A REVIEW OF BEECH FOREST PATHOLOGY

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SYNOPSIS

Aspects of the anatomy and physiology of Nothofagus *spp. apparently relevant to injury to trees by climatic factors, fungi and insects are noted.*

A presumably pathogenic fungus is reported spreading from inner to outer sapwood from the vicinity of Platypus *tunnels in living trees. It has so far been found in* N. menziesii, N. solandri *var* cliffortioides, N. fusca *and* N. truncata. *Its success as a pathogen appears to depend on its transmission to innermost sapwood of living trees by* Platypus.

Observations and experiments suggest that Platypus *attack is not restricted to weakened trees. Proximity to sources of emerging brood and to freshly felled or windthrown material appear to be two important factors determining whether or not trees are attacked. Trees of a sufficient diameter to contain an appreciable core of heartwood died following heavy attack; smaller trees which suffered comparable attacks recovered but were left with a core of dead and discoloured sapwood which is here termed pathological wood.*

The buprestid, Nascioides enysi, *previously considered to be an important factor in mortality of* Nothofagus, *is found to develop beyond an early larval stage only if the inner phloem, cambium and outermost sapwood lose the capacity to produce gums in response to wounding, a condition characteristic of dead tissue.*

INTRODUCTION

At the fifth Forest Research Institute symposium, "Beech Forestry in New Zealand" in 1964, J. S. Dugdale presented a paper on insects thought to be damaging to beech, and J. W. Gilmour contributed on the pathogenic fungi. These two papers fairly represented the state of knowledge on damaging organisms at that time. Both speakers agreed that the limited knowledge available did not permit a definite assessment of their impact on the health and growth of beech trees.

Morgan (1966) was of the opinion that *Nascioides enysi* kills beech trees during outbreaks, and discussed various ways of preventing outbreaks. At the same time he maintained that only those trees predisposed by a range of postulated damaging agents were likely to be killed.

The beech forestry symposium did not include a contribution on the physiology of beech trees, as there was no worker in this field. The role of damaging organisms cannot be interpreted without regard to the physiology of the host, especially its responses to damage. Sound forest management must be based on forest pathology and on crop tree phenology, par-

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ticularly growth and reproduction. Clearly, management needs information on beech tree physiology.

The following observations and sometimes debatable deductions are set down here in the hope that they may spur competent studies.

ANATOMY AND PHYSIOLOGY OF BEECHES

The following fragmented observations apply to red beech, *Nothofagus fusca*, unless otherwise specified, but are probably applicable to the other New Zealand species to some extent.

The rooting habit is shallow (Conway, 1952, p. 294; Williams and Chavasse, 1951, p. 221) whether trees grow on shallow soils over rock, on morainic or alluvial gravels, or on deep, permeable, volcanic ash deposits such as those of the central North Island. The disposition of the roots apparently indicates that they require a high level of aeration since trees commonly die if spoil is deposited over the roots by floods, slips or roading. The shallow rooting habit makes them prone to windthrow. In windthrown trees insects and fungi harmful to healthy standing trees may reach local outbreak levels. During seasonal droughts their shallow root systems make beech trees particularly susceptible to moisture stress.

Diurnal stem moisture deficits in summer may be high. Four samples were taken from each of two mature and two pole-sized mountain beech (*N. solandri* var. *cliffortioides*) growing on the lower slopes of Mt. Grey, Canterbury. In all 16 samples the moisture content of the outer 12.5 mm of sapwood was found to be only 50% of the oven-dried weight in the early afternoon of a particularly hot summer day. These trees appeared healthy at the time, and subsequently survived. The corresponding diurnal deficit in sapwood inside this zone was less marked, the moisture content being higher than that of the outer wood. Sapwood moisture content in healthy red beech is about 90 to 120% when the entire sapwood band is included in the sample.

