Threats to New Zealand’s indigenous forests from exotic pathogens and pests

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ABSTRACT

The principal pathways by which forest pathogens and pests enter New Zealand are in debris inadvertently trapped in cargo (both sea and air) as well as in imported used vehicles. The regions which dominate our trade and passenger travel are Australasia and the Northern Hemisphere, and they are also the major sources of contaminants arriving in New Zealand. Case studies of Dutch elm disease in Europe (Ophiostoma spp.), chestnut blight in North America (Cryphonectria parasitica), European gypsy moth in North America (Lymantria dispar), and pine wilt nematode in Japan (Bursaphelenchus xylophilus) show that major pathogen and pest invasions are the result of east-west movement of these organisms in the temperate Northern Hemisphere. There are no records of invasion of temperate forest pathogens and pest between the Northern and Southern Hemispheres. This is due to the divergent floristic history and biogeography of the continents of the Northern and Southern Hemispheres. New Zealand is biogeographically linked with Australia, South America and Africa and this is the most likely source of devastating pathogens. Similarly pest threats will also come from these areas, although widely polyphagous insects from the Northern Hemisphere are also a potential problem. The pathogen of Araucariaceae, Podocarpaceae, Nothofagaceae and Myrtaceae that could threaten the New Zealand members of these families are reviewed. Impact scenarios were developed for the effect on native forests from the establishment of the pathogens Chalara australis (myrtle wilt), Puccinia psidii (guava rust). Impact scenarios are also developed for two pests that successfully established, Orgyia thyellina (white spotted tussock moth) which was eradicated and Eriococcus orariensis (manuka blight) which failed to become a major pest due to a fungal parasite. The risks to New Zealand’s forest were deemed to be low from C. australis, low to moderate from P. psidii, low to medium from O. thyellina, and medium to high from E. orariensis. An extensive bibliography is provided.

Keywords: pathogens, pests, Dutch elm disease, chestnut blight, pine wilt, risk assessment, myrtle wilt, guava rust, white spotted tussock moth, manuka blight, New Zealand

1. Introduction

Man’s dependence on agriculture and horticulture has dictated that the study of pathogens and pests is orientated to these endeavours. Our knowledge of pathogens and pests in indigenous systems is scant and usually acquired after a major biological disaster. For this reason much has to be inferred from a limited number of cases studies and then extrapolated from these if sound judgements are to be made in assessing what the risks are and how to alleviate them. There is no doubt from these case studies that failure to anticipate and control pathogens and pests is costly.

This report was commissioned by the Department of Conservation to ‘Provide an assessment of the likelihood and consequences of the arrival and establishment in New Zealand’s indigenous forest or other natural ecosystems of insect and fungal pathogens capable of causing adverse effects’. This is a huge task and through discussion it was agreed to limit the report to the most prominent indigenous native tree families: the Araucariaceae, Podocarpaceae, Nothofagaceae, and Myrtaceae. These families were selected because of their importance in the landscape, their cultural importance to both Maori and non-Maori New Zealanders, and their biological significance as dominant trees. Also predacious insects, such as wasps and ants, which have been very successful invaders of new habitats, and are capable of causing significant change forest ecosystems have been excluded.

The first task of this report was to examine data on pathogen and pest interceptions accumulated by Forest Research, and trade and migration data collected by Statistics New Zealand. Then fungal pathogen and pest (insects and nematodes) case studies were examined to identify the type of pathogens and pests that could threaten New Zealand’s indigenous trees and where they might come from. Once the types and sources were identified the literature was examined to identify any known pathogens and pests that might be a threat to New Zealand’s indigenous trees. Organisms identified in the literature search were used to develop impact scenarios should they arrive in New Zealand. Finally the likelihood of arrival of each organism and the threat that it poses to indigenous forest was estimated and the risk assessed.
2. Pathways by which pathogens and pests enter New Zealand

The quarantine database, referred to as BUGS, records information on wood and bark boring insects intercepted at ports, which have been sent to Forest Research for identification (Bulman 1990). The source of these interceptions is almost solely from inspections of wooden packaging, logs, or sawn timber entering sea ports. The database was interrogated to determine where intercepted insects originated, and on what types of cargo or packaging they were found. Information stored in BUGS has been collected since 1948.

At present, databases on other types of intercepted organisms are still being developed. Easily accessible information on interceptions of plant debris, fungi or sapsucking insects collected from material other than wooden packaging was limited. For instance, used machinery and cars, external surfaces of containers, air cargo and overseas passengers are risk pathways for new pathogen and pest introductions. Some data have been collected since 1994 and stored in a rudimentary spreadsheet, an analysis of these data was undertaken.

In 1988, Peter Gadgil and John Bain compiled a list of first records of insects and fungi found on tree species since 1950 (Carter 1989). Data on newly recorded pathogens and pests that affect trees have been kept since then. These data were examined to show likely pathways by which new insects or fungi could establish in indigenous forests.

Rather than presenting data by country of origin which in many cases contains little ‘biological’ information, the data has been grouped by regions. In determining these regions, biological, cultural, and political borders were considered. The Floristic Kingdoms of Good (Good 1964; Woodward 1997b) and the Zoogeographic Provinces of Sclater & Wallace (Woodward 1997a) were used to provide a biological basis for these groupings. North America corresponds with the Nearctic province and includes Canada, the USA and Mexico. Europe is the Palaearctic province without China, Korea, Japan, and northern Africa but including the middle east to the Red Sea and across to the Pakistan border. China, Korea, Taiwan and Japan are grouped as North Asia based on biological and cultural similarities. Africa is the continent of Africa to the Mediterranean and Red Sea, it also includes Madagascar and the islands of the western half of the Indian Ocean. The Oriental province has been divided into Asia South West and Asia South East. Asia South West includes Pakistan, Bangladesh, Sri Lanka, India and the Himalayan states bordering China. Asia South East includes all states south of the Chinese border, the Philippines, and Indonesia to the Papua New Guinea border. Australia and Papua New Guinea comprise Australasia. All of the tropical and subtropical oceanic islands of the Pacific are in the Pacific but the Hawaiian islands are excluded as they are included in North America. South America corresponds with the Neotropical province which includes all of South America, central America to the Mexican border and the Caribbean island states.
2.1 PATHWAYS AND NATURE OF THE THREAT

Many potentially harmful agents have been intercepted by import quarantine inspectors since the 1950s. Total interceptions of wood and bark boring insects sent to Forest Research for identification averaged almost 380 per annum from 1988 to 1997, an increase of 150 per annum over the previous 10 year period (Figure 1). There was an apparent decline in the number of interceptions during the mid to late 1960s, but this was due to Quarantine Officers being instructed to send only those samples that were approved by their senior Officers. The policy regarding the referral of samples for identification was rescinded in 1972, which lead to an increase in the recorded number of interceptions. The number of interceptions sent for identification peaked in 1990 at 597.

![Figure 1. Interceptions of wood and bark borer (1948–1997).](image)

2.2 INTERCEPTIONS BY REGION OF ORIGIN

Over the last 20 years, Europe (mainly Germany, Italy, Netherlands, Russia and the United Kingdom) was the most common origin of wood and bark borer interceptions (Figure 2). Asia North (China, Hong Kong, Korea, Japan, Taiwan) and Asia South East (mainly Indonesia, Malaysia, Singapore and Thailand), also contributed a significant number of intercepted insects. The number of intercepted insects from Europe has declined over the last 10 years and a greater number of insects were intercepted from Asia South East. Significantly fewer goods are imported from Asia South West (India, Pakistan and Sri Lanka) compared with Australasia (Figure 8), yet both regions contribute approximately the same proportion of interceptions.
2.3 **RISK ASSOCIATED WITH PACKAGING**

The type of host material in which wood and bark boring insects were found is given in Figure 3. Two thirds of all interceptions were found in casewood and dunnage. Not surprisingly, considering the data consisted of wood and bark borers, 80% of interceptions were in wooden packaging; and 18% were found in sawn timber, logs, piles and other bulk wooden material, but only 2% were found in wooden cargo (cricket bats, furniture, hand crafts, etc.).
Figure 4 shows that the proportion of wood and bark borers intercepted in dunnage has decreased over the last 10 years and the number of interceptions found in casewood and pallets has increased. This reflects the increased use of wooden packaging and the efforts quarantine authorities have made to discourage importers from using contaminated dunnage.

2.4 PATHWAYS ASSOCIATED WITH NON WOOD AND BARK BORING INSECTS

Since mid 1994, data from contaminants other than wood and bark boring insects sent to Forest Research for identification have been collated. Most of the samples sent were contaminants from used cars, containers and ships, and mainly consisted of plant debris and insect material (Table 1, Figures 5 and 6). Scale insects, moths, plant material with aphid damage, and egg masses of several invertebrate species have been found on such material. Many genera of sporulating fungi, including *Fusarium* and *Phytophthora* (both of which contain species of pathogenic fungi) have been identified on the plant debris.

A major study to determine the proportion of containers imported into New Zealand whose external surfaces are contaminated by organic material or organisms is in progress. Preliminary results show that almost 40% of all containers examined (from a random sample) had some type of external contaminant. The percentage of these contaminants that constitute a quarantine risk has not been determined, but *Fusarium*, *Ophiostoma* and *Phytophthora* spp. have been isolated from soil contamination, and gypsy moth egg masses were found in several consignments.

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>NUMBER RECORDED</th>
<th>TYPE OF CONTAMINANT</th>
<th>NUMBER RECORDED</th>
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<tr>
<td>Air container</td>
<td>24</td>
<td>Wood decay fungi</td>
<td>24</td>
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<tr>
<td>Other</td>
<td>19</td>
<td>Insect</td>
<td>358</td>
</tr>
<tr>
<td>Container</td>
<td>218</td>
<td>Plant debris</td>
<td>766</td>
</tr>
<tr>
<td>Machinery</td>
<td>65</td>
<td>Soil</td>
<td>29</td>
</tr>
<tr>
<td>Ship</td>
<td>140</td>
<td>Wood</td>
<td>135</td>
</tr>
<tr>
<td>Vehicle</td>
<td>574</td>
<td></td>
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<tr>
<td>Not recorded</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1312</td>
<td>Total</td>
<td>1312</td>
</tr>
</tbody>
</table>

Figure 5. Source of contamination (wood and bark boring insects excluded).

Figure 6. Type of contamination (wood and bark boring insects excluded).
2.5 RISK ASSOCIATED WITH PASSENGER ARRIVALS

The clothing and luggage of air passengers is a recognised pathway by which new pests and fungi (in particular) could arrive in New Zealand. Baker (1966) reported that 65 fungal species were cultured from shoes of air travellers arriving in Honolulu.

Gadgil & Flint (1983) examined 45 tents brought in by air passengers at Auckland International Airport during December 1981. The fabric from the roof of the tents was vacuumed, with air passing through a filter that retained all detachable material greater than 0.2 µm in diameter. The contents of the filters were examined under a microscope and no spores of forest pathogens were seen. However, the sampling method employed did not remove all the spores, and the filters were only examined by one pathologist. Organic and inorganic debris was present in all tents, 9 of which had ‘abundant’ debris present. The debris consisted of grass stems and leaves, leaves of broadleaved plants, and conifer needles. Live insects were found in 6 tents. Gadgil & Flint concluded that the gross plant and animal debris, and live insects carried in or on tents, posed a major risk. This risk appears to be particularly relevant to indigenous forest, as it is safe to assume that most of the travelling owners of tents will be camping in National Parks or other indigenous forest areas.

Sheridan (1989) conducted two studies at Wellington Airport in 1980 and 1982 where clothing of 137 and 97 passengers respectively was vacuumed and spores caught in double-sided sticky tape. Pathogenic fungi comprised 17% of the total spores collected. Sheridan concluded that the likelihood of passengers introducing new pathogen into New Zealand was high, although he was also including pathogens of agricultural crops, particularly rusts, in his evaluation.

Figure 7 was derived from data supplied by Statistics New Zealand. The data comprised overseas visitors by country of last permanent residence and this was categorised into regional groupings. Data for 1998 were available to the end of April, and have been extrapolated to estimate arrivals for the full year. There has been a steady increase in the number of visitors entering New Zealand. Visitor numbers from Asia North peaked at almost 400,000 in 1996 and then declined. More visitors continued to arrive from Australia and Europe, whereas visitor numbers from North America remained relatively constant. Sheridan (1989) stated that the number of international visitors to New Zealand increased from 500,000 in 1983 to 700,000 in 1987. In 1997, the number of overseas visitors reached 1.5 million. It appears very likely that numbers of overseas visitors will continue to increase, particularly from Australia, Europe and North America.

The trend for Asian visitors over the next five years is less certain, but it seems probable that visitor numbers from this region will continue to decrease.

2.6 IMPORTS TO NEW ZEALAND FROM 1988 TO 1998

Data on overseas trade imports for April–March years from 1988/89 to 1997/98 were obtained from Statistics New Zealand. Information on packaging is not kept, so each trade category was examined and the categories which appeared
Figure 7. Overseas visitor arrivals (1988–1998).

Figure 8. Imports of packaged cargo by region (1988–1998).
to include cargo that would be imported in bulk were excluded. For instance, all petroleum products, fertilisers, sugar, mineral ores, slag and ash, cement and lime were excluded. Some packaged cargo would have been inadvertently excluded, and some bulk cargo included, in the final data but this was unavoidable.

The total quantity of cargo imported has increased steadily over the period examined (Figure 8). Australasia (Australia and Papua New Guinea) accounted for the most imports, followed by Asia North, North America and Europe. Over the last two years the quantity of imports from North America decreased, but the quantity of goods from Africa, Australasia and Asia North has increased significantly. Future trends are difficult to predict, but there is nothing to suggest that over the next five years the trend towards more imports from Asia and Australia will not continue.

<table>
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<td>Northland</td>
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<td>Auckland</td>
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<td>Coromandel</td>
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<td>Bay of Plenty</td>
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<td>Taranaki</td>
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<td>Gisborne</td>
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<td>Wairarapa</td>
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<td>Nelson</td>
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<td>Marlborough</td>
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<tr>
<td>Marlborough</td>
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<tr>
<td>Buller</td>
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<tr>
<td>Kaikoura</td>
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<tr>
<td>Westland</td>
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<tr>
<td>North Canterbury</td>
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<tr>
<td>Mid Canterbury</td>
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<tr>
<td>Chatham Islands</td>
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<tr>
<td>Mackenzie</td>
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<tr>
<td>South Canterbury</td>
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<td>Otago Lakes</td>
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<td>Central Otago</td>
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<tr>
<td>Dunedin</td>
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<td>Fiordland</td>
</tr>
<tr>
<td>Southland</td>
</tr>
<tr>
<td>Stewart Island</td>
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<tr>
<td>Not recorded</td>
</tr>
</tbody>
</table>

Grand Total        | 53      | 17      | 74      | 76      | 127    | 93      | 220    | 5.71    | 9.30    |

* Crosby et al. (1976)
2.7 NEW RECORDS OF PATHOGENS AND PESTS AFFECTING TREES AND WOODY SHRUBS

In the period from 1950 to 1987 for insects, and from 1956 to 1987 for fungi, an average 3.7 new records of insects or fungi per year affecting trees and woody shrubs in New Zealand were made (Table 2). From 1988 to 1997 a further 93 (9.3 per year) new records have been listed, increasing the average number of new records per year to 5.0. Discoveries of newly recorded fungi (76) greatly outnumbered insects (17) during the 1988 to 1997 period. Of the 93 new records from 1988 to 1997, 57 (61%) were found in port environs. This compares with 38% found in the port environs during the earlier period. New recordings averaged 3.0 per year in the Auckland region from 1988 to 1997 and all were in urban areas within 5 km radius of the ports. The Bay of Plenty biological region hosted the most new recordings in areas outside the port environs, 14 newly recorded fungi and one insect were found there over the last 10 years.

