Aspects of the Natural Regeneration of the Kauri
(*Agathis australis* Salish.)*

R. V. Mirams

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Abstract

Ecological studies in the Waitakere Ranges indicate that there is a lack of naturally occurring regeneration in the Kauri forest. On the other hand, in parts of the ranges where the kauri forests have been cut down and are now covered with *Leptospermum* shrubland, there is an abundance of kauri regeneration. A study of the climatic and edaphic factors, the quantity, availability and germinability of kauri seed indicates that the above-mentioned difference in regeneration is not due to any of these factors. Although large numbers of seeds fall to the ground in all of the *Leptospermum* and kauri communities studied, many are unable to germinate as they are destroyed by a large orthopterous insect (*Hemideina thoracea*), it is also shown that the moisture content of the soil is important to the seed at the time of germination and later to the young seedlings. The viability of sound kauri seeds is low, dropping from 100% to less than 5% when stored under ordinary atmospheric conditions. The status of the kauri forest is discussed, whether it be subclimax, relict, or member of a cyclic community. Some of the differences in regeneration may be explicable in terms of one or more of these concepts.

Introduction

The present day occurrence of the kauri (*Agathis australis*) is limited, it extends from the North Cape to the Bay of Plenty in the east and Kawhia on the west. It does, however, form distinct communities, but many of these have been exploited since the colonisation of the Dominion because of the value of the timber. Attempts are now being made to preserve the species and the present study is a contribution to the problem of its survival.

The first phase in the study of the survival of any species is its capacity for natural regeneration; this falls into a number of phases—e.g.,

1. the production, distribution and germination of kauri seeds, and the various factors affecting these;
2. the survival of recently germinated and young seedlings;
3. the subsequent growth of these seedlings into saplings, etc., and factors affecting their subsequent growth and development.

The present paper is concerned with the essential preliminary—i.e., the capacity for natural regeneration, and the first two of the above-mentioned phases.

This investigation has been carried out in the Waitakere Ranges, a system of low hills to the west of Auckland City, whose average elevation is about 330 metres (1,000 feet), one or two peaks and ridges, however reach to 550 metres (1,800 ft). The topography is generally rugged.

Before the advent of European settlement, the ranges were covered with temperate rain forest dominated by *Agathis australis* or communities of the *Podocarp-broadleaved* species. Much of this bush has been milled and is now in the process of regenerating through *Leptospermum* scrubland. A considerable portion of the range is a waterworks reserve, and here the forest is in a relatively undamaged state.

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CLIMATE

For the five years 1944-48, the average annual rainfall at three of the Waitakere stations was

Waitakere ... 70.22 ins (178.5 cms)
Nihotupu ... 90.53 ins (230 cms)
Huia ... 84.66 ins (215 cms)

For comparison, the average rainfall in Auckland City for the same period was 51.44 ins (130.5 cms).

The rainfall everywhere in the ranges is high with quite an appreciable variation from station to station. The fall is fairly uniformly distributed throughout the year, although heavier during the winter months.

Measurements of temperature and relative humidity were made in the Leptospermum scrubland and in the kauri forest for a period of about fifteen months during 1949 and 1950.

During January and February, maximum temperatures as high as 80° F. were quite frequently recorded, but from May to August the maximum was often below 60° F. The minimum temperatures do not show these seasonal variations to such an extent. In the summer period the daily range of temperature is as much as 25° F. falling to 10°-15° F. in the winter.

The main feature of relative humidity readings was the long duration of high humidities in the scrub and forest. The relative humidity is usually at a level not far from saturation for many hours each week, it also does not often fall below a value of 50% (a level which is significant for the seeds to remain viable).

The daily temperature and humidity curves show an almost exactly opposite variation. The lowest temperature is usually reached just before sunrise, and from that time onward there is a rise in temperature over a period of four to five hours. The maximum value for the day is attained at noon or soon afterwards, and may last, with minor fluctuations, for periods of up to four hours, or it may commence to fall again almost immediately. The rapidity of this rise and fall of the temperature and the range is dependent on the season. During overcast and wet weather, there is a tendency for the temperature to remain at a fairly constant level for several days. The basic form of the diurnal variation curve is recorded, although it is very much flattened. The relative humidity is at its highest levels during the night hours, and there is a decrease as the temperature rises, often as much as 30% in one hour. The lowest reading for the day is during the noon hour. As with the maximum temperature, this minimum relative humidity can be either of short duration (most usual) or it may persist for some hours, with minor fluctuations. From the minimum level there is a steady rise until the maximum value near saturation point is attained. In damp weather and when rain is falling, the humidity tends to remain static, in sympathy with the temperature at a uniformly high level. This phenomenon is more pronounced in winter and spring with their frequent rainy days than at other periods.

The regular daily patterns of temperature and relative humidity are essentially similar in the Leptospermum scrubland and in the kauri forest.

SOILS

The underlying rock in the ranges is andesitic (basic), and this has given rise in most areas to soils of the brown granular clay sub-group of the brown loam group. Except for two very small areas of recent soils developed from alluvium, the remainder of the region is covered with soils belonging to the skeletal group (Grange-Soil Map of N.Z. Sheet 2. 1947). Wright (1951) has pointed out that long cycles of kauri on an area will eventually lead to the impoverishment of the soil and the formation of swamp and barren "gumland" communities. This stage of development does not appear to have been reached in the Waitakere Ranges.
Determinations of the pH of the soils in various localities and in different communities were made using the glass electrode. Samples were taken from the surface litter, and at a 2in–4in horizon. The range in Leptospermum communities for the surface horizons was 4·5–6·1, and the kauri forest 4·5–5·3, for the lower horizon 4·3–6·1 and 4·4–5·6 respectively. There is not a great range of pH in any of the communities, and in all cases the litter and soil is distinctly acid, with a somewhat lower value for both horizons in the kauri forest.

The only other soil property regularly investigated was that of soil moisture. Samples were taken in a number of regenerating Leptospermum and ricker* communities at more or less weekly intervals during 1949 and 1950. The samples were dried in the laboratory at 105° C. and the moisture content expressed as a percentage of the dry weight. The moisture content for duplicate determinations varies considerably for the surface layers which in many cases is nearly all raw humus: it is this layer, however, which provides the germinating seed and the young seedling with its water supply. The variation in moisture content of duplicate determinations of the same sample from the 4in–6in horizon is almost nil. The moisture content values are not intended to be taken as absolute, but they are of assistance in showing the general trends of soil moisture during the course of the year.

