

INSECTS DAMAGING BEECH (*NOTHOFAGUS*) FORESTS

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INTRODUCTION

The distribution of living and fossil *Nothofagus* in the southern hemisphere (Skottsberg 1949) suggests the possibility that it once played a part in colonising primitive and unstable soils comparable with that played by *Pinus* in the northern hemisphere. Each genus includes species which colonise rocky soils of mountain ranges and glacial, alluvial and volcanic deposits; each genus is, or has been, represented from circumpolar regions to the highlands of the tropics. Those species best adapted as pioneers are most tolerant of variations in soil moisture, nutrients and temperature, but either require insolation of the soil for germination or are intolerant of shade as seedlings so that little regeneration survives under closed canopy. Since adjacent trees are commonly interconnected through root grafts, deaths of individual stems do not normally provide root space for the development of seedlings. Larger gaps in the canopy resulting from storm damage or other natural causes of group mortality tend to be rapidly filled with dense regeneration. For these reasons, forests of pioneer species are typically even-aged except near advancing margins or where group mortality has occurred (Wardle 1970, Wardle 1974, p. 23 for *Nothofagus solandri*). Mortality as a result of competition in even-aged stands ensures a continuing supply of host material in addition to that provided intermittently by climatic damage and senescence for those organisms which thrive on weakened or moribund tissues. Such a coupling of extensive geographic distribution and mortality resulting from intraspecific competition has probably provided environments conducive to the evolution of aggressive insects and pathogens of forest trees. To the extent that this is so, comparison of the insect complexes of *Pinus* and *Nothofagus* may be meaningful although the genera belong in

different subdivisions of the Spermatophyta.

A further reason for attempting such a comparison arises because *Pinus* has been extensively managed in conjunction with its endemic complex of insects and diseases, while stem rots and insect damage in untended stands of New Zealand *Nothofagus* have seriously restricted utilisation (Johnston 1972). There is little doubt that the New Zealand beeches — especially silver beech (*N. menziesii*) — could become a much more valuable hardwood resource if insect and rot defects could be obviated. With this purpose in mind, it is relevant to enquire whether the insect problem is any less capable of solution in *Nothofagus* than it is in *Pinus*.

THE INSECTS INFESTING *PINUS* AND *NOTHOFAGUS*

It seems characteristic of forest trees belonging to pioneer genera that they support a numerous and diverse fauna of insects, a few of which precipitate the local losses of canopy trees which these tree genera are so well adapted to withstand. Most of the insects which utilise living tree tissues are present in numbers which are controlled by the physiological state of the host as well as by parasites and predators. Water stress in the host has the effect of reducing the translocation of photosynthesate; increased photosynthesate levels in foliage accelerate the development of defoliators and sapsuckers. Water stress in the stem has the effect of reducing the rate of flow of gums and resins which are produced in response to wounding, so that insects and attendant fungi can enter and establish themselves more readily. Nitrogen levels in soils affect the water uptake of roots (Goyer & Benjamin 1972) and thus affect the susceptibility of trees to insect damage. Pioneer trees persist on infertile and shallow soils from which highly soluble nitrogenous compounds tend to be leached. In brief, it appears that the

susceptibility of pioneer species to insects is directly related to moisture stress — in part induced by overstocking and hence intraspecific competition, in part by seasonal variations in soil moisture, and in part because of impaired root uptake of moisture associated with the low nitrogen levels of the soils where they persist. Whether one considers *Pinus* or *Nothofagus*, few of the insects are restricted to one host species, though the relative abundance may vary both between hosts and between sites.

1. Sap-suckers

Eriophyid gall mites are associated with all New Zealand species of *Nothofagus*. Pouch galls certainly occur on leaves of *N. fusca* and *N. solandri* and probably on the other two species. Flower buds of *N. fusca* are galled, and other bud galls occur in all the species. Most conspicuously, terminal buds of *N. menziesii* form "witches' brooms" when they are invaded by eriophyids. Eriophyidae seem to be more common on angiosperms than gymnosperms.