The majority of new introductions recorded between 1988–1997 were fungi causing leaf spots, followed by other fungi (mainly those causing cankers and dieback), then defoliating and sapsucking insects (Figure 9). Only 4% were wood boring insects, which suggests the quarantine system of inspecting wood and wooden packaging is effective. Fifty-four percent of newly recorded organisms were found during port environs surveys, carried out by Ministry of

![Figure 9. Type of newly recorded organism (1988–1997).](image1.png)

![Figure 10. Means of discovering new organism (1988–1997).](image2.png)


<table>
<thead>
<tr>
<th></th>
<th>EXOTIC HOSTS</th>
<th>INDIGENOUS HOSTS</th>
<th>TOTAL</th>
<th>EXOTIC HOSTS PER YEAR</th>
<th>INDIGENOUS HOSTS PER YEAR</th>
</tr>
</thead>
<tbody>
<tr>
<td>1988–1997 insects</td>
<td>17</td>
<td>0</td>
<td>17</td>
<td>1.7</td>
<td>0.0</td>
</tr>
<tr>
<td>1988–1997 fungi</td>
<td>58</td>
<td>18</td>
<td>76</td>
<td>5.8</td>
<td>1.8</td>
</tr>
<tr>
<td>Total</td>
<td>75</td>
<td>18</td>
<td>93</td>
<td>7.5</td>
<td>1.8</td>
</tr>
</tbody>
</table>
Forestry, Forest Health Advisers (Figure 10). Forest surveys accounted for the discovery of a further 30%, the remaining discoveries were made by members of the public. Of the 18 new recordings found on indigenous hosts, 72% were found during port environs surveys. Of the average 9.3 new records per year from 1988 to 1997, 7.5 per year (81%) were found on exotic hosts, and 1.8 per year (19%) were found on indigenous hosts (Table 3).

Table 4 lists the newly recorded organisms found on indigenous hosts over the last 10 years. Of the 18 organisms, none were recorded as causing significant damage to their hosts, and none were judged as serious by specialists at Forest Research. No newly recorded insects have been found on indigenous species over the last 10 years. Leaf inhabiting fungi accounted for 16 of the records, with one stem canker and one fungus causing branch dieback completing the list. The great majority of these fungi (72%) were found in the port environs, but very little indigenous forest surveillance is carried out. Between July 1997 and June 1998 inspections were undertaken, by the Ministry of Forestry, at Mt Egmont, Ruahine, Urewera, Kaweka Forest Park, Rimutaka, Maruia, Lewis Pass, and Charleston. At present indigenous forest surveillance consists of ad hoc inspections which are generally carried out over one day, no structured system is in place. In contrast, exotic forest surveillance is carefully planned and combinations of aerial surveys, surveys from vehicles, and transect surveys on foot are systematically carried out. The intensity of surveys is determined by the location of the exotic forest—‘high risk’ locations are surveyed more intensively than those forests planted in locations where the risk of exotic organisms being introduced is low. If a structured system of indigenous forest surveillance was in place, one might expect that a greater proportion of new records would be made from indigenous forest areas, notwithstanding the fact that a new record from these areas would not necessarily indicate a new introduction of an exotic

<table>
<thead>
<tr>
<th>HOST NAME OF ORGANISM</th>
<th>DISORDER</th>
<th>LOCATION</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coprosma sp.</td>
<td>Cercospora sp.</td>
<td>Leaf spot</td>
</tr>
<tr>
<td>Coprosma sp.</td>
<td>Coniothyrium sp.</td>
<td>Leaf blight</td>
</tr>
<tr>
<td>Corynocarpus laevigatus</td>
<td>Deuteromycotina: Coelomycetes</td>
<td>Leaf loss</td>
</tr>
<tr>
<td>Corynocarpus laevigatus</td>
<td>Phomopsis sp.</td>
<td>Leaf spot</td>
</tr>
<tr>
<td>Corynocarpus laevigatus</td>
<td>Phyllosticta sp.</td>
<td>Leaf spot</td>
</tr>
<tr>
<td>Dodonea viscosa.</td>
<td>Pseudomonas sp.</td>
<td>Leaf spot</td>
</tr>
<tr>
<td>Freycinetia banksii</td>
<td>Glyphis sp.</td>
<td>Leaf spot</td>
</tr>
<tr>
<td>Griselinia sp.</td>
<td>Elsinoe sp.</td>
<td>Leaf spot</td>
</tr>
<tr>
<td>Myoporum laetum</td>
<td>Cercospora sp.</td>
<td>Leaf spot</td>
</tr>
<tr>
<td>Myoporum laetum</td>
<td>Cercospora sp.</td>
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<tr>
<td>Myoporum laetum</td>
<td>Mucosphaerella sp.</td>
<td>Leaf blight</td>
</tr>
<tr>
<td>Notobagrus solandri</td>
<td>Deuteromycotina: Coelomycetes</td>
<td>Leaf spot</td>
</tr>
<tr>
<td>Pittosporum tenuifolium</td>
<td>Vizella tunicata</td>
<td>Leaf spot</td>
</tr>
<tr>
<td>Prumnopitys ferruginea</td>
<td>Discosporium sp.</td>
<td>Branch dieback</td>
</tr>
<tr>
<td>Prumnopitys ferruginea</td>
<td>Discula sp.</td>
<td>Leaf blight</td>
</tr>
<tr>
<td>Pseudo pancreas colensoi</td>
<td>Deuteromycotina: Coelomycetes</td>
<td>Leaf spot</td>
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<tr>
<td>Pteridium esculentum</td>
<td>Camarosporium sp.</td>
<td>Stem canker</td>
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<tr>
<td>Solanum aviculare</td>
<td>Cercospora sp.</td>
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</tr>
</tbody>
</table>
organism. The lack of base line data for native forest can be exemplified by Rimutaka Forest Park, which had a published fungal flora of only 32 species as of May 1997. A non-funded survey was carried out and the number of species expanded to 142 representing a 433% increase in the number of known species from this area (Ridley & Taylor 1997).

2.8 DISCUSSION

Wood and bark borers were intercepted at our ports at an average of 380 per year over the last 10 years. Nearly one third of all interceptions came from cargo originating in Europe. Asian cargo also seems to be a likely source of interceptions, particularly India, Pakistan and Sri Lanka, countries from which the number of recorded insect interceptions appears to be disproportionate to the quantity of cargo imported. Most wood and bark borers were found in casewood and pallets; dunnage now appears to be a less common source of insects, compared with 15–20 years ago. Wooden cargo is not a significant source of infestations, 98% of recorded interceptions over the last 25 years were found in packaging, logs or sawn timber. Wood and bark boring insects comprise only 4% of the newly recorded organisms recorded over the last 10 years, which is probably a good reflection of New Zealand’s stringent quarantine system. Other pathways are obviously contributing to the establishment of exotic insects and fungi during the last 10 years.

Fungal leaf spots contributed 52% of the new records, followed by other fungi (mainly associated with branch and stem cankers), and sapsucking and defoliating insects. Many of these organisms would have to enter the country on plant material, and Figure 6 shows plant debris comprised 59% of the 1,312 samples received at Forest Research during 1994–1997. Of the 713 samples of plant debris where the source was recorded, 568 (80%) were from vehicles. Vehicles are therefore likely to be a significant pathway for foliage pathogens, and possibly sapsucking insects, to enter New Zealand. Ministry of Agriculture and Forestry officials have recognised the need for stricter controls on the cleanliness of imported vehicles and the revised import health standard has encouraged major importers to ensure vehicles are cleaned overseas. Increased attention to inspections in New Zealand and overseas should effectively reduce the percentage of undetected vehicles carrying significant amounts of plant debris and other material (K. Glassey, MAF, pers. comm.).

The external surfaces of containers often have soil, or animal and plant debris, attached to them. Almost 40% of containers sampled in one study were contaminated to some extent, so it appears likely that pathogenic fungi, and, to a lesser extent, insects could well be introduced by this pathway.

The risk associated with air passengers is real, but difficult to quantify. It has been demonstrated that fungal spores are carried on passengers’ clothing and effects, and tents and camping equipment have been recorded containing live insects and plant debris. The significant increase in air passenger arrivals over the last 20 years is of concern, and can only increase the risk of organisms being introduced by this path. Significantly, many tourists spend time in parks, reserves and forests while they are in the country.
Of the 93 newly discovered pathogens and pests recorded over the last 10 years, 18 were associated with indigenous hosts. Nearly all (89%) were leaf inhabiting fungi, and none were recorded as causing significant damage to their hosts. It is expected that targeted surveys of indigenous forests (especially camping areas and locations that tourists commonly frequent) would result in a greater number of newly recorded insects and fungi on indigenous hosts. Over 70% of the new organisms on indigenous hosts are recorded from port environs surveys and their hosts were either planted, or regenerated on ‘waste ground’. Because the native fungal flora is so poorly known it is in most cases difficult to determine whether these records represent new introductions or undescribed native species.

New Zealand’s most significant source of imports (see Figure 8) and overseas visitors (see Figure 7) is Australasia yet this region contributed less than 15% of wood borer interceptions between 1993 and 1997. Whereas Asia South West, which is a very minor source of trade, contributed almost 10% of the wood borers intercepted over this period. This trend indicates that major trade and passenger routes do not necessarily indicate the source of major interceptions, rather that the type of cargo and cargo practices in the exporting country can be of more significance.

The major lesson that can be learnt from this exercise is that it is not possible to predict specifically the source and nature of new introductions. Rather it is a matter of anticipating the possibilities based on experience and general trends in observations made by field operatives. Based on this line of reasoning one would anticipate that surveys of air cargo, passengers and aircraft from Australia would intercept a number of organisms simply because of the volume of traffic and the short distance between Australia and New Zealand. Another area of concern again on the trans-Tasman route is sports gear, and in particular golf equipment. Recent discoveries of the defoliating insects—*Uraba lugens* (Crabtree 1997; Morgan 1998) on golf courses in Mt Maunganui, and *Dicranosterna semipunctata* at Remuera golf course in Auckland—indicate how easily a pathogen or pest could be picked up from an Australian golf course, and rapidly transported to New Zealand (where many golf courses have Australian specimen trees) and inadvertently liberated.
3. Case studies of invasions by pathogens and pests

To recognise potential threats to New Zealand’s indigenous trees it is necessary to examine the progress of invasions of pathogens (an epiphytotics) and pests (an epizootic) that have occurred in forest systems overseas. Through the use of well-documented case studies it should be possible to identify the means of entry of pest pathogen into a forest ecosystem, the impact the pathogen had on the indigenous vegetation, the environmental and economic costs, and any steps taken to alleviate the problem. Four cases have been selected: Dutch elm disease in Europe, chestnut blight in North America, European gypsy moth (Lymantria dispar) in North America and pine wilt disease caused by a nematode (Bursaphelenchus xylophilus) in Japan.

3.1 Dutch Elm Disease Caused by *Ophiostoma ulmi* and *O. novo-ulmi* in Europe

The genus *Ulmus*, comprising some 40 species, has been one of the most useful trees in the Northern Hemisphere. Because of the combination of beauty and hardiness against wind, salt, drought and cold, elms have been widely planted in recent centuries in Europe; to provide shade trees in towns and cities, shelterbelts in exposed areas and to furnish rural landscapes (Richens 1984). Dutch elm disease, has caused the demise of a major part of the elm population, and in the short space of 70 years led to a profoundly altered landscape.

The fungi responsible—*Ophiostoma* spp.—cause a vascular wilt disease, and are vectored by bark beetles: in Europe the main vectors are *Scolytus scolytus* and *S. multistriatus*. The fungus is introduced into the xylem of healthy trees by feeding adult beetles. The beetles breed beneath the bark of dead and dying trees, the pathogen sporulates prolifically in the larval galleries and emerging adults carry the fungal spores on their bodies. New host plants may also become infected via natural root grafting, the fungus moving in the vascular system through the roots from tree to tree. The *Ophiostoma* spp. causing Dutch elm disease are confined to species of *Ulmus* and the closely related genus *Zelkova*. North American species of *Ulmus* are extremely susceptible to the disease and those of Europe are only slightly less so. Some of the Asian elms are resistant (Heybroek 1983).

There have been two pandemics of the disease in the Northern Hemisphere in this century. The first, which appeared in several locations in Europe around 1918–1921 spread both west to Britain and North America, and east through Europe and eventually to Asia. The epidemic died down by the 1940s but losses of elm trees ranged from 10%–40%, depending on the country and the composition of elm species (Peace 1960). The second, and far more destructive pandemic began in the 1970s (Gibbs & Brasier 1973) and, although recorded initially in Britain, is thought to have begun some years earlier in the Moldova-
Ukraine area of eastern Europe. Within a decade of the onset of the second pandemic, over 20 million of an estimated 30 million elms in Britain were dead, and by the 1990s the figure had risen to well over 25 million (Brasier 1996). A similar scenario has been enacted in other European countries and in North America. As more trees sickened and died more breeding material became available for the bark beetles, populations escalated and increased fungal transmission to new hosts followed.

The first pandemic was caused by *O. ulmi*, and many trees infected with this fungus recovered from the attack. A popular hypothesis has been that the pathogen was imported into Europe and that it originated in China: this theory was based on the Chinese species of elms being highly resistant to the pathogen. However in a survey across China in 1987 no evidence of the disease could be found (Brasier 1990). The origin of *O. ulmi* remains obscure. The second pandemic was caused by a fungus which initially appeared to be a more aggressive strain of *O. ulmi*, but was subsequently found to be a new species, *O. novo-ulmi* (Brasier 1991). *Ophiostoma novo-ulmi* exists as two closely related forms, the Eurasian (EAN) and the North American (NAN) races which arose separately in the different continents (Gibbs & Brasier 1973). Both races are now present in Europe and the NAN race is thought to have entered Britain in infected logs, from where it spread into Europe. The movement of infested logs is thought to have been the primary means of long-distance dispersal of these fungi (Brasier & Gibbs 1973). There are two theories for the emergence of *O. novo-ulmi*, the first that it is native to the Himalayas, a region with unique elm species which are not susceptible to Dutch elm disease. Or second, that it arose as an unusual interspecific hybrid between *O. ulmi* and *O. piceae* or *O. himal-ulmi* (Brasier 1995) (See further comments under myrtle wilt).

Three main approaches to the control and management of Dutch elm disease have been investigated. These are; control or manipulation of the insect vectors and prevention of spread, control of the fungus, and selection and breeding of resistant elms.

Considerable success in slowing down the rate of spread of Dutch elm disease through a rigorous sanitation programme has been demonstrated in parts of Britain (Greig & Gibbs 1983). Prompt removal and destruction of all dying and dead trees eliminates the breeding material of the bark beetle vectors, thereby markedly reducing beetle populations. Felling of infected trees is accompanied by digging trenches and severing root connections to prevent root-graft transmission to adjacent trees and restrictions on the storage and movement of elm timber. A number of case-histories illustrate the effectiveness of such campaigns in restricting spread of the disease and results of some are shown in Tables 5, 6, and 7.

Insecticides such as DDT and methoxychlor have had some controlling effect on insect populations but use of these chemicals has largely ceased due to environmental concerns (Phillips & Burdekin 1982). There have also been attempts to reduce insect populations using a ‘trap-tree’ technique. Elms were poisoned and baited with pheromone to induce mass attack by *Scolytus* spp. whose brood then failed to develop within the treated trees (O’Callaghan & Fairhurst 1983). Natural biological control of beetle populations by the fungus, *Phomopsis oblonga*, which grows in the bark of elms has been demonstrated
(Webber 1981). *Scolytus* will avoid wood infected with *P. oblonga* where there is a choice, and if forced to use such material for breeding the numbers of viable offspring produced are decreased. A proactive use of this natural system has been limited in effectiveness by the preference of the fungus for only some elm species.