Rainfall, being the chief source of water supply, largely determines the amount and variation of the soil water content, although those factors controlling evaporation from the surface are also of primary importance. Unfortunately, no atmometer determinations are available.

The moisture content of the surface horizons in all of the communities reached high levels and at times—April to November—exhibited great fluctuations. There would sometimes appear to be something in the nature of supersaturation; free water could often be squeezed out of the sample by pressure of the hand. Values of more than 250% were frequently reached. During the remainder of the year—the summer period—there is considerably less water present in the soil layers, the average value being about 80%. A surprising feature is the uniformity throughout the year of the moisture content of the 4in–6in horizon, the average value being approximately 60%. There are, especially in the surface horizons, considerable variations at the same time among the various communities; nevertheless, the seasonal trends are the same in all of those where measurements were made and probably also in the kauri forest. There appears to be a direct correlation between seed germination, survival of young seedlings, and the moisture content of the soil.

PART I.—QUADRAT INVESTIGATIONS OF NATURAL REGENERATION

In the Waitakere Ranges, all degrees of inter-mingling of the forest are to be found from a pure kauri stand to a type of forest dominated mainly by species of Podocarpus and Dacrydium, the broad leaf, Beilschmiedia tawa not being common. These are some of the members of the ultimate climax, but the forests in this region do not appear to have reached a great degree of stability.

It is obviously impossible to follow a single succession from its initiation to the ultimate climax, and resource has therefore to be made to the study of a number of examples of the same succession at different developmental stages contemporaneously. Similarly it is not possible to see kauri forest initiation to-day. The commencement of secondary forest can, however, be observed in the natural regeneration which usually occurs after the forest has been destroyed or damaged. It is realised that the sequence of events which we see to-day giving rise to a new kauri forest may be, and probably are, vastly different from the succession which gave rise to the kauri forest which we now see and which is dominated by trees that are many hundreds of years old.

* Immature growth form of kauri.
A very brief description of the subsere and the kauri forest will suffice, as these various communities have been adequately described by Cockayne (1928). The succession of events is as follows: After the short-lived initial communities of grasses, and herbs there develops a tea-tree or manuka scrub. It is a typical shrub community with Leptospermum scoparium—the dominant—present in considerable numbers. In the early stages the ground is covered with a mass of Gleichenia circinata. Beneath this fern, which is often one metre and more deep, are to be found many of the forest tree seedlings, including Agathis. With the passage of time the fern dies out, Leptospermum scoparium grows larger, the allied Leptospermum ericoides enters the succession and becomes a co-dominant. Many individuals of the numerous species which go to make up the kauri forest are now seen as small saplings growing beneath the tea-tree canopy. L. ericoides is usually by now completely dominant, but it is eventually over-topped by individuals of Agathis which at this stage have a characteristic conical form. (Plate 43, fig. 2.) The Leptospermum ericoides persists for a considerable period, first as a co-dominant but later as a subdominant, and there comes into being what may be called "a forest of kauri rickers". These rickers, which often form dense stands, increase in both diameter and height until eventually there is developed a community, little different from the mature forest. The main difference is the smaller size and very much larger number of individuals of kauri in the former type. The ground is now covered with a heavy tussock-like growth of "kauri grass", Gahnia xanthocarpa and Astelia trinervia, which frequently reaches a height of two to two and a-half metres. (Plate 44, fig. 2.) By the time the mature kauri tree has developed, it has become the only dominant. Even in a dense stand, the trees are not close together but may be separated by distances of fifteen to twenty metres. There are also a number of smaller trees of other species but only one, Knightia excelsa, reaches into the sub-canopy layer. The canopy in the pure stand is quite irregular, being formed of the large rounded heads of the mature kauri tree. (Plate 43, fig. 1.)

The occurrence and distribution of natural regeneration was investigated by a series of quadrats laid down in the various successional stages, five types being recognised.

(1) Young Leptospermum.
(2) Older Leptospermum (usually lacks the ground layer of fern and rush found in the first type). (Plate 43, figs. 3, 4.)
(3) Leptospermum—Agathis community.
(4) Kauri ricker community. (Plate 44, fig. 1.)
(5) Kauri forest. (Plate 44, fig. 2.)

A quadrat size of 36 sq. m. was decided upon from the species-area curve. Myers (1948) in a more comprehensive study of minimal area in Leptospermum shrubland also found that the minimal area for this community was 36 sq. m.

On every quadrat a list of all the species encountered was made. In addition, counts of all the individuals of Agathis were made. These individuals were classified into one of the six size-age groups listed below in order that a better picture of regeneration could be obtained. (Plate 43.)

Class I
Small seedlings with cotyledonary leaves only. The majority of these individuals are from the current year's seed fall, but retarded individuals are occasionally found which have come from a previous fall.

Class II
Seedlings with up to about twelve leaves and not more than ten centimetres in height; branching of the stem not apparent.

Class III
Seedlings between ten and fifty centimetres high, with a number of branches both lateral and terminal.
Class IV
Slender saplings with a stem not more than five centimetres in diameter. The height varies from fifty centimetres to four metres or more.

Class V
Saplings and small rickers five to fifteen centimetres in diameter.

Class VI
All individuals whose stem is more than fifteen centimetres in diameter.
A total of eighty-four quadrats were laid down, sixty of which were thirty-six square metres in area, the remaining twenty-four being one hundred square metres. The number of species occurring in the sixty smaller quadrats are eighty-six, with the addition of the twenty-four larger quadrats a further ten species were added, making a total of ninety-six.

Natural regeneration is considered first as the total number of individuals of Agathis in each of the five successional types, and secondly as the distribution of the size-age classes in these communities. In both cases, the data is taken from twelve 36 sq. m. quadrats in each of the five community types.

Table I.—No. of Individuals of Kauri in Various Communities.