Heavy attacks by spittle bugs belonging to the genera *Tilophora* and *Aphrophora* (Cercopidae) may kill tops, branches and sometimes young trees of *Pinus*. Pine aphids (*Eulachmus* and *Cinara*) and *Pinus* spp. (Adelgidae) are common, especially when pines are subject to drought. The scale insects of *Pinus* include species of *Matsucoccus* and *Drosicha* (Margarodidae), *Toumeyella* (Coccidae) and the armoured scales *Lepidosaphes* and *Phenacaspis* (Diaspididae). *Nothofagus* is not affected by spittle bugs or aphids. *Nothofagus solandri* growing in dry regions supports large numbers of *Ultracoelostoma assimile* (Margarodidae) on thick barked parts of the stem. Honey dew is produced by scale insects in such quantities on the stems of *N. solandri* that it is utilised by commercial apiarists. On *Nothofagus* the Eriococcidae are represented by 22 species, of which only one has other hosts. An armoured scale, *Inglisia* sp., occasionally reaches outbreak levels on *N. fusca* during seasonal droughts. During droughts the upper crowns can become completely defoliated and the lower foliage and that of the understorey is smothered with sooty moulds. It appears that populations of this scale insect are normally

controlled by parasitic fungi. When moist conditions are restored, the fungi rapidly regain control and crowns appear to recover completely.

Whereas *Nothofagus* recovers well after outbreaks of sap-sucking insects, resin reactions to stylet punctures in *Pinus* tend to restrict conduction and this may result in the death of smaller stems.

2. Defoliators and Foliage Miners

Amongst other defoliators and foliage-miners feeding on *Nothofagus* are three species of *Proteodes* (Oecophoridae). *P. carnifex* occurs on all the species, normally in low numbers. Outbreaks of *P. carnifex*, which may persist and spread for several seasons, are known only on *N. solandri*. During outbreaks, trees may be severely defoliated during the summer but usually produce some new foliage before the winter. Occasionally no new foliage appears until the following spring. Even with two successive seasons of severe defoliation there is no indication that trees are either killed or so weakened that they succumb to other insects or pathogens. Other tineoid defoliators of *Nothofagus* are sometimes common on the foliage of larger trees though the injury they cause appears to be well tolerated.

Tortricoid defoliators of *Pinus* include the pine budworms (*Choristoneura* spp.) which prefer to feed on the bases of the most recently produced needles. Defoliation for several successive years greatly reduces wood growth and may so weaken the trees that they become susceptible to bark beetle attack. *Nothofagus* supports a number of Tortricidae at least three of which also occur on other hosts. *Epichorista emphanes*, which feeds exclusively on *Nothofagus* spp., is the only one of these which occurs in outbreak numbers. Outbreaks have been localised, do not appear to last for more than one season and are not known to cause any long term injury to the trees. A related family affecting *Pinus*, the Olethreutidae, includes the pine tip moths (*Rhyacionia* spp.), the shoot moths (*Eucosma* spp.), and the pitch nodule moths (*Petrova* spp.). While lacking olethreutids, all species of *Nothofagus* are affected by *Carposina*

eriphylla (Carposinidae) the larva of which feeds on inner bark and callus at the margins of wounds. Its chief importance seems to be that it enlarges wounds made by other insects and delays healing.

Caterpillars and pyraloid moths which affect *Pinus* include the webworm *Tetralopha robustella* (Pyralidae) in the eastern U.S.A., the inner bark borers, or pitch moths, of the genus *Dioryctria*. *Dioryctria* spp. cause the formation of resin pockets which become included in the wood. No Pyralidae damage *Nothofagus*.

Bombycoidea are represented on *Pinus* by *Dendrolimus spectabilis* (Lasiocampidae) and *Coloradia* spp. (Saturniidae). Most damaging lasiocampids (e.g. *Malacosoma* spp.) and saturniids are associated with hardwood hosts, but the former do not occur in New Zealand and the latter are represented only by the introduced eucalypt silk moth *Antheraea eucalypti*.

