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

by

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CHAPTER 1

INTRODUCTION
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1.1 The regeneration of plants

Regeneration of plants from seed involves the passage through a series of life stages which have different sensitivities to environmental conditions. The regeneration niche is an expression of the requirements for a high chance of success in the replacement of one mature individual by a new mature individual of the next generation (Grubb 1977). The regeneration niche can be seen as a statement of the tolerance ranges for survival and the requirements for growth as seed becomes seedling and so on through the ontogeny of the plant.

Cohorts of plants generally experience their greatest mortality during the regeneration phase; therefore there is an huge potential at this stage for differential selection of individuals with attributes associated with increases in fitness. The high mortality at this stage is associated with the relative severity of the environment near the surface of the soil, and with the susceptibility to damage of plants with very limited reserves and few meristems.

The regeneration phase is important because differentiation between species in this phase has the potential to influence the species richness of a community of plants. The importance of the regeneration phase for the maintenance of species richness in a plant community, which has been discussed by Grubb (1977), is related to the enormous influence of chance at the relevant scale of environmental variation. The element of chance refers to both the presence of viable propagules of the species at the site and the microenvironmental
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conditions in the vicinity of the seed and seedling.

The potential for the manipulation of community composition by modification of conditions in the regeneration phase has implications for the management of both weedy and desirable species. In order to realize this potential it is necessary to understand the environmental control of these processes and the way in which they may be manipulated.

1.2 The regeneration of Eucalyptus

Plants of the genus *Eucalyptus* are widely distributed in Australia and may be found in a wide range of environments varying in altitude from sealevel to treeline at 2000 m, and in latitude from southern Tasmania to the tropical regions north of Australia. The 440 species of the genus (Chippendale 1976) show a large degree of morphological variation ranging from the multiple-stemmed 'mallees' of drier areas and high altitude areas through the short-boled single-stemmed trees of open woodlands to the giant single-stemmed trees of the tall forests which occur in higher rainfall areas.

The regeneration niche of the eucalypts has been discussed extensively by Cremer et al. (1978) who discuss some of the variation in the requirements necessary for the regeneration of species from different environments and conclude that the single most important factor in the successful regeneration of many eucalypt species is fire. The sensitivity of various species to fire and the intensity of the fires to which they are exposed lead to a wide range of responses which may be characterized by the degree and mode of regeneration of individuals following the fire. The range of these responses, from the
decimation of the extant population and obligate regeneration from seed (e.g. *Eucalyptus regnans*), to facultative regeneration from seed in addition to regeneration of adults. The regeneration of adults ranges from resprouting from lignotubers (e.g. *Eucalyptus incrassata*, *Eucalyptus pauciflora*), to various levels of stem resprouting observed in species such as *Eucalyptus pilularis*, *Eucalyptus dives* and *Eucalyptus delegatensis* (Jacobs 1955). Two species in which the limitations to regeneration in the absence of fire has been studied are *E. regnans*, which grows on deep soils in high rainfall areas and is discussed by Ashton & Willis (1982) and *E. incrassata*, a mallee species growing in the semi-arid areas (Wellington 1981).

*Eucalyptus regnans* forests tend to be even aged stands in which the trees have established following fires, which may occur once every century or so. The established trees are unlikely to survive the high intensity fires when they do occur and regeneration of the forest proceeds from seed. Seed does germinate under the understorey, which is well developed in these forests, although the survival of the germinated seedlings may be limited by the presence of lipids in the soil. Seedlings which do survive establishment die within 2 years. Antagonistic microorganisms in the soil associated with the living roots of the established trees have been implicated in the death of these seedlings in a mature forest. In addition to the limitations imposed by the soil, light may also become limiting for the plant as it passes from the seedling phase, when the leaves are normal to the incident light, to the juvenile phase when the leaves become pendulous. Fire removes the limitations imposed by the biological and physical environment and permits the seedlings to establish and grow vigorously.

*Eucalyptus incrassata* populations tend to have an uneven age
distribution because many individuals are likely to survive the more frequent fires (about 20 year intervals) which occur in the mallee shrublands, and regeneration may proceed by resprouting from the lignotuber or from seed. Comparison of the water status of seedlings of *E. incrassata* at sites which differed in the time since fire showed that the seedlings in a stand burnt 4 years previously had far lower water potentials than those growing in an area which had been burnt one year previously (Wellington 1984). This observation suggests that the effect of fire is to increase the availability of water in the upper layers of the soil by temporarily removing the transpiring canopy of the adult trees. In the absence of fire seedlings germinated and emerged but then died during the first summer in the mallee.

