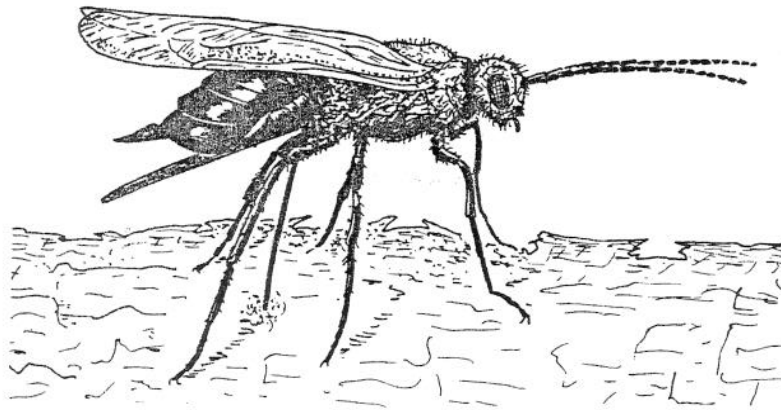


CHAPTER 20

SIREX IN AUSTRALASIA

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1. INTRODUCTION

Woodwasps or horntails (Siricidae) are primitive phytophagous hymenopterans that naturally infest a variety of coniferous and hardwood trees throughout North America, Eurasia, North Africa, and Japan.^{10,13,27,36,42,43,55,75,78} Although woodwasps have been reported to be responsible for economic degradation of otherwise marketable timber,^{5,35,55,73,77,85} such infestations are more symptomatic of a prior pathological condition than a primary cause of tree mortality.¹⁹ Therefore, in their natural habitat, woodwasps are secondary to other predisposing agents, which may include defoliation or debilitation of trees by insect and/or fungal attack,^{6,19} fire or smog damage,^{15,16} and mechanical injury.⁴⁶

An exception to the secondary status of woodwasp attack was first recognized in New Zealand during the 1940s, when the woodwasp, *Sirex noctilio* Fabricius, was found attacking and killing apparently healthy Monterey pines, *Pinus radiata* D. Don.⁶⁶ In contrast to the northern hemisphere, where *S. noctilio* infestations were rare and localized, the primary nature and toxicity of the attack on *P. radiata* resulted in severe tree loss in New Zealand and subsequently in Australia.^{33,70}

Both Australia and New Zealand lack extensive areas of fast-growing indigenous softwoods, but the introduction of *P. radiata* more than compensates for this deficiency with exceptional rapid growth and wood production over a wide range of climates and site conditions. Australian plantations alone supply 33% of the annual production of saw and veneer logs, pulpwood, preservative-treated round logs, and sleepers.²

Historically, *S. noctilio* became established in New Zealand around 1900,⁵⁶ but it was not until some 45 years later that severe and extensive losses occurred. During 1946–1954, approximately 30% of 120,000 ha of *P. radiata* was destroyed.⁶⁸ In 1952, *S. noctilio* was discovered in a 1100-ha *P. radiata* plantation at Pittwater, Tasmania³³ and by 1958 had destroyed 40% (range 30–80%) of trees aged 23–28 years.⁴⁸ In 1961, the wasp was discovered in the mainland state of Victoria and has since spread throughout that state and to forests in the adjacent states of South Australia and New South Wales, and the Australian Capital Territory.⁴

The capability of *S. noctilio* to kill individual *P. radiata* posed a potential threat to a rapidly expanding postwar timber industry. Initial control attempts in New Zealand and Tasmania involved the introduction and release of parasitoids collected in Europe by the Commonwealth Institute of Biological Control (CIBC), but a concerted program of research and control in Australia had to await the discovery of the wasp in mainland plantations in 1961–1962.⁵⁹

In 1962, the National *Sirex* Trust Fund and National *Sirex* Fund Committee were established to finance immediate containment and eradication procedures in Victoria, and research into all facets of the *Sirex* problem. All field research was initially undertaken in Tasmania and included investigations on (1) biological control and the biology, behavior, and ecology of *S. noctilio* and its parasitoids by the Division of Entomology, Commonwealth Scientific and Industrial Research Organisation (CSIRO); (2) insect–host tree interactions, including susceptibility and resistance to attack, tree breeding, and sil-

vicultural practice by the Forestry and Timber Bureau; and (3) insect-fungus relationships and evaluation of chemical control by the Department of Entomology, Waite Agricultural Research Institute, University of Adelaide. Subsequent research was conducted at the CSIRO *Sirex* Biological Control Unit established at Silwood Park, England, and from the mid-1970s by state forestry departments, notably the Victorian Forests Commission.⁵⁹

2. LIFE HISTORY AND ECOLOGICAL RELATIONSHIPS

Woodwasp larvae cannot feed, grow, and develop without prior alteration and conversion of host-tree tissue into readily assimilable forms. This conversion is performed by *Amylostereum* and *Stereum* spp., basidiomycetous fungi that are mutualistically associated with, and vectored by, siricid females.^{14,17,20,78} Female siricid larvae acquire and store the fungus as arthrospores within abdominal hypopleural organs,⁶⁵ which are recontaminated after each moult; ultimately, in the adult stage, arthrospores are lodged and nurtured within paired intersegmental, mycangial sacs at the base of the ovipositor.³⁰ Inoculation of new hosts with arthrospores is associated with oviposition. The relationship between the fungi and woodwasps is species-specific, with the exception of *Xeris spectrum*, which carries no fungus but deposits eggs into other siricid-infested wood.³¹ The fungus associated with *Sirex noctilio* is *Amylostereum areolatum* Fries (Boidin).³²

The general life cycle of *Sirex* in Australia takes 12 months but may range from 3 to 36 months, depending on tree size (volume) and the degree of insolation and/or shading.⁵⁸ An adult sexual dimorphism in color exists, with females being steel-blue and males possessing orange abdomens.¹⁰ Adult emergence commences early in summer (early December) and continues to April, with peak emergence in February.⁶⁰ On emergence both sexes fly to tree tops, where they aggregate in predominantly male swarms. Mating occurs on the upper branches and the original photopositive response of the female is replaced by a host-location response. Mated females leave the swarm to seek trees as suitable oviposition sites. In the absence of mating the host-location response becomes increasingly dominant and unfertilized eggs are deposited. Such haploid eggs develop into males. Flight activity and mating frequency is favoured by temperatures greater than 20°C.

Sirex females are attracted to physiologically stressed trees. High girdling of pruned trees results in the region below the girdle becoming attractive some 10 days after the operation. At this time, the permeability of the bark tissue of the attractive region to water vapour and monoterpenes is twice that of the upper, nonattractive region.^{18,50} The major monoterpenes, α - and β -pinene, elicit the greatest electroantennogram response⁷⁴ and arrestment in flight mill olfactometers, and trees baited with either solvent extracts of bark or the two monoterpenes alone, or in combination, have been preferentially attacked. That attraction actually occurs was evidenced by the flight to and searching behaviour of female wasps on fly wire screen surrounding but 6 cm from attractive stem sections.

Following the location of host trees, *Sirex* females walk over the bark surface and assess the tree as a potential oviposition substrate by probing the phloem with the ovipositor. Acceptance or rejection can occur after one or two probes. Eggs are deposited within drill shafts bored into the outer sapwood by the abrasive action of the ovipositor and removal of wood particles by a pair of reciprocating valvifers⁵ (Fig. 1a).