In the main part of the stem of mature trees the sapwood is generally about 6 to 7 cm in radial thickness. In silver beech (*N. menziesii*) sapwood thickness is probably greater. Since the cross-sectional area of the conducting tissues between roots and crown is probably constant, at flanged bases where the circumference is greatly increased, the thickness of sapwood is correspondingly decreased. The moisture of the sapwood in an unstressed tree decreases from the outer, most actively conducting, tissues inwards, reaching a minimal value at the transition zone between sapwood and the moist heartwood. As mentioned above, at times of maximum transpiration losses the outermost sapwood may temporarily have a lower moisture content than the layers inside it, suggesting that radial movement of moisture in sapwood is a relatively slow process.

The initiation of heartwood formation appears to depend on girth rather than on age. A red beech, from the central North Island, aged about 150 yr and 19 cm d.b.h. was found to have no normal heartwood (although there was an irregularly shaped small core of reddish dead wood associated with ghost

moth wounds). Another tree from the Maruia district, was only about 70 years old, with 71 cm d.b.h., and all except the outer 7 cm appeared to be normal heartwood. It can be postulated that heartwood is formed when the cross-sectional area of conducting tissue exceeds that required to maintain an adequate flow of water between roots and crown. In changing from sapling to pole form, stems increase in girth most rapidly in the section between ground level and a height of about 60 cm. If the rate of heartwood formation depends on the rate of increase in girth locally, then heartwood at the base of the stem would be formed both earlier and more rapidly than elsewhere. Is there a possible connection between the possibly more rapid formation of heartwood in the lower parts of the stem and the fact that butt rots are usually restricted to this region? Is the concentration of those heartwood extractives which impart natural durability the same in heartwood at the base as in heartwood at breast height?

Because of the extractives deposited in cell walls of heartwood, this tissue tends to resist decay by saprophytic fungi. Since decay-causing fungi do not thrive under anaerobic conditions, the high moisture content of red beech and hard beech (*N. truncata*) may also play a part in resisting fungal decay. Even in those species with less durable heartwoods, decay fungi require a pathway from the outside to the dead tissues of the core. Dead roots could provide entry points for butt rots, just as dead branch stubs provide pathways for core rots of the upper stem. As the height of the stand canopy increases, lower branches are progressively suppressed and die. Whether a comparable functional suppression and death of elements of the root system occurs is apparently unknown. *Armillaria mellea* (Gilmour, 1966) is the commonest cause of butt rot in beech heartwood but does not appear to advance from the heartwood into the inner, least resistant sapwood. (Inner sapwood is considered "least resistant" because gum reactions are least vigorous here.) In sapwood adjacent to butt rots, to dead branch traces and wounds, bright red substances are secreted. These substances may be fungicidal, but, whether this is so or not, there is visible evidence that sapwood responds physiologically to proximity with decay fungi. Where this response is evoked, the fungi appear to be contained. Local accumulations of these red substances do not appear to affect normal wood functions.

Reactions to wounding of the stem must be taken into account when evaluating the various roles of insects and fungi. When holes are drilled mechanically through the bark and into the sapwood of healthy trees, the innermost phloem and the outermost sapwood break down in a lens-shaped area surrounding the wound and release gums. The maximum length of this response is variable, but it commonly extends further above the wound than below it. The maximum tangential width of the response occurs at the wound, and is approximately three times the diameter of an isolated wound. When several wounds occur close together, their response zones coalesce, forming large pockets containing gum and detritus surrounded by callus. This reaction to wounding

appears to be analogous to the formation of kino veins in eucalypts (Skene, 1965), although, in the latter, tissue breakdown occurs only in the outer xylem. The gums of *Nothofagus*, like eucalypt kino, could be polyphenolic glycosides (Dr V. Harwood, pers. comm.) but are even more soluble in cold water than is eucalypt kino so that gum exuded on to the surface of the bark tends to be washed off at the next rain. Sapwood that inwardly bounds the zone which breaks down produces gums intracellularly, particularly in the ray and parenchyma cells; some of this gum passes into vessels. In some microscopic sections brown contents have been found within the tapered ends of fibres, suggesting that protoplasm persists in these elements which the textbooks say die soon after elongation. The intensity of the gum response to wounding tends to diminish as the inner sapwood is approached. W. Faulds (pers. comm.) has found that the extent of gum response is minimal when sterile holes are drilled and plugged with sterile cotton-wool plugs. The wound response is greatly amplified when holes are left open, or when micro-organisms are deliberately introduced. He has also found some evidence that the extent of the response varies with the particular micro-organism introduced; greatest response so far is obtained by introducing an unidentified fungus cultured from the inner sapwood of a tree which had recently died following *Platypus* attack.

