ENTOMOLOGICAL AND OTHER FACTORS IN THE ECOLOGY OF A PINUS RADIATA PLANTATION

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INTRODUCTION

Kaingaroa Forest contains approximately 115,000 acres of *Pinus radiata* D. Don. Of this acreage there are 15,000 acres on which the trees are so poor that the areas have been scheduled for conversion to other species. These trees are short and heavily branched and many have multiple leaders; these areas were mostly understocked in the early stages. The reasons for this condition are to be found in the climatic factors, such as frost and wind, and in the soil conditions, which result from the high elevation, climatic factors and poor drainage. These soil conditions were indicated in the original flora by the presence of *Dracophyllum subulatum* Hook f. The adverse site factors, particularly frost damage, predisposed the trees to attack by fungi such as *Phomopsis strobi* Syd. and *Diplodia pinea* (Desm.) Kickx. It might be possible to grow a commercially acceptable crop of *P. radiata* on these sites after they had been drained and treated with fertilisers so as to improve the soil and increase the frost hardiness of the trees. For a forester however it is easier to change the species than to modify the site.

The remaining 100,000 acres consist of about 50,000 acres classed as fairly good and 50,000 acres classed as good. The fairly good sites contain many trees with double leaders or otherwise of poor form. Trees on these sites suffer severely from wind damage and are liable to attack by needle fungi such as *Lophodermium pinastri* (Sch. ex Fr.) Chev. and *Naemacyclus niveus* Sacc.; the predisposing cause appears to be excessive humidity, especially during hot wet summers. Trees on good sites are subject to damage by wind and fungi but the resultant crop is superior both in quality and volume.

The main factors influencing the development of a stand on one of the best sites will be described and their effects traced from the time of planting in 1922. The details apply only to areas of similar age and site and must not be taken to apply to areas on other sites or during different climatic cycles. Only those factors which appear to have been of greatest importance will be dealt with. No doubt many events have passed unobserved or unrecorded or have been misunderstood at the time. In retrospect the exact influence of any one factor can only be inferred. No sequence of events has yet been exactly repeated and probably never will be. The presence of the forest, apart from all other factors, has so changed the site conditions that nothing but repeated fires, or another eruption, could bring about a return of the conditions present before planting commenced. Planting has now been replaced, to a large extent, by natural regeneration and the resulting stands differ in many features from the forests first established.

The site under consideration is at an elevation of about 1700ft. at latitude 38deg. 20min. S.

SOIL FACTORS

Before planting commenced, the area under consideration was covered by manuka scrub up to 15ft. high, or by bracken fern. The vegetation was burnt and the soil was destroyed where manuka had stood. The following is a soil description of a plot in Compartment 1125 near the southern limit of the basaltic lapilli from the Tarawera eruption.

1. On surface, ½ in. litter of pine needles, pollen cones, twigs and small branches.
2. 2–3 in. of dense black loamy sand consisting of basaltic lapilli from the Tarawera eruption of 1886 and the remains of soil typical of bracken fern, pH 4.9.

3. 17 in. of pumice from the Kaharoa eruption in about the year A.D. 1000. There are two distinct zones: first, 9–10 in. dark (reddish) brown, grading into lighter brown, gravelly sand; then 7 in. banded gravelly sand and coarse loamy sand.

4. The fossil soil which formed on the ash beds of the Taupo eruption about 120 A.D. made up of 5 in. dark brown grading into lighter brown coarse sandy loam and 5 in. grey coarse sand with Taupo pumice fragments. This appears to be water-carried and may be a post-Taupo lake bed. There follows 15 in. consisting of 1 in. orange red coarse sand, 12 in. yellowish brown fine, grading to coarse, pumice gravel and 2 in. gravelly sand.

5. At greater depths coarse sandy loam of older ash showers continues to the underlying ignimbrite rock.

Roots probably penetrate as far as the rock and have been found as far down as holes have been dug. The soil material is all acidic except for the Tarawera lapilli which have not yet commenced to disintegrate. However the soil is reasonably fertile but low in potash and phosphate. Water percolates readily through the soil in most places. The water-holding capacity of pumice is high.

