had dormant seeds, belonged to this group although not all of them do (for example E. perriniana, E. glaucesens). Not all of the members of the group exhibit seed dormancy (for example E. sieberi). The dormancy of the seeds must therefore be associated with more subtle differences than the gross anatomy of the seed coat.

Grose (1963) showed that the presence of the inner integument was sufficient to prevent germination since seed of E. delegatensis did not germinate when the inner integument was intact but germinated readily when both the inner and outer integuments were removed. This observation shows that the presence of the inner integument is sufficient to prevent germination, but does not show that the cause of dormancy resides entirely in the inner integument. The mechanism behind the action of the inner integument in inhibiting germination has not been investigated. Removal of the seed coat may not remove all of the constraints on growth present in the seed of this species since

Grose (1963) also found that the rate of growth of excised E. delegatensis embryos was lower than those which had germinated without interference.

Grose (1963) postulated that the dormancy of E. delegatensis was mediated by a restriction of gas exchange by the seed coat which leads to a limitation of oxygen supply to the embryo. He based this assertion on the stimulation of germination in dormant seed by atmospheres which were high in oxygen. Bachelard (1967) disagreed with this view and maintained that the dormancy of both E. delegatensis and E. pauciflora seed was the result of mechanical restraint imposed on the embryo by the seed coat. The evidence tendered by Bachelard (1967) was that germination never occurred when the seed coat could resist the elongation of the embryo (cutting the seed coat on the sides compared to cutting the coat at either the micropylar or cotyledonary end) although the embryo was partly exposed to the atmosphere. Bachelard's observations do not exclude the limitation of gas exchange as a limiting process in the breaking of dormancy of intact seeds because they do not provide evidence of changes in either the strength of the seed coat or the strength of the embryo in the breaking of dormancy by stratification. If the dormancy of E. pauciflora was mediated by the restraint of the seed coat then concurrent studies of the changes in the strength of the seed coat and the strength of the embryo as dormancy is broken, such as those of Esashi & Leopold (1972) with Xanthium seeds, may lead to further insights into the mechanism of dormancy. Such an experimental approach would be of little use if the breaking of dormancy is mediated through changes in the permeability of the seed coat to oxygen as Grose (1963) suggests.

The studies reported in this thesis have set out to describe the

responses of the seed to its environment and are important in describing the responses which a mechanism of dormancy must explain. The main aspects of this response are listed below-

1. The strength of innate dormancy of seed increases with increasing altitude of collection.
2. Larger seeds have a weaker dormancy.
3. Dormancy is induced at temperatures above 9°C in both stratified and unstratified seed with measurable responses occurring in a period of 5 days or more at 15°C .
4. Dormancy is broken at temperatures below 9°C (optimum temperature of 5.5°C) with measurable changes in a period of 10 days or more.
5. The rate at which dormancy is broken begins to decline at a water potential of -4 bars and is negligible at a water potential of -10 bars.
6. The dormancy of individual seeds is not associated with their water content.
7. The range of temperatures which are suitable for germination increases as the dormancy of the seed is broken.
8. As the dormancy of a seed sample is broken the rate of germination increases.
9. Soaking seed in solutions of gibberelic acid will break dormancy

(Bachelard 1967).

10. The dormancy of seed is associated with the seed coat (Boden 1957, Bachelard 1967) and possibly only the inner integument (Grose 1963).
11. Treatment of seed in atmospheres high in oxygen breaks dormancy (Grose 1963).

Many of the responses listed above could be attributed to either increases in the force exerted by the embryo or to a weakening of the seed coat or both and it would be pointless to speculate on the detailed mechanism of dormancy in the absence of information on changes in these characters.

8.4 Regeneration of *Eucalyptus pauciflora*

Regeneration niche was defined by Grubb (1977) as an expression of the requirements for a high chance of success in the replacement of one individual by a mature individual of the next generation. The chances of success during the regeneration of *Eucalyptus* have been associated, in the first instance, with the occurrence of disturbances such as fire and flood, and then with seasonal changes in the suitability of the climate for regeneration (Florence 1981).

The chances of successful regeneration of eucalypts from many environments are closely linked to seasonal conditions (Cremer et al. 1978), which places an emphasis on mechanisms which cue the timing of germination to favourable seasonal conditions. The timing of germination is critical for the survival of the seedling because it is the stage when the seedling is least tolerant of environmental extremes of temperature and moisture availability yet is in an environment near the surface of the soil, which is potentially most extreme and variable.