The sapwood which reacts by producing gums intracellularly is subsequently dead tissue, a property it shares with heartwood. However, it appears to lack the extractives which make heartwood resistant to rot fungi. In freshly cut samples, sapstain fungi invade this killed sapwood in preference to any other woody tissue, and heartrot fungi preferentially destroy it in living trees. Similar wood has been termed "false heartwood", "affected wood" and "pathological wood". A second phase in the development of pathological wood is its inclusion in the heartwood circle. During this process ray-like extensions of the transition zone, in transverse section widest, and in radial longitudinal section longest at the wound, come to include the gum-suffused sapwood. The time sequence of these various events has not been worked out. However, the effect of the two main processes is the formation of a core of stained dead wood which, in discs, has radial prolongations aligned with radial wounds. Similar periodic formations of pathological wood occur in rimu (*Dacrydium cupressinum*) where the cause of radial injury is unknown. In rimu this material is commonly called "intermediate wood" or "intermediate heartwood". In beech, true heartwood is subsequently formed at the new transition zone so that non-durable pathological wood becomes included in heartwood. Apart from the old stellate boundary indicating earlier radial wounds (commonly caused by *Platypus*), pathological wood and heartwood are difficult to distinguish visually. Earlier conflicting experiences on the natural durability of beech heartwoods could well be accounted for if some test samples included pathological wood.

Seasonal leaf fall is characteristic of beech trees, the season differing with species. Unseasonal and abnormally severe leaf fall has been observed when beech trees were severely attacked by *Platypus* and also when a scale insect reached outbreak levels on red beech during a seasonal drought. When abnormal leaf fall is induced, bare or sparsely leafed twigs first appear at the apex of the crown or at the ends of branches which project beyond the main mass of the crown. These parts appear to be those from which transpiration losses would be accelerated by sun and wind, and it could be considered that leaf fall therefore appears to be initiated by a deficit between moisture lost and moisture supplied through the stem. This point needs investigation. Buds may later burst on denuded twigs. If the onset of moisture stress is rapid, leaves are not shed but rapidly turn from green to brown without yellowing. This sort of foliage wilt occurs when trees are felled in summer. It also occurs on outlying branches of trees attacked by *Platypus*, and more rarely throughout the entire crown. In one instance the foliage of a standing red beech turned from green to brown in one week in October. Branches where this sort of wilt occurs do not appear to recover. In fact, the sapwood trace which supplied the branch dies back in an elongate triangular pattern. In contrast, death of sapwood does not occur below the origins of pruned branches or those subject to normal suppression, so it seems that branches which die of wilt offer unusually favourable conditions for the introduction of heart rots into the main stem.

OUTLINE OF PATHOGENIC FUNGI

A leaf spot caused by *Trabutia nothofagus* occurs on red beech and mountain beech (which commonly hybridize) but not on the remaining *Nothofagus* species. Silver beech, which does not form hybrids, is the sole host of three species of *Cyttaria* gall-forming fungi. *Armillaria mellea* is recorded as a root, butt and white heart rot from all except hard beech, in which it is recorded only as a white heart rot. *Polyporus berkeleyi* is the only other fungus recorded as a butt rot. A variety of species of *Coltricia, Coriolus, Fomes, Fomitopsis, Hymenochaete, Inonotus, Polyporus* and *Poria* are recorded as heart rots of one sort or another. The above fungi are recorded by Gilmour (1966). Specific host relationships are not to be expected if the butt and heart rots are essentially saprophytic. Whether *Armillaria* is pathogenic on beech roots is not entirely clear. The same fungus can be shown to colonize branches of felled trees in contact with the ground, and, as mentioned above, it does not appear to invade sapwood at the transition zone when it occurs as a butt rot. Therefore it does not appear to be an aggressive pathogen of beech and may, in fact, succeed only in moribund or freshly dead tissues.