<table>
<thead>
<tr>
<th>Community</th>
<th>Size-Age Classes</th>
<th>No. of quadrats on which individuals of Agathis were found (Total = 12)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
<td>II</td>
</tr>
<tr>
<td>Young Leptospermum</td>
<td>6</td>
<td>63</td>
</tr>
<tr>
<td>Proportion</td>
<td>7.5</td>
<td>78.8</td>
</tr>
<tr>
<td>Older Leptospermum</td>
<td>22</td>
<td>213</td>
</tr>
<tr>
<td>Proportion</td>
<td>7.7</td>
<td>74.2</td>
</tr>
<tr>
<td>Leptospermum-Agathis</td>
<td>34</td>
<td>233</td>
</tr>
<tr>
<td>Proportion</td>
<td>6.9</td>
<td>47.2</td>
</tr>
<tr>
<td>Ricker Agathis</td>
<td>10</td>
<td>262</td>
</tr>
<tr>
<td>Proportion</td>
<td>2.3</td>
<td>61.6</td>
</tr>
<tr>
<td>Kauri forest</td>
<td>23</td>
<td>88</td>
</tr>
<tr>
<td>Proportion</td>
<td>16.2</td>
<td>62</td>
</tr>
</tbody>
</table>

A second set of quadrats 10 m. x 10 m. provided the following results, which are very similar to those obtained from the smaller quadrats, apart from the larger numbers of individuals.
It can be seen from the above table that there is considerable variation in the total number of individuals of all size-age classes in the various communities examined. The smallest number of individuals is found in the young Leptospermum, the highest at the middle stage of the succession. The number of individuals in the kauri forest is also relatively low, much lower than would be expected even for the class I individuals. There is adequate seed available for the germination of many more seedlings.

In the young Leptospermum it is only to be expected that the density of Agathis will be low, since invasion by this and the other forest species has only just commenced. This fact was reflected in the absence of kauri from almost half of the quadrats and the small numbers on several of the remainder. The absence of individuals in classes V and VI is also due to the early age of the community at this stage. By the time an older Leptospermum community has developed, there has been a considerable increase in the number of individuals of all age classes, especially classes II and III. There has been a slight increase in the numbers in class IV, and class V is now represented by a solitary specimen. The increase in total numbers is probably due as much to the "accumulation" of seedlings as to the operation of any factor more favourable to their growth. In spite of the increase in numbers there is evidence to show that there is a considerable mortality of young kauri seedlings; these results only show the "end point" of their survival at the time of counting, they do not show what the trends in survival are.

The next stage of the sere is an ectonal community in which Agathis becomes codominant with the giant tea-tree Leptospermum ericoides. The most noticeable feature of this stage is the presence for the first time of individuals of the oldest size-age class. It must not be thought that the individuals of this class in this community are at all comparable with those of the same class in the kauri forest. Many of them will not yet be producing seed and those that are, only small quantities. This added seed source much nearer to hand is probably partially responsible for the large increase in the number of class II seedlings. It is possible, too, that conditions in the community are more favourable for the germination and survival of small seedlings. On the whole, it can be said that natural regeneration is at its greatest in the Leptospermum-Agathis community.

There is a change from the sub- or co-dominance of Agathis by the time the ricker community develops. There is apparently a slight decline in the regenerative capacity of the sere as shown by the reduction in the number of class IV and V seedlings. Further evidence on this point is the absence of one or other of the various size-age groups on almost all of the quadrats. The ricker community gradually changes into a mature forest. In the kauri forest, there is a decrease in the number of individuals of Agathis and a steady increase in the size of those remaining. The diameter of any of the adult specimens examined was not less than sixty centimetres, and many were considerably larger than this. The first point to be noticed about this community is the small number of individuals of all age classes and more importantly the complete absence of individuals of class V in all probability showing that domination by Agathis is now on the downgrade because it is apparently not replacing itself. The largest individuals of class IV were not more than two or three centimetres in diameter and can scarcely be considered as potential replacements for some of the dominant individuals. If a community is to maintain itself as a stable climax, the dominant species must be able to reproduce themselves so that there is formed a more or less even aged stand. If the seedlings of tree species cannot meet the competition of lesser species, whether it be in the herb or shrub stratum, such trees must eventually disappear from the community. The small number of individuals of all age classes and the complete absence of class V indicates that, at least in some of the strata, Agathis is not competing successfully. Permanent or true dominance involves the ability to compete successfully in all strata of the
community and *Agathis* is certainly not doing this. It might be argued that there are sufficient individuals in class IV allowing for a considerable mortality, to maintain the stocking of class VI at its present level. However, the forest is surely old enough for individuals of *Agathis* intermediate between class IV and class VI to have developed and the fact that they have not already done so indicates that they may not under the present environmental conditions. At the same time, it does not seem possible to regard the members of class IV as potential replacements of the present mature individuals. The greatly reduced occurrence of seedlings of *Agathis* on quadrats within the mature forest is harder to explain for this community than for any of the others. Collections of seed by means of traps have shown that there is more than sufficient seed falling to the ground in one season to produce the number of seedlings of all ages recorded, let alone those which are only in the cotyledonary stage (size-age class I). The activities of at least one insect are responsible for the destruction of a large proportion of the seed; this does not explain, however, the complete absence of one of the size-age classes and the small number of individuals in the remainder.

**Previous Views on Natural Regeneration**

Although there is quite a volume of literature bearing upon the kauri, one finds on examination that most of it is in the broadest of terms. As far as the occurrence and distribution of natural regeneration is concerned, we have such statements as the following. Cockayne (1908 and 1928) says that “he notices usually nothing between seedlings and old trees. Whereas outside the forest in the manuka scrub kauri can be seen coming up in abundance and here trees of all ages are seen.” Cheeseman (1914a) also mentions “the comparative absence of young kauris in a mature kauri grove.” Hutchins (1918) states that it is evident that the tea-tree can act as a nurse for the regeneration of kauri and the forest generally.

The phenomenon of succession in the New Zealand forests has been recognised from the earliest days. Cockayne (1928), while recognising the fact, does not regard the kauri forest as forming part of the climax community but considers that it will be replaced by a community dominated by broad-leaved trees, perhaps *Beilschmiedia taraire*, *B. tawa* or *Weinmannia sylvicola*.

One of the tests for a climax community is that it must be capable of reproducing itself, since it represents the last stage of succession so long as the climate remains the same. The climax must therefore be a stable community, in which the oldest individuals, dying, are replaced by their own kind, leaving the character of the community unchanged. As will be shown later, the kauri forest does not appear to be reproducing itself and it cannot therefore be considered to be the climax. It might be a subclimax community of long persistence apparently having a dominant similar in life form to that of the ultimate climax. It is also possible that the kauri forest may be a relict or post-climax and that the few areas now remaining are survivals of once more extensive kauri forests. Wood indistinguishable from that of the present day *Agathis australis* has been found in Miocene coals in the south of the South Island (Evans, 1934).