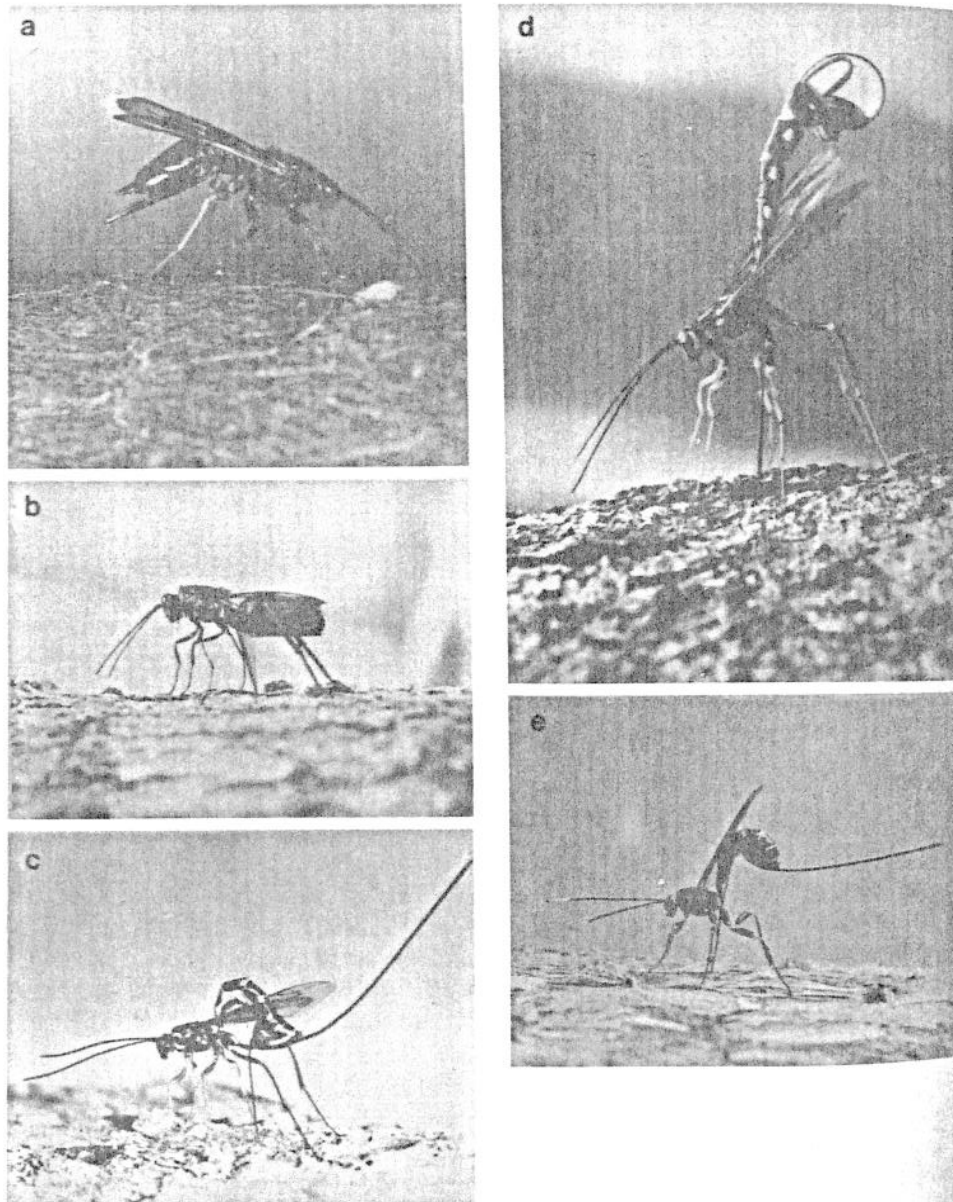


FIGURE 1. *Sirex* and parasitoids. (a) *Sirex noctilio*. (b) *Ibalia leucospoides*. (c) *Rhyssa persuasoria*. (d) *Megarhyssa nortoni nortoni*. (e) *Certonotus tasmaniensis*.

Initial acceptance does not necessarily result in immediate oviposition, as eggs are placed only in situations that maximize the probability of survival.⁴⁷ In the early stages of an attack, a high proportion of single drills are made, but the incidence of eggs in these drills is low. However, *A. areolatum* arthrospores and secretions derived from a large mucous gland reservoir are inoculated into the lumen of the drill holes.²⁴ When two drills

are made, eggs only occur in the first drill and arthrospores and mucus are secreted into the second. As many as six drills may be made in the sapwood through an outer single drill and, irrespective of number, the last drill is always egg free but contains mucus and arthrospores. The capacity to vary the number of drills and hence eggs, is related to the vitality of the tree as expressed by the osmotic status of the phloem tissues.⁴⁷ Single drills are made when the tree is suboptimal, and increasing numbers of eggs are deposited as the tree's vitality and capacity to resist attack decline in time following successful attack. Aspects of tree susceptibility and resistance to attack are considered below.

Eggs usually hatch within 10–15 days, but viable eggs and first-instar larvae have been recovered from the base of large trees 10 months after attack. Such delayed hatching is attributed to the existence of low temperatures beneath the canopy for most of the year, inhibiting fungal growth as well.⁴⁷ On hatching, first-instar larvae feed on yolk fragments and fungal mycelia occupying the lumen of the drill hole. Second instars and subsequent stages feed through fungus-infested wood tunneling with the grain to create galleries of increasing diameter and whose general characteristics vary according to conditions of moisture content, aeration, and fungal activity. The number of instars varies from 6 to 12, but a minimum of 3 larval moults has been reported to result with very small adults.⁶³

Greater numbers of instars are associated with larvae that experience suboptimal conditions during their development. Such factors as high moisture and consequently poor fungal growth or physical barriers such as resin patches result in more frequent moults and changes in gallery direction. Final adult size is directly related to the volume of fungus-infested wood displaced during development. Pupation occurs in the spring, when air temperatures increase and the moisture content of the larval habitat limits fungal growth.⁴⁷

2.1. Tree Mortality and Resistance Mechanisms

Sirex has been reared successfully from *Pinus*, *Abies*, *Picea*, *Larix*, *Pseudotsuga*, and *Auricularia* spp., and treatment of *Pinus sylvestris* and *Picea sitchensis* trees with *Sirex* arthrospores and mucus, or oviposition, has been reported to cause death.⁷⁶ However, the interaction of the *Sirex* and Radiata pine is the only one in which the primary role of the insect in causing tree death has been substantiated.

The development of short-term periods of physiological stress within individual host trees appears sufficient to result in attraction and attack by *Sirex*. Stressors may involve damage by wind or felling operations, defoliation, herbicides, fire, cone harvesting, or thinning, particularly when it occurs during the *Sirex* flight season.^{46,48,50,52,54}

Irrespective of cause, the injection of mucus into the sapstream, followed by its translocation to the foliage, results in the inhibition of translocation and a reinforcement and extension of the original stress condition. The chemical nature of the mucus is unknown, but its stability at high temperatures suggests that it has a low molecular weight, while its mode of action is to induce premature senescence.²⁹ The effect of the mucus is to alter the water balance of needles drastically through tissue desiccation and collapse of the phloem elements.

Consequently, the duration of a temporary deviation from normal physiological conditions is extended to increase the probability of additional attack and inoculation of the tree with arthrospores and mucus. At the same time, the rupture of xylem elements by ovipositor probes results in the invasion of air into the tracheids creating a suitable milieu

for germination and growth of the fungus. Progressive coalescence of drying patches originating from individual points of inoculation results in the invasion of the fungus throughout the xylem and heartwood.^{21,22}

Although the fungus was originally considered the sole pathogenic entity, it is now thought that tree death results from the combined effects of mucus and fungus. The mucus reinforces the original stress condition by impairing translocation, which in turn favors vigorous establishment of mycelia, which then occlude the xylem of the tree. Acting together, the insect and fungus create a suitable habitat for continued fungal growth and larval feeding. Trees successfully attacked by *Sirex* are characterized by a generalized chlorosis, or yellowing, of the crown, followed by needle fall and death that may occur 2 weeks to 8 months after attack. Such variation may be associated with locality and site characteristics and their influence on tree resistance mechanisms.