In silver, red, hard and mountain beeches which have earlier been attacked by *Platypus*, darkly stained areas occur in the inner sapwood, or sometimes in pathological wood. Wood from *Platypus*-attacked black beech (*N. solandri* var. *solandri*)

has not been examined. Fungal hyphae can be shown to be present in this stained wood. Such hyphae have been found in more than 50 sections from 12 trees, which included examples of *N. menziesii* from Southland, *N. fusca* from Reefton and Ahaura districts, *N. truncata* from Reefton district, and *N. solandri* var. *cliffortioides* from Canterbury. Hyphae are sometimes not found at the external apices of stains, but can then be demonstrated within stain margins. It appears that the staining is largely caused by gums, which are often formed outside the zone where the hyphae occur. The hyphae are invariably septate, and the walls of those of larger diameter are pigmented. Pigmented septate hyphae can be shown to be continuous with smaller diameter septate hyphae which are not pigmented but which stain readily with aniline blue. These in turn are sometimes found to be continuous with extremely fine hyphae, less than 1 μ in diameter. In some sections hyphae occur predominantly in the vessels, with short branches penetrating adjacent ray and parenchyma cells; in others hyphae pass radially from one ray cell to the next. Wherever such hyphae are found, ray and parenchyma cells, and sometimes the tapered ends of fibres, have brown (presumably gummy) contents. If these cells were capable of reacting to the presence of the hyphae, it follows that they were alive at the time. In cross-sections of the stem, gum barriers can be shown to occur outside the most darkly stained areas and where hyphae are apparently advancing radially outwards. These observations on host reactions suggest that one or more species of sapwood pathogen is involved. If more than one is involved, then the complex would appear to be related since all have pigmented septate hyphae and depend on *Platypus* for transmission. *Platypus* species do not appear to discriminate between those species of *Nothofagus* which coexist; all *Platypus* attack all *Nothofagus*. It is the writer's opinion that one pathogen is involved rather than a complex of competing species. Bearing in mind the inadequacies of present knowledge, this theory reasonably accounts for observations made so far. Experiments to test the pathogenicity of a fungus with characteristics like those described here have been started.

Because outer sapwood has a high moisture content, secretes coloured substances which are possibly fungicidal, and forms gum barriers, invasion of the sapwood from the outside is an improbable event. If, however, the fungus is introduced into sapwood of low moisture content and possibly lower defensive capacity through the walls of a tunnel which is kept aerated and relatively free of gums by the activity of an insect borer, conditions are probably most favourable for initial establishment of the pathogen in host tissues. Its introduction and initial establishment appears to be a critical phase in its as yet unknown life history. The males of all three species of *Platypus* make radial entry tunnels in living beeches. These tunnels curve through a right-angle to become tangential close to the transition zone if such a zone is present. If it is absent, the tunnel continues in a radial direction towards and often through the centre.

Platypus activity alternates between excavation at the tunnel
face and ejection of wads of wood strands. Nest extension by
a pair of parents may continue for up to 10 months. Com-
pletion of the tunnel is not, however, essential for the estab-
lishment of the pathogen which may be established in the
first tangential arm made by a male alone. Trees may die
although none of the attempted nests produce *Platypus* brood.
No other insects boring in living beech trees make tunnels
which are located at the transition zone, so no other insects
are equally adapted to serve as vectors for the postulated
pathogen. Success of the pathogen therefore seems to depend
on its transmission by *Platypus* to low-moisture sapwood, or
perhaps to earlier formed pathological wood.

OUTLINE OF DAMAGING INSECTS

Since Dugdale's review of beech insects in 1964, there has
been little change in the state of information concerning gall-
forming mites and cecidomyid flies, lepidopterous defoliators,
ghost moth and cerambycids which damage stems, or scale
insects. Exceptions are Mrs Marianne Horak's (1970) study of
Proteodes carnifex in mountain beech and Morgan's (1966)
paper on *Nascioides enysi.* Dugdale, summarizing an internal
report, stated that defoliation of mountain beech at Mana-
pouri so weakened trees that *Nascioides* was able to develop
successfully in them. More recent observations do not con-
firm this opinion. No widespread deaths of mountain beech
followed the recent outbreaks which Mrs Horak studied in the
Te Anau and Nelson Lakes regions. Trees are known to flush
after two successive seasons of severe defoliation and there
appears to be no increase in the incidence of *Platypus* attack
or of successful invasion by *Nascioides* as a result of defoli-
ation. J. S. Dugdale (pers. comm.) advises that Entomology
Division, DSIR, have records of a caterpillar (*"Heliostibes"*
callispora) which feeds in the bark of twigs of 4 to 15 mm
diameter of all the beech species; of unnamed weevil larvae
which kill elongating shoots of regeneration of red and silver
beeches; and of an apionine weevil which makes galls in
twigs of silver beech.