Butterfly larvae which feed on *Pinus* foliage include those of *Spindasis takanonis* (Lycaenidae) in Korea and Japan and the ponderosa pine butterfly *Neophasia menapia* (Pieridae) of western North America which may kill its preferred host during outbreaks. *Nothofagus* species do not support butterfly larvae.

The Geometridae which feed on *Nothofagus* include the general feeders *Selidosema suavis* and *Declana floccosa*. *S. productata* is common on beech but also occurs on other hosts. *D. feredayi* and *Tatasoma fasciata* appear to occur exclusively on *Nothofagus*. Outbreaks of these geometrids on *Nothofagus* are unknown, although local outbreaks of *S. suavis* have occurred on *Pinus radiata* in Canterbury. Geometridae are usually of minor significance on endemic *Pinus* though a number of species belonging to *Semiothisa*, *Ectropis*, *Zethenia*, *Nepytia*, *Lambdina*, *Eufidonia*, etc., are known to feed on pine needles.

The larva of the black hawk moth, *Hyloicus caliginus* (Sphingidae) occurs on pine foliage in China, Japan and Korea, but again there is no counterpart affecting the New Zealand beeches.

Sawflies belonging to the genera *Neodiprion*, *Nesodiprion* and *Diprion* (Diprionidae) and *Acantholyda* and *Cephalcia* (Pamphiliidae) defoliate *Pinus*. Some of these are serious forest

pests which have no counterpart on *Nothofagus*. Some adult buprestid beetles, e.g. *Buprestis apricans*, feed on pine needles for several weeks before mating and ovipositing. Each adult *Nascioides enysi* has been found to consume ten leaves of *N. menziesii* per day (Morgan, 1966). In each case adult buprestids are plainly a part of the defoliating complex of insects, but in neither case has their relative importance been established. Adult chafer beetles (Scarabaeidae) feed on foliage of both *Pinus* and *Nothofagus* while their larvae feed on roots. Several species of *Odontria* are numerous in monotypic *N. solandri* forest but as yet their significance is unknown.

In general, in their countries of origin, *Pinus* species are periodically subjected to severe defoliation by a great variety of caterpillars and sawfly larvae. During outbreaks severe defoliation may check wood growth, weaken trees so that they become susceptible to bark beetle attack and even kill them. On the other hand outbreaks of an oecophorid moth which last for more than one season and extend over considerable areas affect only one of the indigenous *Nothofagus* species (*N. solandri*); even in this case the trees rapidly regain full foliage and no long term injuries stem from defoliation.

3. Inner Bark Feeders

The bark feeding habits of caterpillars of *Carposina eriphylla* in *Nothofagus* and *Dioryctria* spp. in *Pinus* have been briefly mentioned above and many of the sap-sucking insects are essentially dependent on these tissues. In addition, the larvae, the adults (or both) of beetles belonging to the Buprestidae, Cerambycidae, Scolytidae and Curculionidae feed on inner bark.

Buprestids belonging to the genera *Melanophila* and *Chrysobothris* are especially associated with suppressed, dying or freshly felled *Pinus*. Eggs may be laid on living trees which are growing very slowly, but development of the larvae is retarded until radial growth ceases (Anderson 1960). Two buprestids, *Neocuris eremita* and *Nascioides enysi*, are found in *Nothofagus* forests. Larvae of the former occur in small diameter dead branches of *Nothofagus* but