Resistance to *Sirex* wasp attack can be summarized under three traditional categories: nonpreference, antibiosis, and tolerance.⁶⁴ Nonpreference is observed when an initially attractive tree is rejected by the attracted wasp. This is commonly observed when a tree is damaged by localized wounding such as the removal of a phloem sample. Individual wasps may be attracted to these sites but, following a number of probes of the phloem with its ovipositor, often reject the site and leave the tree. Similarly, apparently normal trees attacked by three to four females on 1 day may be followed by a second attack some 10–12 days later or not be reattacked at all.⁵⁰

Antibiosis in response to *Sirex* attack involves resinosis and polyphenol formation²³ (Fig. 2). Resinosis, a phenomenon similar to the hypersensitive reaction⁷¹ and dynamic wound response¹¹ of bark beetle attack, is a nonspecific wound reaction that is dependent on water status and maximum cell turgor for complete expression. This expression includes both flooding of the drill and impregnation of surrounding wood with resin. Polyphenol formation involves the transformation of current photosynthate into two fungistatic polyphenols, pinosylvin and pinosylvin monomethyl ether.³⁷ These two polyphenols occur, along with three other nonfungistatic polyphenols, in the heartwood of radiata pine. Polyphenol production does not occur in response to a physical wound and is therefore a specific response to the invasive agent, *Amylostereum areolatum*. Furthermore, the dependence on current photosynthate as opposed to stored starch as the carbon source for these polyphenols emphasizes the importance of the effect of mucus in the pathology syndrome, as it directly inhibits translocation of photosynthate.

Tolerance to sustained *Sirex* attacks has not been investigated but undoubtedly entails the suppression of the mucus effect. This can be achieved in either of two ways. First, transpiration may be so reduced that the rate of mucus transport is insufficient to elicit a toxic effect in the needles. Such a condition could apply during drought periods when transpiration may fall to less than 10% of the predrought value.⁷² Second, premature senescence and shedding of affected needles has been interpreted as a hypersensitive reaction resulting in the elimination of toxic mucus from the tree.²⁹ Extreme variability in response, which ranged from rapid needle chlorosis and wilt to no apparent effect, was observed when either detached shoots were placed in mucus solutions or mucus was injected into seedling trees.²² Breeding for such resistance traits was not successful, even though needles from different trees retained their order of sensitivity to mucus when tested throughout the year.¹² Under field conditions, rapid development of chlorosis and wilt of the youngest needles is almost always associated with susceptibility to attack, whereas

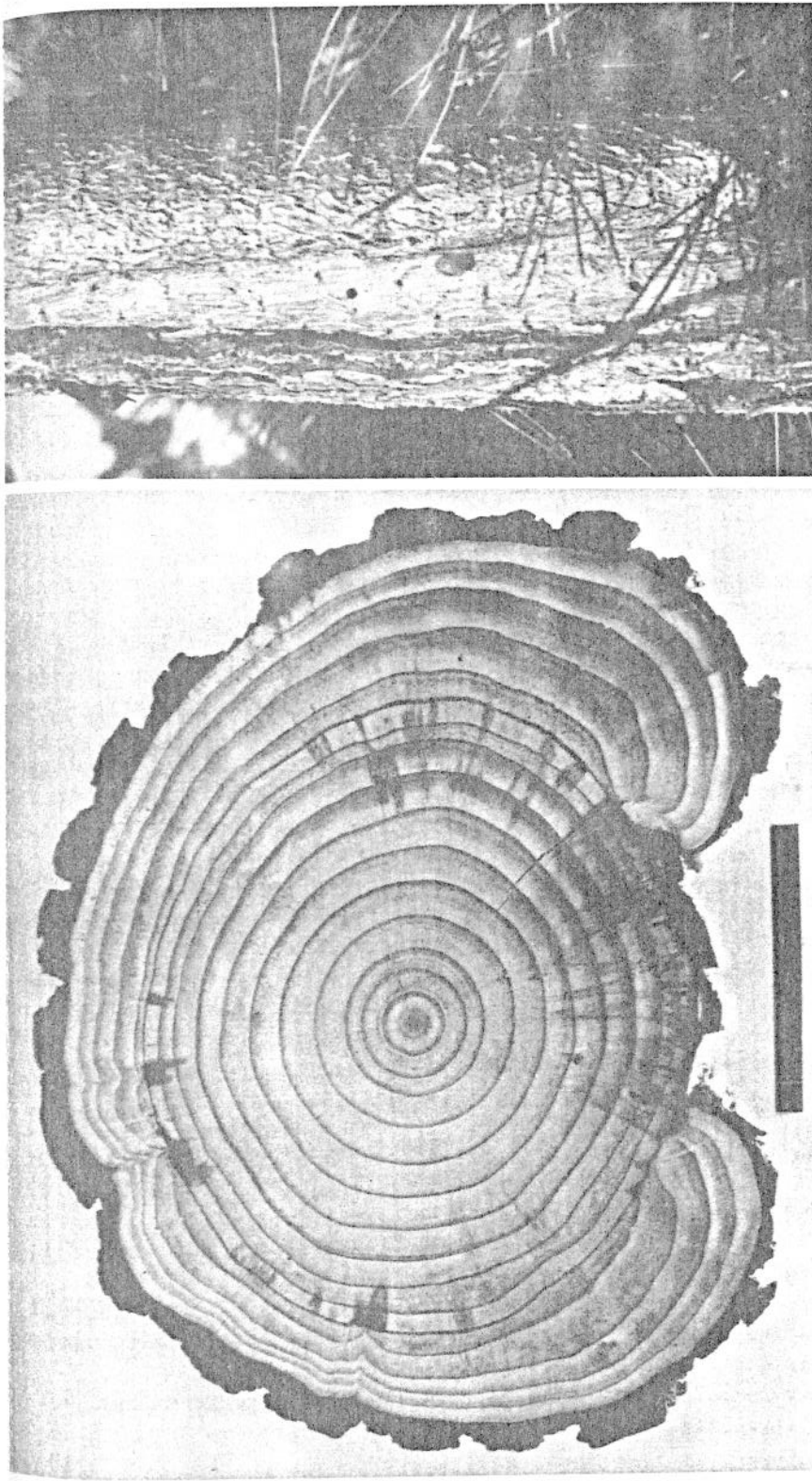


FIGURE 2. Transverse section of Radiata pine tree (right) partially killed by *Sirex* attack 6 years before felling. Note resinosis and polyphenols associated with drilling and concentrated in killed sector, which contains emergence holes (right).

chlorosis and needle fall of more mature foliage and stem needles, but not meristematic needles, occurred on those trees that most often tolerated and resisted attack. Elongation of the leading shoot of Radiata pine is positively correlated with diurnal changes in diameter, and shrinkage of the leader shoot does occur in actively growing trees under high transpirational load.⁴⁴ By contrast, diurnal variation in transpiration declines from 600 ml/m² day to 200 ml/m² night predrought to a constant 50 ml/m² 34 days after final watering.⁷² Therefore, under drought conditions, it can be inferred that the supply of mucus to the needles is reduced and, of equal importance, that the target cells are metabolically dormant at this time. The response of droughted, watered, and untreated control trees to forced *Sirex* attack emphasized the importance of transpiration rate. Watered trees succumbed most rapidly and droughted trees took 2–3 months to die, while control trees were intermediate in their response.¹²

2.2. Parasitoids, Predators, and Pathogens

Prior to the establishment of the National *Sirex* Fund Committee program, attempts at biological control of *Sirex* were limited to the introduction of *Ibalia leucospoides* (Hochenwarth) and *Rhyssa persuasoria* Linnaeus into New Zealand and Tasmania.⁸⁰ The former parasitoid attacks *Sirex* eggs and early-stage larvae and the latter mature larvae in the spring. Both parasitoids are commonly associated with siricids in the Northern Hemisphere (Fig. 1b,c).