Some new information is available as a result of current
studies on *Platypus*. It was earlier supposed by many (*e.g.,*
Anon., 1957) that *Platypus* attacked weakened trees—even that
the presence of *Platypus* attack was indicative of debility in
the tree. However, *Platypus* attack was induced experimentally
in every one of 12 trees selected as healthy, and observations
in an area where some trees had been felled 1 and 3 years
previously made it clear that undamaged and apparently
healthy trees were subject to attack by field populations,
particularly if large head logs or stumps lay nearby. Both the
felled material and the standing trees were indiscriminately
invaded. When freshly felled material was stacked around
trees all were attacked, but the intensity of the attack varied
with the distance from a source of emerging beetles. Follow-
ing massive attack (maximum density of 968 to 1291 holes
per square metre of bark) three red beech larger than 35 cm

d.b.h.o.b. died within 2 to 4 years of the first attack. Four smaller trees (29, 25, 21 and 20 cm d.b.h.o.b.) suffered abnormal leaf fall and some twig dieback, but survived despite thinning of the crown. On felling such trees, cores of pathological wood, gum pockets surrounded by a band of callus, and new sapwood outside the callus were found. In two consecutive seasons following experimentally induced *Platypus* attack, and after an extended period during which there was severe thinning of the crown, a small diameter red beech increased in diameter at the rate of 8 to 10 mm per year although in the four years immediately prior to attack its diameter had increased at the rate of 4 to 5 mm per year. During the relevant period no adjacent trees were removed. This phenomenon was interpreted (D. A. Rook, pers. comm.) as implying that the carbohydrate component of the gums was later made available, but since the volume of living tissue which could make demands on it was greatly reduced a large part of it was available for the formation of new wood.

In a footnote, Dugdale stated that *"Platypus* attacks weakened trees 1-2 years before *Nascioides* and that irrespective of *Nascioides*, *Platypus* entry holes are associated with lenses of dead cambium and an associated inwardly projecting zone of dead wood." These areas of dead cambium surrounding *Platypus* entry holes are now interpreted by the writer as part of a defensive reaction to wounding rather than the work of a pathogenic fungus. Dugdale's observation that *Platypus* attack might precede *Nascioides* attack (presumably of the cambial zone) is worthy of further examination, especially now that the need for a prior weakening in some undisclosed way can be dispensed with. In fact, as soon as it was suspected that *Platypus* could cause terminal dieback and death of beech trees, it became necessary to evaluate afresh the role of *Nascioides* in beech deaths. It was found that live early instar larvae were present in the branches of healthy beech trees in every month of the year. Measurements of the head capsule widths of such larvae show that all belong to the one instar, and that no increase in head capsule width occurs in such material from one oviposition season to the next. In dissecting out these larvae, dead specimens were frequently found in tunnels swamped with gum which gives the tunnels their characteristic dark reddish or blackish appearance—the more recent the gum flow, the lighter the colour of the gum. Since the most vigorous gum reaction occurs in tissues on either side of the cambium, there seemed little prospect of the larvae attaining the cambial zone while these tissues retained their capacity to react to wounding. In trees which were evidently dead following *Platypus* attack, somewhat larger larvae were found in the cambial zone. Their tunnels were still characteristically longitudinal and did not engrave the sapwood. There was no evidence of gum reactions where their tunnels had reached the cambium. In patches of phloem which were still bright in colour and apparently alive, the *Nascioides* larvae were smaller in size, and in some cases had not developed beyond the size found in the thick-walled phloem of healthy branches. It thus appears that *Nascioides*