are not restricted to beech. *Nascioides enysi* has long been regarded as an important cause of beech mortality (Cockayne 1926, Morgan 1966) and is restricted to the beech species. The writer has recently suggested (Milligan 1972) that *N. enysi* larvae do not develop beyond the first instar unless they reach the inner phloem, and are prevented from doing so by host gum reactions as long as the tissues remain alive. Still more recently, it has been observed (J.A. Wardle pers. comm.) that early larval mines of the buprestid in pole sized *N. solandri* occur exclusively in those stems in which growth is suppressed. It follows from this observation that ovipositing *N. enysi* must select specific physiological conditions in the host. Similar conditions must prevail, at least temporarily, in branches of healthy trees since larvae also occur there. Since *N. enysi* do not oviposit when the temperature is below 22°C, and higher temperatures are required in the absence of direct sunlight (Morgan 1966), it seems likely that stem moisture stress is associated with attractiveness to ovipositing females. If the stress is of a temporary nature the larvae fail to develop; if it is indicative of a moribund condition they are able to reach the cambial zone and to complete their development. *Nothofagus* mortality previously attributed to *N. enysi* is now more convincingly interpreted as a consequence of *Platypus* attack (see below): the part played by *N. enysi* appears to be closely comparable with that played by *Melanophila gentilis* and *M. drummondi* in the death of pines.

The larvae of many longhorn beetles (Cerambycidae) feed in the inner bark of forest trees. As a rule, the trees are dead when they are selected as host material. The sawyer beetles, *Monochamus* spp., lay their eggs on dying and freshly felled *Pinus*. Later, larval mines enter the wood causing appreciable losses of otherwise salvagable standing timber and of stockpiled pulpwood. In parts of Japan adults of a species of *Monochamus* have the habit of biting holes in the thin bark of the upper stem of pines, and in doing so infect the wounds with a nematode which invades the wood and rapidly kills the trees. Longhorn beetles which damage *Nothofagus* are essentially wood feeders, and will be considered below.

Some species of bark beetles belonging to the genera *Dendroctonus*, *Ips*, *Blastophagus* (*Myelophilus*) and *Cryphalus* (Scolytidae) are the cause of most insect damage in the areas where *Pinus* is endemic. Outbreaks are commonly initiated by wind throw or droughts. *Blastophagus piniperda* and *B. minor* occur throughout the Palaearctic region but are absent from North America. Broods are reared in the inner bark of recently killed trees and the beetles feed in the leading shoots of young *Pinus* before they establish brood galleries. Damage to apical shoots during maturation feeding leads to the formation of bushy trees which are of little use for timber production. Aggressive species of *Dendroctonus*, *Ips* and *Cryphalus* bore into and feed on the inner bark of living *Pinus*. While *Dendroctonus* attacks tend to occur mostly in the lower parts of the trunk, those of *Ips* are concentrated in thinner barked regions and *Cryphalus* attack branches and tops. Sapstain fungi carried either in specialised organs or externally on the body surface (Francke-Grosmann 1963) invade sapwood adjacent to the tunnels and play a part in interrupting conduction so that the crown wilts and the tree dies when a sufficient number of attacks are concentrated on it. Brood galleries may extend from the initial feeding tunnel or may be made in other parts of the killed tree. Although weakened trees are preferentially attacked, adjacent healthy trees are killed when broods emerge some 4-5 weeks later. This leads to group mortality, which occasionally extends over large areas. Up to five broods are produced over the warmer months, so outbreaks develop rapidly. Losses (of the order of 1 billion board ft/year) caused by *D. brevicornis* attack on ponderosa pine in the Pacific Coast States of U.S.A. over a 25 year period were almost 1½ times the increment, and more than 10 times greater than losses by fire (Anderson 1960). Bark below the green crown may be completely stripped by feeding adults of *Ips grandicollis*, which later make brood galleries in the lower parts of the killed tree. Outbreaks of *Ips avulsus* during droughts in Texas, U.S.A., have necessitated extensive sanitation salvage operations. The role of *Cryphalus* species in tree

mortality is less well documented, but some are said to predispose trees to attack by other bark beetles. The Scolytidae of indigenous *Nothofagus* are represented by one (or perhaps two) species of *Hypocryphalus*. These are commonly found in small branches of felled trees and seem to be restricted to dead or moribund tissues.

