

THE PINUS RADIATA/SIREX NOCTILIO RELATIONSHIP AT ROTOEHU FOREST

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Summary

An outline is provided of stand development and mortality in *Pinus radiata* at Rotoehu forest. Factors possibly conducive to this heavy mortality are discussed. It is indicated that there is no simple primary cause, but that an interrelationship of natural competitive effects with a superimposed and dependent population of *Sirex noctilio* forms the underlying mechanism. A hypothetical pattern for this mechanism is given, together with likely measures for controlling it.

1. Introduction.

Pinus radiata was the first species to be used when planting began at Rotoehu Forest in 1937. Its early manifestation of vigour indicated that it would be a major, if not the most important, species. In 1946-8 and subsequently, however, the stands suffered such excessively high mortality as to cause considerable concern for the future. As a result the planting of *P. radiata* was discontinued in favour of other pines which did not exhibit such disconcerting losses. More recently the pendulum of opinion has swung back in the other direction. Alternative species all have disadvantages of their own, and none is able to measure up to the phenomenally rapid height and diameter growth of *P. radiata*.

It is therefore of importance to determine the effect of mortality on stands of this species, and to attempt to elucidate the underlying causes of death. If these are mainly climatic, e.g., periodic drought years—and one must expect periodic outbreaks of mortality—then there would appear to be little that the forester can do about it. The extent of the impact of mortality on stand development and volume production will largely determine whether or not the species is to be judged climatically unsuitable. On the other hand, if more circumscribed edaphic factors are primarily responsible, there is a possibility of overcoming the problem by correct siting or by the application of the putatively deficient trace elements. Whatever the cause, a thorough understanding of the predisposing factors is essential in order that one may formulate methods of control, and that development may be directed towards the ends dictated by the objects of management of the forest.

This paper is intended as a contribution towards a fuller understanding of the wider problems of *P. radiata* development, and as a record of data gathered in the course of studying it within the more limited environment of Rotoehu Forest. It is necessarily incomplete

and tentative only. Attention is confined to those stands planted at 6 ft. x 6 ft. spacing, and which have not been thinned.

2. Development of *Pinus radiata* stands.

Since 1947 the establishment of mortality plots and the annual enumeration of stands over a range of age-classes has enabled a considerable quantity of data regarding the incidence of mortality to be built up. Annual figures for residual live stocking are tabulated in Appendix I, together with number of trees dying in the year of enumeration. E. R. Lewis, Biometrician, Forest Research Institute, has analysed these data, with the following results:

TABLE 1

	Degrees of Freedom	Sum of Squares	Mean Square	Variance Ratio	
Age of Stand	1	16038	16038	15.13	Highly significant
Stands of same age, in different years.	6	9196	1533	1.45	Not significant
Residual	17	18026	1060	—	

The analysis is only approximate in that systematic differences between stands were ignored.

He interprets these results as follows: "Mortality definitely depends on the age of the stand, but there is no evidence in these data that it is in addition influenced by the year or season."

The same clear correlation of mortality with age may be depicted in the form of a histogram, as in Fig. I; and its effect on the residual live stocking is shown as a residual stocking/age curve in Fig. II. It can be seen that although individual stands show some fluctuation from year to year, yet they all follow the same trend remarkably closely. The very steep drop in the stocking over the period from six to eleven years old is an arresting feature of this curve, eliminating over 50 per cent. of the originally established trees in the short space of six years.

What is the effect of this mortality on the other stand statistics and, in particular, how does it affect volume production?

Height growth is virtually unaffected, but continues at a very uniform rate of six feet per annum, at least up to an age of sixteen years. The average curve of stand top height is superimposed for comparative purposes on the mortality curve in Fig. II.

Diameter growth of the residual stand is registered against age in Fig. IV, together with mean d.b.h. of trees dying in any one year at different stages of development. The rate of d.b.h. growth diminishes slightly from about the sixth year onwards. This is correlated with a very sharp drop in diameter growth at stump height at or about the seventh year.

Basal area exhibits a very rapid increase up to the age at which mortality commences, and then gradually levels off until, at about