larvae do not kill beech trees. If the inner phloem and cambium lose the capacity to react to wounding, the larvae are ideally placed to move into these presumably more nutritious feeding grounds in advance of other insects, such as cerambycid larvae, which might utilize them following the next oviposition season. The supposition that the longitudinal tunnels amongst the fibre bundles of the thick-walled zone of the phloem seriously interfere with the function of this tissue, and so weaken the tree, is hardly tenable when one notes that, in North Island beech forests, ghost moth larvae (*Aenetus virescens*) commonly interrupt more than half of the bark of branches without appreciably debilitating either the branch or the tree as a whole.

The chief changes in thinking about beech insects since the 1964 Beech Forestry Symposium are that, in the writer's opinion, *Platypus* appears to be the vector of a fungus which invades the sapwood, either killing the trees or causing the formation of pathological wood in the core. Secondly, that deaths previously attributed to *Nascioides* were probably caused by a pathogen associated with *Platypus* because *Nascioides* does not appear to be the vector of any pathogenic organism. *Nascioides* does not appear to develop beyond an early larval stage unless it reaches inner phloem and cambium, yet it cannot penetrate this zone without evoking a vigorous gum reaction while the tissues remain alive.

PROBLEMS IN THE MANAGEMENT OF BEECH

Current proposals envisage, after utilization of standing timber, some 70,000 ha to be developed as productive beech forest with the addition of eucalypts where an adequate stocking of beech seedlings cannot be obtained. A further 38,000 ha are to be perpetuated as beech forest. One cannot predict what the net annual return from this large and at least potentially valuable resource would, or could, be. *Because* it is a large resource, efforts should be made early in the experiment to ensure that it is as productive as knowledge and available manpower can make it.

We know that eriophyid mites make galls in flower buds and that weevil larvae feed in the galls. We know that good seed years follow hot dry summers, but the looking so far has been in the seed trays rather than in the tree tops. Why should good seed years follow good summers? Could it be that mite populations are reduced in hot, dry summers so that fewer buds are damaged next season? Is this something peculiar to the physiology of beech? Neither of these considerations would seem to apply because cabbage trees and flax also flower prolifically after a hot, dry summer. If primordia are laid down in the autumn, how is their formation affected by the weather of the previous months? Can the mechanism be simulated? These are not solely academic questions. Management envisages leaving, say, five seed trees per acre at the time of felling. These could be killed as a result of *Platypus* attack within two years, perhaps before a mast year. If it could be shown that the fall of viable seed could be increased in non-

mast years, possibly by using a systemic insecticide, I think forest managers would like to know about it. It could make the difference between having potential beech forest or a scrub hardwood jungle.

Secondly, all those with experience of the utilization of beech acknowledge that heart rots greatly detract from the value of the standing crop. This paper suggests that there may be a relationship between *Platypus* attack, the formation of pathological wood, and the incidence of heart rots of the upper stem. This is still little more than a reasonable suggestion; someone must produce the facts and figures before useful advice can be given on the control of rots. If *Platypus* is a prime cause we need to know more about *Platypus* control, which in turn requires that more be discovered about changes in *Platypus* populations and about *Platypus* behaviour. Again apparently academic studies can have a real bearing on economic forestry.

Thirdly, for those interested in pulping beeches, the question of how polyphenols are distributed in clean sapwood, pathological wood and heartwood may be of real concern, especially if an industry is to deal with 850,000 m^3 of material a year. If polyphenols reach a high level in pathological wood, and the formation of pathological wood can be controlled, then forest managers must aim to keep this class of material to a minimum.

The problems of beech management are scarcely realized as yet, but management of an indigenous forest with its indigenous insect and disease complex will be comparable with managing spruce in spruce budworm country, jack pine with jack pine sawfly and aggressive bark beetles, Scots pine with *Myelophilus* and *Hylobius*, eucalypts with phasmatids and termites. To date we have not had this sort of experience.

Forest managers in other parts of the world have learned to call in their research teams and field experts during the planning stages of operations—not after the action, when the damage has been done. As I see it, now is the time for management to demand that the necessary research be done.

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