CLIMATIC FACTORS

It is a common fallacy to suppose that heavy rainfall and wet years are good for trees. *P. radiata* is adapted to a mild climate with a rainfall of 25-30in. and a dry summer. The rainfall at Kaingaroa ranges from 32 to 77 inches with an average of 58 inches, of which it is estimated that only about 30in. can be utilised by trees; the remaining 30 or 40in. leaches salts from the soil and favours fungi which attack the foliage. Summers having up to 30 days without rain are beneficial for *P. radiata*. Dry summers with the equivalent of up to 50 days without rain do no apparent harm, but more intense drought than this has the effect of intensifying competition, giving dominant trees an advantage over smaller trees. Following the 1946 drought, in which there was the equivalent of 60 days without rain, an epidemic of *Sirex noctilio* Fab. caused widespread mortality among the smaller trees in the *P. radiata* stands. In stands of Douglas fir (*Pseudotsuga taxifolia*) no killing agent was present and no spectacular mortality resulted, but the advantage given to the dominants by the drought is now evident.

Wind has been the most important of the climatic factors. Planted at 8 x 8ft spacing

FIGURE 1. P. radiata *42 years old, showing strong effects of wind on crowns in overstocked stands.*

the trees have little room for crown expansion and, as they become taller, the arc through which the crown moves, in even a moderate wind, becomes considerable. The trees do not move together, as a field of wheat, but in such a way that two neighbouring trees generally are moving in opposite directions and there is a continual clashing together of branches. As a result each crown occupies the centre of a circular area which increases each year and which represents the area moved over during the frequent moderate, and the more rare severe, winds which occur in this district. The frequent violent contact between crowns injures branches and growing points, killing buds and giving access to fungi, particularly *Diplodia pinea*, which kill back the leaders and branches. Any tree which has become overtopped by its neighbour cannot grow upwards without having its leader killed back by the lower branches of the taller tree. As a result of this sway, crowns in crowded stands are small, branches tend to be upright, and the canopy is light.

Wind is an important factor in breaking apart the leaders of forked trees; trees with double leaders must ultimately split as their height increases and as leverage becomes greater. On poorly drained areas shallow-rooted trees are uprooted, and on other areas trees may be broken off by severe gales. These losses are important because they most frequently affect the dominant trees. Double leaders are frequently large-crowned wolf trees which have suppressed their neighbours. When they split they make a large gap and may break or push over other trees as they come down.

Frost is important only in newly planted or regenerated areas and snow is almost unknown.

To sum up, wind controls the form of the crown at any spacing and assists in the eliminating of suppressed trees; it may cause losses through windthrow or breakage of dominants. Extremes of drought or wetness assist the growth of dominants and assist in the elimination of suppressed trees. Drought favours the development of insect outbreaks and high humidity favours attack by fungi. Lightning damage, resulting in killing of areas of ¼ to ½ acre in area, is sporadic throughout the forest.

During the summer of 1960–61 the compartment described was struck by lightning. About two acres of the best trees had dead crowns and four acres were felled to salvage the timber.

BIOTIC FACTORS

The influence of pigs and deer upon an established forest does not appear to be as great as might be expected, although pigs may be an important factor in the development of a tree fern understorey. Birds are probably important but little is known about their exact status in the forest.

Some 137 species of insects have been recorded as associated with the *P. radiata* forests. Of these 37 are defoliators, 33 are predators or parasites, 12 are sap suckers and 55 are wood borers, scavengers, or of no known significance. Only 7 are of exotic origin. With the exception of *Sirex noctilio* no species has caused appreciable mortality or damage in Kaingaroa Forest, but some of the early multiple leaders may be the result of attack by tortricids.

Caterpillars of the following 17 species of native Lepidoptera have been recorded feeding on *P. radiata* foliage:—

Selidosema suavis (Butl.)
S. fenerata (Felder)
S. dejectaria (Walk.)
S. leucelaea (Meyr.)
Declana floccosa (Walk.)
D. leptomera (Walk.)
D. hermione (Hudson)
Asthena pulcharia (Dbldy.)
Heliostibes atychioides Butl.
Tortrix excessana (Walk.)
T. flavescens (Butl.)
T. conditana Walk.
Capua plagiatana (Walk.)
Ctenopseustis obliquana Walk.
Austrotortrix postvittana (Walk.)
Cnephasia jactatana (Walk.)
Oeceticus omnivorus (Fered.).