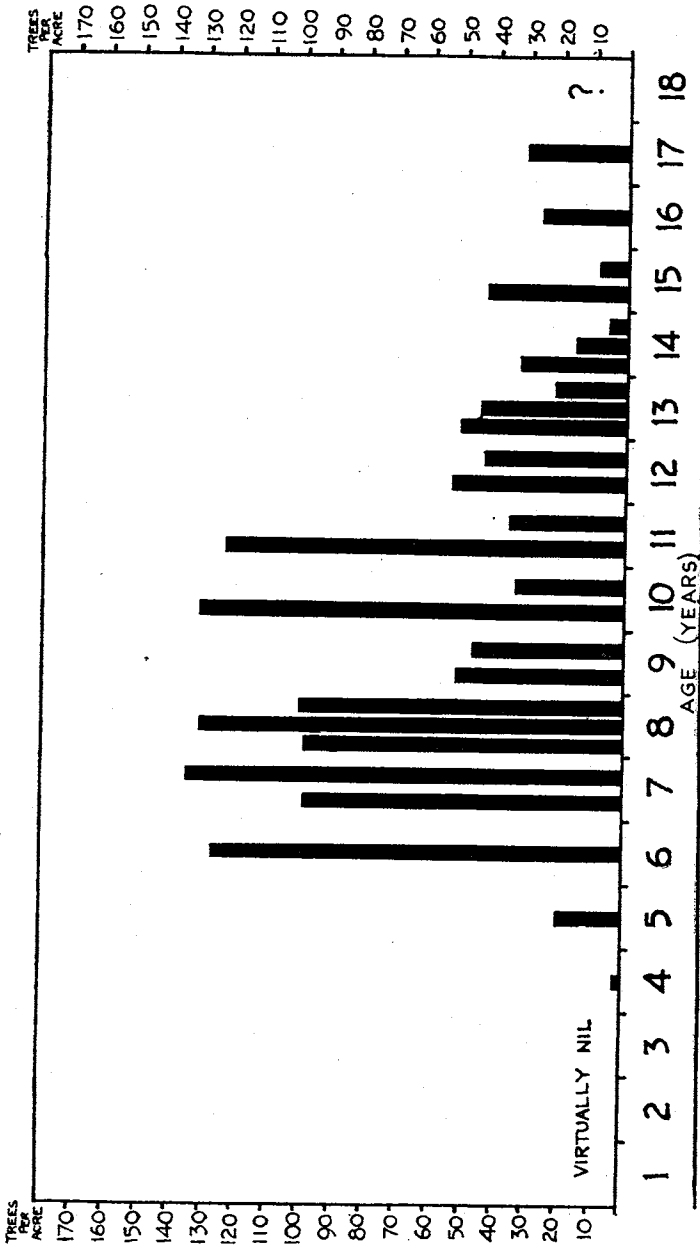


Figure 1. Mortality due to Sirex noctilio correlated with age.

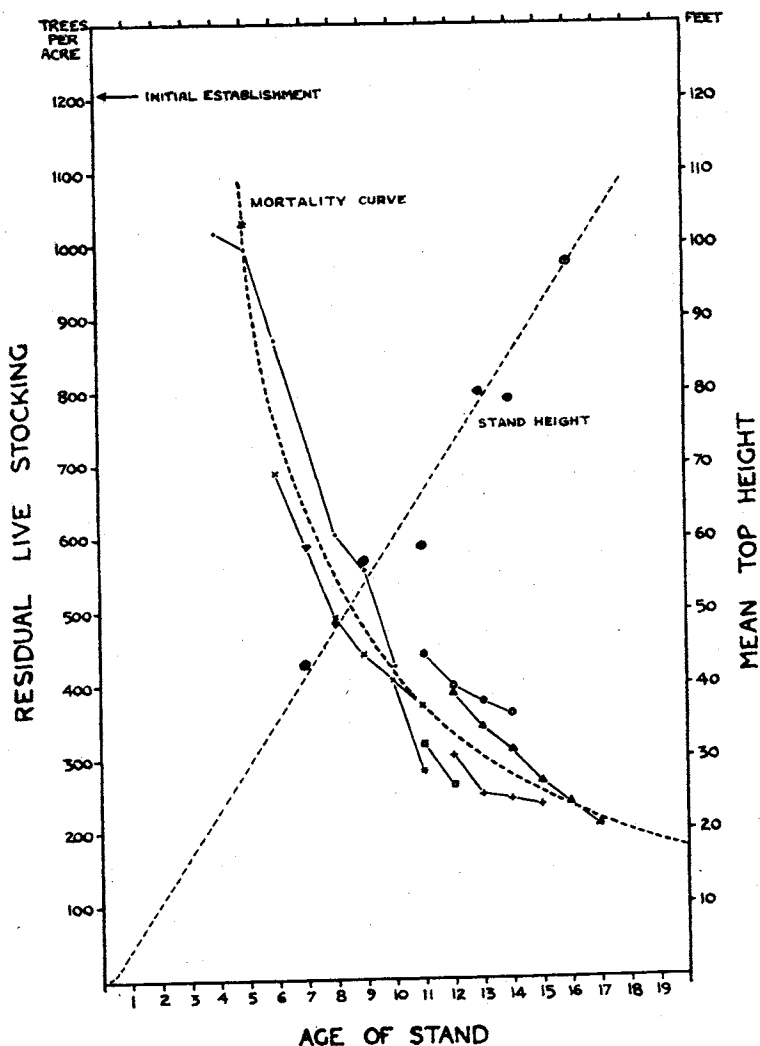


Figure 2. Comparison of mortality with stand top height.

sixteen years, it shows signs of maintaining an equilibrium level at or about 145 sq. ft. per acre. Individual stands may rise somewhat above this figure but in a year or two drop back again through a rather heavier loss of trees than normal.