Concerted exploration in Europe by CSIRO officers from 1963–1971, supplemented by collections in North America, Japan, and Nepal by both CIBC and CSIRO, resulted in the introduction of 21 species and subspecies of parasitoids into Australia. Following laboratory rearing, testing, and quarantine, 10 species were released, 5 of which became established.⁸¹

In Tasmania, the most effective parasitoid was *Megarhyssa nortoni nortoni* Cresson (ex. California), which, with *R. persuasoria*, caused a significant reduction in a *Sirex* population at Pittwater between 1965–1974 (Fig. 1d). Key factor analysis indicated that these two parasitoids, combined as a guild, acted in a delayed density-dependent manner, whereas *I. leucospoides* apparently acted in a density-independent way.^{82,83} By contrast, *Ibalia* spp., *I. leucospoides*, and *I. ensiger* Norton were the most effective parasitoids in Victoria, causing an average mortality of >20%. *Megarhyssa nortoni* (strains *nortoni* and *quebecensis* Provancher) averaged less than 12% mortality, and *R. persuasoria* has failed to establish in Victoria. Differences in the efficiencies of *Ibalia* spp. between Pittwater and Victoria appear to be related to differences in the rate of mortality of trees in different climatic zones. At Dulverton, northern Tasmania, *Ibalia* spp. caused 40% mortality during 1979–1980. Resinosis, a density-independent mortality factor, is the most likely factor obscuring a functional relationship between *Ibalia* and *Sirex* at Pittwater.

Indigenous parasitoids, particularly *Certonotus tasmaniensis* Turner in Tasmania³⁸ and *Guiglia schauinslandi* Ashmead in New Zealand,⁶⁸ have successfully parasitized *Sirex* larvae.

In addition to parasitoids, avian predators have been observed attacking *Sirex*.⁵¹ Sixteen of a total of 42 species of birds recorded at Pittwater were implicated in the predation of both male and female woodwasps. Three species, the Dusky Wood Swallow,

Spine-tailed Swift, and Raven, predominantly attacked the mating swarms, which not only affected a numerical reduction but also reduced mating frequency as many single-attacked trees generated exclusively male or significantly high male to female ratios.

Both parasitoids and avian predators are responsible for the significant destruction of immature and adult stages of *Sirex*. Another less apparent but extremely efficient natural enemy was discovered in New Zealand in 1962.⁸⁶ Dissection of some *Sirex* adults demonstrated hypotrophy of the ovaries and hypertrophy of the testes and, within the ovaries, apparently normal eggs were found to be full of juvenile nematodes. The nematode was subsequently described as *Deladenus siricidicola* Bedding (Neotylenchidae),⁸ which, together with a second species, *D. wilsoni* Bedding, has a unique life cycle involving extreme female dimorphism.⁷ The neotylenchid form is free living and mycetophagous, feeding exclusively on *Amylostereum areolatum*, while the other possesses many diagnostic features of the Allantonematidae and parasitizes *Sirex* larvae. Hormones associated with insect pupation apparently trigger the rapid development of the reproductive system of the nematode, the ovoviviparous release of nemas into the hemocoel of its host, and their migration to the reproductive organs. The female *Sirex* is sterilized by the infection but is still able to locate host trees and oviposit normally, depositing arthrospores and mucus, but nematode-filled egg cases. The nematodes escape from the egg to feed on the fungus for many generations within the tree until, in the presence of an active siricid larvae, adult infectives are formed. These mate and then penetrate the larvae to reinitiate the cycle. Many parasitic strains of *Deladenus* spp. have been introduced into Australia, but only *D. siricidicola* has been released, for it only attacks *Sirex* larvae. *D. wilsoni* attacks both *Sirex* and the rhyssine parasitoids.

The remarkable life cycle of *D. siricidicola* has unique features that facilitate its use as a biological control agent. The mycetophagous form can be produced in the laboratory on fungus cultures and inoculated into *Sirex* infested trees in the field.⁹ Artificial inoculation of felled infested trees results in virtually 100% parasitism, and flight and oviposition by infected females rapidly disperses the nematode throughout the forest.

3. PATTERNS OF NUMERICAL BEHAVIOR

The *Sirex* wasp in Australasia is associated predominantly with Radiata pine, which is grown on sites of variable quality that frequently experience hot, dry summers. Despite such conditions, woodwasp populations usually remain relatively low, with an annual turnover of 5–10 trees/ha.

Sirex outbreaks are characterized by an eruptive increase in tree mortality, followed by a rapid decline to endemic levels.⁶⁷ The duration of outbreaks ranges from 4 to 10 years, in the absence of parasitic nematodes.

3.1. New Zealand Outbreaks

Despite the woodwasp's presence in this country for >70 years, significant tree losses, due directly to *Sirex* attack, did not occur until the mid-1940s. Outbreaks in forests within the Rotorua region were attributed to overstocking and drought. Summer rainfall

from December 1945 through February 1947 was about 50% of the long-term average, with 1945–1946 being the driest year on record at Kaingaroa.⁶⁶ Paradoxically, greater tree mortality occurred in thinned stands adjacent to overstocked and, presumably, more drought-affected trees. This preferential attack in thinned compartments was attributed, at the time, to “the ‘effect’ of solar radiation on the bark (phloem) of trees with thin crowns.”⁷⁰ In areas of 9-year-old regeneration, it was observed that trees pruned and thinned during January–March 1946 were extremely vulnerable. This phenomenon was witnessed again in 1947–1948, and it was postulated that fresh resin elicited attraction and mass *Sirex* attack. High mortality in 20-year-old trees was also associated with pruning operations during *Sirex* flight, and a decreasing tendency for the wasp to attack trees at greater spacing intervals was observed.⁶⁶

A severe drought occurred in 1945–1946, and *Sirex* populations increased through 1946–1947. Higher rainfall (90 mm/month) was experienced in the summer of 1947–1948, however, and *Sirex* activity declined. Rains were moderate (75 mm/month) in the summer of 1948–1949, with generally overcast and cool conditions prevailing. Unexpectedly a massive increase in *Sirex* activity occurred in this year and 25–30% mortality of trees was estimated over 300,000 acres of forest.⁷⁰ Surveys at Rotoehu Forest showed wide variation in tree susceptibility from year to year, as expressed by differences in the numbers of trees initially thought to be dying and those actually killed (Fig. 3a).⁴⁰ In subsequent years, *Sirex* numbers stabilized at subeconomic levels.

In one decade, official forest policy changed from terminating the Radiata pine planting program in favor of species not attacked by *Sirex* to its reintroduction. This about-face was attributed to the recognition of certain facts about the consequences of thinning and pruning operations during the growing season and the importance of appropriate stocking intensity with tree age (size). Furthermore, alternative softwood species failed to compare with the superior qualities of Radiata pine. Indeed, *Sirex* wasp was referred to as a beneficial insect through its thinning effects.^{40,70} However, the unpredictability of its outbreaks in space and time serve more as a reminder of poor or delayed management practices.