Of the exotic insects *Pineus laevis* Mask. may be mentioned. Crawlers of this aphid appear to be spread by wind, the winged forms having no apparent function in New Zealand. It is now controlled by *Leucopsis obscura* Hal. and seldom becomes very numerous. *Hylastes ater* is of importance only in its attack on regeneration.

THE *Sirex* COMPLEX

Sirex noctilio is normally only capable of killing trees debilitated by some predisposing factor. One *Sirex* female can cause death only when the tree is already very sickly. Concentrated attack by many *Sirex* can kill progressively less sickly trees as the numbers of *Sirex* increase. A female *Sirex* will lay from 25 to 500 eggs, depending upon its weight. The killing agent is a fungus deposited with the egg in holes drilled in the tree by the ovipositor or in holes drilled but abandoned without an egg being laid. *Sirex* is facultatively parthenogenetic, producing females from fertilised eggs and males from unfertilised eggs. Eggs are laid in living trees and oviposition tends to become concentrated just below the lowest green branch. On hatching the larva tunnels with the tracheids consuming both the wood and the fungus which has invaded the wood ahead of it. After about the 7th instar it turns inwards and later, when fully grown, usually moves outwards to pupate just beneath the surface.

In normal years the males greatly outnumber the females, and copulation takes place in the tops of trees on hot, sunny days. However the female has no time to waste since she must deposit as many eggs as possible before her fat-body is exhausted. She therefore starts ovipositing without copulating if the weather is not favourable. On an average only one female will complete the cycle from each batch of eggs. In the 1946 drought summer conditions were favourable for copulation and trees were easily killed. Consequently in 1947 there were many more *Sirex* than normal and a much higher proportion of females. The average size and egg-laying capacity of the females was also greater than normal and a one-year, instead of a two-year, life cycle predominated. The summers of 1947 and 1948 were also favourable for copulation and the result was the epidemic outbreak culminating in 1949.

The importance of *Sirex*, then, depends upon the number of females and their ability to lay fertilised eggs. When adequate thinning cannot be carried out, *Sirex* is beneficial because it kills unwanted trees. In epidemic numbers it may kill too many trees or damage trees it cannot kill. Biological control is therefore important. There are three introduced and one native parasite, all of which play their part in keeping the numbers of *Sirex* below the epidemic level. *Rhyssa persuasoria* L. is active in the early spring; the female drills into the wood, stings the *Sirex* larva, and deposits an egg upon it. The *Rhyssa* grub devours the *Sirex*. *Rhyssa* is effective in killing fully developed larvae which otherwise would have had a good chance of becoming adults, and is important in destroying the females which could bring about a rise in population if conditions were suitable. *Rhyssa* is limited in that the adult requires food and is active at a time when few flowers are available. Without food it may be unable to lay more than one or two dozen eggs. A second species, *Rhyssa lineolata* Kirby, has been accidentally introduced and may become important as it has a slightly different life cycle from *R. persuasoria*. *Ibalia leucospoides* Hochenw. is active at the same time as the *Sirex;* it requires food but many flowers are available at this time. *Ibalia* oviposits in the eggs of *Sirex*. It is limited in that it must locate the eggs within ten days of their oviposition and its success depends upon the successful development of the *Sirex*. On the other hand *Ibalia* will increase with the *Sirex*, whereas *Rhyssa* will always be one year behind.

The native *Guiglia schauinslandi* (Ashm.) Benson attacks *Sirex* larvae in the same manner as *Rhyssa* but is smaller and keeps mainly to the tops of trees. It has an alternative host in *Stenopotes pallidus* Pasc.