It is known from the work of Cranwell and Von Post (1936) that climatic conditions in the Post-glacial were, at times, more favourable than they are now, and it is possible that during one of these Post-glacial warm periods in addition to one in earlier times, *Agathis* extended over more than its present range. It is unfortunate that kauri pollen does not preserve well (Cranwell, 1940). The kauri will today grow in gardens and parks as far south as Invercargill, possibly because of the lack of competition such as would occur in an integrated community.

Finally, there is the possibility of a cyclic complex such as is mentioned by Watt (1947), in which one community having developed to the maximum is replaced by
another which has grown up within it, it, in its turn, being replaced. It is suggested that the kauri forest alternates with and is replaced by a community dominated by some or other of the podocarps (Podocarpus and Dacrydium spp.) and broad-leaved species (Beilschmiedia and Weinmannia). Forest dominated by these species occurs intermingled with the kauri forest, there being a range from a pure podocarp-broad-leaved-community through a mixed podocarp-broad-leaved-kauri community to a pure stand of kauri.

The fact that the kauri forest may not be the climax community may possibly explain the apparent non-replacement of the species and the small number of individuals to be found in the mature forest as compared with the other successional phases. The early communities are on the upgrade while the kauri forest is apparently degenerating. The fact that Agathis does regenerate in the Leptospermum communities under the present climate indicates that the cause of its degeneration may be in its actual constitution and its effect on its own internal environment. All of the regenerating communities examined are on the sites of former kauri forests, and this is further evidence in support of the above conclusions.

**Discussion**

It has been shown that natural regeneration occurs more abundantly in the tea-tree communities than in the kauri forest. Not only are more individuals of Agathis found in the seral communities with the exception of the young Leptospermum, but in the mature forest there is a vast gap between the largest sapling, which is never more than two to three centimetres in diameter, and the adult trees one to two and more metres in diameter.

There must be a number of reasons for these differences in regeneration in the various communities. There is no evidence to show that seed supply is a factor limiting regeneration, the seed which germinates forming only a small fraction of the total which falls, even in the Leptospermum, where it must be transported often over considerable distances. As far as the kauri forest is concerned, although there are few seedlings compared with the number of seeds which were collected, it appears that the failure of regeneration in this particular community is in the subsequent lack of growth of small individuals of Agathis into saplings and small trees.

If the lack of seed is not the cause of the failure of natural regeneration in the kauri forest, we must look for differences in some of the factors operating in the various communities, or else in some variation brought about by the plants themselves. Variations in the site, aspect, topography, climate, soil, etc., cannot be ignored in attempting to explain the differences in the occurrence and distribution of natural regeneration. As far as their direct effect is concerned the differences, from the available data, are not sufficient to account for these wide variations in the numbers of individuals in the various communities. Light (a factor influencing the growth of Agathis but not directly analysed), while appearing to have no effect on germination, may be insufficient in the mature forest for the optimum growth of small individuals of kauri. A supposedly light-demanding tree such as the kauri cannot be expected to grow very successfully beneath a heavy canopy, formed in this case of individuals of the same species.

Root competition is another factor which may be responsible for the poor growth of kauri saplings in the kauri forest. McKinnon (1945) mentions it as a factor and says "kauri seedlings on a quadrat whose boundaries were trenched to below the general root level have shown a significant improvement in size and vigour as compared with an adjoining control quadrat". The time between trenching and the publication of the above report was approximately three and a-half years.

It is interesting to note that remnants of former kauri forests, stumps, etc., have been found in many of the tea-tree communities investigated. This would suggest that the differences in regeneration are to be found in the dynamics of the various
communities and are not so much a result of physiographical and physical differences, except in so far as these may be modified by the present plant cover. It is possible that there are actions and reactions between the various plant species and combinations of species that may have an effect which is responsible for some of these differences. There is a great difference in the structure and physiognomy of the communities studied, but many, if not all of the characteristic species are to be found throughout the succession. There is some evidence from individual quadrats that the effect of one plant on another may be responsible for some of the differences of regeneration; in some cases the small number of individuals of Agathis and the reduced number of other species is due to the presence of one species tending to produce conditions not entirely favourable. The effect of these species—e.g., Gleichenia circinata, Schoenus tenus, Cyathea dealbata (leaf debris) and Freycinetia banksii is to produce a blanket-like layer of living and dead plant material over the surface of the soil which forms an unsuitable seed bed.

Sando (1936) lists the following as possible causes of the failure of kauri to regenerate:

1. Excessive leaf litter and dense floor covering of “kauri grass”.
2. The dense shade produced by Beilschmiedia taraire and Dioxylum spectabile and also the dense undergrowth of Cyathea medullaris and C. dealbata on shady faces in old workings.

Cockayne (1928) and McKinnon (1945) also mention the aggressiveness of certain floor plants, among which are some of those listed above.

A further point which must be considered is whether Agathis australis is the dominant of the climax community. It is suggested that it is not and that it may either be a subclimax, a relict or post climax, or one of the communities of a cyclic complex. In each of these cases, there must be a replacement by or alternation with another community, and it seems probable that once the kauri forest has reached its full and characteristic development it commences to decline slowly within the succession prior to its replacement.

The fact that Agathis does regenerate in the Leptospermum communities under the present climate indicates that the cause of the degeneration of the present kauri forest is rather in the actual constitution of the forest community and its effect on its own internal community environment.

PART TWO

FACTORS AFFECTING NATURAL REGENERATION

The developing cones of Agathis australis are borne on the tips of the branches, male and female cones being on the same tree. When the cone is mature, the scales do not open to allow the seeds to fall out as is the case with most conifers, but disintegrates completely, the scales falling off the central axis. The majority of the scales bear one winged seed which usually becomes detached from the scale before it reaches the ground. The cones vary in size and the number of seeds which they contain. The proportion of seeds which are sound (on the basis of a cutting test) varies from 0-90% of the total number of seeds per cone; larger cones usually contain a higher proportion of sound seeds. In bulk lots of seed the sound proportion is about 30-35% of the total.

SEED FALL AND DISPERSAL

A number of one metre square seed traps were constructed and placed in the various communities being studied. (Plate 44, fig. 2.) Collections of seeds were made during the two seed years 1949 and 1950, twelve traps were used during 1949, and fifteen during 1950. The object of placing out the traps was to find out how many seeds were falling to the ground in the various communities being studied.
The efficiency of the seed traps, both from the point of view of retention of caught seed and its protection from animals after trapping was tested by means of suitably marked seeds placed in the traps at the beginning of the period of collection. In only one case was there any serious loss of marked seed from a trap, in many a complete recovery was made. In some of the traps one or two of the marked seeds were found to be damaged in a characteristic manner, these damaged seeds were also found among the collections of naturally fallen seeds. The indications were that the sound seeds were selectively eaten by an insect or insects.