Protection of trees against fungal invasion by injection with systemic fungicides has had some success. However, treatment is so expensive that it can only be justified on valuable specimen trees (and success is not guaranteed) (Phillips & Burdekin 1982). Some biological control of the fungus has been achieved by injection of species of the bacterial genus *Pseudomonas*, which hinder fungal growth, into the xylem of newly infected trees (Scheffer 1983).

In the Northern Hemisphere populations of *O. novo-ulmi*, viruses (d-factors) carried in the cytoplasm which reduce growth and reproductive ability of the fungus have been found (Brasier 1983). Viability of the asexual spores of

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TABLE 5. NUMBER AND PERCENTAGE OF DISEASED TREES IN LOCATIONS WHERE A SANITATION PROGRAMME WAS RIGOROUSLY FOLLOWED.

<table>
<thead>
<tr>
<th>YEAR</th>
<th>BRIGHTON</th>
<th>HOVE</th>
<th>NETHERLANDS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NO. OF DISEASED TREES FELLED</td>
<td>% OF REMAINING ELM POPULATION</td>
<td>NO. OF DISEASED TREES FELLED</td>
</tr>
<tr>
<td>1975</td>
<td>228</td>
<td>1.15</td>
<td>100</td>
</tr>
<tr>
<td>1978</td>
<td>266</td>
<td>1.41</td>
<td>416</td>
</tr>
<tr>
<td>1981/2</td>
<td>160</td>
<td>0.87</td>
<td>169</td>
</tr>
</tbody>
</table>

TABLE 6. NUMBER AND PERCENTAGE OF DISEASED TREES IN LOCATIONS WHERE ONLY A PARTIAL SANITATION PROGRAMME WAS MAINTAINED.

<table>
<thead>
<tr>
<th>YEAR</th>
<th>JERSEY</th>
<th>MERSEYSIDE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NO. OF DISEASED TREES FELLED</td>
<td>% OF REMAINING ELM POPULATION</td>
</tr>
<tr>
<td>1975</td>
<td>7500</td>
<td>3.75</td>
</tr>
<tr>
<td>1978</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1981/2</td>
<td>25,000</td>
<td>20.00</td>
</tr>
</tbody>
</table>

TABLE 7. CUMULATIVE TOTALS OF TREES FELLED FROM 1975 TO 1981/82*.

<table>
<thead>
<tr>
<th>LOCATION</th>
<th>TOTAL TREES REMOVED 1975-1981/82</th>
<th>PERCENTAGE OF 1975 POPULATION LOST</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brighton</td>
<td>1,775</td>
<td>8.9</td>
</tr>
<tr>
<td>Hove</td>
<td>1,788</td>
<td>41</td>
</tr>
<tr>
<td>Netherlands</td>
<td>Approx. 580,000</td>
<td>Approx. 18</td>
</tr>
<tr>
<td>Jersey</td>
<td>83,200</td>
<td>69</td>
</tr>
<tr>
<td>Merseyside</td>
<td>12,760</td>
<td>69</td>
</tr>
</tbody>
</table>

* Figures derived from Greig & Gibbs (1983).
infected *O. novo-ulmi* is markedly reduced, the degree depending on the particular virus. For an elm to be infected a beetle must carry a defined spore load: too little and infection does not occur. In Europe about 62% of *Scolytus scolytus* and about 16% of the smaller *S. multistriatus* carry sufficient spores to initiate a new infection in *Ulmus procera*. Thus the release of selected d-factors is considered to have considerable potential for increasing the number of ineffective vectors (Sutherland & Brasier 1997).

Selection and breeding of elms resistant to Dutch elm disease has been undertaken in several countries. A number of clones developed in the Netherlands incorporating crosses between European elms and *U. wallichiana* from India show moderate to good resistance. Hybrids with the Asian *U. pumila* also show promise (Heybroek 1983). However the resistant selections differ markedly in form and in vigour and cannot be regarded as ever replacing the elms of Europe (Brasier 1996). Manipulation of the elm genome to increase resistance to fungal invasion is being actively explored and anti-beetle genes are being considered for insertion into the plant (Brasier 1996).

### 3.2 CHESTNUT CANKER IN NORTH AMERICA CAUSED BY *Cryphonectria parasitica*

*Castanea dentata* (American chestnut) was once one of the most important trees in the mixed hardwood forests of eastern North America ranging from Maine to Georgia and west to Indiana and Illinios. Chestnuts comprised 25% of these forests which covered 81 million hectares (Liebhold et al. 1995). In virgin forests large chestnuts were commonplace with trees to six hundred years old and averaging 1.2-1.5 m in trunk diameter (with some 2.4-3.0 m) and 24.4-30.5 m tall. *Castanea dentata* unlike other nut trees produced heavy crops every year and were a major cash crop for many families in Appalachia. The nuts were important as seasonal food for bear, deer, wild turkey, squirrels, and passenger pigeons. The timber was important for its use in telegraph poles, railway sleepers, heavy construction, shingles, paneling, fine furniture, musical instruments, pulp, plywood, and tannins (Anon. 1995a). It is not now possible to know what ecological and economic effects the loss of an estimated four billion trees in fifty years has had (Mansfield 1998).

The chestnut blight, caused by *Cryphonectria parasitica*, was first observed in New York City in 1904 (Anagnostakis 1996c). The pathogen spread rapidly averaging 40 km per year and successfully colonised the entire range of *C. dentata* in approximately 40 years (Kuhlman 1978; Liebhold et al. 1995). By the 1950s, the host had been essentially eliminated as a forest tree (Anon. 1995a).

The source of the pathogen was speculated to be from Asian species of *Castanea* introduced into North America and a search in Asia found the fungus there in 1913 (Anagnostakis 1996a, 1996b). The pathogen reached Europe in 1938 attacking *C. sativa* but due to its lower susceptibility and its geographical distribution it had only a limited effect in Italy and southern France (Mittempergher 1978).

The primary thrust of the attempts to manage the disease, by the US Department of Agriculture and the Connecticut Agricultural Experimental Station, was to
breed resistant hybrids combining the best features of the American chestnut with the disease resistance of the Asian species. The USDA breeding programme was unsuccessful and was discontinued in 1960 but the Connecticut programme has continued (Anon. 1995b; Anagnostakis 1996d). In 1983 ‘The American Chestnut Foundation’, a non-profit organisation, was formed (Anon. 1995b). Its mission is to restore the American chestnut as an integral part of the eastern North American forest ecosystem. Using backcrossing techniques the Foundation intends to create a hybrid between the American and Chinese chestnut which is indistinguishable from the American but with the blight resistance of the Chinese. It is expected that the total breeding project will take 30–50 years but with the first releases of resistant trees within 10 years.

In the 1950s spontaneous healing of cankers on C. sativa was observed in northern Italy (Mittempergher 1978). Work conducted in southern France found that the healing process was the result of the conversion of the virulent pathogen to a non-virulent form. It was also found that this was transmissible and the non-virulent strains were called ‘hypovirulent’ (MacDonald & Fulbright 1991). Over the next 25 years the European chestnut recovered naturally. Then in 1977 hypovirulent strains were also found in Michigan, and extensive surveys have found it in other states (Fulbright et al. 1983). Hypovirulence was associated with a double-stranded ribonucleic acid strand which may have been virus transmitted. Research is still being conducted to best utilise these hypovirulent strains. The major stumbling block to successful utilisation is the loss of mature chestnuts in the majority of North American forests. Survival and spread of the hypovirulent strains appears to be dependent on mature trees being available for its long term survival and increase. In the present system C. dentata survives as a minor understorey plant and only increases in size and number if there is disturbance creating gaps in the canopy. In such sites the chestnuts grow rapidly but this is followed by a rapid increase in the virulent strain which kills the developing trees. Due to the slow growth rate and reduced sporulation rate of the hypovirulent strains they are unable to increase as rapidly as the virulent strain does and therefore are unable to effectively shift the population from a virulent to a non-virulent form as occurred in Europe (Griffith 1989).

3.3 EUROPEAN GYPSY MOTH (Lym antr ia d ispar) IN NORT H AMERICA

The gypsy moth, Lymantria dispar (Lepidoptera: Lymantridae) is native to most of temperate Europe, Asia and northern Africa within the latitudes 20°–60° N where the annual rainfall is 250–1000 mm and the temperature isotherms are 15°C to 27°C for July and −18°C to −12°C for January (Montgomery & Wallner 1988).

Lymantria dispar is considered to be one of the most serious pests of forests (Montgomery & Wallner 1988) and has been recorded from more than 600 species of plants (Baranchikov 1989). There are at least two distinct strains of L. dispar (Ferguson 1978), the European strain and the Asian strain. Proceeding westward from East Asia to western Europe, adult and larval colouration
patterns become less variable and the females progressively lose the ability to fly (Schafer et al. 1984). The European strain also has a distinct preference for hardwoods whereas the Asian strain has a broader host range which includes conifers. *Lymantria dispar* exhibits its greatest biological variability in East Asia and that is the probable origin of the species.

*Lymantria dispar* was introduced into North America in 1869 by Leopold Trouvelot, a no doubt well-meaning but misguided astronomer with an interest in insects. He brought gypsy moth egg masses to his home in Medford, Massachusetts in an attempt to develop a disease resistant strain of silk moth. Some caterpillars escaped and established in the area. The first outbreaks of gypsy moth were not recorded until nearly 20 years later when caterpillars threatened to overrun Medford. To quote from Dunlap (1980):

‘The startled townspeople discovered caterpillars in astounding numbers, swarming through trees, eating leaves, and coating the ground below with droppings. People swept insects from their sidewalks, porches and clothes; carried umbrellas to ward off droppings and falling caterpillars; and even wore face nets’.

Since 1869 *L. dispar* has spread slowly but gradually from Medford at an average rate of 20 km per year. As the North American population is of the European strain of *L. dispar*, the female moths are incapable of flight and this has retarded its spread. The range of *L. dispar* in North America includes all of the northeastern USA and portions of the southeast and midwest, as well as Ontario, Canada. A number of isolated populations have become established in western states of the USA as the result of inadvertent spread by man. These western populations are subject to eradication attempts and *L. dispar* is not, as yet, considered to be permanently established in these states. There have been several incursions of the Asian strain of *L. dispar* into North America since 1991 and these have been the subject of eradication attempts. It is too early to say whether these have all been successful but the Asian strain is not considered to be established in North America at this time.

From time to time *L. dispar* populations expand enormously and may defoliate large areas of forest, horticultural and ornamental trees (Cowley et al. 1993). In Europe, because of the abundance of natural enemies the outbreaks are generally short-lived (DeBach & Rosen 1991), although there have been periods of severe and extensive forest defoliation (Montgomery & Wallner 1988). In Japan and China *L. dispar* is recognised as a pest, but severe widespread outbreaks are apparently rare (Schafer 1980; Schafer et al. 1984). In contrast, North American outbreaks in *Quercus* dominated forests, can last from 2 to 5 years and reoccur at intervals of 4 to 12 years (Anon. 1997b). At its peak in 1981 (Figure 11) some 5.2 million hectares of forest were recorded as being defoliated by *L. dispar* in the USA (McManus et al. 1989). The decline in these outbreaks is the result of the buildup of insect pathogens and predators, and from starvation (Anon. 1997b).

The preferred hosts of the European *L. dispar* include species of *Quercus*, *Malus*, *Liquidambar*, *Alnus*, *Tilia*, *Betula*, *Populus*, *Salix*, and *Crataegus*. Young larvae tend to be limited to the preferred host genera while older larvae feed on a greater range of genera. Furthermore, during outbreaks caterpillars will feed on almost all plants species available (McManus et al. 1989).
The effects of *L. dispar* on the environment in North America have been profound (Figure 11) (Gottschalk 1990; Anon. 1995c). It is recognised that hardwood trees that lose 50% or more of their leaves will refoliate later in the growing season. However repeated defoliation will lead to twig and branch dieback, and fine root death with the latter resulting in reduced water and mineral uptake. Consequently growth losses of up to 33% are not uncommon and may still be evident up to 3 years after defoliation. Furthermore, physiological changes as a result of defoliation weakens affected trees and makes them more vulnerable to attack by other pests and pathogens (Anon. 1997b; McManus et al. 1989).

Defoliation and subsequent mortality can have profound effects on stand structure. Mortality in some stands has been as high as 80–100% but this is very much the exception rather than the rule. The first time *L. dispar* defoliates an area, between 15–35% mortality can be expected. Mortality is greatest when defoliation is greater than 60%. Death rates are typically much higher amongst subdominant than dominant trees and repeated defoliation may result in single storied stands. Defoliation can also cause significant changes to stand composition with moderate to heavy defoliation accelerating forest succession to more shade tolerant species. The most favoured hosts of *L. dispar* in North America are various species of *Quercus*. Forest dominated by *Quercus* has been dramatically altered by this pest, with shifts in species composition and loss of forest cover due to regeneration failure (Gottschalk 1990).

Changes in species composition of the vegetation will also have significant effects on forest fauna. Diversity of insects, birds and other animals may be altered during outbreaks due to loss of food resources. Research in eastern North America has found that bird species that prefer closed-canopies will
abandon defoliated forests while open canopy birds increase in number. The use of chemical and biological insecticides has also had deleterious effects on non-target lepidopterans (Anon. 1997b).

Attempts to control *L. dispar* have included chemical and biological insecticides, and biological control. Biological insecticides have been based on the bacterium *Bacillus thuringiensis var. kurstaki* and the nucleopolyhedrosis virus (NPV) which have been formulated for commercial use (McManus et al. 1989). Biological control ranges from the planting of food plants such as *Amelanchier* spp., *Corylus* spp., *Fagus grandifolia* and *Carya* spp. to encourage predatory and parasitic insects, insectivorous birds, rodents and other small mammals, to the introduction of biological control agents (Anon. 1997b). These agents include the predatory beetle *Calostoma sycophanta* and parasitoid wasps such as *Ooencyrtus kuvanae* (Anon. 1997c). Educational programmes have also been developed, such as ‘Michigan’s Gypsy Moth Education Program’, to teach individual home owners methods to reduce *L. dispar* number in the urban landscape (Anon 1997b).

The *L. dispar* has long been considered one of the most important forest insects in the USA and enormous sums of money (Figure 12) have been spent in eradication and control campaigns. Despite this, outbreaks continue to occur and the insect is still spreading, albeit at a slower rate. The cost to the community through the loss of trees in the urban landscape, the damage and losses in commercial forestry¹, and damage to the environment are incalculable. It would appear that *L. dispar* is firmly entrenched in north-eastern North

![Figure 12. Expenditure ($US) on gypsy moth suppression programmes in the USA (1980–1995).](image)

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¹ The Pennsylvania Bureau of Forestry estimated total losses due to gypsy moth in Pennsylvania between 1969 and 1987 to be 180 million m³ on 5 million ha, worth $219.6 million.
America and eradication is probably now impossible. The majority of management options are now aimed at maintaining \emph{L. dispar} populations at a ‘level considered tolerable’ (McManus et al. 1989).

3.4 \textbf{PINE WILT DISEASE CAUSED BY A NEMATODE (\emph{Bursaphelenchus xylophilus}) IN JAPAN}

Pine wilt disease was first noticed in Japan in the early 1900s (Yano 1913) but the causal agent (a nematode, \emph{Bursaphelenchus xylophilus}) was not identified and described (as \emph{Bursaphelenchus lignicolus}) until 1972 (Mamiya & Kiyohara 1972). The disease is characterised by the rapid wilting and death of the host. The nematode is transmitted by beetles of the genus \emph{Monochamus} (Coleoptera: Cerambycidae).