Volume yield must be considered in relation to mortality. The so-called net volume production refers to total living volume of the stand at any age. If to this is added the accumulated volume of

trees which have died, one obtains gross volume production, representing the full productive potential of the site under *P. radiata*. From these two values of productivity, corresponding mean annual volume increments have been computed. They are plotted against age in Fig. III.

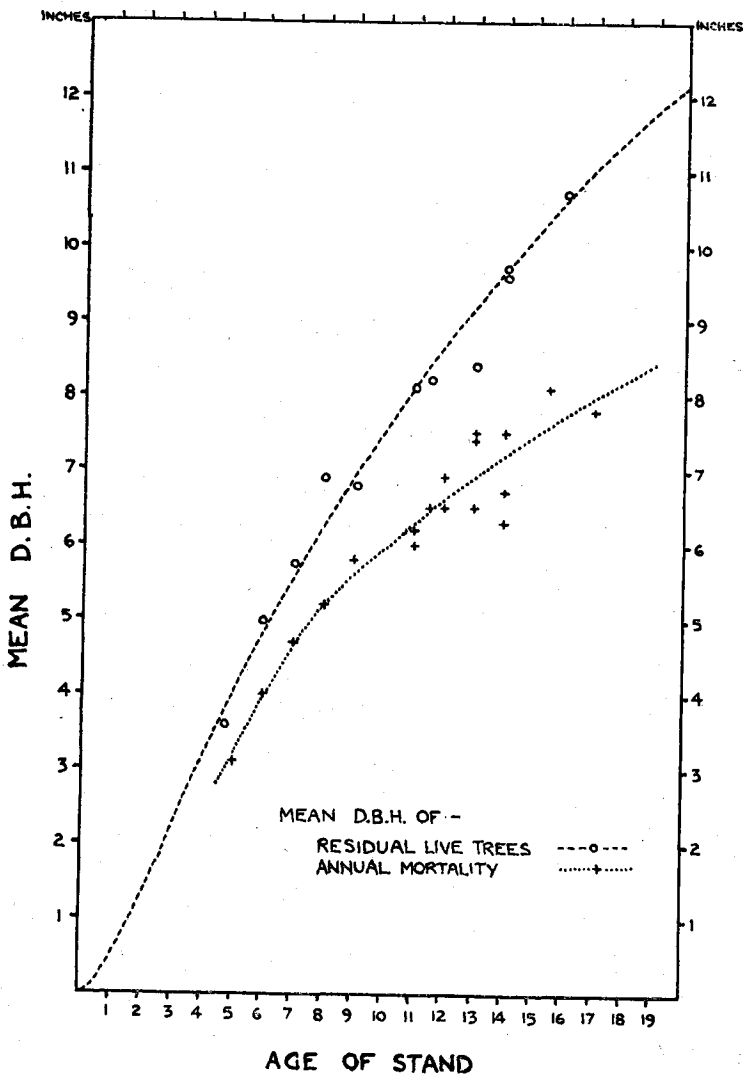


Figure 3. Comparison of potential and actual volume yields.

From these data it is clear that the loss of productivity due to mortality in *P. radiata* is substantial, reducing a potential mean annual increment of 450 cu. ft. per acre to an actuality of just over 300 cu. ft. per acre at fifteen to eighteen years old. It happens that at the age which the oldest stands have just attained (i.e. Compts. 1 and 2, planted 1937—now seventeen years old) the M.A.I's show signs of levelling off. Much will depend on whether the residual stands can continue over the next few years to make sufficient volume growth to offset annual mortality by a margin of 300 cu. ft. per acre per annum. Another point which should be noted is that stocking, as quoted herein, includes all living trees at any age, regardless of thriftiness, degree of suppression, malformation of stem or misshapen crowns. Even on the best stocked areas of the seventeen year old stands it is difficult to find on any acre as many as 100 dominant or co-dominant trees of good form.

Past losses cannot therefore be accepted with complacency, particularly if they forecast, as they appear to do at Rotoehu, that similar losses will be a developmental feature of future *P. radiata* plantations on this forest. A number of pressing questions arise:

- i. Does a mean annual increment of 300 cu. ft. per acre represent the maximum forest productivity which average sites at Rotoehu can sustain? If not—
- ii. What aspects of normal development are predisposing to mortality, and to what extent are these affected by other factors?
- iii. What measure of control can be exercised, and how?