The cones of Agathis ripen in the late summer and seedfall commences during the latter part of February and continues until mid-April. The seed was collected and removed from the traps at intervals until the fall was over. It was then sorted into the following categories—sound seed, blind seed (distinguished by the cutting test) and damaged seed. In nearly all cases the damaged seed was originally sound, parts of the embryo and endosperm usually remaining.

**TABLE II.—SEEDS COLLECTED IN EACH COMMUNITY.**

These are average values for the number of traps in each community.

<table>
<thead>
<tr>
<th></th>
<th>Blind</th>
<th>Sound</th>
<th>Damaged</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1949</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kauri Forest (5 traps)</td>
<td>80</td>
<td>41</td>
<td>18</td>
<td>139</td>
</tr>
<tr>
<td>Ricker (Cascades) (3 traps)</td>
<td>70</td>
<td>32</td>
<td>10</td>
<td>113</td>
</tr>
<tr>
<td>Ricker (Swanson) (1 trap)</td>
<td>83</td>
<td>5</td>
<td>—</td>
<td>88</td>
</tr>
<tr>
<td>Old-Leptospermum (2 traps)</td>
<td>25</td>
<td>3</td>
<td>1</td>
<td>30</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>1950</th>
<th>1950</th>
<th>1950</th>
<th>1950</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Blind</td>
<td>Sound</td>
<td>Damaged</td>
<td>Total</td>
</tr>
<tr>
<td>Kauri Forest (6 traps)</td>
<td>71</td>
<td>37</td>
<td>20</td>
<td>129</td>
</tr>
<tr>
<td>Ricker (Cascades) (3 traps)</td>
<td>46</td>
<td>28</td>
<td>8</td>
<td>82</td>
</tr>
<tr>
<td>Ricker (Swanson) (1 trap)</td>
<td>113</td>
<td>14</td>
<td>3</td>
<td>130</td>
</tr>
<tr>
<td>Old-Leptospermum (2 traps)</td>
<td>26</td>
<td>7</td>
<td>1</td>
<td>34</td>
</tr>
<tr>
<td>Young-Leptospermum (3 traps)</td>
<td>7</td>
<td>4</td>
<td>—</td>
<td>11</td>
</tr>
</tbody>
</table>

It is clear that the number of sound seeds reaching the ground is considerable, especially in the ricker and the kauri forest. An interesting comparison can be made between the total number of sound seeds (sound + damaged in above table) reaching the ground and the number of seedlings of size-age classes I and II occurring on the quadrats. It is obvious from these comparisons (see Table V) that in all of the communities there is sufficient seed available to account for the seedlings of the above two age classes, even in the Leptospermum, where seed must be transported by the wind. It can be fairly safely concluded that lack of seed in any community is not the cause of failure of natural regeneration.

As with all winged seeds, that of the kauri finds its means of dispersal in wind action and gravity. In order to find out the lowest wind speed necessary to keep the seeds afloat, use was made of a small vertical wind tunnel. Air was drawn upwards through the tunnel by means of a fan. The speed at which the air moves up the tunnel being controlled by adjusting a shutter in front of the fan; closing the shutter reducing the flow of air in the tunnel, and thus its speed. The air-speed in the tunnel was measured by observing the changes in level in a water micromano-meter connected to a pitot head in the tunnel. Sound seeds were introduced through a small aperture at the top of the tunnel so that they tended to float upwards in the current of air. The flow of air in the tunnel was reduced as successive samples of seed were introduced until a point was reached when the seeds just began to sink. From these determinations it was found that the wind speed necessary to keep the seeds afloat was between 3.5-4 feet per second. Foley (1950) in a brief account reported that the mean rate of fall of sound kauri seed was approximately 3.5 feet per second and for mixed lots (sound and blind) 2.5 feet per second. He timed the rate of fall of the seed in an open light well.
In order to make use of this value as applied to the dispersal of seeds in the forest, a measurement of wind speed in the forest canopy was necessary. This was carried out by means of a Casella-Robinson three-cup anemometer. A pulley was attached at a height of 23 metres (80 feet) to one of the upper limbs of a large kauri. By means of a cord passing over this pulley it was possible to raise and lower a small wooden platform to which the anemometer was attached. The anemometer is an integrating instrument and only average values of the wind speed could be obtained for a given period. Measurements on any one day were taken over a total period of up to about seven hours, during which time the instrument might be read and reset to zero six or more times. The average wind speeds for these short daily periods were computed; the range of these speeds is shown in Table III together with the average wind speed for the total daily period. Observations were made for a total period of more than sixty-three hours spread over twelve days during the period of seed fall.

### TABLE III.—WIND SPEED READINGS.

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<th></th>
</tr>
</thead>
<tbody>
<tr>
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<td>235</td>
<td>3.4–3.45</td>
<td>5.4</td>
</tr>
<tr>
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<td>236</td>
<td>3.6–3.30</td>
<td>4.6</td>
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<tr>
<td>29/3/50</td>
<td>323</td>
<td>2.55–4.25</td>
<td>3.3</td>
</tr>
<tr>
<td>31/3/50</td>
<td>432</td>
<td>3.1–5.6</td>
<td>4.5</td>
</tr>
<tr>
<td>1/4/50</td>
<td>411</td>
<td>0.4–2.3</td>
<td>1.8</td>
</tr>
<tr>
<td>2/4/50</td>
<td>346</td>
<td>5.4–7.7</td>
<td>6.5</td>
</tr>
<tr>
<td>3/4/50</td>
<td>390</td>
<td>3.6–4.3</td>
<td>3.8</td>
</tr>
<tr>
<td>4/4/50</td>
<td>420</td>
<td>1.7–2.75</td>
<td>1.9</td>
</tr>
<tr>
<td>5/4/50</td>
<td>129</td>
<td>2.3</td>
<td>2.3</td>
</tr>
<tr>
<td>18/4/50</td>
<td>180</td>
<td>1.6–4.1</td>
<td>2.8</td>
</tr>
<tr>
<td>19/4/50</td>
<td>390</td>
<td>0.3–3.0</td>
<td>2.3</td>
</tr>
<tr>
<td>20/4/50</td>
<td>390</td>
<td>1.7–3.0</td>
<td>2.3</td>
</tr>
</tbody>
</table>

The average wind-speed for the total period of the observations was 3.5 feet per second; for 54.3% of the time of the observations the average recorded wind-speed was below 3.5 feet per second. The wind conditions within and without the canopy layer must be vastly different, but it is considered that on every day there would be winds of sufficient velocity to transport the seed over some distance. The average wind-speed recorded in the forest canopy is almost identical with that found from the wind-tunnel as being of sufficient velocity to keep the seed afloat. Baldwin (1942, p. 24) says “that the distance that wind may carry the seed is conditioned very largely by the rate of fall”. The lack of high enough wind speeds in the kauri forest does not appear as if it would be a limiting factor in the carriage of kauri seed, although how far the seed will be carried is difficult to estimate.