Yano (1913) reported the death of pines (\emph{Pinus densiflora} and \emph{P. thunbergii}) in epidemic proportions at Nagasaki, Kyushu in 1905. The outbreak was controlled by burning all the dead trees (Kobayashi 1981). In 1925 the disease was reported 50 km north of Nagasaki (Mamiya 1988) and by the late 1930s was present throughout most of Kyushu and Shikoku. Annual losses of timber were about 400,000 m$^3$. Pine wilt disease was found in Honshu in 1921 and during the 1930s and 40s spread northwards through that island. During World War II all attempts at control were abandoned and during this period the disease spread rapidly (Mamiya 1988). By the late 1970s the disease had spread to northern Honshu and in 1979 timber losses of 2.4 million m$^3$ were recorded: in 1980 the Japanese government spent $35$ million in control operations (Mamiya 1984). Today pine wilt disease is found throughout most of Japan where pines occur (a major exception is Hokkaido) (Evans et al. 1993), and it is considered to be the most serious pest of forest trees there (Mamiya 1984).

Since about 1970 \emph{Bursaphelenchus xylophilus} (and pine wilt disease) has spread into China, Korea and Taiwan and is thought to have reached these locations from Japan (Mamiya 1988). In China it is restricted to the provinces of Jiangsu, Anhui, Guangdong, Shandong and Zhejiang, and in Korea to the province of Pusan (Evans et al. 1996).

In 1979 pine tree deaths associated with \emph{B. xylophilus} were discovered in the United States (Dropkin & Foudin 1979). Subsequent research showed the nematode to be native to North America and to have been introduced into Japan, presumably about the turn of the century (Holdeman 1980; Dropkin et al. 1981). It almost certainly reached Japan in pine logs or lumber and established there independently of its North American vectors. In Asia \emph{B. xylophilus} is transmitted by indigenous species of \emph{Monochamus} beetles.

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2 \emph{B. xylophilus} was first described in the United States as \emph{Aphelenchoides xylophilus} (Steiner & Buhrer 1934). Later it was described again as \emph{Bursaphelenchus lignicolus}, when recognised to be the causal agent of pine wilt disease in Japan (Mamiya & Kiyohara 1972). The synonymy was recognised in 1981 (Nickel et al. 1981).
Bursaphelenchus xylophilus occurs in all areas of North America where pine forests exist (EPPO/CABI 1996) with a single report of its presence in Mexico (Dwinell 1993). There is also a record of B. xylophilus in dying pines in Nigeria (Khan & Gbadegesin 1991), but this has not been confirmed by specialist taxonomists (Evans et al. 1996). Similarly, the report by Harrachi et al. (1990) of a Bursaphelenchus sp. in wilted Pinus baleensis in Morocco has not been confirmed.

In contrast to the Asian experience, widespread mortality of pines has not been recorded in North America (Dropkin et al. 1981; Nickle 1981; Wingfield 1983) except in exotic species, most notably in the European Pinus sylvestris. It is by far the most commonly affected host reported from North America (Linit et al. 1983) and belongs in the same section of the genus Pinus as the susceptible Asian pines (e.g. P. densiflora and P. thunbergii).

Considerable work has been carried out in both Japan and the United States to assess the susceptibility of various pine species to B. xylophilus (Futai & Furono 1979; Dropkin et al. 1981; Kondo et al. 1982; Wingfield et al. 1984). Unfortunately there are many contradictions in the literature; many of these can be plausibly explained but some cannot. In general, Japanese work indicates that members of the subsection Sylvestres of the genus Pinus are most susceptible to the disease (although some, e.g. P. massoniana, are apparently resistant) and that the vast majority of North American species of pines are resistant to a greater or lesser degree (Bain & Hosking 1988).

Inoculation studies in the United States have often given conflicting results and generally more species have been reported susceptible to the disease than indicated by the Japanese work. In the United States nearly all of the inoculation studies were carried out using seedlings, whereas much of the Japanese work used older trees, very often in plantation field experiments. For example, in Japanese inoculation studies P. echinata and P. strobus (two North American pines) were ranked as highly resistant, i.e. no trees were killed (Mamiya 1972; Kobayashi 1978), but in inoculation tests with seedlings of these species United States workers recorded 100% mortality (Dropkin & Foudin 1979).

Of great significance are the results of Wingfield et al. (1984). These workers inoculated large numbers of P. banksiana, P. resinosa and P. nigra with B. xylophilus in a forest situation and failed to kill or damage any of them. The inoculum used was sufficient to kill more susceptible species, and also seedlings of the above three pine species in greenhouse inoculation studies.
4. Implications of pathogen and pest case studies for New Zealand

4.1 Pathogens Implications

The major conclusion drawn from these case studies is that pathogenic fungi do not tend to jump great taxonomic distances. All of the great epiphytotics created by the inadvertent introduction of pathogens into new areas have been dependent on the presence of a closely related host species. So in the case of Dutch elm disease what was probably only a minor pathogen of Asiatic elms became an aggressive pathogen of North American and European elm species, as did the causal agent of chestnut blight. Pathogenic fungi tend to be conservative in the number of hosts they attack, and are often confined to a single plant species, genus or family. Such conservatism is the result of co-evolution with the host, evolving defence mechanisms against the pathogen, and the pathogen evolving methods to overcome the defence. This results in pathogens becoming highly adapted and specific to their hosts. This specificity can be so integrated that a study of the systematics of the pathogen allows an understanding of the systematics of the host, as in the case of Cyttaria and Nothofagus (Korf 1983). Therefore to be able to predict the source of a threat it is necessary to understand the biogeography of the host. For instance in the case of Castanea dentata (American chestnut), in considering generic specificity of pathogens it would be likely that a new pathogen would come from another species of Castanea outside of the natural range of C. dentata. The natural distribution of the genus Castanea is limited to the Northern Hemisphere temperate zone or the Boreal floristic kingdom (Good 1964). The Boreal floristic kingdom spans Europe, Asia and North America and represents the fragmentation of the Laurentian flora through plate tectonic movement. Thus in the Northern Hemisphere spectacular epiphytotics have been the result of east–west movement of pests and pathogens across the Boreal floristic kingdom. This also explains the lack of any epiphytotics resulting from the north south movements of pathogens between the Northern and Southern Hemispheres.

As New Zealand forests have developed from a Gondwanan forest it will be amongst the other Gondwanan remnants that we should look for potentially devastating pathogens. This conclusion is supported by two observations. First, New Zealand has been subjected to one hundred and fifty years of introductions of plants mainly from the Northern Hemisphere. Approximately 2100 species of overseas plants have become naturalised (Nicol 1997), but despite this there has not been a single documented ingress of pathogenic fungi into native forest (McKenzie 1998). Second, floristically New Zealand’s forests are related to the forests of the Southern Hemisphere and this is reflected in its mycoflora. For example Leupteutypa podocarpi is a foliar fungus initially described from Podocarpus nubigenus in Chile and subsequently found on P. drouyniana in
Western Australia and *P. totara*, *P. acutifolius*, *P. nivalis* and *P. halli* in New Zealand (Ridley et al. 1997). It is therefore reasonable to assume that the fungi, most likely to penetrate native forest whether they are pathogens or not will come from forests of a similar floristic and climatic composition.

4.2 PESTS IMPLICATIONS

There are very few ‘tested’ generalisations about biological invasions and most rely on probabilistic predictions of which species is likely to arrive, establish and naturalise (Gilpin 1990; Daehler & Strong 1993). The requirements for successful invasion of a new habitat by insects are taken as: a viable reproductive founder population, a suitable climate, minimal ‘predation’ and a suitable food resource. Accepting the idiosyncrasies of reproductive systems and founder effects and the mild New Zealand maritime climate, a potential immigrant must find a suitable supply of food and lack significant predation for its population to expand and establish. Natural migrants are invariably winged adults, which, with extremely rare exceptions, would be free of, and unlikely to be accompanied in flight by, specific parasitoids. If the founding population of any life stage is small the successful co-establishment of specific parasitoids is also likely to be diminished. The assumption for most establishing immigrant insects is that the major constraint to population expansion is the availability of food.

The current accepted dogma is that plants are not passive targets for herbivores and that phytophagous organisms co-evolve with their host plants. Related insects tend, therefore, to feed on related plants and though capable of surviving on other hosts or artificial diets, the response cues necessary for various behaviours are absent. This results in either feeding and dispersal not being initiated and the insect dies, or feeding not being initiated but dispersal is triggered so that the insect seeks a suitable host. This can be seen when populations of newly arrived phytophages, constrained only by host availability, turn to alternative hosts during population outbreaks, e.g. *Phyllonorycter messaniella* (oak leaf miner) attacked *Nothofagus*, and *Phylacteophaga froggatti* (eucalypt leaf miner) attacked *Betula* before the introduction of specific parasitoids (Forest Research, unpublished data).

Some insect groups have circumvented plant defences by feeding on dead material (most wood borers) or by avoiding ‘green cell’ defence systems by tapping directly into the photosynthetic stream (sapsuckers). These two groups are well represented in the naturalised immigrant fauna of New Zealand (see Fig. 9), but the leaf feeders (lepidopteran caterpillars), particularly those from the Northern Hemisphere are not. This is despite the fact that globally Lepidoptera are the most significant forest defoliators and have overcome major abiotic and biotic hurdles to achieve their prominence, as in the case of *Lymantria dispar*.

The long period of New Zealand’s geographic isolation is reflected in the high degree of endemism in its flora. The prominent families of Nothofagaceae (Nixon 1982; Jones 1986; Hill & Jordan 1993), Podocarpaceae and Myrtaceae are confined almost exclusively to the Southern Hemisphere, with elements in
New Zealand, Australia, New Caledonia and South America. It follows then that Northern Hemisphere green cell feeding insects, unless they are very broadly polyphagous, would not find the New Zealand endemic flora a suitable food resource.

There are over 180 exotic forest and timber insects established in New Zealand and the vast majority of them are found on exotic host plants. Only a relatively small number of these introduced insects have been found feeding on indigenous plants and with the major exception of *Eriococcus orariensis* none have caused any significant damage. Some examples of established exotic ‘forest’ insects and recorded indigenous hosts are presented in Table 8 (Spiller & Wise 1982; Forest Research, unpublished data). All of the insects listed are phytophagous sapsuckers and feed on live plants, with the exception of *P. messaniella* which is a leaf miner. This suggests that threats to New Zealand’s indigenous forest well may come from sapsucking insects rather than from grazing insects such as lepidopterans. For instance *Scolypopa australis*, the Australian passionvine hopper, has been implicated in the sudden decline of cabbage tree (*Cordyline australis*) (Beever et al. 1996).

<table>
<thead>
<tr>
<th>INSECT</th>
<th>HOST</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Scolypopa australis</em> (Hemiptera: Ricaniidae)</td>
<td>Coriaria, Leptospermum, Muehlenbeckia</td>
</tr>
<tr>
<td><em>Trialeurodes vaporariorum</em> (Hemiptera: Aleyrodidae)</td>
<td>Pittosporum, Senecio</td>
</tr>
<tr>
<td><em>Hemiberlesia rapaz</em> (Hemiptera: Diaspididae)</td>
<td>Hoheria, Leptospermum</td>
</tr>
<tr>
<td><em>Icerya purchasi</em> (Hemiptera: Margarodidae)</td>
<td>Leptospermum, Hoheria, Pittosporum</td>
</tr>
<tr>
<td><em>Aspidiotus nerii</em> (Hemiptera: Diaspididae)</td>
<td>Carpodetus, Coprosma, Corynocarpus, Laurelia, Sophora, Vitex</td>
</tr>
<tr>
<td><em>Lindingaspis rossi</em> (Hemiptera: Diaspididae)</td>
<td>Leptospermum</td>
</tr>
<tr>
<td><em>Myzus persicae</em> (Hemiptera: Aphididae)</td>
<td>Hebe, Pittosporum, Vitex</td>
</tr>
<tr>
<td><em>Siphanta acuta</em> (Hemiptera: Platidae)</td>
<td>Coprosma</td>
</tr>
<tr>
<td><em>Aphis gossypii</em> (Hemiptera: Aphididae)</td>
<td>Hebe, Pittosporum, Vitex</td>
</tr>
<tr>
<td><em>Macrosiphum euphorbiae</em> (Hemiptera: Aphididae)</td>
<td>Hebe, Pittosporum</td>
</tr>
<tr>
<td><em>Ceroplastes sinensis</em> (Hemiptera: Coccidae)</td>
<td>Hebe, Leptospermum, Myrsine, Olearia, Vitex</td>
</tr>
<tr>
<td><em>Eriococcus orariensis</em> (Hemiptera: Eriococcidae)</td>
<td>Leptospermum</td>
</tr>
<tr>
<td><em>Phyllonorycter messaniella</em> (Lepidoptera: Gracillaridae)</td>
<td>Notobogus</td>
</tr>
</tbody>
</table>
5. Potential threats from pathogens to New Zealand forests

In the previous section the flora of the Southern Hemisphere was identified as a major source of pathogenic threats to New Zealand's indigenous tree species. Due to the sheer number of species involved a purely pragmatic approach was taken and the search of the literature for pathogenic fungi limited to what might be considered the dominant forest species in New Zealand: the conifers (Araucariaceae and Podocarpaceae), the southern beech (Nothofagaceae), and the ratas (Myrtaceae). However, the recorded global invertebrate fauna of the Araucariaceae, Podocarpaceae, Nothofagaceae, and Myrtaceae is both too numerous and diverse to be assessed for threats in its entirety, and a risk assessment is further constrained by a lack of ecological theory of invasion to aid prediction, although the presence of suitable host material and regulatory guilds are obviously significant (Kay 1999a).

As stated in section 4.2, past experience and biogeography favours the establishment of Hemiptera (sapsuckers) as the most likely pests for colonisation of New Zealand's flora. This section will focus on the potential threats to the flora from this insect group as Hemiptera possess a 'weediness' of character often exhibited by invasive organisms. They often incorporate a number of fecund asexual generations in a multivoltine life cycle, which, coupled with their relatively small size, passive dispersal and an ability to bypass some plant defenses, are beneficial for colonising organisms.

New Zealand will always be exposed to temperate invertebrates accompanying trade goods. The bulk of trade is sea-borne and north-south transportation of pests is presumably restricted by the duration of the voyage, a seasonal asynchrony of pests and hosts and possible thermal shock encountered when passing through the tropics. Conversely, east-west transportation of pests is not so prejudiced by biological constraints but, with the exception of Australia, has in the past been limited by the lack of strong trading relationships (Kay 1989; Walsh & Kay 1996).

The dominant elements of the New Zealand flora also predominate in other Southern Hemisphere landmasses. If it is accepted that insect host selection is basically phylogenetically conservative, and that insects travel along trade routes, then the greatest potential threat to New Zealand's indigenous forests should be seen as Southern Hemisphere Hemiptera moving from, or via, Australia.

Hemiptera may damage plants in a number of ways. Typically, they feed on new succulent plant growth, and may cause stunting, distortion/galling or wilting. A number of mesophyll feeders can inject toxic saliva which causes necrosis of plant tissue, while others are vectors of serious plant disease microorganisms. The exposure to a novel insect threat as well as a new disease organism would pose a significant evolutionary hurdle. A third effect is that the sugary excreta of aphids, psyllids and coccids, dropping on leaves and stems adjacent to, or
below, high populations of these sapsuckers supports, the growth of black sooty mould. This growth may impede normal photosynthetic function and may influence the health of the host or adjacent tree species.