The answer to the first of these questions is "no!" Under other species, e.g., *Pinus patula* and *Pinus taeda*, similar sites attain an actual net production of 400 cu. ft. per acre per annum. Since *P. radiata* can produce at least this volume increment elsewhere, it is clear that some element of the normal environment (climatic, edaphic or biotic) at Rotoehu is proving unfavourable; and to the extent of 100-150 cu. ft. per acre per annum.

The most obvious factor of normal stand development which is likely to lead to mortality is competition between the trees themselves. Mortality due to suppression may not only be expected, but is even a necessity within any developing plantation. Corresponding with the phenomenal development of *P. radiata* is a very marked and early differentiation into crown classes, a strong expression of dominance and suppression. That competition and suppression are the major factors in predisposing a portion of the crop to mortality is strongly indicated by a number of features:

- (a) at least 80 per cent. of the mortality is always comprised of trees from the intermediate or suppressed sections of the stand;
- (b) the lesser mean d.b.h. of trees dying, as compared with the mean d.b.h. of the residual crop (Fig. IV);
- (c) the postponement of mortality in young plantations until the stage following canopy closure, when competition ensues. This is further reinforced by the associated decrease in rate of

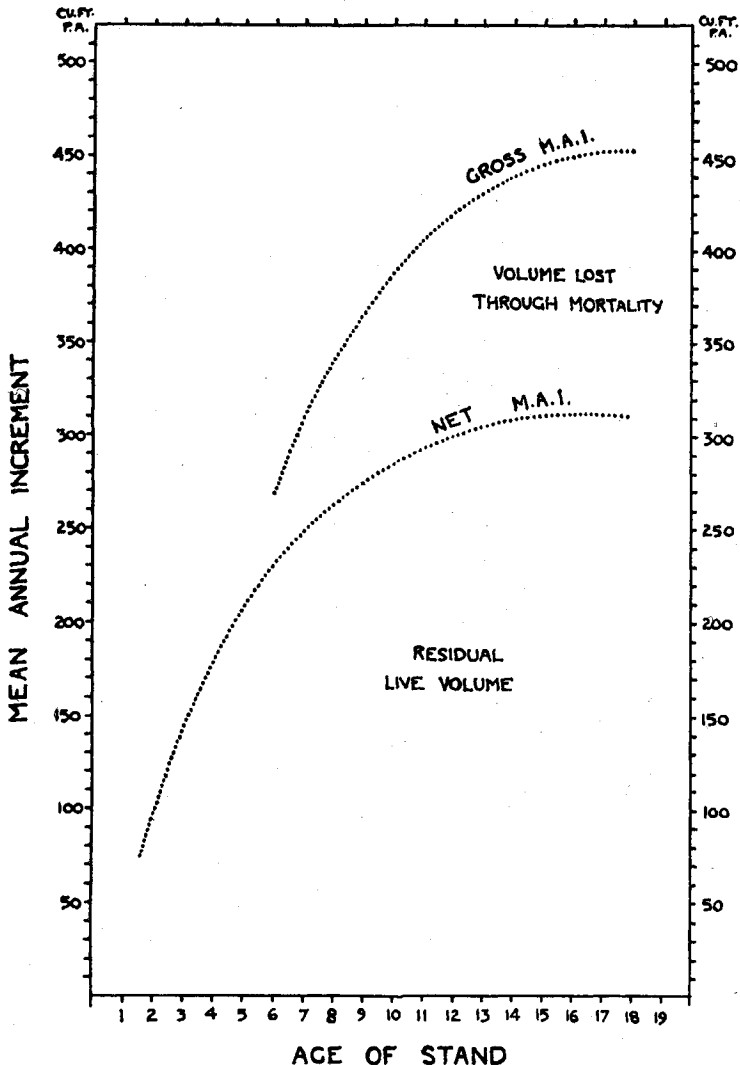


Figure 4. Comparison of lesser mean d.b.h. of the dying trees with the mean d.b.h. of the residual crop.

- d.b.h. growth and of diameter increment at stump height;
- (d) the much lower percentage mortality in shelter belts and marginal rows of plantations;
 - (e) and finally, the evidence afforded by spacing trials. Thus, at Rotoehu, mortality in the replication plots in Compt. 29 is directly correlated with spacing, as follows:

TABLE 2

Initial Spacing:	3x3	4x4	5x5	6x6	8x8	10x10	12x12	15x15 ft.
Percentage mortality at:								
6 years	60	56	50	42	20	24	—	—
8 "	89	83	79	59	38	37	28	10

If one takes all these items of evidence into consideration, integrating them with the initial demonstration that mortality is a developmental feature of unthinned 6 ft. x 6ft. stands, the importance of competition (whether for light, moisture, and/or inadequate nutrients is uncertain) and suppression as predisposing factors is manifest.