3.2. Australian Outbreaks

3.2.1. Tasmania

Sirex was first discovered in the Pittwater plantation in 1952. However, evidence of its presence since 1947–1948 was found when the course of the outbreak was reconstructed by determining the frequency and age of *Sirex*-killed trees.⁴⁸ This analysis suggested that the outbreak developed from random foci within the compartment and that maximum tree mortality occurred some 10 years after the year of introduction. Resinosis and polyphenols within attacked but surviving trees indicated that a marked increase in resistance to attack commenced 8 years after *Sirex* introduction (Fig. 3b). Insect survival within trees declined through the outbreak reflecting the greater vigor and resistance of surviving trees. Numbers of oviposition drills per unit area of bark and the proportion of multiple drills also increased during summers experiencing above-average rainfall.

The Pittwater plantation was situated on sand dunes with a water table in the study

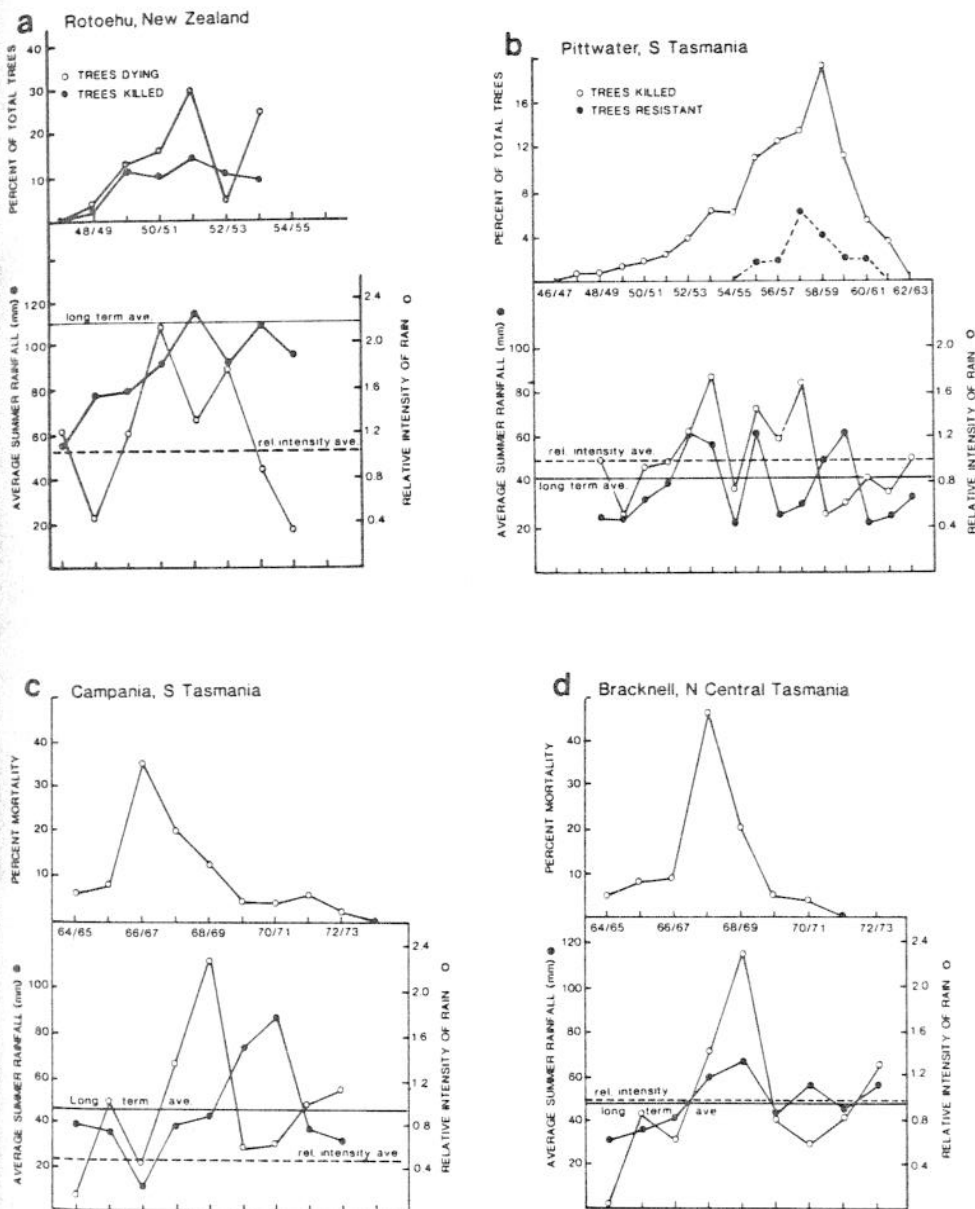


FIGURE 3. Relationship between the percentage of *P. radiata* trees attacked by *Sirex* and average summer rainfall (December–March) and the intensity of February rainfall relative to the summer average at locations in New Zealand (a) and Tasmania (b–d).

area at 2.4 m. Tree mortality was 68% at this site, with mortalities ranging from 30 to 80% in areas with deeper and shallower water table levels, respectively.

In common with the New Zealand experience, Pittwater was also disturbed by forestry operations during the *Sirex* flight season. Commencing in 1948–1949, and in response to postwar shortages of softwoods, the largest trees at Pittwater were selectively harvested. This practice of high grading caused damage to understory trees and produced large quantities of slash, in which the *Sirex* population increased.

A separate investigation of *Sirex* in Radiata pine regeneration at Pittwater from 1965–1974⁸² showed that peak mortality occurred in 1968–1969 and that tree kill was influenced significantly by severe defoliation by the larvae of a geometrid, *Chlenias* sp.⁵²

A small plantation at Campania, located 25 km north of Pittwater, was infested by *Sirex* during the early 1960s but in 1966–1967 a sixfold increase occurred, followed by a rapid decline to preoutbreak levels⁸³ (Fig. 3c). The only significant environmental features at this plantation were an elevated site with shallow soils overlaying parent rock and excessive hot air temperatures (approximately 40°C for ~6 hr) on February 7, 1967, a date on which disastrous fires destroyed large areas of southern Tasmania with great loss of life.

Coincident with the Campania outbreak, a fivefold increase in tree mortality was observed in 1967–1968 in a small plantation Bracknell, north-central Tasmania⁸³ (Fig. 4d).

Three plantations with the Scottsdale district of northeastern Tasmania were attacked by *Sirex* during the late 1960s and early 1970s. All plantations consisted of multiple age plantings and were in need of thinning. The Mt. Helen outbreak was monitored from 1968 to 1975. Growth-ring analysis on dead trees indicated that small numbers of trees were killed as early as 1965. Peak tree mortality occurred in 1971–1972, and the greatest frequency of resistance was observed during the preceding season. Increases in *Sirex* populations at Mt. Helen and to a lesser extent at the Cuckoo plantation, some 10 km east, was influenced by forestry operations and wind (Fig. 4a). Thinning during the *Sirex* flight season occurred at both plantations, and the impact of localized damage on tree attractiveness and susceptibility was evidenced in the death of 14 elite trees chosen for their growth rate and form and damaged during the flight season by the selective removal of cones and cone-bearing branches for seed. Levels of tree mortality were less at the Cuckoo plantation and it was recorded that Mt. Helen had approximately 5% of stems with evidence of crown damage or breakage and limb run compared with less than 1% at Cuckoo. This damage was caused by wind in the more exposed Mt. Helen plantation.⁵⁰

At the Retreat plantation, some 14 km southwest of Mt. Helen, no real evidence of *Sirex* was detected until 1968–1969, when a small area of the forest was found to be infested. This locality had experienced severe wind damage in February that had caused stem breakage, lodging, and excessive crown damage. During this particular storm, dominant trees were observed to rotate violently and damage the foliage and branches of adjacent codominant and subdominant trees.⁵⁰