5.1 CONIFERS (ARAUCARIACEAE AND PODOCARPACEAE)

The Araucariaceae and Podocarpaceae are ancient conifer families. The Araucariaceae contains three genera: *Agathis* with 20 species extends from the Philippines to New Zealand and from Malaysia to Fiji; *Araucaria* with 16 species is found in South America, Australia, New Caledonia, New Zealand and Norfolk Island (Spore 1974); and *Wollemia* with 1 species is limited to a few small populations in New South Wales (da Silva 1997). The Podocarpaceae contains approximately 150 species in 15 genera and is distributed throughout the Southern Hemisphere and extending into Indonesia, South East Asia, southern China, Japan, the West Indies (Spore 1974). New Zealand has 17 species in these families (Table 9) (Poole & Adams 1990).

As ancient families of slow growing conifers, the resource allocation theory (reviewed by Sibly 1997) dictates that Araucariaceae and Podocarpaceae should

| TABLE 9. NEW ZEALAND INDIGENOUS SPECIES OF ARAUCARIACEAE AND PODOCARPACEAE. |
|-----------------------------|-----------------------------|
| **FAMILY**                  | **SPECIES**                 |
| Araucariaceae               | *Agathis australis*         |
| Podocarpaceae               | *Podocarpus totara*         |
|                             | *P. totara var. waibensis*  |
|                             | *P. hallii*                 |
|                             | *P. acutifolius*            |
|                             | *P. nivalis*                |
|                             | *P. nivalis var. erectus*   |
|                             | *Prumnopitys ferruginea*    |
|                             | *P. taxifolia*              |
| Dacrycarpus dacrydioides    |                            |
| Dacrydium cupressinum       |                            |
| Halocarpus kirkii           |                            |
| *H. biformis*               |                            |
| *H. bidwillii*              |                            |
| Lagarostrobus colensoi      |                            |
| Lepidothamnus intermedius   |                            |
| *L. laxifolius*             |                            |
| Phyllocladus trichomanoides |                            |
| *P. glaucus*                |                            |
| *P. aspleniifolius var. alpinus* |                        |
be well defended from insect attack and there are numerous reports of insecticidal properties attributed to the so-called ‘secondary compounds’ of this group of plants (Barrington et al. 1993; Kubo et al. 1984; Briggs & Kingsford 1974). Sapsuckers which tap directly into the photosynthate conductive issues, may avoid these compounds.

5.1.1 Pathogens of Araucariaceae

Three rusts are known from Araucariaceae. Aecidium fragiforme occurs on Agathis palmerstonii in northern Queensland, A. alba, A. dammara and Agathis spp. in Malaysia and Indonesia, A. labillardieri in New Guinea, and A. vitiensis in Fiji (Punithalingam & Jones 1971; Hadi et al. 1996). Aecidium balansae occurs on A. ovata, A. moorei and Agathis sp. in New Caledonia (Punithalingam & Jones 1971). The third rust species Caema sanctae-crucis occurs on Araucaria araucana in Chile (Petersen 1968) with its alternate stage of Mikronegeria fagi found on Nothofagus alpina, N. obliqua var. obliqua, N. obliqua var. macrocarpa, and N. glauca (Butin 1969; Oehrens & Gonzalez 1977).

5.1.2 Pathogens of Podocarpaceae

Only a single rust has been described from Podocarpaceae and this is Caema peltatum on Phyllocladus trichomanoides in New Zealand (Shaw 1976). An alternate Mikronegeria on Notrofagus has never been located. Other Caema species are known from Southern Hemisphere conifers in the Araucariaceae (Petersen 1968) and Cupressaceae (Petersen & Oehrens 1978).

The Coryneliaceae comprise some 15 species occurring predominantly on Podocarpaceae in Australasia, South America, Africa and Asia (Johnston & Minter 1989). New Zealand has a single species, Corynelia tropica, occurring on Podocarpus totara, P. ballii, P. nivalis and P. acutifolius (Hood 1985). It is also recorded from Chile on P. salignus (Johnston & Minter 1989).

Johnston (1991) has reported 6 species of Bivallum from Southern Hemisphere Podocarpaceae and Cupressaceae. The species occurring on Podocarpaceae are B. zelandicum on Dacrydium cupressinum from New Zealand, B. microstrobi on Microstrobos niphophilus from Tasmania, and B. podocarpi on Podocarpus salignus and P. nubigenus from Chile.

5.1.3 Pests associated with Araucariaceae and Podocarpaceae

The aphid genus Neophyllaphis has about twelve species which are associated with Araucariaceae and Podocarpaceae in the Southern Hemisphere, the mountains of the tropics, China and Japan. Three species are recorded from Podocarpus in Australia. They are not recorded as pests, but relatively small populations typically cause stunting and curling of new growth on young or mature trees. Heavy attack can stunt the growth of seedlings (Blackman & Eastop 1994). Only N. totarae is recorded in New Zealand. Parasitoids of N. totarae are not recorded, but it is unlikely that this lone representative would support a parasitoid guild which could effectively control introductions of new species.
The coccid *Conifericoccus agathidis* feeds on young succulent leaves and stems of *Agathis* spp. in Australia. It has been recorded as a severe pest of *Agathis* plantations of up to 40-year-old trees, in Queensland. Repeated defoliation by this insect may result in the death of trees and this coccid has effectively curtailed the establishment of *Agathis* plantations in Queensland. It also appears that *C. agathidis* has readily spread to southeast Queensland on nursery stock. The genus *Conifericoccus* is unrecorded in New Zealand. Control of an accidental introduction would have to rely on generalist coccid predators and parasitoids. These are largely unknown but probably reasonably extensive, given the diversity of the coccid fauna in New Zealand (Hoy 1963).

Other coccids, *Eriococcus araucariae* and *Nipaecoccus aurilanatus* were recorded in New Zealand in the late 19th century (Maskell 1879, 1890), but have only ever been recorded on introduced *Araucaria* species.

### 5.2 NOTHOFAGACEAE

The Fagaceae traditionally contains eight genera of which seven are distributed in the Northern Hemisphere and tropics and one, *Nothofagus*, in the temperate Southern Hemisphere. *Nothofagus* was considered to represent a relic Gondwanan element of the family (Wardle 1984). However *Nothofagus* has now been allocated to its own family the Nothofagaceae and is thought to have closer affinities with the Betulaceae than the Fagaceae (Nixon 1982; Jones 1986; Hill & Jordan 1993). *Nothofagus* is divided into three groups on the basis of pollen type. The *brassi*-type which is limited to the montane forests of New Caledonia and New Guinea, and the *menziesii*-type and the *fusca*-type which are both found in Australia, New Zealand and South America (Table 10) (McQueen 1976; Poole 1987).

### TABLE 10. *Nothofagus fusca* AND *menziesii* TYPE POLLEN GROUPS AND SPECIES.

<table>
<thead>
<tr>
<th>fusca-TYPE</th>
<th>menziesii-TYPE</th>
</tr>
</thead>
<tbody>
<tr>
<td>New Zealand</td>
<td></td>
</tr>
<tr>
<td><em>N. fusca</em></td>
<td><em>N. menziesii</em></td>
</tr>
<tr>
<td><em>N. solandri</em> var. solandri</td>
<td></td>
</tr>
<tr>
<td><em>N. solandri</em> var. cliffortioides</td>
<td></td>
</tr>
<tr>
<td><em>N. truncata</em></td>
<td></td>
</tr>
<tr>
<td>Australia</td>
<td></td>
</tr>
<tr>
<td><em>N. gunnii</em></td>
<td><em>N. cunninghamii</em></td>
</tr>
<tr>
<td><em>N. moorei</em></td>
<td></td>
</tr>
<tr>
<td>South America</td>
<td></td>
</tr>
<tr>
<td><em>N. alessandrii</em></td>
<td><em>N. obliqua</em> var. obliqua</td>
</tr>
<tr>
<td><em>N. antartica</em> var. antartica</td>
<td><em>N. obliqua</em> var. macrocarpa</td>
</tr>
<tr>
<td><em>N. antartica</em> var. bicrenata</td>
<td><em>N. glauca</em></td>
</tr>
<tr>
<td><em>N. betuloides</em></td>
<td><em>N. alpina</em></td>
</tr>
<tr>
<td><em>N. dombecyi</em></td>
<td></td>
</tr>
<tr>
<td><em>N. leoni</em></td>
<td></td>
</tr>
<tr>
<td><em>N. pumilio</em></td>
<td></td>
</tr>
<tr>
<td><em>N. nitida</em></td>
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</tr>
</tbody>
</table>
5.2.1 Pathogens of Nothofagaceae

The family Ophiostomataceae which contains a number of pathogens and sapstain fungi including \textit{Ophiostoma novo-ulmi}, the causal agent of Dutch elm disease, \textit{Chalara australis}, the causal agent of myrtle wilt in Tasmania, and \textit{Sporotrix} sp. causing beech dieback in New Zealand (Faulds 1977). In Tasmania, \textit{Chalara australis}, a sapstain fungus, causes severe wilting and death of \textit{N. cunninghamii}. It is a major cause of gaps in natural \textit{N. cunninghamii} stands but the most severe mortality occurs in forests subjected to human disturbance (Kile et al. 1989). Mortality associated with \textit{C. australis} has not been observed in the other Australian species (\textit{N. gunnii} and \textit{N. moorei}) although the fungus was consistently reisolated from stained wood of artificially inoculated \textit{N. gunnii}. Experimental inoculation of the South American species \textit{N. glauca}, \textit{N. leoni}, \textit{N. obliqua}, \textit{N. alpina} and \textit{N. alessandra} showed some discoloration of the sapwood. However no such discoloration occurred in the New Zealand species \textit{N. menziesii} and \textit{N. solandri} var. \textit{diffortiioides} despite \textit{N. menziesii} being closely related to \textit{N. cunninghamii}. \textit{Ophiostoma nothofagi} with a \textit{Sporothrix} anamorph and \textit{O. valdivianum} have been reported from \textit{Nothofagus} in Chile (Butin & Aquilar 1984; Seifert et al. 1993).

Only two rusts are known from \textit{Nothofagus}: \textit{Mikronegeria fagi} and \textit{Micronegeria alba}, from Chile. Both species have been reported to infect \textit{Nothofagus alpina}, \textit{N. obliqua} var. \textit{obliqua}, \textit{N. obliqua} var. \textit{macarcarpa}, and \textit{N. glauca} (Butin 1969; Oehrens & Gonzalez 1977; Peterson & Oehrens 1978). Their alternate states occur on coniferous hosts, \textit{M. fagi} with \textit{Caeoma sanctae-crucis} on \textit{Araucaria araucana} (Petersen 1968), and \textit{M. alba} with \textit{C. espinosae} on \textit{Libocedrus chilensis} (Oehrens & Gonzalez 1977; Petersen & Oehrens 1978). There appears to be no published account of the effects of these rusts on their \textit{Nothofagus} hosts but Peterson & Oehrens (1978) describe witches’ brooms being formed on infected \textit{Libocedrus chilensis}.

In Europe powdery mildews attack species of \textit{Quercus}, \textit{Malus}, \textit{Crataegus}, \textit{Acer}, \textit{Corylus} and \textit{Platanus} and other hardwood trees (Strouts & Winter 1994). Viney (1970) considered the powdery mildew caused by \textit{Microsphaeria alphitoides} on \textit{Quercus robur} responsible for failure of this species to regenerate in Belgium and France. It is also thought that \textit{M. alphitoides}, in tandem with root pathogens, drought and insect attack led to substantial dieback of \textit{Q. robur} in various parts of Europe in the early part of the twentieth century (Phillips & Burdekin 1982). Walker (1983) reviewed the distribution of plant pathogenic powdery mildews in the Southern Hemisphere revealing that few indigenous woody plants were susceptible to powdery mildews and that existing records were usually cultivated or nursery plants. Two powdery mildews have been reported from South American \textit{Nothofagus} forests: \textit{Uncinula magellanica} on \textit{N. antartica} and \textit{U. nothofagi} on \textit{N. antartica} var. \textit{bicrenata} and \textit{N. pumilio} (Havrylenko 1995). There is no information available on damage, if any, caused by these pathogens but these hosts belong to the \textit{fusca} pollen groups as do three of the New Zealand \textit{Nothofagus} species and they could possibly be susceptible to pathogenic attack.
5.2.2 Insects associated with Nothofagaceae

As one would expect, New Zealand’s smaller landmass harbours relatively few invertebrates associated with *Nothofagus*, particularly in comparison with South America. For example, five hemipteran families are associated with *Nothofagus* in New Zealand, but twelve in South America.

*Eriococcus* (all species of which may not form a monophyletic group of scale insects) occurs throughout the world on a wide variety of tree hosts. *Madarococcus* was erected for a few New Zealand species, and differs from *Eriococcus* by only a single character. All species of the Eriococcidae with spatulate suranal setae belong to one of these two genera, and all appear to be confined to *Nothofagus*. Humphries et al. (1986) give a cladistical collation of *Eriococcus* associated with *Nothofagus* from which potential risk can be deduced. For example, the South American species *Eriococcus eurytbrich* and *E. navarinensis*, because of their host associations, could be considered a threat to New Zealand’s *N. menziesii* and *N. fusca*-types respectively. However, an accidental introduction would probably be controlled by the presumed, but largely unrecorded, parasitoid guild associated with the numerous *Eriococcus* spp. and *Madarococcus* spp. on *Nothofagus* in New Zealand.

On the other hand, three related, but distinct, genera of aphid associated with *Nothofagus; Neuquenaphis, Neosensoriaphis* (9 species in South America) and *Taiwanaphis* (4 species in Australia, and only one (*T. nothofagi*) in New Zealand) do represent a threat to New Zealand *Nothofagus* because of the probable paucity of parasitoids in New Zealand. These aphids are not recorded as pests, but their biology is not well known. Some appear to feed on more than one host (Blackman & Eastop 1994). The host specific parasitoids (*Pseudephedrus* spp.) associated with these aphid genera have not been recorded from New Zealand and, even if present, may be too host-specific to contribute significantly to the control of introduced South American species.

5.3 MYRTACEAE

The Myrtaceae has its greatest diversity in the Australasian and South-East Asian region and in Central and South America, and with a few additional species in southern Africa. The family is subdivided into the fleshy fruit Myrtoideae and the dry fruited Leptospermoideae. The Myrtoideae are strongly represented in Australasia, South-east Asia, Central and South America and by two genera in southern Africa. In contrast the Leptospermoideae are chiefly found in Australasia, and with only one genus in the Americas and two in southern Africa. The New Zealand flora contains fourteen species of Leptospermoideae, in three genera, and four species of Myrtoideae in three genera (Table 11) (Poole & Adams 1990).

5.3.1 Rusts of Myrtaceae

Walker (1983) tabulated 43 species of rust occurring on Myrtaceae. All but 3 were recorded from Central and South America and all of these from the subfamily Myrtoideae. In 1994 a new rust was found on *Kunzea ericifolia* in Western Australia (Shivas & Walker 1994), giving a total of 2 myrtaceous rusts
from Australia and 2 from India. Of the American species *Puccinia psidii*, guava rust, has been recorded attacking Australian species of *Callistemon, Eucalyptus* and *Melaleuca* species cultivated in South America. Species of *Eucalyptus* attacked in Brazil include *E. citriodora, E. cloeziana, E. grandis, E. maculata, E. paniculata, E. pirocarpa, E. punctata, E. saligna, E. tereticornis* and *E. urophylla* (Anon. 1985). The Australian tree *Melaleuca quinquenervia* has become an invasive weed of natural areas in southern Florida (Liebold et al. 1995). In January of 1997 a significant epiphytotic caused by *P. psidii* was reported by Rayachhetry et al. (1997) and it was speculated whether this rust could be used as a biocontrol agent of melaleuca. There appear to be no records of cultivated New Zealand Myrtaceae having been attacked by *P. psidii*.

The Australian rust *Uredo xanthostemonis* has been reported on *Xanthostemon paradoxus* and *X. eucalyptoides* from the Northern Territory (Walker 1983). The host species are placed in the subfamily Leptospermoideae, *Metrosideros* alliance, *Xanthostemon* suballiance by Briggs & Johnson (1979).