One may take it that excessive mortality ensues when this critical process of re-adjustment is upset. Further questions then follow—what are the extraneous environmental factors which thus interfere, and how do they operate?

A thesis that it is the general climatic environment which is unsuitable seems untenable. One would not expect the climate prevailing over Rotoehu forest to be inadequate in any important respect. An average annual rainfall of 65 inches per annum, and a P/E ratio which puts it into Garnier's humid mesothermal class (Garnier 1950) compares favourably with either its natural habitat or the major areas of successful introduction overseas. Moreover the overall healthy appearance and vigour of the crop are inconsistent with any meteorological elements being unsuitable—unthrifty appearance is one of the first signs of such trouble. Furthermore, whether one proceeds in the direction of warmer, more humid conditions (e.g., Matakana Island), or cooler, drier climates (e.g., Golden Downs, Dusky, Beaumont), one can find areas where *P. radiata* will maintain higher stockings per acre and attain higher net productivity than at Rotoehu. Finally, *P. patula*, *P. taeda* and *P. elliotii* all derive from areas of high rainfall regime—and should show the effects of any inadequacy sooner than *P. radiata*. In fact they are, to date, considerably more productive.

Proceeding to a brief consideration of edaphic factors, one is on more uncertain ground. Indeed, one of the possible explanations for the health of the Matakana Island *P. radiata* is a relatively high water table. However, if a seasonal soil moisture deficit is responsible it is peculiar that there is no manifest correlation of mortality with different site types at Rotoehu. The range of topography and slope is considerable, and independent studies have indicated that the moisture relations of, for example, typical plateau sites are very different from those of basins and valley sites. As might be expected, the latter receive a disproportionate share of precipitation in the form of run-off; and this is reflected by certain differences in the soil profile. One would expect that under these circumstances such sites would carry a heavier stocking and exhibit less mortality, age for age, than drier ridges and plateaux. In fact the reverse seems to be the case. Where edaphic factors are at fault the most familiar pattern is

that of the mosaic, or patchy stand development, similar to that arising on northern gumland soils. An obvious exception to this pattern is where some trace element or nutrient is in deficient supply. This possibility cannot be excluded. Nutrient plots have actually been established since 1949. They could perhaps well be extended.

It has already been shown that mortality is intimately connected with the normal course of stand development. An obvious corrective is to anticipate this suppression by drastic thinning, and such silvicultural treatment was therefore applied to Compt. 27 in 1949 at an age of five years. Stocking was reduced from 1030 down to 480 trees per acre. By 1953 however, continuing mortality had reduced this to only 344, which is well below the average unthinned survival curve level of 480 at the age of nine years. Moreover, many of the dead trees were vigorous, well formed dominants. A similar phenomenon is, as a matter of observation, common throughout these stands; that is, although most of the mortality takes place in the actively competing and subordinate elements of the crop, a by no means negligible number of healthy dominants are also killed. This can be illustrated by an analysis of annual mortality over the crucial period for two half-acre plots in Compt. 27.

TABLE 3

Year	1950	1951	1952	1953	1954
Age of stand	6	7	8	9	10
Percentage of dead trees above average height	6%	9.9%	13.8%	13.6%	4.7%
Percentage of dead trees of average height	55.2%	50.4%	51.1%	59.1%	25%
Percentage of dead trees below average height	38.8%	39.7%	35.1%	27.3%	70.3%
Total number of dead trees	127	135	131	47	131

(In order to avoid any possibility of subjective bias, the status of trees is taken as in the year of assessment prior to mortality.)

The fact that a number of otherwise perfectly healthy dominants suddenly succumb every autumn, and that the percentage tends to increase up to a certain point, strongly suggests that some factor is acting not only in conjunction with, but also overriding, the normal course of competition and suppression. This is further confirmed by the mortality which occurred in the case of the thinned stand mentioned above.