The elements of the environment which limit the survival of seedlings in the absence of fire are replaced by other limitations to survival following a fire. It is the response of the seedling to environmental conditions during regeneration which will be examined in this thesis. The eucalypts show considerable variation in the processes involved in regeneration; specializations such as seed dormancy, differences in the optimum temperature for germination (Boland *et al* 1980) and the growth rate of seedlings (Davidson & Reid 1980, Noble 1983) have been identified in *Eucalyptus*.

*Eucalyptus pauciflora* offers the opportunity to examine the changes in the processes of regeneration in relation to altitude in the species which is distributed to the upper altitudinal limit of the eucalypts. Many environmental factors change with altitude including temperature, rainfall and the incidence of frost and snow (Costin 1954). The reduction in temperature and associated increase in the number of frosts and incidence and duration of snow cover (Slatyer *et*
results in a delay in the beginning and a hastening of the
end of the growing season with increases in altitude (Costin 1954,
Slatyer & Morrow 1977). In addition to a reduction in the length of
the growing season the conditions during the growing season become
cooler with increases in altitude which reduces the potential for
growth even further as altitude increases. The changes in the
environment are also associated with changes in the morphology (Green
1967) and physiology (Slatyer 1978) of the species and these changes
have been interpreted as increasing the chances of survival and growth
of the populations of \textit{E. pauciflora} growing in those environments.

1.3 The regeneration of \textit{Eucalyptus pauciflora}

\textit{Eucalyptus pauciflora} (Sieb. ex Spreng.) is a long lived tree
which has a wide distribution from sea level to treeline (2000 m)
(Boland et al. 1984); it occurs extensively at higher altitudes in the
Great Dividing Range in eastern Australia. The morphological
differentiation of \textit{E. pauciflora} with altitude is such that different
ecotypes were considered to be different species until Pryor (1954)
suggested that the variation in morphological characters, such as tree
height, canopy form, capsule and leaf shape which were being used to
differentiate between the species could be considered to be continuous
in response to changes in environmental factors. This proposition was
supported by Green (1967, 1969a, 1969b) who demonstrated that the
variation in a range of morphological and phenological characters in
\textit{E. pauciflora} was genetically controlled and varied continuously with
altitude, and that the characters which had formerly been used to
differentiate between the species were not stable and discrete.

Physiological \textit{proc. ses} were also found to vary in \textit{E. pauciflora}
populations from different altitudes. Slatyer (1977) found that there was a decrease in the optimum temperature for photosynthesis and a reduction in the rate of photosynthesis at the optimum temperature with increases in the altitude of seed source. Harwood (1976) showed that the frost tolerance of this species increased with altitude of seed source.

The regeneration of a species from seed depends on some seed being in suitable place and physiological state to ensure the germination of the seed and survival and growth of a seedling to the stage of reproductive maturity. The studies in the following chapters investigate the influence of the physical environment on the process of the regeneration of *E. pauciflora* from seed. The ontogenic sequence from seed to established tree may be influenced by the environment at all stages from the production of the seed to the establishment of a seedling. The role of the environment in determining the outcome of this sequence will depend on the type and extent of the response which it elicits and the degree to which this response pre-empts the response to environmental conditions subsequently. I will now discuss the life history of *E. pauciflora* concentrating on the influences of the physical environment at various stages and the potential for that influence to control the timing of the process of regeneration.

The production of seed begins with the development of flower buds in the summer and autumn of the year prior to flowering; flowering occurs in the period from November-January (Boland *et al.* 1980). *E. pauciflora* flowers profusely at irregular intervals but in most years some trees flower at all altitudes. Observation of the widespread and heavy flowering which occurred in the Snowy Mountains in 1982 showed that there was a delay of 2 weeks in the onset of flowering
of *E. pauciflora* from 960 m to 1850 m and that the flowering extended over a period of 4 weeks to 6 weeks. The development of the seed is completed by the summer following flowering (Cremer et al. 1978).

*Eucalyptus pauciflora*, in common with most eucalypts, does not have a large, long-lived seed bank in the soil (Howard & Ashton 1967), because almost all the seed will germinate within a year of dispersal from the capsules. The canopy seed bank has several cohorts of capsules and the timing of dispersal of seed from the capsules is the first point at which the timing of germination may be influenced. The frequency of flowering and the persistence of the capsules in the canopy makes it unlikely that there would ever be a paucity of seed for regeneration, although the amount of seed in the canopy will vary depending on the time since the last flowering.

The dispersal of seed is dependent on the local environment of the parent tree, and may occur before or after the seed is shed from the capsule. Seed dispersed inside the capsule probably has a reduced chance of becoming an established seedling because of destruction of the seed by predators or pathogens before the seed is shed from the capsule (Cremer et al. 1978). The association between the climate and the shedding of *Eucalyptus* seed in southern Australia is well documented with a tendency for seed to be shed in late summer and autumn (*E. regnans*, Cremer 1965, Cunningham 1960; *E. delegatensis*, Grose 1963) although some seed is shed at all times of year. Fire may stimulate a large and synchronized seed fall (*E. regnans*, Cunningham 1960, Cremer 1965b; *E. diversicolor*, Christensen 1971; *E. incrassata*, Wellington 1981; *E. delegatensis*, O'Dowd & Gill 1980).