4. Wood-borers

Pinus is little affected by wood-boring caterpillars, though minor damage is caused in North America by larvae of the clear-wing moth *Parharmonia pini* (Aegeridae). All species of *Nothofagus* are susceptible to damage by the larvae of the ghost moth, *Aenetus virescens* (Hepialidae), but *A. virescens* fortunately is absent from the South Island. Early instars of *A. virescens* feed under a silken tent, often at twig bases, on the bark of seedlings. As they grow the larvae migrate to larger and woodier stems in which they bore "7"-shaped refuges, the long arm parallel with the stem axis and the shorter one extending to the surface. From this shelter, and concealed from the outside by a silk tent, the larva feeds on inner bark and callus induced at the margins of the wound. The bark is often eaten away for more than half the circumference of small stems and branches, and the wounds are a common cause of breakage during gales or snowfalls. When the bark of poles becomes too difficult for the larvae to penetrate they tend to move further up the stems; old damage then becomes overgrown by new wood. Cores of damaged wood tend to be of greater diameter in *N. menziesii* than in *N. fusca* or *N. truncata*, and this appears to reflect the earlier development of resistant bark in the latter two species. Wetas (*Hemideima* spp. : Tettigoniidae) take over the caterpillar refuges, enlarge them and keep the entrances open for many years. When the wetas emerge to forage after dark they serve as vectors of sapstain and rot fungi. As long as the tunnels are kept open, aerobic conditions favour the spread of rots. Core rots associated with old ghost moth damage are usually most extensive in *N. menziesii*. Current ghost moth damage may be found in the branches of mature trees of all the *Nothofagus* species as well as in hosts belonging to other families.

Pinus is affected by Hymenopterous wood-borers belonging to the family Siricidae. As a rule these are of minor importance in endemic pine forests, but *Sirex noctilio*, which has been accidentally introduced into New Zealand and Tasmania, has occasionally caused extensive damage in plantations of *Pinus radiata*. Outbreaks have been associated with sustained droughts and overstocked stands. *Sirex noctilio* lays its eggs in the wood of living trees, often in greatest numbers just below the green crown. A fungal symbiont introduced with the eggs causes wilting of the crown and death of the tree. Only if the wood dies do the larvae develop. Brood is also reared in logging wastes, windthrown trees and those snapped off in gales or snowfalls. The nearest relative of the siricids in *Nothofagus* is *Xiphidryia dunniana* (Xiphidryidae), the larva of which develops in dead twigs and small branches. There is no evidence that *X. dunniana* kills the twigs which it utilises.

Buprestid and cerambycid wood-borers associated with *Pinus* seem able to gain entry to the wood only through wounds which are incompletely covered with resin and are therefore unimportant except in forest produce and as agents which break down the stumps and other forest wastes. Upper parts of *Nothofagus* regeneration are girdled and killed by larvae of the longhorn beetle *Navomorpha lineata*, which later hollow out the lower living stem. Eggs of *N. lineata* are frequently laid at wounds such as those made by ovipositing cicadas. Similar damage occurs in small branches of *Nothofagus* trees and occurs in many other hosts. Where poles or larger trees of *N. solandri* (and occasionally *N. fusca*) closely associated with *Leptospermum* they may be damaged by larvae of the longhorn beetle *Ochrocydus huttoni*, for which *Leptospermum* is the usual host. Larval tunnels in the sapwood are large, predominantly vertical, and free of frass. The frass is ejected through small openings which are cut from the larval galleries to the exterior. Wetas utilise the flight holes, pupal chambers and larval galleries of *O. huttoni* just as they use ghost moth refuges. Damage is unusual, except in *N. solandri* (which is little sought after as a timber producing species) and even in this host, diminishes in frequency with distance from scrub margins.