In north and northwestern Tasmania, *Sirex* populations remained at low densities in a number of government- and company-owned plantations during the 1970s, but significant tree mortality occurred on two major plantations in 1980–1981 (Fig. 4b). Branches Creek plantation, which consisted of unthinned >10-year-old trees, experienced 30% mortality within two compartments from 1980 to 1984. In the other plantation, at Dulverton,

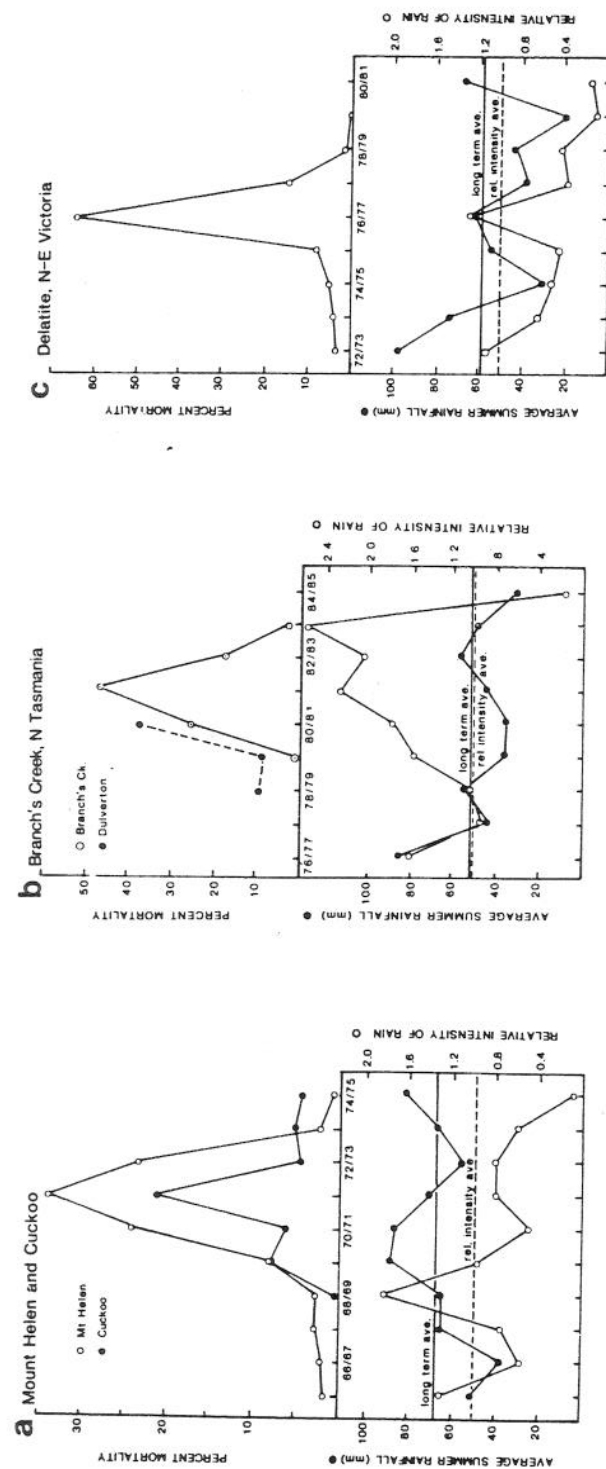


FIGURE 4. Relationship between the percentage of *P. radiata* mortality due to *Sirex* attack and average summer rainfall (December–March) and the intensity of February rainfall relative to the summer average at locations in Tasmania (a–b) and Victoria (c).

mortality increased gradually from 10% in 1977–1978 to 30% in 1980–1981. These increases in *Sirex* activity were attributed to drought, but the Dulverton outbreak was aggravated by thinning operations during the flight season of 1980–1981. One feature of the infestation at Branches Creek was that trees on poor sites with chlorotic needles were not attacked. Suppressed, subdominant, and then codominant trees growing on moister sites were particularly susceptible.³

3.2.2. Victoria

Sirex was discovered on mainland Australia in 1961 in the state of Victoria; until the early 1970s, control attempts consisted of the detection and eradication of infested trees and the release of parasitoids. In 1972, *Sirex* was discovered at Delatite plantation and in the subsequent 7 years destroyed approximately 12% of the marketable volume, notably in 12–15-year-old unthinned stands. Mortality ranged from 63 to 77% in the most severely affected stands. The remarkable feature of this outbreak was that 41–54 of the total mortality occurred during the 1976–1977 season alone, and tree losses were significantly greater in unthinned stands.⁴⁵ In addition, this outbreak occurred despite the presence of both parasitoids and nematodes in the plantation.

A sequence of progressively lower summer rainfalls occurred from 1972 to the end of the decade. Despite this and the large number of *Sirex* emerging from trees killed in 1976–1977, overall mortality declined markedly after 1978 (Fig. 4c).

4. HYPOTHESES FOR CAUSE OF OBSERVED POPULATION BEHAVIOR

Factors that seem to have contributed to the observed changes in *Sirex* populations, as reflected by annual tree mortality in the areas described, have been drought, thinning, and pruning during the *Sirex* flight season, and damage by any one of a number of agencies, including wind, fire, excessive dry heat, and mechanical wounds associated with selective harvest.

One hypothesis suggests that physiological stress due to any cause promotes damage responses characterized by increased transpiration and stem respiration, suppressed photosynthesis, and translocation. Such changes affect overall water relationships and lead to increased permeability of phloem to water and essential oils.⁵⁰ Experimentally girdling, which physically blocks translocation, leads to enhanced phloem respiration for 10 days, at which time phloem shrinkage occurs through direct loss of water. *Sirex* attacks occur coincidentally with these changes. A similar phenomenon is observed when trees are conditioned by the drilling activity of caged wasps. In this case, the mucus inhibits translocation and causes enhanced phloem respiration and stem shrinkage at 10 days and coincident attack by wild females.

Reduction of photosynthesis and labile and stored carbohydrates favours multiple drilling and increases the number of eggs laid and their survival because resinosis and polyphenol formation are dependent on cell turgor and terpenoids on the supply of labile carbohydrates, respectively. The rupture of xylem vessels experiencing high water tensions by drilling with subsequent invasion of air favours optimal conditions for growth of *Amylostereum areolatum*. The immediate and delayed effect of mucus on tree physiology

and water status plus the progressive occlusion of the xylem vessels by the fungus results in tree death.^{21,22,50,53}

All experimental treatments that result in predictable *Sirex* attack on individual trees involve a rapid change in the physiological status of the host tree.⁴⁶ This situation contrasts with the effects of drought, commonly regarded as a major cause of outbreaks.^{3,45,66}

Growth in Radiata pine is closely correlated with rainfall and limited by extremes of temperature and evaporation during summer. Consequently growth may cease prior to the *Sirex* flight season (Fig. 5a) or may be progressively reduced during summer (Fig. 5b), primarily according to variations in water availability. In both instances, photosynthesis and transpiration decline, root growth ceases, and levels of starch and monosaccharides fall.⁷²

Most Radiata pine plantations in Australia experience drought or shortages of water to varying degrees every summer. Such shortages progressively develop from late spring to early summer, with cessation of growth occurring before *Sirex* emergence occurs. Radiata pine trees adapt in time to tolerate periods of extreme water shortage and this tolerance to drought is expressed in zero growth and minimal levels of respiration and transpiration.⁷² This quiescent stage may be sustained in seedling trees for 30 weeks, during which time, in the absence of watering, transpiration declines from 400 g to about 4 g/day.²⁵

In contrast to the gradual adaptation to water shortage, Radiata pine resumes a high level of efficiency in most physiological functions within 24–48 hr of rewatering.^{25,72} Absorption of rainwater by the foliage of water-stressed Radiata pine trees has also been demonstrated.⁴¹

In the light of the capacity of the host tree to adapt to, and tolerate, extended periods of drought, it is hypothesized that other influences occur during the flight season, which act catastrophically to alter host tree physiology rapidly. Such influences could be provided by unseasonal above-average rainfall, which would break the tree's quiescence or tolerance to drought. Subsequent to this, and in the absence of further rain, a rapid transition from a photosynthetically active to an acutely water deficient tree would occur. Cessation of growth is accompanied by active shrinkage of phloem tissue, which signifies an increase in tissue permeability. Thus, during the shrinkage phase water vapor and monoterpenes are essentially squeezed out of the tree, thereby increasing the probability of attack, which in turn depends on the degree of physiological impairment of individual trees. The role of the *Sirex* mucus in the initial stage of attack is to sustain the impairment and thereby increase the duration of attractiveness and attack and probably susceptibility.