The most obvious factor is, of course, *Sirex noctilio*. Rawlings (1948) has indicated that this insect, together with its fungal symbiont, is capable of acting as a primary parasite, and has expressed his opinion that in many cases it undoubtedly does so. Moribund trees are, almost without exception, previously attacked by *Sirex*, though a few very small suppressed trees escape. Moreover, the transformation effected within a few weeks by heavy attack on a healthy, vigorous dominant forces one to conclude that *Sirex* can and does act in such cases as a primary parasite. Where a predisposition exists, as in most cases of

disease induced by the physical environment, one should be able to recognize at least the majority of potentially moribund trees a year or two in advance. For the forester such recognition is essential if he is to carry out a thinning on anything like a rational basis. As a test of ability to recognize such individuals, on the basis of general symptoms such as vigour, thriftiness, colour, etc., forecasts were made in 1950 and 1951 of the mortality expected in the above stand. Forecast status was recorded tree by tree and compared in the following year with actual status. Summarized as follows:

	1951	1952
Actual mortality in these years was	135	131 p.a.
of which, only the following had been forecast during the previous year:	25	36
In addition, trees forecast dead, but still alive a year later, numbered	17	5

If the number of trees not forecast is added to the number incorrectly forecast, and the sum is expressed as a percentage of actual mortality, we obtain an expression of the error. This was 94% and 76% respectively! It will be noted that much the greater portion of this error was made up of trees which were apparently completely healthy at time of forecast. Of the trees "wrongly" assessed as moribund, all died in subsequent years.

As a follow-up, attempts were made to find some feature which would enable one to "pin-point" susceptible trees in advance of death. These mainly hinged on morphological characters such as crown-type, branching and internodes etc. All were entirely unsuccessful. This was half expected, since, to be apparent, such morphological indices would have to be genetically linked with the physiological characters which presumably constitute the real difference between susceptible and resistant trees—competitive ability for the moment disregarded. This difference remains obscure right up to the point at which attack by *Sirex* occurs, thereafter being only too apparent. One is reluctant to admit that attack is entirely haphazard, even if superficial appearances so dictate. Apart from this, the role of the *Sirex*/symbiont association as the immediate cause of death seems inescapable.

3. Development of *Sirex noctilio* populations

One of the most obvious features emerging from the above study was the importance of intensity of attack in causing any trees to succumb. Intensity of attack would be largely dependent on the number of female *Sirex* available in the stand. Here one is up against a population problem. Survival of *Pinus radiata* may largely depend upon whether or not it is attacked by *Sirex*—but the very existence of the latter most certainly depends on breeding material being available. Moreover, if large quantities of such material are killed and utilized by the insect in the early years, it follows that there must be correspondingly less available for the future. It becomes of con-

siderable interest, therefore, to ascertain just how many *Sirex* actually emerge from the trees of different sizes, ages and years of mortality.

Over the years 1951-54 trees were felled in different stands and actual counts taken of the number of *Sirex* emergent from such stems. In all, 31 trees were examined, ranging from four inches to twelve inches d.b.h., and from seven to sixteen years old at time of death. If emergences are grouped by diameter of one-foot stem sections a very strong correlation appears:

TABLE 4

Section diameter, inches o.b.	1	2	3	4	5	6	7	8	9	10
No. emergence holes per cu. ft. i.b.	Nil	260	465	392	342	311	252	254	216	152

It would seem that, on the average, material of three to four inches in diameter is most efficient in producing *Sirex* under conditions normally prevailing at Rotoehu.

The overall totals for emergence from each tree are plotted against total stem volume i.b. in Fig. V. It was clear from the outset that considerable variation existed, both in the numbers and size of *Sirex* emerging from any one size class of tree. Rawlings (*in verbo*) has indicated the complexity of the factors, apart from tree-size, which influence overall emergence. Nevertheless, these data can be used to outline a tentative pattern for the interaction which occurs between the two populations, the developing *P. radiata* stand and *Sirex noctilio* on Rotoehu forest.

Taking first the simplest case, as presented by the average curve of mortality (Fig. II). The number of trees dying in each year and their mean stem volume can be tabulated as follows:

TABLE 5

Age of stand:	Average No. of trees dying	Mean vol. per dead stem	No. <i>Sirex</i> per stem (Fig. V)	Average No. <i>Sirex</i> per acre (hundreds)
5	50	0.5	260	130
6	235	1.0	550	1293
7	120	1.6	690	828
8	95	2.1	760	722
9	70	2.8	860	602
10	60	3.6	960	576
11	50	4.3	1050	525
12	35	5.2	1160	406
13	35	6.2	1280	448
14	23	7.2	1400	322
15	23	8.4	1550	356
16	19	9.7	1710	325