### Germination

Several writers in the past have expressed conflicting opinions on the longevity of kauri seed. Some, Sando (1936), McKinnon (1937b) and MacMorrin (1946) saying the seed does not remain viable for much longer than one year under normal storage conditions. Hutchins (1918) on the other hand says that “the predominant opinion is that kauri seed may remain dormant for as long as thirty years”.

An attempt was therefore made to discover what time the seed will remain viable under various storage conditions and also to what extent various factors affect germination.

The “cutting” test as a means of ascertaining the proportion of sound seed in a sample has already been mentioned. It should be emphasised that the cutting test is not a measure so much of the germinability of seed but that the seed has been fully formed.
When this series of kauri seed experiments was commenced in 1948, germinations were carried out using nursery boxes with soil as the medium. A number of the boxes were in an unheated glasshouse, the remainder being in the open and shaded to various degrees.

Watt (1919) working on the English oakwoods, found that there were considerable variations in the rate of germination of the acorns when they were placed in different positions. It was thought that the position in which the kauri seed was placed in relation to the soil surface might have some bearing on germination.

Significantly better germinations were obtained in two cases. In 1949 and 1950, germination experiments were transferred to the laboratory, the seeds being sown in sand, in petrie dishes placed in incubators at 24° C. The seeds were placed in the sand with the wing in the air, the lid of the petrie dish being raised by means of a square cover slip in order to ensure better air circulation. Good results were obtained using this method, and all of those which follow were obtained by using it.

AGE OF SEED AND RETENTION OF VIABILITY

Rapid viability tests are of considerable importance where time does not permit of lengthy germination tests. In this series of experiments, use has been made of the salts, sodium biselenite (NaHSeO₃) and 2.3.5 triphenyl tetrazolium chloride. Viable tissue placed in solutions of these substances will, under suitable conditions, assume a red colour, its intensity and extent depending on the degree of viability of the material under test.

The technique for both salts was as follows: the seeds to be tested (one hundred sound ones in each case) were placed in a beaker containing distilled water and then put overnight into an incubator maintained at 24° C. This preliminary soaking facilitates removal of the embryo, and in no way affects the results. The embryos were then excised and placed in the test solution for a period of up to eight hours, again at 24° C. After this time the embryos were washed in water and sorted into the following categories:

1. at least half of the embryo intensely coloured
2. the embryo showing a spot of colouration
3. no colouration
4. embryos obviously dead (decayed, etc.) on excision, and therefore not soaked in the test solution.

In the case of sodium biselenite, a 2% aqueous solution was used. The method is essentially a modification of Eidmann's as given in Baldwin (1942, p. 183).

The tetrazolium method was originally described by Lakon (1942) for cereals but the paper was unobtainable and a re-description of the method in English (Lakon, 1949) was seen only after most of the work described had been completed and use had therefore to be made of other methods of embryo classification. A 1% aqueous solution of 2.3.5. triphenyl tetrazolium chloride was used.

Within the limits of the apparatus available, as many replicates as possible were used in each series of experiments; in a few cases it was not possible to have any. In some of the later experiments, germinations indicated that the single sample result was probably correct, but in one or two cases further replicates were obviously necessary.

The course of germination is shown in Figure 1. There is a steady fall in the germination of kauri seed from 100% at the time of collection to only 5% in mid-July, four and a-half months later; and by mid-November, it is down to less than 1%. The results obtained by the rapid viability test methods, although somewhat higher, show the same trend as the actual germinations. It is evident from these results that the viability of kauri seed drops rapidly when the seed is stored under ordinary atmospheric conditions.
Fig. 1.—Graph showing the course of germination of kauri seed from two sources. The results obtained by the use of rapid viability tests are also shown.

The problem of loss of viability in seeds is not a simple one, and many complex factors and combinations of such factors are responsible. Among the methods employed by various workers to lengthen the life span of seeds are low temperature storage, drying, and by controlling the moisture content of the storage atmosphere, to mention only two. MacMorrant (1943) gives some preliminary figures for the effect of low temperature storage on kauri seed viability. She showed that seed which had an original average germinative capacity of 50% would not germinate at all after two years’ storage, at room temperature. Seed which was stored at a temperature of 10–15°F, however, had a 32% germination after the same period. Low temperature then has an effect which enables kauri seed to retain its viability for a longer period than normal. This result may, of course, have been due to the effect of lowered humidity as the result of the lowered temperature, no attempt was made to separate the two factors of low temperature and low humidity as the result of a low temperature. As early as 1902, MacQueen stated “that a high degree of dryness is the key to retention of viability.” This result is in line with many recent investigations. The degree of dryness which the seed ultimately attains is related to the relative humidity of the storage atmosphere, and an experiment was devised in which kauri seed was stored in containers over sulphuric acid solutions of known concentration. At constant temperature, the acid solutions produce an atmosphere of constant known humidity. Seed was stored in the following relative humidities—10, 25, 35, 50, 60 and 75% R.H. and in a container with a similar volume of distilled water. Germination experiments were commenced on the seed after 49 days' storage, and further lots were withdrawn after 159 and 378 days. At the same time as the germination experiments were made, the moisture content of the seed was determined.

The results of this experiment are shown in Figure 2. They indicate that the seeds which were stored at the lowest relative humidity retained their viability for
Fig. 2.—Germination and moisture content of kauri seed after storage for varying periods in atmospheres of different constant relative humidities.

The greatest length of time. The loss of viability of seed stored in the atmosphere cannot be due to drying, for in the above experiment the seed which germinated in the largest numbers had the lowest moisture content.
Fig. 1.—An adult Kauri growing above regenerating *Leptospermum* scrubland. Fig. 2.—A Kauriicker. Fig. 3.—A *Leptospermum* community, small seedlings of Kauri are to be found beneath the fern (*Gleichenia sp.*) Fig. 4.—Transitional *Leptospermum-Agathis* community, numbers of Kauri saplings of various sizes can be seen.