The studies in this thesis have shown that the regeneration niche of *E. pauciflora* includes a requirement for a period of cold moist conditions which brings about a delay in the timing of germination. This delay is likely to be associated with increased survival of individuals since emergence in spring reduces the chances of exposure of a newly emergent seedling to the lethal environmental conditions of summer and winter whilst giving the seedling the longest possible growing season before it is exposed to the rigours of the subsequent winter. Reciprocal transplants of seed between altitudes have shown that the critical element of the seed dormancy of *E. pauciflora* is the

balance between the strength of the dormancy and the capacity of the environment to break dormancy, since this determines the effectiveness of dormancy in timing germination.

Eucalyptus pauciflora is one of sixteen species of Eucalyptus in which innate seed dormancy has been recorded (Table 8.1). Of the species which possess innate seed dormancy twelve occur in cold, higher altitude environments of southern Australia which receive snow. Most of these species are classified in Morocalyptus, Section Renantharia, Series Obliquae (MAK). The requirement for a period of cold, moist conditions as part of the regeneration niche of these species is presumed to minimize germination in autumn and promote it in spring as it does in E. pauciflora.

The timing of germination has been shown to be critical for maximizing the survival of individuals up to the stage of seedling emergence in E. pauciflora, however regeneration may still be prevented at a later stage in plant development.

The regeneration of E. pauciflora in the absence of disturbances such as fire is rare (Slatyer pers. comm.). The limitations to regeneration in the absence of fire in Eucalyptus regnans and E. incrassata were discussed in Chapter 1 in which it was shown that the increased chances of successful regeneration are associated with transient changes in resources following fires in these species. Fire has been associated with increased chances of successful regeneration through increases in light and the 'ashbed effect' Pryor (1963). Fire also results in a plethora of changes in the soil which include increases in nutrient availability, changes in the composition of the soil microflora (Renbuss et al. 1972), and the removal of allelopathic substances

TABLE 8.1

Species of Eucalyptus which have innate seed dormancy¹

SPECIES	REQUIREMENT	CLASSIFICATION ²
Subgenus <u>Monocalyptus</u>		
amygdalina	stratify 4 weeks	MATEH
delegatensis	stratify 6,8,10 weeks	MAKBE
kybeanensis	stratify 6 weeks	MAKKA
mitchelliana	stratify 6 weeks	MAKLA
pauciflora	stratify 4 weeks	MAKHA
regnans	stratify 3 weeks	MAKCA
stellulata	stratify 3 weeks	MAKMA
Subgenus <u>Symphyomyrtus</u>		
behriana	light	SUDGA
camaldulensis	light	SNEEPA
flocktoniae	stratify 4 weeks	SIT:T
glaucescens	stratify 6 weeks	SPINH
microcarpa	light	SUL:DB
microtheca	light	SUADF
nitens	stratify 3 weeks	SPITG
perriniana	stratify 3 weeks	SPINN
spathulata	light	SIDCDA

¹ from Appendix 2, Boland et al. (1980)² Pryor & Johnson (1971)

The requirement for disturbance in the regeneration niche does not detract from the critical importance of the many other processes which ensure that the regenerating plant has a high chance of survival. The timing of germination, mediated by seed dormancy, has been shown to be one such process in Eucalyptus pauciflora.

8.5 Relationship to other studies

The results of studies reported in this thesis and the studies of Grose (1960) on E. delegatensis are very similar. Both show that control of the timing of germination, through the processes of induction and breaking of dormancy and germination and the processes appear to have a similar response to temperature in the two species.

The apparatus (gradient plate) and statistical techniques used in the studies of the dormancy and germination of E. pauciflora seed permitted precise definition and analysis of the temperature responses of these processes in E. pauciflora. Temperature influences both the direction and rate of change in dormancy and these studies showed that the changes in dormancy are very sensitive to the temperature conditions. A change in temperature from 6° C, which favours the breaking of dormancy, to 9° C would result in the induction of dormancy. There was also an indication that the rate of induction of dormancy depends on temperature but this was not fully investigated.

The responses noted in constant temperature studies were consistent with changes in dormancy observed in seed exposed to field conditions, however there is the need for further work on the action of variation in temperature over a range which spans the 6° C to 9° C region.

Comparison of field studies showed that seed dormancy changed in response to changes in weather conditions in both E. delegatensis (Grose 1960) and E. pauciflora: these changes acted to prevent seed from germinating in autumn and winter and cue germination to spring.

Dormancy mechanisms which cue germination to a favourable time of year have been described by many workers (Karssen 1980, Levins 1969). The investigations reported in this thesis show that dormancy has survival value in E. pauciflora. The variation in the strength of dormancy of seed from different altitudes may be considered adaptive and the response of dormancy to environmental conditions provides the means by which the germination of the seed is synchronized with the environment.