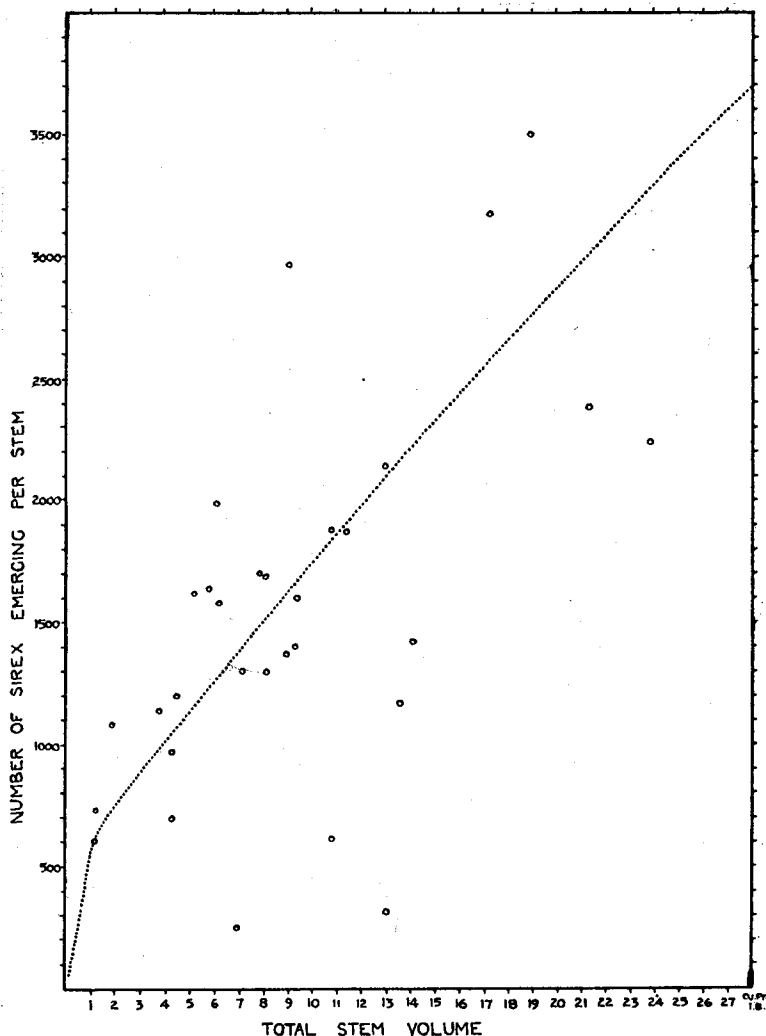


Figure 5. Comparison of the overall totals of emergence of *Sirex noctilio* from each tree plotted against total stem volume *i.b.*

Only a fraction of these total numbers are, of course, female. At Rotoehu the observed proportions ranged from 1 female: 9 males (Compt. 23 in 1953) and 1 : 10 (Compt. 27, 1953) to only 1 : 35 (Compt. 23 in 1952). Although the above population estimates give some idea of the relative weight of attack which a stand must sustain from year to year, all too little is known about what absolute level of population is dangerous, what intensity of attack different tree-

classes can resist, or even what percentage of the females is able to attack with any degree of success. The size-range of adult *Sirex* at Rotoehu is very great, individuals ranging from 9 mm. up to a length of at least 40 mm. Quite apart from the differences in egg-laying capacity of different sized females (Cf. Rawlings 1953, p. 27), a considerable proportion of the lower size-range of females must be impotent through having ovipositors too short to be effective.

Within a natural environment the pattern will be very much more complex than is indicated above. One must bear in mind that we are dealing not with a single population, but with two which are interacting, each of which has its own peculiar responses. Nothing that has been said above precludes the possibility of very severe drought or other climatic conditions from being the immediate cause of large numbers of *P. radiata* dying. The writer's concern has been to record that apparently comparable losses at Rotoehu are correlated not with vagaries of climate but with the normal course of stand development. The possible effect of weather on the *Sirex* population is another matter altogether, and one must turn to the pathologist to ascertain what these may be. The effect of wind or rain for instance at the time of the copulatory flights must adversely affect the percentage of females fertilized. Owing to the haploid-diploid character of males and females of this species, the generation of the following year would then have a higher percentage of males than average. Other things being equal, this would result in an abnormally high percentage of females in the ensuing year—and so on, the oscillation tending to magnify itself in each succeeding generation. Such oscillations should manifest themselves in a biennial fluctuation of mortality; that they do not do so to any marked extent indicates that there is some counter-acting mechanism, e.g., a mosaic of separate populations with some degree of inter-migration of the surplus males or females. The two mortality plots in Compt. 27 show a suggestive fluctuation of mortality, each out of phase with the other, over the crucial 6-9 year period.

TABLE 6

Age:		5	6	7	8	9	10
Percentage mortality	Plot 27	7.9%	12.7%	9.3%	16.1%	10.1%	9.2%
in each year	Plot 28	7.2%	13.2%	14.2%	8.2%	15.1%	11.3%

Whether this is due to the above cause is another matter.