*Facing page 674.*
Fig. 1.—A Kauri ricker community. Fig. 2.—The Kauri forest. The Kauri “grass” and a number of the characteristic species are shown. Fig. 3.—A seed trap in the Kauri forest.
Kauri seedlings. Fig. 1.—Individuals of Classes I, II, and III. The Class I seedling second from left. Fig. 2.—Class II. Fig. 3.—Small individual of Class IV.
Numerous germinations were conducted in which the effect of varying temperatures, light and pH of the germination medium were studied. It was found that the kauri seeds appeared to tolerate considerable variation in these factors with little apparent effect on final germination.

A further factor studied was the effect of moisture supply on the rate of final germination of kauri seeds. The seeds of Agathis are falling from the end of February until early April. During this period, the deep litter layer and the upper soil horizons—upon which the germinating seed is dependent for its moisture supply—become indicate that if the seed is going to germinate at all, it must do so immediately as there are several factors which tend to reduce or prevent it altogether—e.g., high very dry. Evidence for this has been presented earlier. Germinations of kauri seed humidities, low soil moisture content, and the attacks of an insect.

In order to study the effect of available moisture on germination an experiment was devised in which six degrees of watering, and consequently moisture supply were established. Equal weights of cleaned dried quartz sand were placed in large petrie dishes, one hundred sound seeds were sown in the sand in the usual manner. The dishes were placed in an incubator at $24^\circ$ C. The same total amount of distilled water was applied to each dish in the manner indicated below over a period of twenty-one days.

**TABLE IV.—GERMINATION AND THE DEGREE OF WATERING.**

<table>
<thead>
<tr>
<th>Amount of Water Giver per Day, Arbitrary Units.</th>
<th>Number of Times Applied</th>
<th>Time of Application</th>
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</thead>
<tbody>
<tr>
<td>0.1</td>
<td>22</td>
<td>Every day</td>
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<tr>
<td>0.2</td>
<td>11</td>
<td>Every second day</td>
</tr>
<tr>
<td>0.3</td>
<td>7</td>
<td>Every third day</td>
</tr>
<tr>
<td>0.7</td>
<td>3</td>
<td>Every seventh day</td>
</tr>
<tr>
<td>0.1</td>
<td>2</td>
<td>Every eleventh day</td>
</tr>
<tr>
<td>2.2</td>
<td>1</td>
<td>First day only</td>
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*First Experiment, commenced 16/5/50*

<table>
<thead>
<tr>
<th>Amount of Water/Day</th>
<th>No of Applications</th>
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<th>24/5</th>
<th>26/5</th>
<th>29/5</th>
<th>31/5</th>
<th>2/6</th>
<th>6/6</th>
<th>8/6</th>
<th>Final</th>
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<tr>
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<td>1</td>
<td>1</td>
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<td>19</td>
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<td>27</td>
<td>27</td>
<td>27</td>
</tr>
<tr>
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<td></td>
<td>4</td>
<td>12</td>
<td>17</td>
<td>19</td>
<td>21</td>
<td>21</td>
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<tr>
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<td></td>
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<td></td>
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<td>10</td>
<td>15</td>
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<td>14</td>
<td>25</td>
<td>26</td>
<td>32</td>
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<tr>
<td>2.2</td>
<td>1</td>
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<td>19</td>
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*Second Experiment, commenced 13/6/50*

<table>
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<th>19/6</th>
<th>21/6</th>
<th>26/6</th>
<th>30/6</th>
<th>4/7</th>
<th>11/7</th>
<th>Final</th>
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<tr>
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<tr>
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<td>12</td>
<td>15</td>
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<td>15</td>
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</table>

The final germination figures indicate that those seeds which received a large proportion of their available water supply at the commencement of the experiment had the best germination. This is to be expected because large amounts of water are rapidly imbibed by seeds in contact with a moist substratum during the early stages of germination. If there is insufficient moisture in the soil at this time, the seed will be unable to complete germination. It should be noted that the dish which
received all of its water at once dried out steadily during the course of the experiment, and at the conclusion was in fact drier than any of the other dishes. Seeds which were slow to start germinating under these conditions would thus encounter less favourable conditions towards the end of the experiment than those in dishes which had a more or less continuous though perhaps limiting supply of moisture during the whole period. The results of the second experiment are somewhat anomalous in that those seeds which received all of their water supply at once had as low a germination as those which received it throughout the course of the experiment. There has also been a drop in the overall germinative capacity of the seeds, and this may also have contributed to the result obtained. It was impossible to have any replicates in this series of germinations; the results obtained indicate their great desirability.

The conclusion to be drawn when the above factors are taken into account is that, as far as kauri seeds are concerned, moisture supply appears to play an important role in the number of seeds germinating and that an adequate supply is apparently essential at all stages.

An interesting observation was made in 1948 before these experiments were commenced. Seed sown in the field, fully protected from predators, during early April, following a very dry summer together with further dry weather after sowing, resulted in few seedlings. At the time it was thought that this was due to the low moisture content of the soil, and in view of the above results, this is probably the case, although doubtless other factors were also operative.

ANIMALS AND KAURI SEED

It had long been suspected by the writer that some animal was destroying large numbers of the sound seeds before they were able to germinate. In order to find out the nature of the animal, seed was germinated in the field both with and without the protection of wire gauze cages which excluded all animals except subterranean ones. Studies were also made with seeds which had been marked on the wing with aluminium paint.

Birds were early eliminated as the predators; the mesh of the wire covering on the cages being small enough to exclude them. A search had, therefore, to be made for some lower organism as numbers of the seeds were eaten beneath the cages.

Small quantities of these marked seeds were placed in many locations in all of the communities studied. The seeds showed on re-collection and examination that most of the sound seed was eaten during the first night, or at the latest during the second night. The blind seed did not appear to be touched in any way at all. The seed which had been eaten was scattered over an area little greater than that it originally occupied and was all eaten in a characteristic manner. It had the appearance of having been crushed by a pair of powerful jaws and the oily contents then eaten. A number of metal pipes three inches in diameter and approximately fifteen inches in length were sunk into the soil in one of the Leptospermum communities for the purpose of trapping insects. These traps proved efficient in use, and a number of wetas (Hemideina thoracica) were caught. The weta is a large orthopterous insect with heavy mandibles; a number were taken into the laboratory and left overnight with kauri seed. This seed was found to be eaten in the same manner as that recovered in the field.