*Melampsora eucalypti* and *Melampsora* sp. have been recorded on *Eucalyptus globulus* and *E. citriodora* respectively from India. Examination of the type material of *M. eucalypti* failed to find any rust according to Walker (1983). Also when Walker attempted to confirm the identification of Upadhyay & Bordoloi’s (1975) *Melampsora* sp. on *E. citriodora* no material could be located and requests for fresh material was unsuccessful. It would appear that unless further specimens are found it is unlikely that there are anyrusts attacking *Eucalyptus* species in India.

### 5.3.2 Foliage pathogen of Myrtaceae: *Aulographina eucalypti*

The leaf pathogen *Aulographina eucalypti* occurs commonly as a leaf and twig pathogen of eucalypts in south-eastern Australia and Tasmania having been reported on 38 species (Wall & Keane 1984). It is also known from Queensland (Walker 1996) and the Northern Territory (Yuan 1996). The fungus has been inadvertently introduced into the United Kingdom (Sporer 1981), New Zealand (Dick 1982), Hawaii (Wall & Keane 1984), Brazil (Ferreira 1989), South
Africa (Crous et al. 1989) and Chile (Wingfield et al. 1995). In Australia *A. eucalypti* has been recorded from *Angopohora costata*, a genus closely allied to *Eucalyptus*, and from the introduced South American Myrtoideae genus *Feijoa sellowiana* (Walker 1983, 1996). Walker (1996) reports it on Ericaceous hosts, *Arctostaphylos stanfordiana* and *Arbutus unedo*, from North America and Europe. This led Walker to comment on the risk of introduced fungi jumping from the somewhat predictable (*Feijoa, Myrtaceae*) to the unpredictable (*Arctostaphylos* and *Arbutus, Ericaceae*). The health status of the host in both of these reports are unknown and these may represent highly localised opportunism rather than a move to a new host. There are as yet no reports from outside of Australia of *A. eucalypti* occurring on hosts other than *Eucalyptus* spp.

### 5.3.3 Stem canker of Myrtaceae: *Cryphonectria cubensis*

*Cryphonectria cubensis* has become a significant pathogen of *Eucalyptus* spp. in tropical areas of Brazil, Central America, Florida, Hawaii and Western Samoa (Hodges et al. 1979; Hodges 1980), Cameroon (Gibson 1981), India (Sharma et al. 1985) and South Africa (Wingfield et al. 1989; Conradie et al. 1990). It is only recently that *C. cubensis* has been found in native stands of *Eucalyptus* (*E. marginata*) in temperate Western Australia (Davison & Coates 1991; Davison & Tay 1995). The only other known host is *Syzygium aromaticum* (Hodges et al. 1986), the clove, which has been dispersed throughout the tropics from its native range in the Molucca Islands of Indonesia. It is believed that the fungus has been inadvertently carried to most tropical areas on *S. aromaticum* plants destined for either clove production or as tropical ornamentals (Hodges et al. 1986). If that is indeed the case then the fungus was already well established as a minor pathogen before the arrival in most cases of *Eucalyptus* spp. for use in plantation forestry. However there is still an anomaly in the presence of *C. cubensis* in Western Australia which has yet to be explained but suggests that non-tropical Myrtaceae could be at risk in the future.

The original host of *C. cubensis* was *Syzygium aromaticum* a member of the subfamily Myrtoideae whereas *Eucalyptus* is a Leptospermoideae. This represents a jump of both genus and subfamily. Hodges et al. (1986) inoculated stem segments of a number of Myrtaceae but only obtained fungal growth on four of the thirteen species trialed (*Eucalyptus saligna*, *Syzygium aromaticum*, *Syncarpia glomulifera* and *Eugenia megacarpa*). Similar inoculation trials were conducted by Swart et al. (1991) who showed that *Eucalyptus grandis*, *Psidium guajava* and *Syzygium cordatum* were also susceptible.

### 5.3.4 Pests associated with Myrtaceae

It is virtually impossible to identify specific threats to the New Zealand Myrtaceae given the huge number of Hemiptera associated with this quintessential Australian plant family, exemplified by the 600 species of *Eucalyptus*. Australia is our nearest and largest trading partner and a continual stream of establishing Australian forest insects is recorded in New Zealand. The folly of attempting to grow pest-free *Eucalyptus* in this country has been reiterated by Kay (1989, 1999b). If the Australian Hemiptera have co-evolved
with the vast ‘Eucalyptus’ assemblage (Pryor & Johnson 1971) they may well be constrained to a relatively narrow host range within the Myrtaceae and pose little threat to New Zealand endemics. However, this does not seem to be the case for some Australian immigrants. The eucalyptus leaf-mining sawfly, *Phylacteophaga froggatti* was found on a number of unrelated hosts, including *Quercus* and *Betula* when first recorded in New Zealand (Kay 1986).

It is pertinent to this exercise that of the 37 recorded species of Australian Hemiptera established in New Zealand, 13 are recorded from myrtaceous hosts, but only four have established on indigenous plants (*Leptospermum* spp.), which have conspecifics in Australia. It could be argued that New Zealand endemics are relatively resistant to invertebrate attack (Kay 1999a) and that the conspecific status of *Leptospermum* and *Kunzea*, or their pioneer life strategy of ‘run rather than fight’—i.e. precocious seeding and colonisation of transient, disturbed sites—renders them more susceptible to colonisation. A possible threat to *Leptospermum* is the aphid *Anomalaphis casimiri*, recorded from an ornamental variety (Blackman & Eastop 1994).

The role of pathogens and pests in the decline of *Metrosideros* forest in Hawaii is thought to be secondary to either abiotic factors or moribund even-aged stands, although pathogens and pests may have accelerated the decline (Mueller-Dombis 1985; Stoner 1977).
6. Impact scenarios of invasions of potential forest pathogens

Impact scenarios have been developed for two pathogens capable of attacking New Zealand’s indigenous tree species: myrtle wilt of *Nothofagus* and guava rust of Myrtaceae. These pathogens have been selected because there is a wealth of published data on which to base scenarios and to lift them above the level of mere conjecture. Similarly impact scenarios have been developed for two insects: the lepidopteran *Orgyia thyellina* (white spotted tussock moth) and the sapsucker *Eriococcus orariensis* (causal agent of manuka blight). Both these pests had successfully established in New Zealand however, *O. thyellina* was successfully eradicated (Bain 1998; Hosking 1998) and *E. orariensis* began to decline after the inadvertent introduction of a fungal parasite (Zondag 1977b). As they did initially establish, a wealth of published and unpublished data exists on which to base the scenario and to contemplate what could have happened if man or natural intervention had not occurred.

6.1 MYRTLE WILT OF *Nothofagus* CAUSED BY *Chalara australis*

*Nothofagus cunninghamii* (myrtle) is the most common of the dominant tree species in many of the rainforest communities of Tasmania. Locally severe, but widespread mortality was first reported by Howard (1973) in both disturbed and undisturbed forests in north-west Tasmania.

Tree death was caused by a new species, *Chalara australis* (Kile & Walker 1987), and was associated with accelerated attack by an ambrosia beetle *Platypus subgranosus*. Naturally infected trees take from less than 1 year to more than 2.5 years to die from the time of initial infection (Kile & Walker 1987). Elliot et al. (1987) reported that in a survey of 20 rainforest sites 9.4% to 53.4% of *N. cunninghamii* trees were attacked. Although high disease levels were seen to occur in unmodified sites, activities such as roading and logging led to increased levels of infection and mortality.

*Chalara australis* is taxonomically closely related to the causal agents of several tree diseases. The most serious of these is oak wilt, caused by *Certocystis fagacearum* (= *Chalara quercina*) which has proved devastating to many species of oak in North America. *Chalara neocaledonia*, the species most similar to *C. australis*, is the cause of a vascular wilt disease of *Coffea robusta* (coffee) and *Psidium guajava* (guava) in New Caledonia (Witthihn et al. 1998). *Ceratocystis virescens* which is responsible for a disease of *Acer saccharum* in the United States and is also found in logs and lumber of several hardwood species (including *Fagus* spp.) has *Chalara* asexual stages with close affinities to *C. australis*. Although several other species of *Chalara* occur on the Fagaceae, most are saprophytes with some causing sapstain and timber degrade. *Chalara quercina*, in North America and the *Chalara* stage of *Ceratocystis fimbriata* are the only 2 species parasitic on Fagaceae. Several species of
Chalara have been found on Nothofagus spp. in New Zealand (Nag Raj & Kendrick 1975) but none have proved to be parasitic.

Kile (1989) showed that young plants of Nothofagus menziesii and N. solandri var. cliffortioides were not susceptible. However Kile & Walker (1987) found mature trees of N. cunninghamii were more susceptible to C. australis than seedling or saplings. Thus mature trees of New Zealand species could be susceptible to this disease.

Infection of wounds by airborne and/or water-borne spores is considered to be the main method for the establishment of new infections. Spores can be either liberated from mycelium growing on the surface of infected trees or other wood surfaces, or by wind-borne frass contaminated with spores and mycelial fragments from beetle tunnelling in infected tissue. There is also evidence of below ground spread, probably through either root grafts, root contact, or below-ground vectors. Kile & Hall (1988) demonstrated that C. australis was not dependent on P. subgranosus for transmission or for entry to the trees, although P. subgranosus is of some significance in disease spread through liberation of contaminated frass and creation of wounds in stressed trees. However 3 New Zealand species of Platypus, P. apicalis, P. caviceps and P. gracilis, would be capable of playing an important part in transmitting such a pathogen were it to find a susceptible host in this country and become established. There would appear to be no climatic barriers to the growth of the fungus in most parts of New Zealand.

Faulds (1977) provided experimental proof that mortality of Nothofagus fusca associated with pinhole borer (Platypus spp.) attack was the direct result of invasion of sapwood by Sporothrix sp., a fungus which is a frequent contaminant of Platypus beetles. Dieback and mortality of other Nothofagus spp. with similar symptoms and damage and with Platypus attack is presumed to be caused by the same pathogen. Platypus and Sporothrix have also been found to be associated with mortality of Weinmannia racemosa (Payton 1989). Sporothrix is one of the typical asexual stages of many Ophiostoma species, including O. novo-ulmi. A sexual stage of the fungus causing mortality of Nothofagus and Weinmannia has not been found though another Ophiostoma, along with its Sporothrix and Graphium asexual states has been collected from the bark at the entrance of a Platypus tunnel. This second Ophiostoma does not have any known pathogenic capability. It is therefore quite possible should C. australis become established in New Zealand for it to be vectored by a Platypus species.

The possibility that hybridisation between a virulent pathogen introduced from overseas and a closely related native fungus might occur, and give rise to a parasite capable of seriously damaging our indigenous flora has been considered in depth with regard to the recent introduction of Dutch elm disease to New Zealand. Dr C. Brasier (Forestry Commission, Great Britain) a world expert on Dutch elm disease visited New Zealand in 1993 following the outbreak of Dutch elm disease in Auckland. He raised the possibility that O. novo-ulmi may be capable of hybridising with the Sporothrix sp. known to cause mortality of Nothofagus fusca leading to a new, more virulent strain. The two fungi could very conceivably come into contact through the activities of Platypus species. Although principally found in Nothofagus spp., two of the three Platypus species in New Zealand have a very wide host range (Milligan 1979) including species of Ulmus (Forest Research records). Platypus apicalis is particularly
partial to elm, and brood rearing has been recorded in dead or dying trees, stumps and logs of Ulmus spp. Since the establishment of Dutch elm disease in Auckland in 1990 and in Napier in 1993 Platypus apicalis attack of debarked stumps of elms, felled because of O. novo-ulmi infection, has been recorded at both locations. The monitoring of developing broods has been carried out at several sites and the capability of new emerging adults to carry spores of O. novo-ulmi has been demonstrated (L. Bulman, Forest Research, pers. comm.). These beetles could carry the fungus to Nothofagus where it could come into contact with the Sporotrix sp.

If this contact occurred there was the possibility that, through a process of hybridisation and evolution, Sporotrix could acquire genes for vascular wilt toxins and the ability to avoid elicitation of host defence mechanisms from O. novo-ulmi, and thereby initiate an epidemic in Nothofagus forests. Because of this concern a series of mating experiments using isolates of O. novo-ulmi from Auckland crossed with isolates of Ophiostoma and Sporotrix from Nothofagus from all parts of New Zealand were carried out. In all attempted matings hybrids failed to form. Thus the likelihood of a hybrid forming between O. novo-ulmi and co-generic fungi from Nothofagus appears extremely remote. Such a scenario would be far more likely to result from the arrival of a fungus from an area with forest types with close affinities to those in New Zealand (such as Tasmania) than from the Northern Hemisphere Dutch elm disease fungus Ophiostoma novo-ulmi.

New Zealand has approximately 6.24 million hectares of native forest (McKelvey 1995) of which pure or mixed Nothofagus forest forms 4.25 million hectares or 68% (Wardle 1984). Nothofagus forms the framework for a unique assemblage of organisms. Beech forest can range from sea level to the tree line at 1000–1350 m. At any one site in the altitudinal and latitudinal range of the genus, the diversity of vascular plants may only reach just over thirty species. However, over its entire range many species are involved and Wardle lists 100 of the most characteristic and important species. Wardle (1984) lists 24 species of native birds that are either partially or fully dependent on beech forest habitat. Horak (1970) found that of 700 species in 140 genera of Agaricales (Fungi), known at that time from New Zealand, 50% were found in Nothofagus forests.

Man’s dependence on beech forest is related to where it has survived clearance. The most extensive beech forests occur on steep land and survive as protection forest. The 1913 New Zealand Royal Commission on Forestry recognised the value of these forests in protecting the soil, conserving water, preventing floods and providing shelter from wind. Protection forests form the water catchments for 1.432 million urban dwellers (McKelvey 1995). There is no doubt that beech is very important for the maintenance of New Zealand’s biodiversity and for its economic well being.

6.2 Puccinia psidii OR GUAVA RUST OF MYRTACEAE

Puccinia psidii was first recorded on Psidium guajava (guava) in Brazil in 1884. In 1934 there was a rust epiphytotic in Jamaica on Pimenta officinalis (pimento) which destroyed their pimento oil distillation industry (MacLachlan
1938; Anon. 1985). MacLachlan (1938) found that there were two strains of *P. psidii* present in Jamaica, one strain infecting *Pimenta officinalis* and *P. acris* but not *Syzygium jambos, Eugenia malaccensis* and *Psidium guajava*. The second strain infected *S. jambos* and *E. malaccensis* but not *P. officinalis, P. acris* and *Psidium guajava*. Neither the *Pimenta*, nor the *Syzygium* strain of quava rust were capable of infecting guava.

The first report of *P. psidii* on eucalypts was on *Eucalyptus citridora* in Brazil in 1943 (Joffily 1944). Since then it has also been found to infect, *E. cloeziana, E. grandis, E. maculata, E. paniculata, E. pirocarpa, E. punctata, E. saligna, E. tereticornis* and *E. urophylla* (Anon. 1985). Castro et al. (1983) found that *E. cloeziana, E. grandis, P. guajava* and *Myrciaria cauliflora* could all be infected by inoculum derived from *P. guajava* but there was some host-pathogen specificity. Similarly Ferreira (1983) was able to infect *Callistemon speciosus, E. grandis, S. jambos* and *M. cauliflora* with inoculum derived from *E. grandis* and *S. jambos*, but not *P. guajava*. However, inoculum derived from *P. guajava* would only infect *P. guajava*.