4. *The Interaction and its control.*

The pattern that has been outlined above may now be summarized as follows:

Competition and suppression in even-aged *P. radiata* stands planted at 6 ft. x 6 ft. on Rotoehu forest commence at about four or five years, becoming acute by the sixth, seventh, and eight years. *Sirex noctilio* gains a foothold in the plantation during about the fifth year; until this age stems are still too small to carry larvae, as already

shown. It establishes itself in the weakened subordinate element of the stand during the sixth and seventh year when maximum numerical losses of trees occur. *Sirex* populations attain their peak levels between the sixth and ninth year, depending on oscillations of the proportion of sexes, advantageous weather conditions, etc. During the crucial eighth and ninth years, however, the *Sirex* hordes, although preferentially attacking suppressed trees, are forced through lack of these to attack a higher percentage of healthy dominant trees than have been attacked previously. Thereafter the *Sirex* population, as it meets more vigorous resistance, begins to tail off from its peak level. From about the fourteenth year onward a residual population maintains itself in the few weaker trees which drop behind each year, occasionally flaring up locally to take a few dominants.

How can this pattern be modified to suit the objects of management?

In the first place it would appear premature to carry out a thinning as early as five years. Too little is known about the ability of *P. radiata* to resist attack. There is no doubt that, quite apart from effects of suppression, some trees are more resistant than others. Because it is not at present known how to recognize them prior to attack does not mean they are non-existent. Bark thickness is obviously one morphological character of importance. At the physiological level resin production may well be another: if attacked trees are classified according to the amount of resin flow from oviposition punctures, it is found that of those which merely show beads of resin, three or four times as many die within one year as of those which show long or copious streaks of resin. Subsequently to the thinning of Cpt. 27 already mentioned, *Sirex* reduced the residual stocking by over 25 per cent., probably because susceptible individuals had been left behind.

The best time for thinning would seem to be at seven years, after the most susceptible trees have been killed by *Sirex*. Objectives would be to eliminate such trees, but to hit the *Sirex* population before it could divert its depredations to the valuable dominants of good form. Removal of the weaker subordinate elements *in toto* is also important; otherwise *Sirex* has a base on which it can carry over for years to come, sporadically breaking out and killing trees which can ill be spared.

Investigations are needed to determine what degree of fluctuation there is in the proportion of sexes from year to year within any one area. If such fluctuations do occur over extensive areas the winter of thinning should be chosen to follow a season in which the proportion of males had been low. It is obvious that one is only on the fringe of the problems to be solved. What is the effect of felling attacked trees on the number of *Sirex* subsequently emerging therefrom? Will lopping the branches off at an early stage reduce the number? At what age does slash become unattractive for oviposition? Any method which will reduce population levels must be beneficial,

whether the method promises to be permanent and widespread, e.g., the introduction of *Ibalia leucospoides* and the establishment of *Rhyssa*, or whether it is limited to one compartment and one rotation, e.g., adequate thinning. Similarly any possibility of building up inherent resistance to attack should not be neglected. For this reason it is important to collect all *P. radiata* seed locally and from the best trees in stands which have passed through the ordeal of massed *Sirex* attack.

In conclusion, at Rotoehu forest *Sirex noctilio* should be regarded not as an abnormality, but as a normal biotic constituent of the environment of *Pinus radiata*. The objective should be not to exclude it altogether, but by silvicultural and biological control to prevent populations from attaining peak levels of aggression. From the standpoint of population dynamics one may regard a stand which has attained the age of twelve years without progressive attack (or thinning) as being in an explosive state. Postponement will make the eventual eruption so much the more devastating.

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APPENDIX I

MORTALITY OCCURRING IN THE YEARS 1947-1954 AT ROTOEHU

Source of Data	1947	1948	1949	1950	1951	1952	1953	1954
Compt. 27, planted 1944	—	1018	998	871	736	605	558	427
Mean of 2 half-acre plots	—	—	20	127	135	131	47	131
Compt. 29, planted 1942	—	692	—	494	442	408	372	—
Mean of replication plots III & IV	—	—	99	99	52	34	36	—
Compt. 22, planted 1940	590	490	—	—	444	400	378	362
Five 1/10th acre plots. One acre plot	—	100	—	—	—	44	22	16
Compt. 2, planted 1937	—	—	301	250	244	235	—	—
Mean of eight quarter-acre plots	—	—	—	51	6	9	—	—
Compt. 1, planted 1937	—	—	389	344	311	267	240	208
One acre mortality plot	—	—	—	45	33	44	27	32
Compt. 27, planted 1944	844	842	—	—	—	—	—	—
Mean of five 1/10th acre plots	—	2	—	—	—	—	—	—
Compts. 1 & 2, planted 1937	407	283	—	—	—	—	—	—
Mean of ten 1/10th acre plots	—	124	—	—	—	—	—	—

Mortality is expressed as the number of trees dying per acre in any one calendar year i.e., those trees dying in the autumn immediately prior to enumeration, and those moribund trees which succumb during the remainder of the winter and in the following spring.

— No data available.