The predation of dispersed seed is likely have a critical
influence on the survival of the seed. Grose (1963) showed that the number of seedlings of E. delegatensis could be increased by spraying the ground with insecticide after planting and Cremer et al. (1978) noted that the number of seedlings establishing from seed could be increased by insecticide treatment of the seed. More recently the predation of seeds placed on the ground has been examined in detail in E. regnans forests by Ashton (1979) who showed that up to 65% of seed was removed by ants within 2 weeks of placement. Similar rates of seed removal were noted by Wellington & Noble (1985) for E. incrassata.

The size of the seed represents the 'capital' available for the development of the new plant and may vary within a population and between populations. The size of seed within a population had an important bearing on the size and early growth rate of the seedlings of E. maculata and E. sieberi (Grose & Zimmer 1958c), E. delegatensis (Grose 1960). The seed sizes of different populations also have been associated with differences in growth rate of seedlings of E. viminalis (Ladiges 1974). Indirect evidence for a decrease in the size of the viable seed of E. pauciflora with increasing altitude (Boland et al. 1980) can be obtained by comparing the mean numbers of viable seed for samples of the low altitude E. pauciflora ssp. pauciflora and higher altitude E. pauciflora ssp. niphophila form. This comparison may be confounded by a changing proportion of chaff in the seed sample, but needs to be resolved to determine whether the 'capital' is different for ecotypes growing at different altitudes.

The absence of a long-lived seed bank in the soil under E. pauciflora forests (Howard & Ashton 1967) suggests that all of the seed either dies or germinates within a year of dispersal. It is the processes which control the timing of germination which have a critical
role in ensuring that the establishment of the seedling occurs at a
time which ensures the greatest chances of survival and growth of the
seedling. The timing of germination of the seed in response to its
environment can be controlled at three stages: before dispersal,
between dispersal and the breaking of dormancy and during germination.
The essence and impact of the interaction between the seed and its
environment is markedly different in each of these stages.

A large proportion of *E. pauciflora* seed is dormant at dispersal.
Dormancy is one means by which environmental conditions which are
unfavourable for plant processes are avoided. The disadvantage of
dormancy is that it also constitutes a time when an individual is not
competing for resources (Harper 1977). The critical elements of a
dormancy strategy are the timing of the induction and the breaking of
dormancy in relation to conditions which are favourable for germination
of the seed and emergence, survival and growth of the seedling.
Increases in fitness due to dormancy are likely to be attained by
minimizing the loss of competitive advantage and maximizing the
survival of the individual in the prevailing conditions.

*Eucalyptus pauciflora* exhibits a variable degree of dormancy at
dispersal which increases with altitude (Grose 1957) and which will
determine the chances of germination when the seed reaches the ground
after dispersal. The dormancy of *E. pauciflora* seed is broken by cold
moist conditions (stratification) (Pryor 1954). Seed from higher
altitudes may be expected to have a dormancy which requires a longer
period of stratification since the chances of seed breaking dormancy
before winter, due to the lower temperatures at higher altitudes,
expose the seed to the possibility of germination, either during late
autumn or winter which would be fatal (Slatyer pers. comm.).
The dormancy of the seed at dispersal may also be expected to vary with the conditions of seed extraction and dispersal because these conditions are a broad indicator of the conditions on the seed bed (season). The particular advantages of such a response would seem to be the modification of the response of the seed to the soil environment immediately after dispersal. Such a response could be important for seed dispersed in the spring, when conditions are suitable for establishment but the chances of prolonged periods of low temperatures for breaking dormancy are remote, or alternatively, in autumn when the chances of successful establishment are low but the chance of breaking dormancy is high.

The changes in the dormancy of the seed following dispersal could be expected to show some sensitivity to temperature since it is known that low temperatures will break the dormancy in *E. pauciflora* and, in *E. deletratensia*, that exposure to higher temperatures will increase dormancy in fresh seed.

Grose's (1953) work with *E. deletratensia* suggests that interaction between the dormancy of the seed and the environment could be expected to continue with subsequent experiences contributing either by breaking or by enhancing dormancy until the dormancy status of the seed coincides with the threshold for germination for that seed. His studies showed that the sensitivity of the seed to the temperature environment is dependent on its moisture content, with higher moisture contents facilitating more rapid responses.

The effect of moist conditions at the higher soil temperatures of summer and autumn will be to increase the duration of dormancy breaking
conditions required to break dormancy, and so to ensure that the seed is less likely to germinate in late autumn or winter. The importance of the apparently reversible response exhibited by the breaking and induction of dormancy in moist seed is that it provides the seed with a mechanism for integrating the effects of past environmental conditions.