The attacks of leaf-eating insects on seedlings have been mentioned by Millar (1925); damage caused by leaf-eaters has been observed on a number of kauri seedlings, in no case is it considered likely that they would succumb. One of the native parrots (Nestor occidentalis) has been reported by Oliver (1930) to feed on kauri seeds, using its strong beak to break open the cones. Sando (1936) thinks that the attacks of the parrots are a factor in causing the premature fall of kauri
cones. These parrots have been observed in the Waitakeres, but the present writer is not of the above opinion.

One can also mention here the effect of an unidentified fungus which causes the "damping off" of considerable numbers of young seedlings soon after germination. The usual symptoms are in the nature of collar rot. Sando (1936) mentions a fungal infestation of immature or unopened cones, the organism responsible being *Pestalozzia funerea* (Fungi imperfecti).

The effect of the weta eating the seed is considered to be important as a biological factor in natural regeneration, with next in order the collar rotting fungus. The actions of birds attacking the cones and insects the seedlings appear to be of much lesser importance.

The action of man as a biotic agent must also be mentioned. Vast areas of forest in New Zealand have been destroyed by man's agency, and it is in fact through the direct action of man that we find the numerous *Leptospermum* thickets in various parts of the country. Man by his very acts of destruction, is causing the devastated areas to regenerate and, as is shown in the present paper, the kauri forest is regenerating by the natural process of succession in many of these areas. Dansereau (1951) says "the mere breaking up of the continuity of certain communities can be genetically harmful, even in the case of climax associations. There is reason to suspect that such is the case of the kauri (*Agathis australis*) forest of northern New Zealand."

### The Survival of Small Kauri Seedlings

Observations were made on the survival of small seedlings in the young *Leptospermum, Leptospermum-Agathis* and in a ricker community. Counts of the individuals were made at more or less monthly intervals. (See Table V.)

Mortality is high soon after germination, at this stage the unidentified collar-rotting fungus is the causal organism. A slight increase in numbers at this time is probably due to individuals that have come from seeds that were slower to germinate. During the winter months there is usually a steady fall in the number of individuals until the period of high temperatures and low soil moistures in late December, January and February, when there is a second, usually quite sudden, drop in numbers. The death of the seedlings in this case is apparently due to the high temperatures together with the low moisture supply causing them to die from wilting. The older seedlings are apparently just as liable to succumb to these summer temperatures as those which are younger.

A comparison between the survival of young seedlings and soil moisture content during the summer months shows the relationship of low soil moistures and the seedling deaths Sando (1936) mentions the leaf-litter as a factor preventing regeneration, also McKinnon (1945) who says "the depth of the litter layer and the fibrous humus layer of the soil leads to heavy mortality amongst seedlings during prolonged dry weather, roots not having penetrated to the A horizon of the soil."

The following table has been constructed in an attempt to relate all the available field information. A comparison between the number of size-age class I seedlings on an area of one thousand square metres and the number of sound seeds which could be found on a similar area indicates that few seeds can germinate and the seedlings survive for one year. The major portion of this difference can possibly be attributed to the weta destroying a large number of the sound seeds, thus preventing their germination; low soil moistures at the time of seed-fall and high relative humidities causing loss of viability are further factors affecting the germination of the seed under field conditions. After germination, some of the seedlings die by the action of a collar-rotting fungus, and when somewhat older low soil moistures are a cause of death by wilting. Numerous other agencies and combinations of such agencies must also take their toll An exact comparison between the amount of seed estimated to be on the ground and the number of seedlings after, say, one year can only be an
approximation; nevertheless, some interesting points emerge. From field counts on the survival of seedlings a percentage survival from size-age class I to size-age class II was worked out, and this has been applied to the actual number of class II seedlings recorded from the quadrats. The figure obtained was then multiplied by six, which is thought to be the maximum age of this class, no account being taken of earlier deaths apart from the fact that only a percentage of the actual number of class I seedlings is used as a basis for the calculation. It has already been said that natural regeneration is at its best in the old Leptospermum community, and this fact is supported by the above data. The percentage germination in the old Leptospermum is almost six times that in the preceding young Leptospermum and considerably more than that in the ricker and kauri forest communities. This greater germination must be brought about by the occurrence of environmental conditions more favourable to germination at this stage in the sere. The percentage of seeds germinating in the kauri forest is low, almost as low as in the youngest Leptospermum, where the seed source is by no means as close as it is in the kauri forest. In the transition of seedlings from less than to more than one year old the actual per cent. survival is highest in the old Leptospermum. The number of seedlings calculated to be present in the ricker community after six years is almost the same as the number actually present. Before any definite conclusions can be reached much more long term information is required.

**Discussion**

It has been shown that kauri seed is able to germinate under a wide range of laboratory conditions. Under natural conditions, however, before the seeds are able to germinate they are subjected to the attacks of an insect which destroys a large proportion of the sound seed before it has a chance to germinate, thus very considerably reducing the number of seedlings which may eventuate from a seed-fall.

Another factor of importance is the relative humidity of the atmosphere in which the seed is present. Kauri seed stored in the laboratory under ordinary atmospheric conditions loses its viability rapidly, and it has been shown that one of the factors concerned is a high humidity in the storage atmosphere. The best germinations were obtained from seed which was stored at constant relative humidities of 50–65%. These levels are much below those recorded in the forest communities, where there is almost full saturation for many hours each week. It is therefore evident that the seed must germinate soon after reaching the ground or else it will lose viability because of high humidities. There must also be a ready supply of moisture available when it reaches the ground or else germination is unable to proceed. Field observations of soil moisture content indicated that the surface soil horizons are driest at
the time of seed fall, and there may be insufficient water available from them for the seeds to germinate. As far as the survival of small seedlings is concerned there is an agreement between low moisture content of the surface soil horizons during the summer months and the death by wilting of young seedlings.

The above two factors—viz., insect attacks on seeds and a low level of soil moisture at the time of seed fall apparently operate more or less uniformly in all communities and therefore cannot be considered to be responsible for the major differences in regeneration found in these communities. The cause of failure of regeneration in the mature kauri forest has not been definitely established. It is suggested that further studies of the seed and seedling soil-moisture relationships would be worthwhile. At the same time, investigations of the ecological relationships of the various communities should be continued.

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R. V. Mirams,
3 Ingram Road,
Remuera,
Auckland, S.E.2