Such a hypothesis would explain the results of droughting and watering experiments in which watered trees were more susceptible to *Sirex* attack than droughted trees. Such a result is dependent on rates of transpiration which, following *Sirex* attack, determine the rate at which mucus enters the foliage. In truly droughted trees, transpiration is minimal, and noneffective dosages would occur.

Although thinning, pruning, and felling during the *Sirex* flight season undoubtedly aggravated tree susceptibility, outbreak periods often coincide with periods of below-average but increasing summer rainfalls; greater tree mortality often occurs when dry summers were interrupted by intense, above-average rainfall of short duration. These two associations are shown in Figs. 3a–d and 4a–c: (1) average summer rainfall (mm) for the period December through March, and (2) the intensity of either February or March

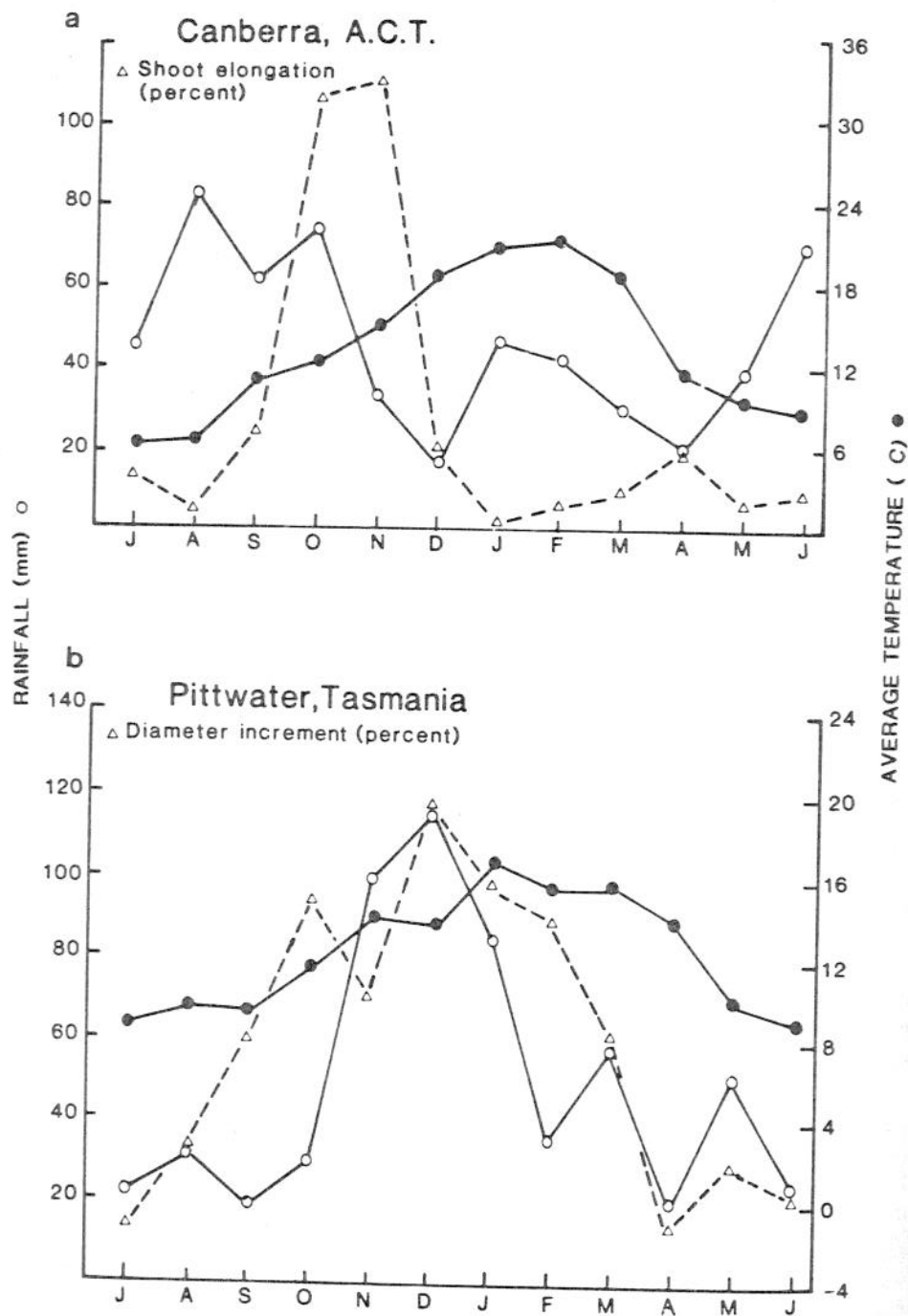


FIGURE 5. Growth of *Radiata* pine at (a) Canberra (A.C.T.) and (b) Pittwater (Tasmania) relative to rainfall and temperature. Growth monitored at the two sites by shoot elongation and diameter increment, respectively.

precipitation relative to the summer monthly average. The February–March period coincides with the peak emergence of *Sirex* in southeastern Australia, Tasmania, and New Zealand. Earlier rains in December or January may act to extend the growing period of *Radiata* pine, in contrast with those of February and March, which may break drought tolerance and reinitiate growth.

The series of graphs indicate the following data:

1. After a period of drought years at Rotoehu, New Zealand, a greater number of trees were attacked during wetter summers and subsequent tree mortality was greatest in 1950–1951 and 1952–1953, years with drier summers interrupted by above average rains in February. In 1951–1952, a season of more uniform and average precipitation, comparatively fewer trees were killed relative to the high proportion of trees initially observed to be dying (Fig. 3a).
2. The Pittwater outbreak coincided with a period of fluctuating summer rainfall but relatively intense February rains. Reduced tree mortality coincided with a year of below average rains (1954–1955), while high mortalities and increased frequencies of resistance to attack were associated with a period of dry summers with intense February rains (Fig. 3b).
3. A relatively dry summer with high February rains preceded a more intense summer drought and high tree mortality at Campania in 1966–1967. During this period, February rainfall was 5 mm, followed in early March by 11 mm. Tree mortality declined with increasing summer and less intense intermittent rains (Fig. 3c).
4. After three seasons of below-average rains, a pattern of ascending but still below-average rains was evident at Bracknell, with significant tree mortality occurring in a year marked by relatively intense February rains. As with Campania, tree mortality declined as summer rains became more average and February rains less intense (Fig. 3d).
5. Trends in tree mortality at the Mt. Helen and Cuckoo plantations in northeastern Tasmania were similar, although tree losses were more severe at Mt. Helen due to more severe wind damage in February 1969. The winds were accompanied by above-average rains, and together the two forces most probably acted to initiate the outbreak. Prior to this event, no change in *Sirex* status was observed despite below average rains (Fig. 4a).
6. At Branches Creek, a significant mortality of ~9% of all trees was recorded in 1980–1981 despite no evidence of *Sirex* presence previously. Summer rains during this and the preceding season were below average and the relative intensity of March rains was significantly high throughout the outbreak period (Fig. 4b).
7. More than 65% of the total mortality of unthinned *Radiata* pine at Delatite plantation, northeastern Victoria, occurred in one season, 1976–1977. Examination of rainfall data indicated that although preceded and immediately followed by dry summers, the 1976–1977 season experienced average precipitation but intense above-average February rains (Fig. 4c).