Species of *Platypus* (Platypodidae) are amongst the first invaders of *Pinus* killed by bark beetles but do not invade the living stems. Coster (1969) found that *P. flavicornis* bored into *Pinus* trees four to six days after they were infested by *Dendroctonus frontalis*. Damage was restricted to the lower few feet of wilting stems where wood moisture content would remain highest. In New Zealand *Nothofagus* forests there are three species of *Platypus* — *P. apicalis* White, *P. gracilis* Broun and *P. caviceps* Broun — which readily breed in freshly fallen trees, logs and stumps. *Platypus caviceps* is not known to breed in any other hosts but the other two may breed in a variety of hardwoods and softwoods. All three species will attack living and apparently healthy *Nothofagus* trees. Rarely, stems only six centimetres in diameter are attacked, but abortive attack is not uncommon in those 15 cm or more in diameter. Brood of *P. apicalis* and *P. gracilis* are known to emerge from nests in large diameter trees which are still alive, but attempted nests of *P. caviceps* fail unless the tree dies. Attacks of *P. apicalis* and *P. gracilis* are concentrated on the lower six metres of the living tree; those of *P. caviceps* also occur in this region but extend up to a height of 21 m. This distribution of attack by the *Platypus* species on living trees is perhaps comparable with that of *Dendroctonus*, *Ips* and *Cryphalus* on living *Pinus*.

When *Nothofagus* trees of sufficient diameter to contain heartwood are attacked, the initially radial *Platypus* tunnel curves through a right angle as the transition zone is approached and then continues tangentially close to this zone. It seems that this change of direction is linked with progressive reduction of moisture content of the sapwood. In stems with no heartwood the tunnel continues towards, and sometimes through, the organic centre. If small stems have been attacked in a previous season, resulting in a core of dead and discoloured wood, the tunnels deviate as the outer margins of the dead core are approached. Fungal hyphae, tyloses in the vessels and dark contents in the ray cells and vertical parenchyma are found in such dead cores. In contrast with heartwood, these cores are readily invaded by sapstain and rot fungi (Milligan 1972).

Evidently a pathogenic sapstain fungus is

transmitted by the beetles and becomes established initially in the innermost sapwood where wood moisture content is least. Butcher (1968) found that *Ceratocystis piceae* was the main cause of staining in untreated sapwood of *N. fusca*, and noted that the same fungus occurs in *N. menziesii*. Staining caused by *C. piceae* was associated with discolouration of ray cell contents rather than with pigmented fungal hyphae. When *Platypus* invades living trees, or when scrapings from nests are introduced into holes drilled in living trees, a sapstain fungus which does have pigmented hyphae and which causes extensive reactions in living wood cells, advances further than other fungi from the wound (Faulds 1973). This fungus, designated "Fungus A" by Faulds, is associated with progressive death of inner regions of the sapwood. It is readily cultured, and the pathogenicity of cultures is being examined; but, so far, it has not been identified. On the other hand, a species of *Ceratocystis* is the dominant component of the flora of older parts of *Platypus* tunnels. The genus *Ceratocystis* (*Ceratostomella*) includes a number of sapstain fungi which are transmitted by the bark beetles which damage pines.

Whereas the bark beetles feed on the inner bark through which they tunnel, *Platypus* and other ambrosia beetles do not feed on wood. Freshly bored tunnels of the New Zealand species soon acquire a lining of yeasts which are the primary food of both adults and larvae. Yeasts are also transmitted by bark beetles, occur in all the feeding stages and are digested, but their precise role in the nutrition of bark beetles has not been determined (Callaham & Shifrine 1960).