The proportion of seed which does not germinate, and is therefore by definition dormant, is, in many plants, closely associated with the conditions of germination (Vegeta 1964). Grose (1963) has shown that the proportion of the seed germinating at temperatures between 5°C and 35°C increases in seed samples of *E. delegatensis* as the dormancy of the seed is reduced by stratification. A response of this type would lead to an increase in the range of temperatures which were suitable for germination as the stratification of the seed on the cold moist soil progressed during winter.

The response of the process of germination to environmental factors finally governs the irreversible commitment of the limited resources of the seed to the job of regeneration. The germination of the seed marks the beginning of a much closer relationship between the seed and the environment which leads to high mortalities of seedling both prior to emergence and between emergence of the cotyledons and establishment of the seedling. It is at this stage that the root and the shoot are exploring the most rapidly variable, unpredictable and extreme environments of the soil and atmosphere with few meristems and meagre reserves in the event of damage. The chances of desiccation, damage by ice heave, flooding, frostling are all enhanced in this zone and contribute to the mortality which is observed prior to establishment.
The observation and manipulation of seedlings which have emerged and established in the field gives some indication of the environments which are favourable for the first stages of regeneration. Noble (1980) investigated the relationship between Poa spp. and regenerating E. pauciflora following a fire near timberline in the Snowy Mountains and concluded that the size and morphology of the seedlings was influenced by the distance from a grass tussock and proposed that the grass had both a protective and competitive role in the environment of the seedlings.

Wimbush & Costin (1979) note that the regeneration of E. pauciflora seedlings is closely related to the physical environment at the soil surface; this determines the degree of flooding, ice heave and drought which, in turn, have important influences on the survival of seedlings. Furthermore, these authors noted that, following the removal of grazing in the subalpine environment, the available gaps were rapidly colonized by shrubby species which prevented the establishment of E. pauciflora for at least 20 years.

In summary the response of E. pauciflora to the physical environment during regeneration may be elucidated further by studies in three general areas

1. The characteristics of the seed and the timing of seed dispersal
2. The timing of germination
3. The survival and growth of seedlings

As will be seen in Section 1.3 the majority of this thesis deals with the second general area, however, aspects of the first and third topics were also investigated.
1.4 A study of the regeneration of Eucalyptus pauciflora

The present study set out to examine the regeneration niche of E. pauciflora by examining the influence of the environment at three critical stages in the process. The first series of studies examined the timing of seed dispersal and the differences in the seed collected at different altitudes, the second series of studies investigated the influence of the environment on the timing of germination and emergence and the third was concerned with the impact of the physical environment on the survival, growth and morphology of seedlings in the field.

The physical environment has been shown to have an important influence on the survival and growth of E. pauciflora (Noble 1980, Harwood 1976). Disturbance has a critical role in the regeneration of this species with seedlings rarely surviving in undisturbed situations. Fire is the most obvious and consistent disturbance and has been implicated in the even aged stands observed. However, the presence of even aged top growth does not, in itself imply synchronized regeneration from seed following fires since a large proportion of the regeneration comes from sprouting lignotubers. No fires of sufficient magnitude occurred to enable examination of the post-fire regeneration of the species during the early part of the study so an alternative approach was sought.

Noble (1980) has shown that the survival and morphology of seedlings establishing in a Poa grass sward could be associated with the distance from the nearest Poa tussock. The distance to the nearest tussock could also be viewed as defining the size of a gap and I set up experiments to investigate the influence of the size of gaps created in a mature tussock grass (Poa spp.) sward on the survival, growth and
morphology of seedlings.

Differences in the microclimate with position in the gap were expected to be important also, and the effect of the position of the seedling (aspect) in the gap was also examined. Grasshoppers and frost caused overwhelming mortality of the seedlings planted in spring 1980 and drought and frost on the seedlings planted in spring 1981. Field studies on the role of nutrients, water, and shading on the growth and morphology of seedlings planted in spring 1982 are not reported in this thesis because the experimental treatments were lost in the overwhelming mortality caused by drought and frost in the autumn of 1982. These site and year specific factors could not be accounted for and these studies were not continued.

Many of the discussions in this thesis assume that successful seedlings emerge in spring and summer. The studies reported in Chapter 7 show this to be the case since seedlings which emerged in autumn died before the next spring and no seedlings which emerged during winter survived. Slatyer (pers. comm.) has observed a similar phenomenon.
1.6 Locations of seed collection, and experimental sites

Figure 1.1 A map showing the location of seed collection and experimental sites in the Snowy Mountains area of South-eastern New South Wales.

Details of the grid reference, altitude, latitude and longitude of seed collection sites are provided in appendix 1.