HISTORICAL ACCOUNT

Compartment 1125 was established by planting in 1922 on ground which had been newly burnt over. Except in bracken-fern areas, the trees received no competition from native vegetation and the crowns closed after about 8 years. After about 12 years the lower branches were dying and the effect of competition between the trees was becoming evident. Up to this time, 1934, there had probably been some damage to leaders by tortricids and fairly widespread attack by *Pineus laevis*. Unseasonable frosts in 1932 caused some damage and were followed by *Diplodia pinea* attack. Some suppressed trees were being killed by *Sirex* but the forest was becoming badly overstocked, with very small crowns and short upright branches.

No great change took place until 1946; at this time the floor was covered by a thick layer of undecomposed needles and twigs and there were no ferns or other undergrowth, although there appeared to be ample light and more than adequate rainfall. The thin and relatively elongated crowns with upright branches tended to collect rain, which ran down the trunks and percolated deeply into the pumice. The soil beneath the litter was of poor structure and contained few earthworms. The previous thirteen years, all with wet summers except 1939, had probably favoured needle fungi and contributed to the poor condition of the crowns. By 1946 then, the stand was in a very dangerous condition with mutual suppression of almost all the trees and there appeared to be no natural thinning agent capable of bringing about an adjustment. The severe drought of the 1946 summer had no apparent effect upon the forest, which was outwardly in better health than before the drought. Actually the drought had had a very drastic effect upon the smaller trees which rendered them susceptible to killing by *Sirex* attack. This enabled the *Sirex* population to build up to epidemic numbers. The *Sirex* population reached a peak in the summer of 1949 but had reverted almost to normal by 1950. Tree mortality also increased yearly and reached a peak in the winter of 1949. Total deaths over the four winters amounted to 30 per cent. of the trees. In 1950 mortality was very slight but a further 10 per cent. of the surviving trees died in 1951. After this thinning there were many important changes in the forest. Branches grew out and sagged down, spreading drips over the forest floor instead of conducting the rain to the trunk. The litter decomposed, there was a great improvement in soil structure, earthworms became plentiful, and white leached zones in the soil began to disappear. Most important of all was the appearance of a great variety of native plants including over 30 species of ferns. Of the ferns the most conspicuous were the tree ferns of which there are now from 200 to 400 per acre over much of the forest. *Dicksonia squarrosa* Swartz. is the most common, followed by *D. fibrosa* Col. and *Cyathea dealbata* Swartz. *C. cunninghamii* Hook. f., *C. smithii* (Hook.) Domin. and *C. medullaris* Swartz. occur in about equal numbers. It is evident that if the forest were not felled or burnt the *P. radiata* could not reproduce itself in competition with the invading native flora. Although the present stands frequently contain a dense understorey of regenerated pine, few of these would survive to produce seed, and seed would find no place suitable for germination. Possibly Douglas fir would eventually take over and species such as rimu, totara, and matai should eventually colonise the sites.

All tree ferns, except *D. fibrosa*, and most of the native shrubs are water-dispersing species, the leaves being resistant to wetting and provided with drip points. *D. fibrosa* is a water-collecting species, water tending to run down the fronds to the crown and collect in the matted fibrous roots, consequently *D. fibrosa* is the most plentiful fern on the dry ridges.

Since 1951 there has been a steady increase in volume over most areas with a light but continual mortality. Most areas appear to be badly overstocked should another drought, similar to that of 1946, occur. What effect the changes in soil, vegetation, and other factors would have in decreasing or increasing drought effects is quite unpredictable.

While the history of this particular forest has been sufficiently well recorded for the salient features and controlling factors to be followed from the time of planting, any sequence of factors could give a very similar end result provided that damage and mortality occurred in moderation and at appropriate times.

CONCLUSION

Up to 1946 no entomological factor had been of much importance in the development of *P. radiata* stands at Kaingaroa. The chief feature had been the lack of natural agents to kill suppressed trees and so to prevent stagnation caused by unrelieved competition. The 1946 drought and *Sirex noctilio* combined to relieve a very dangerous situation through killing the small and deformed trees. At present the condition of the *P. radiata* bears much resemblance to that of 1946 but differs in the age and size of the trees, much lower stocking and the presence of an understorey of tree ferns and shrubs. The effects of another drought summer are awaited with considerable interest.