Aggregation of attack on particular trees is characteristic of, and essential to, aggressive bark beetles. Unless a sufficient number of wounds are made, and a sufficient part of the sapwood exposed to the sapstain fungi which interrupt its conducting function, the tree will not die and so will not become a suitable medium for the rearing of brood. Aggregating mechanisms have been demonstrated in a number of cases. Those beetles which initiate the galleries produce volatile chemicals in the hind gut which, in combination with volatiles emanating from the

wounded host, serve as powerful attractants to others of both sexes. The insect-produced volatiles (pheromones) become adsorbed on faecal material which is discharged an hour or two after feeding begins. Madrid, Vité & Renwick (1972) have recently shown that aggregating pheromones are also produced in the hind gut of male *P. flavicornis*. Observations on the behaviour of New Zealand *Platypus* have for some time indicated the existence of such aggregating pheromones. During the 1972-73 flight season it was found that freshly emerged males of *P. apicalis* emit an odour which is so distinctive that the sexes can readily be separated on this basis alone. So far it has not been shown that the odour is attractive to others of the species under laboratory conditions. In earlier field experiments it was found that trees near cages containing emerging beetles became heavily attacked by wild populations. Since the caged beetles could not reach these trees it appeared that additional odours from the wounded host were not initially essential for attraction of others. On these grounds the existence of an attractant originating from the beetles was deduced.

Attempts to test the attractiveness of chemicals to *P. apicalis* in the laboratory have been confronted with the difficulty that freshly emerged adults are initially attracted to light, and this attraction over-rides those of a chemical nature. Immediately before boring into the wood in the case of the male, or before a female joins a male in a tunnel, the attraction to light must be reversed. Such a phototropic reversal probably occurs as a result of flight (Graham 1961). The "male odour" of *P. apicalis* is emitted soon after beetles emerge, so if the odour detected indicates the emission of an aggregating pheromone some aggregation should occur in flight as well as at the surface of host material.

Droughts have long been recognised as a common cause of bark beetle outbreaks in coniferous forests. That flooding may also render trees susceptible to bark beetle attack (Anderson 1960) is comprehensible if it results in partial death of the root systems, so that the uptake of water by the roots becomes less than transpiration losses during warmer weather. In

either case reduced wood moisture is favourable for the spread of sapstain fungi introduced by the bark beetles. As a practical expedient, logs are stored in ponds or under water sprays so as to limit the spread of sapstain. Although the fungi associated with pine bark beetles have not been found to be particularly virulent pathogens, their association would appear to be an essential one for the success of both organisms. When small diameter *Nothofagus* trees are attacked by *Platypus* the associated pathogen first establishes itself in the drier, innermost sapwood and then spreads outwards until it reaches limits imposed by wood moisture and defensive reactions of the outer sapwood. During seasonal droughts, and especially on severely drained sites, centrifugal advance of the fungus may be accelerated. Radial prolongations of killed sapwood occur at the tunnels and where spearheads of the advancing fungus break through gum barriers. As a rule these small trees do not die, even though they are severely attacked. On the other hand trees which were only lightly and abortively attacked have succumbed to the pathogen when a drought occurred in the following summer, even without a second attack in the drought year. This indicates that the pathogen can survive for at least a year in trees which were only abortively attacked by *Platypus*. Surviving trees are left with a core of pathological wood which is often stellate in section, or, if not stellate, then with the boundaries only rarely coincident with the growth rings. Rot fungi may erode these cores, especially where aerobic conditions prevail close to the *Platypus* tunnels. In field experiments, all *N. fusca* over 35 cm in diameter which were severely attacked died within two to four years. One tree, attacked over the summer of 1965-66 suddenly died in the following October, that is in less than a year. Though susceptibility to this sort of mortality is not necessarily equal in the various species of *Nothofagus*, none is immune. *Platypus* and the associated pathogen have been found to be involved in most instances of deaths of mature *Nothofagus* examined since 1965. An important exception is the recent deaths of *N. truncata* eight to ninety centimetres in diameter in the Rai Valley-Whangamoia area, where dieback and deaths were associated with a stem canker not caused by fungi and not linked with insect attack.