*Puccinia psidii* was first recorded on the Australian genus *Melaleuca*, on *M. leucadendron*, in Florida in 1977 (Anon. 1977). Then a significant epiphytotic in January of 1997 caused by *P. psidii* of *M. quinquenervia* was reported by Rayachhetry et al. (1997). This species has become an invasive weed of natural areas in southern Florida (Liebold et al. 1995). The epiphytotic was so spectacular that it was speculated whether this rust could be used as a biocontrol agent of *Melaleuca*.

Guava rust occurs from north-eastern Argentina, Uruguay, Paraguay, Brazil, French Guiana, Suriname, Gyana, Venezuela, Colombia, northern Peru, Ecuador, the Caribbean and Florida (Anon. 1977, 1985). Thus it ranges from the tropics to the temperate zones at 30° N and 40° S latitude. Carvalho et al. (1994) has reported that a high incidence of infected leaves and twigs of *E. cloeziana* in Bahia, Brazil correlated with a relative humidity of 90% and a temperature range of 15–25°C. Thus there are areas of northern New Zealand that could be suitable for the establishment of *P. psidii*.

*Puccinia psidii* exhibits three features that are of concern. First, the pathogen has in the last fifty years shown that it has the ability to jump from its natural South American hosts in the Myrtoideae to Australasian Leptospermoideae, chiefly in the form of *Eucalyptus*, but also *Melaleuca* and *Callistemon*. In the Myrtoideae it is able to infect a number of South American species in a number of genera but it can also infect species not native to South America as in the case of *Eugenia malaccensis*. Second, it is assumed that, based on the initial records, *P. psidii* is tropical in origin. However, it is showing a definite trend to move towards the temperate zones both in South and North America. Finally, both these trends may be genetically based and a high degree of genetic variability is a feature of *Puccinia* pathogens of crops such as wheat and maize. What we may be witnessing in the Americas is the exposure of a greater number of Myrtaceae to the pathogen and this is selecting for strains that can infect them. Also the presence of a continuous population, in the form of plantation eucalypts, growing over a wider climatic range may be selecting for locally adaptive variants and would explain the results of Castro et al. (1983) and Ferreira (1983).

If an increase in genetic variability is occurring and resulting in the development of an increasing number of host specific strains then this poses a real threat to the
New Zealand species of Myrtaceae. It is possible that the pathogen could become established on any of the 16 species (6 genera) of native or one of the many Australian, European, or South American species present in New Zealand. There are 90 species of exotic Myrtaceae grown widely in New Zealand. These are divided into 86 Australian species (16 genera), 1 European species, and 4 South American species (3 genera) (Palmer 1982; Webb et al. 1988). Thirty of these have become naturalised, 27 from Australia (7 genera) and 3 from South America (2 genera). New Zealand also shares 1 species, *Leptospermum scoparium*, with Australia. Caution must also be taken concerning generic and species limits as they are not necessarily well defined as exemplified by the putative garden hybrid between the New Zealand species *Lophomyrtus bullata* and the Australian *Syzygium australe* (*Eugeniamyrtus smithii*) (Palmer 1982). Therefore, supposed generic barriers to pathogens may not exist in reality.

The cost to New Zealand if only *Leptospermum scoparium* and or *Kunzea ericoides* were severely infected can be gauged from the effect that *Eriococcus orariensis* had on *L. scoparium*. These two species form important hill country protection forest and act as nursery crops in disturbed sites. The cost to New Zealand if *Metrosideros robusta* or *M. umbellata* were to be lost has been well demonstrated in the case of possum (*Trichosurus vulpecula*) which has caused major defoliation over many years (Payton 1988; Pekelharing & Batcheler 1990; Rose et al. 1992). It is probable that defoliation by *P. psidii* will have similar effects. Similarly if *M. excelsa* is attacked a similar sequence of events that led to it’s decline due to possum browsing will probably occur again (Hosking et al. 1989; Hosking & Hutcheson 1993) with consequent environmental and cultural losses (Simpson 1994).

6.3 *Orgyia thyellina* — THE WHITE SPOTTED TUSSOCK MOTH

*Orgyia thyellina* (Lepidoptera: Lymantridae), the white spotted tussock moth, represented an example of an invader with the potential to threaten New Zealand’s indigenous forests. The moth was first recorded in quite high numbers within a limited area of Auckland city in April 1996 (Hutching 1996; Hosking & Holden 1998). *Orgyia thyellina* was broadly polyphagous, well protected from generalist predators, lacked any specific parasitoids, and was from a family containing recognised forest pests, such as *Lymantria dispar*, and with representative species in both the Northern and Southern Hemispheres.

The known host range of the genus *Orgyia* spans some 30 plant families, of which the Fagaceae, Betulaceae and Myrtaceae are well represented, along with species from the Order Coniferales. The recorded host list of *O. thyellina* included plants from 9 families, of which 3 (excluding Nothofagaceae) are represented in the New Zealand flora (Ericaceae, Moraceae and Rosaceae). This list was not considered definitive by the advisory body set up to oversee the eradication attempt, so testing, following standardised procedures, was undertaken at Forest Research to assess the threat this species posed to the indigenous and naturalised flora.

The tests confirmed the published host range of *O. thyellina*, but also expanded it to include 6 additional plant families, 3 of which (Nothofagaceae, Fabaceae
and Oleaceae) had endemic representatives. The additions to the host range were, with the exception of Nothofagaceae, from within the host range of the genus Orgyia and particularly from those plant families well patronised by other Orgyia species. None of the indigenous plant species outside the genus Orgyia host range were accepted as hosts by O. thyellina. Within this host range New Zealand indigenous plant species, with the exception of Gaultheria (Ericaceae), were the least palatable or were non-hosts to the caterpillars.

The most palatable exotic plant species within the host range of O. thyellina was Betula (Betulaceae) while the most palatable indigenous tree species was Nothofagus solandri var. solandri (Nothofagaceae). This reinforced the hypothesis that Nothofagus is more closely related to the Betulaceae than to Fagaceae (Nixon 1982; Jones 1986; Hill & Jordan 1993). It was difficult to assess the threat from O. thyellina. The survival, growth, and development of O. thyellina on the least palatable hosts, was much lower than on its preferred hosts, which suggested that it might not do well on indigenous species. There is evidence to suggest that fecundity within the genus Orgyia, and for O. thyellina, is directly proportional to its body weight (Harrison & Karban 1986; Forest Research, unpublished data). When fed on N. solandri var. solandri, O. thyellina body weight was about half of that considered normal, resulting in a 50% reduction in fecundity. Also the small initial gene pool of the founder population might have limit the ability of O. thyellina to adapt to a new host. However this had to be tempered with O. thyellina being a novelty in the already established fauna, and the possible lack of predators. Fortunately, or unfortunately, many of these questions could not be answered as the containment methods and the blanket aerial spraying of the invested area with the bacterium Bacillus thuringiensis var. kurstaki successfully eradicated O. thyellina (Hosking 1998).

The conclusion drawn from this case study supports the accepted dogma that related insects feed on related plants and that insect/plant interactions are determined by temporal and spatial association. The Lepidoptera from the Northern Hemisphere that we should be most concerned about for the future of our Nothofagus spp. are those polyphagous and oligophagous species with a liking for Betula.

6.4 **Eriococcus orariensis** **CAUSAL AGENT OF MANUKA BLIGHT**

The Eriococcus (Hemiptera: Coccidea: Eriococcidae) species responsible for manuka blight of Leptospermum scoparium was first recognised by DSIR entomologists from a farm in South Canterbury in 1942 (Sewell 1953). The effect of the blight was to kill the affected plant. At that time it was reported to have started on farms in this area, but subsequently reports place the first outbreaks in the Orari Gorge, South Canterbury, in 1936/37 (Hamblyn 1959; Hoy 1961; Zondag 1977b). By 1946 a number of popular articles had appeared and this fuelled enough interest by farmers that by 1948 the sale of manuka blight was being advertised widely (Sewell 1953). The next year an article appeared promoting manuka blight as a biological control agent for L. scoparium (Hoy 1949). The blight had been deliberately introduced into Taranaki and northern Hawke’s Bay in 1947/48 (Hoy 1949, 1961). At this stage a
number of Government agencies involved in forestry and soil conservation became concerned and began recommending to Government the stopping of further deliberate distribution of blight (Anon. 1950; Hoy 1961). With this swing against the deliberate distribution of blight farmers became reluctant to divulge whether the blight was present on their land. However it is known that once blight was established on a farm that the farmer would deliberately spread it around his property. There is also one known case of a farmer hiring a light aircraft to fly infected material from Canterbury to his North Island farm and then dropping it from the air (Hoy 1961).

The concern of foresters and soil conservators resulted in a debate at the 6th New Zealand Weed Control Conference held at Massey Agricultural College in August, 1953. Foresters (Foster 1953) and soil conservators (Cambell 1953) argued that *L. scoparium* was an important nurse crop for the long term management of native timber species and for the stabilisation of hill country. Whereas the view of farmers (Gardiner 1953) and agriculturalists (Hamblyn 1953) can be summed up by a quote from Hamblyn:

‘The agriculturalist considers that the increasing loss to the country of grazing land going under manuka because of the inability of the farmer to face the cost or provide the labour to keep this plant in control, and the prospect of a continuing annual expenditure of vast sums in the endeavour to keep land free from manuka, are of such moment that these considerations outweigh any arguments that can be brought forward against the use of the mealy bug *Eriococcus* in the control of this plant.’

No controls were placed on the artificial spread of the disease and in tandem with localised natural spread the blight had effectively covered the entire North Island and the eastern side of the South Island by 1958. At this time it was difficult to find stands that did not have the insect present (Hoy 1954a, 1961). However, by the late 1950s the effectiveness of the blight was declining, particularly in the North Island (Hamblyn 1959). Initially it was thought to be due to adverse weather conditions, but later a fungal parasite, *Angatia thwaitesii*³, was found to be killing *Eriococcus* (Hamblyn 1959; Hoy 1961). The fungus was so effective that 16 years later Zondag (1977b) was able to report that the blight caused by *Eriococcus* was of little importance.

The *Eriococcus* sp. was named *Eriococcus orariensis* (Hoy 1954b) and it was not for several more years before it was located and mapped in its native Australian range (Hoy 1959, 1961). Its natural range is southern and eastern Australia where it is seldom associated with wide scale death of its host *L.

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³ *Myriangium thwaitesii* was originally described from Ceylon by Petch (1924) and transferred to *Angatia* by Arx (1965). Although Dingley (in Hoy 1961) designated the fungus killing *E. orariensis* as *M. thwaitesii* no evidence to support this identification has been published. Given the geographic disjunction between Ceylon and New Zealand, that *A. thwaitesii* has only ever been reported from Ceylon and New Zealand, and that no other species of *Eriococcus*, whether native or introduced from Australia, is attacked, it is reasonable to assume that the New Zealand fungus is a specific pathogen of *E. orariensis* and not *A. thwaitesii*. It is more likely to be an Australian species that occurs in sufficiently low numbers to have gone undetected in Australia. This parallels the case of the nematode parasite *Beddingia siricidicola* which attacks the wood wasp *Sirex noctilio*. This nematode was discovered and described from New Zealand and consequently discovered in its native European range (Zondag & Nuttall 1977).
*juniperinum* on the mainland and *L. scoparium* in Tasmania. How *E. orariensis* gained entry to New Zealand is unknown. Hoy (1954a) speculated that the insect might have been accidentally imported on ornamental varieties of manuka from Australia, but noted that it did not explain its first appearance in the remote Orari Gorge. W. Cottier (Anon. 1957) commented that it came on either imported nursery stock of *Leptospermum* or was carried to New Zealand on air currents from Australia. However, a number of comparisons can be drawn with the recent illegal introduction of rabbit haemorrhagic disease virus into New Zealand. In both cases a small segment of New Zealand society that stood to gain financially flouted public opinion and the desires of other segments of society. Diseased material was deliberately released and distributors were uncooperative with government agencies. Diseased material was sold, distributed probably through the postal system, and aerial drops of diseased material in uninfected areas were made (Davies 1998). In the case of rabbit haemorrhagic disease virus it is known that diseased material was brought from Australia so it is possible to speculate that manuka blight may have arrived the same way. It is also possible that further introductions occurred and may explain the sudden appearance of *A. thwaitesii* in the Gisborne region, the fungus having inadvertently been introduced with another consignment of infested material from Australia. Cottier’s suggestion that the insect may have been blown to New Zealand on prevailing winds from Australia seems unlikely.

Trans-Tasman transport has been reviewed (Close et al. 1978) and although reasonably common for insects and fungi, deposition of transported insects is usually in the northern and western regions of New Zealand and not on the eastern side of the Southern Alps as required for *E. orariensis*.

*Leptospermum scoparium* is an important species in serial succession, quickly colonising open and disturbed ground especially after fire (Evans 1987; Chapple 1992). It has a remarkably wide ecological range from seaside sands, bogs, dry rock outcrops, or leached gravels, and from sea level to the alpine zones at 1500 m or more (Evans 1987). As the initial species in a succession back to mature forest, *L. scoparium* does not dictate what is to follow but acts as a nurse crop for virtually all forest types including *Nothofagus fusca* in Canterbury (Burrows & Lord 1993), *Weinmannia racemosa* and *Nothofagus menziesii* in Fiordland (Mark et al. 1989), *N. menziesii*, *W. racemosa*, and *Metrosideros umbellata* in the Catlins (Allen 1988), and *Agathis australis* and *Dacrydium cupressinum* in the Waitakere Range (Esler & Astridge 1974). It also creates habitats for bryophytes (Johnson 1976), agaric fungi (Horak 1970) as well as a broad range of other forest margin plants, insects, birds and reptiles (Chapple 1992). As a primary coloniser of cleared ground *L. scoparium* plays a major role in soil stabilisation (Watson & O’Loughlin 1985). Bergin et al. (1995) have shown that the chance of landslide damage on the East Coast of the North Island for a 10-year-old manuka stand was 65% less than pasture and 90% less at 20 years.

Had *L. scoparium* been decimated by *E. orariensis*, then profound changes would have occurred in the New Zealand landscape with consequent economic, social, and environmental costs resulting from loss of forest regeneration and associated land destabilisation.
6.5 DISCUSSION

An assessment of epiphytotics in natural systems shows that pathogenic fungi are generally highly conservative in their host preference. The notion that a pathogen can readily move from species to species is not generally supported by field and experimental observation. Rather, pathogens have co-evolved with their hosts, where selection for novel attack mechanisms in the pathogen are abrogated by selection for counter attack mechanisms in the host. The result of this evolutionary pressure is that a great many pathogens are either limited to a single or small groups of species, or jump only short taxonomic distances and are often confined to a single host genus or family. This argument is supported by the case studies of Dutch elm disease and chestnut blight in Europe and North America, where pathogens have jumped from co-evolved resistant host species to non-resistant host species in the same genus, but outside of the pathogen's native range.

The evolutionary history of the Earth's flora has resulted in a distinct division between those flora derived from the Laurentian land mass, and largely confined to the Northern Hemisphere, and those derived from Gondwanaland and confined to the Southern Hemisphere. This dichotomy has resulted in tree families generally being either confined to the Northern or Southern Hemisphere. This, combined with pathogen host conservatism, means that for an epiphytotic to occur in a native forest a pathogen must move east–west in either hemisphere to encounter non-resistant hosts. Any movement north–south across the equator is likely to be unsuccessful, due to the lack of closely related susceptible hosts. The argument for the lack of north–south movement is circumstantial and based on the manifest failure, so far, of any pathogen to do so. New Zealand is a particularly good case study as large numbers of plants and their pathogens have been imported, but none of the pathogens have succeeded in transferring to native tree species.

For New Zealand the source of potentially devastating tree pathogens will be from the remnants of Gondwanaland: Australia, South America, Africa, and possibly India. The selected host families examined—Araucariaceae, Podocarpaceae, Nothofagaceae, and Myrtaceae—are either exclusively or predominantly confined to these areas. The scenarios developed for *Chalara australis* and *Puccinia psidii* clearly show that there is a risk to the New Zealand flora by pathogenic invasion from other Gondwanan flora.