Nowhere else in the world have species of Platypodidae been implicated as vectors of tree-killing pathogens, so their role in forests has not been related to that of aggressive Scolytidae. Nevertheless a number of similarities appear. One that is perhaps crucial is that drought, and hence wood moisture of the stem, immediately affects the spread of fungi which are introduced by both groups of insects. Only if the fungi spread rapidly is the tree killed. In the case of a bark beetle which completes its life cycle in about two months, eggs are laid about a week after the attack starts, hatch a week after laying and larvae are fully grown after feeding for three weeks (Anderson 1960). Newly hatched larvae probably have least capacity to overcome host resin reactions to wounding, so tissues near the egg gallery must be effectively dead two weeks after attack starts if the larvae are to survive. Anderson remarks that, once large bark beetle populations are developed, even the most vigorous trees are attacked and killed, but the number of offspring produced in such initially vigorous trees is low. Death of vigorous trees, whether of *Pinus* or *Nothofagus*, depends on there being large numbers of inoculated wounds at any one level between roots and crown — or upon concentration of insect attack. To ensure high density attack, aggregating mechanisms are necessary, so it is hardly surprising that initial evidence of aggregating behaviour has been found in New Zealand *Platypus*. *Platypus* life cycles are completed in approximately two years, and small groups of eggs are laid over a considerable period, so it is less dependent on rapid tree death than are the bark beetles. Furthermore, when it attacks living trees in which heartwood is developed, wood with a reduced moisture content for the initial establishment of the pathogen is always available at the transition zone. In fact rapid drying of the stem above a block in conducting tissue may be inimical to the development of brood which depend on yeasts rather than on sapstain fungi.

PLATYPUS AND BEECH MANAGEMENT

Johnston (1972), referring to West Coast *Nothofagus* and beech-podocarp forests, reports that the beech component has been little utilised because of extensive hidden decay and

difficulties in sawing, seasoning and treating. There are, especially in western Southland, extensive areas of *N. menziesii* which is sawn, seasoned and treated without undue difficulty. Furthermore, in mixed *N. fusca* and *N. menziesii* forests elsewhere, the proportion of the latter could readily be increased by selective thinning of the regeneration. Natural *Nothofagus* forests all suffer from the prevalence of insect and rot defects so that little interest has been aroused for their management on a commercial scale.

It seems that much of the stem defect arises directly from sublethal *Platypus* attack on growing trees, but rots of the upper stem are commonly associated with dead branches. If pathological wood has been formed below the crown, rots entering through dead snags may more readily spread downwards. D.A. Franklin (pers. comm.) has shown that rot fungi are absent from branch traces pruned five years previously, so there seems a real prospect of minimising defects if trees are pruned to the height required for a merchantable log, especially if pathological wood caused by *Platypus* attack can be minimised at the same time (see also Franklin 1974, p.19).

A silvicultural regime which would produce beech logs with least defect in the shortest time is plainly needed. Widely spaced saplings of *N. menziesii* arising in a low nurse crop such as *Fuchsia* or *Leptospermum* will break crowns from heights of about six metres and such trees, with large crowns and correspondingly large root circles, are known to increase in diameter at rates of up to 16 mm a year. Short, large diameter trees which were resistant to windthrow could also be produced by thinning the thicket stage of dense regeneration to final crop spacing as soon as the minimum of height growth was obtained. Pruning to an appropriate height would be required. The thinning operation would create minimal *Platypus* hazard because the wastes would be too small to support broods, and the crop stems would be below the diameter susceptible to attack. Windthrow, which favours local outbreaks of *Platypus* in untended stands, would be least likely in a stand of short trees with large root circles. Large crowns would promote most rapid attainment of merchantable diameters, reducing the period of growth during

which the crop was susceptible to *Platypus* damage. The only stage when the crop trees would be prone to damage would be when harvesting commenced, when *Platypus* from the surroundings would be attracted by stumps and logging wastes. However, logging of such a high quality tended stand is at least 50 years away, so there is ample time to perfect methods of controlling *Platypus* populations.

None of the other insects associated with *Nothofagus* seem likely to create serious problems in the management of *N. menziesii*.

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