The two scenarios represent examples of the types of insect—a lepidopteran and a sapsucker—which have great destructive potential. However the evidence from the scenarios would suggest that the threat to New Zealand native flora is not as great as the threat to the naturalised flora from such invertebrate introductions. The extensive list of native plants apparently attacked by exotic pests (Table 8) probably represents the xenophagic, i.e. will eat everything, behaviour of founding populations (Swan 1973). Such founding populations would escape immediate regulation from generalist predators and consequently colonise plants that in the long term would be marginal to their survival.

Sapsuckers (Hemiptera) are typically small and often have complex reproductive cycles which usually incorporate a parthenogenetic stage, i.e. mating is not required. New introductions are therefore difficult to detect and can rapidly establish a viable population from low founder numbers. They thrive in dry regions which promote both insect survival and host stress, the
latter increasing the hosts susceptibility to attack. The Australian species *Eriococcus orariensis* was first recorded from Canterbury, one of the drier regions of New Zealand. However its establishment was facilitated by its New Zealand hosts being the same species as its Australian hosts. *Eriococcus orariensis* New Zealand host, *Leptospermum scoparium*, also occurs in Tasmania, Victoria, and New South Wales (Thompson 1989; Harden 1991) so its establishment on New Zealand provenances was only to be expected. The decline in the severity of manuka blight, attributed to the entomopathogen *A. thwaitesii*, may equally have been the result of the strong natural selection pressure exerted by *E. orariensis* for pest resistance.

The establishment of *Orgyia thyellina* highlighted the fear of a ‘gypsy moth scenario’ occurring in New Zealand. However Niemela & Mattson (1996) argue that the fundamental similarities in the floral and faunal composition of North America and Europe predispose these two continents to a successful interchange of insects. While Barbosa & Schaefer (1997) concluded it is the availability and quality of host plants that is the ‘major driving force determining the spread and abundance of invading species’. The establishment in New Zealand of exotic Lepidoptera is likely to be more difficult than for Hemiptera because of the greater chance of detection and slower population development. The challenge for *O. thyellina* to establish in New Zealand was primarily its host plant preferences. *Orgyia thyellina* developed best on its Northern Hemisphere hosts first, then plants also eaten by other members of the genus *Orgyia*, and then developed least well on other plants including the New Zealand natives. As pointed out in the scenario, potential fecundity declined in proportion to body size and on less suitable hosts could not maintain normal development. The ability of *Orgyia thyellina* to survive on some *Nothofagus* spp. did indicate that it was potentially a threat to these species.

All invertebrate immigrants are aided in their entry into New Zealand by the large range of exotic plants that are established as amenity species about our ports of entry. In particular, fast growing Australian species seem to be favoured. These plantings enable exotic invertebrates to establish a bridgehead from which to expand and possibly adapt to alternative hosts. However the flora of our biggest and closest trading partner, Australia, is dominated by the radiation of two genera, *Eucalyptus* and *Racosperma* (*Acacia* spp.). The consequent and equivalent radiation of phytophagous insects is presumably the result of exploitation of subtle intra-generic differences between the many species in each genus. As a result these insects are probably not well pre-adapted to exploit the unique New Zealand flora.

The temperate Northern Hemisphere insects are disadvantaged not only by the relative isolation of New Zealand, but also the antipodal seasons which tend to restrict entry to New Zealand to egg masses and dormant pupae. Also the majority of insects have only one generation per year which puts them at a competitive disadvantage as well as exposing them to increased predation pressure in New Zealand.

South America may well be the greatest source of potential threats. This continent has some common floristic elements with New Zealand and has a great, but largely unstudied, diversity of insects. Fortunately, at present, it is not a major trading partner, however, this situation could very well change so there is a need to be vigilant.
7. Risk assessment using the four scenarios

Utilising the data and pathways outlined in section 2 and applying them to the known biology reviewed in sections 3–6 it is possible to estimate the likelihood of arrival of the pathogen or pest in New Zealand. Likelihood will be ranked on a scale of: certain—likely—unlikely—very unlikely. Should one of these pathogens or pests successfully establish an assessment of the threat, as low, medium or high, to indigenous forest will be made. Having assessed likelihood and threat to indigenous forest it is then possible to assess the risk, as low, medium or high, to indigenous forests that each example poses.

7.1 Chalara australis

The likelihood of *C. australis*, the cause of myrtle wilt of *Nothofagus* in Tasmania, being inadvertently introduced into New Zealand is ranked as very unlikely. This is because *C. australis* is reliant on water droplet dispersal of its spores, not wind or insect vectors, thus contaminated material would have to be placed in close proximity to a susceptible host for infection to occur. It is also known that some New Zealand species of *Nothofagus* appear to be resistant although this has not been tested rigorously (Kile 1989).

The volume of direct traffic between Tasmania and New Zealand is comparatively low with only 929 passengers arrived from Hobart in 1997, compared with 148,283 from Melbourne. Unfortunately it is not possible to break the Australian trade figures down by state or port but it is likely they also reflect this low traffic volume.

Based on the known biology of *C. australis* the likelihood of its arrival and establishment in New Zealand is considered very unlikely. Should it become established, the natural resistance of New Zealand’s *Nothofagus* species (although not all species have been tested) suggest that there is a low threat from the pathogen. Thus overall the risk to New Zealand’s indigenous forest appears to be low.

7.2 Puccinia psidii

The likelihood of *P. psidii*, the causal agent of guava rust, arriving in New Zealand, like *C. australis* is also unlikely due to the long distance between New Zealand and South America coupled with the low volume of passenger traffic and trade. However this situation could change in the future as the New Zealand Government endeavours to promote trade with South America (Goulter 1998) or if it became established in Australia or Asia (Coutinho et al. 1998).

*Puccinia psidii* is a rust and therefore an obligate parasite requiring either a living infected host or a dead host on which sporulation has commenced as a
means of entry into New Zealand. Any importation of nursery stock of known hosts would require high security quarantine and this eliminates this pathway unless the nursery stock is brought into New Zealand illegally. Therefore the likelihood of arrival is considered very low. If illegal infected or sporulating material did enter New Zealand the spores would have to be wind dispersed to a susceptible host in a climatically suitable area of northern New Zealand. However the apparent variability of this fungus indicates that there is a moderate to high threat to indigenous forest should a cool-tolerant strain be brought in or develop in New Zealand. Thus the threat to indigenous forest would be from low to moderate and consequently the risk low to moderate.

7.3 *Orgyia thyellina*

Based on experience there is a high likelihood of *O. thyellina* (the white spotted tussock moth) arriving in New Zealand. Its native range is Asia North, an area with a high volume of passenger traffic and trade with New Zealand. As this insect is polyphagous it could easily establish on host material surrounding ports and airports and use these areas as a bridgehead to invade our urban and rural environments. However feeding trials suggest that it is unlikely to enter indigenous forests aggressively although there might be population explosions from time-to-time. Based on its known biology it would seem that the threat to indigenous forest would be low to medium and only at times when population pressure pushes it onto less suitable hosts such as *Nothofagus*. Thus the risk to indigenous forest is considered to be low to medium.

7.4 *Eriococcus orariensis*

If *E. orariensis*, causal agent of manuka blight, and its fungal parasite were not already established the likelihood of it arriving in New Zealand from Tasmania is considered unlikely as traffic between these two is low. However, as the insect also occurs in South-eastern Australia importation from there is likely due to the higher traffic volumes. There is a good chance that the insect could be transported to New Zealand in cargo or aircraft and once released could easily find a suitable host within a few kilometres of any port or airport in New Zealand. Thus the threat to indigenous forest would be considered medium to high. The risk to indigenous forest is high as was demonstrated in the 1940s and 1950s. It was only through luck that a parasitic fungus also entered the country, through an unknown pathway, and stopped it from devastating *Leptospermum scoparium* populations.

This case study also exemplifies the risk from the unknown as *E. orariensis* was not known in its native range until it became a pest in New Zealand. Similarly the rust *Puccinia cygnorum* on *Kunzea ericifolia* was unknown in its native range until a consignment of *K. ericifolia* was rejected by New Zealand Quarantine Service (Shivas & Walker 1994).
Where a significant amount of information is available, as in the case of the four scenarios, it is possible to make an assessment of the likelihood of arrival and of threat to indigenous forests should such an arrival occur. However is it possible to be more specific or for that matter to generalise based on hindsight? The answer to that is both yes and no. With our knowledge of the biology of individual species increasing each year it should be possible to make a more detailed assessment of the risk should a particular organism reach New Zealand. But which organisms do we assess? Our knowledge of individual organisms is growing but not at the same rate as new organisms are being discovered. An example of the vagaries of this process is the south-west Australian myrtle rust *Puccinia cygnorum* on *Kunzea ericifolia* which was discovered by New Zealand quarantine inspectors who rejected a consignment of florist foliage. The fungus was subsequently examined in Australia and described as a new species (Shivas & Walker 1994). Based on specifics, we could not have predicted a myrtle rust from this source, as only one other Australian myrtle rust was known and it was limited to two hosts in a small area of the Northern Territory. Rather, generalities in the form of regulations come into play which prevent the entry of woody plant foliage into New Zealand unless it has been treated in a defined and predetermined way.

Our treatment of threats has to be based on a dichotomous approach. One approach is to evaluate the organisms that have caused problems overseas and assess their potential to cause similar problems in New Zealand. Such an assessment is generally well grounded in detail as problem organisms usually generate a reasonable amount of research. In such cases possible pathways of entry are easily identified and active monitoring of these pathways can be conducted. The second approach which covers the huge unknown is generic in concept. In this case we can review the pathways by which goods and people enter New Zealand and compare them with the type of contaminants, whether accidental or deliberate, that accompany them. From this it is possible to define how ‘dirty’ this pathway is and to adjust monitoring to an appropriate level so as to increase the chance of interception and thus reduce the risk of arrival.

The theme of this report has been to identify the source of threat to New Zealand’s native forests. The evidence suggests that the principal threat will come from the temperate Southern Hemisphere although the Northern Hemisphere also poses a lower level of threat particularly in the form of polyphagous foliage insects. However these threats are unevenly distributed as demonstrated in the case of *Nothofagus*. With this particular genus the source of threat is limited to the temperate *Nothofagus* species found in Tasmania, small areas of Victoria, a pocket in southern Queensland, and in Chile and southern Argentina. As already described for *Chalara australis* the likelihood of arrival is low because of the small amount of direct traffic between these locations and New Zealand. Although there is an increase in ecotourism, and the number of travellers circumnavigating the southern end of the world is increasing (Crocker 1998), even with this increase in traffic with South America (Goulter 1998) it is unlikely that there would be any successful establishments of new pathogens and pests from these sources, as long as our present quarantine standards are maintained. The target of the ecotourist is unspoilt
ecosystems such as the Milford, Routeburn, and Heaphy tracks (Sage 1995). The potential of such southern travellers to inadvertently transport pests and diseased plant material in tents, backpacks or boots from southern South America or southern Australia directly into New Zealand’s indigenous forests is indicated by the tent study of Gadgil & Flint (1983).

The New Zealand Myrtaceae are more threatened from importation of pathogens and pests because of the large number of Myrtaceous genera distributed across Australia and a more limited number in South America. However this potential threat has to be tempered with reality. There are some 86 Australian species of Myrtaceae grown or established in New Zealand. These species, and in particular the eucalypts, have an abundant suite of pests and pathogens that either arrived with them or have subsequently established in New Zealand (Bain 1976; Alma 1977; Bain 1977a, b, and c; Zondag 1977a; Dick 1982; Zondag 1982; Nuttall 1983; Kay 1986; Dick 1990; Ridley 1995; Appleton 1996; Crabtree 1997). The inevitability of this process of continuing invasion of Eucalyptus pathogens and pests was commented on by Bradbury (1997). Yet despite this ongoing invasion of eucalypt pathogens and pests not one appears to have made the leap to a native myrtaceous genus. The same holds true for other myrtaceous hosts, for example a Ctenarytaina species has become established in Auckland on the Australian Acmena smithii, but has failed to utilise any other myrtaceous host whether native or exotic (Anon. 1997a; Inglis 1997). The only myrtaceous pest to have successfully established has been Eriococcus orariensis (scenario 4) and this ultimately proved not to be a host range expansion, but merely an extension of its range to an uninfested population of Leptospermum scoparium.

Generally there is a low likelihood of arrival of pathogens and pests that could attack New Zealand’s native woody plants, in the genera examined, from overseas. However it must always be borne in mind that nature is not predictable, because it is impossible to know all of the operating parameters and that ‘Perturbations, starting as tiny fluctuations wrought by individuals, can accumulate to profound and permanent alterations in a much larger world’ (Gould 1991). Whilst acknowledging this, it must be borne in mind that the unthinkable, in terms of profound devastation of an indigenous genus, can occur as has been demonstrated in the Northern Hemisphere by the Dutch elm disease pandemic, the almost total annihilation of the North American chestnut, and the destruction wreaked by the gypsy moth.
8. Summary

The most important pathways for new exotic pathogens and pests of indigenous forests have been estimated to be air and sea containers, used cars, and sporting and camping equipment. The major traffic routes for trade and passengers are from Australasia and Europe, followed by Asia and North America, then much lower levels from the Pacific, Africa, and South America.

Over the last 10 years 61% of newly recorded pathogens and pests were detected in and around ports. 19% were found on indigenous hosts and of these, 72% were found in port environs. The majority of the new records were organisms that could only have entered the country on live plant material or plant debris.

For New Zealand the source of potentially devastating tree pathogens will be from the remnants of Gondwanaland: Australia, South America, Africa and possibly India. The Earth’s flora is distinctly different between the Northern and Southern Hemispheres, and because pathogen generally exhibit host conservatism they must move east–west in either Hemisphere to encounter non-resistant hosts. Any movement north–south across the equator is very likely to be unsuccessful due to the lack of closely related susceptible hosts.

The notion that a pathogen can readily move from species to species is not supported by field and experimental observation. Rather pathogens have co-evolved with their hosts with selection for novel attack mechanisms in the pathogen abrogated by selection for counter attack mechanisms in the host. The result of this evolutionary pressure is that a great many pathogens are either limited to a single or small groups of closely related species, or jump only short taxonomic distances and are often confined to a single host genus or family.

Similarly, herbivorous insects have co-evolved with their host so that the insects have evolved mechanisms to overcome specific plant defences. Consequently this narrows the host range and makes it difficult for insects to move to new hosts. This is particularly true for Australian insects which have co-evolved with a small number of highly species-diverse plant genera by taking advantage of subtle differences between these host species. South America may well be the greatest source of potential threats as it has some common floristic elements with New Zealand and has a great, but largely unstudied, diversity of insects.

Future changes in direct traffic between locations with similar floristic structures, such as South America and Tasmania, could increase the risk of contact with potential pathogens and pests causing organisms for New Zealand.

The risk from the unknown organism is real but unquantifiable. For this reason a quarantine policy should focus on pathways of entry and on generic groupings of pests and diseases rather than on specific organisms. To protect indigenous forests more emphasis should be placed on surveillance of pathways that link countries of the Southern Hemisphere. In particular surveillance should concentrate on air and sea containers, used cars, and used sporting and camping equipment arriving from Australia, South America, Africa and possibly India.
There needs to be more funding of research on the taxonomy and ecology of fungi and insects in indigenous forests to establish a base line from which any newly introduced organisms will be recognised. In association with these baseline surveys, a structured surveillance system for indigenous forests needs to be developed so that limited resources can be deployed to look at the highest risk sites in a manner that will provide the greatest chance of detecting newly introduced pests or diseases.

9. Conclusions

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