These examples, and notably 6 and 7 support the proposed hypothesis that intermittent drought during the *Sirex* emergence season contributes significantly to woodwasp outbreaks by increasing tree attractiveness and susceptibility through rapid physiological

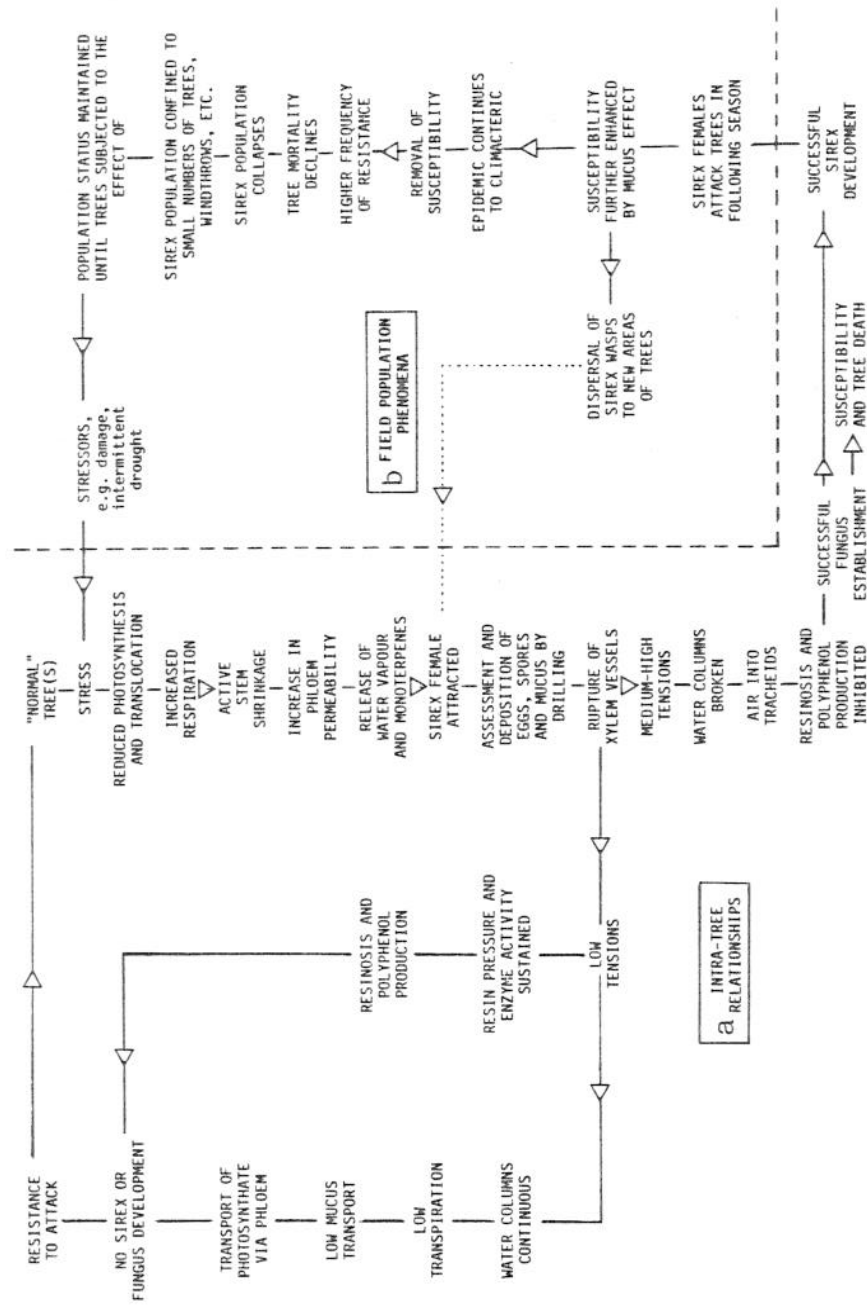


FIGURE 6. Proposed mechanism to explain (a) factors affecting susceptibility and resistance of *Radiata* pine to *Sirex* attack, and (b) changes in *Sirex* populations as reflected by tree mortality.

changes following rains of short duration. The proposed mechanism is summarized in Fig. 6.

5. MANAGEMENT IMPLICATIONS

Given the presence of the *Sirex* wasp and its capacity to exploit short-term disturbances within plantations, new plantations should be established in areas of low risk from fire and wind damage and in areas that experience dry summers, due consideration should be given to the probability of rain during the *Sirex* flight season. In established plantations, thinning and pruning schedules should be adhered to, but only during the late autumn and winter, and never in the summer months. Similarly, if felling during the summer is unavoidable, then clear felling with appropriate disposal of slash would be less harmful to remaining trees than selectively logging. Unprocessed logs also require protection from *Sirex* degrade through application of insecticide sprays.^{34,39}

Attention to site conditions and timing of forestry operations would help prevent *Sirex* outbreaks. However, because of the unpredictability in the occurrence and intensity of stress agents, natural enemies should be introduced and established in order to suppress and stabilize resident populations. Distribution of nematodes through plantations by either female wasps or by planned artificial inoculation of *Sirex* infested trees contributes significantly to population control by reducing the reproductive capacity of the population. However, nematode parasitism does not affect the ability of female wasps to kill trees and, unless high levels of parasitism are sustained, high tree mortality can occur. The spectacular Delatite outbreak, in which 70% of the trees in unthinned areas were killed in 1 year, occurred despite the presence of both parasitoids and 40% nematode infection rates.⁶¹

The observation that high girdling of pruned trees during the flight season results in highly predictable attack 10–12 days later suggested that lure trees can be used to detect the presence of *Sirex* and avert attack from more valuable trees.⁵⁴ In a plantation of 12,000 trees, 80% of the girdled trees ($N = 55$) were attacked, compared with less than 1% of untreated trees, most of which were in the vicinity of girdled trees.

Tree girdling has also been used in New Zealand to increase the incidence of nematode parasitism,⁷ but variability in the frequency and success of attacks, plus high establishment costs, limited the continued deployment of this method. A practical solution to this problem was discovered during field evaluation of different herbicides as thinning agents.⁵⁷ Trees, injected basally with 20% Dicamba (3,6-dichloro-2-methoxybenzoic acid) at 1-ml/10-cm circumference attracted wasps and, although not all treated trees were attacked, treatment during spring was 80% effective and was not detrimental to the development of parasitoids, fungus, or nematodes.⁶²

The management strategy currently being used in high-risk plantations in Australia is to treat batches of low-quality trees with Dicamba in the spring. Attacked trees are then felled in autumn and inoculated with nematodes to maximize infection and attain sterilization rates in excess of 90% after 2 years.⁶³ This strategy concentrates the *Sirex* population in known locations and at the same time maximizes parasitism by insect parasitoids and nematodes.

In exceptional circumstances, significant tree mortality can still occur. Proper sur-

veillance of forests during the flight season is required to ensure effective control. Unseasonal and unexpected events, such as wind or rain storms, should be considered potential stressors and initiators of *Sirex* outbreaks. Proper documentation of local plantation meteorological events should be accompanied by continual monitoring of tree growth to truly establish and identify the causal mechanisms of the observed effects of outbreaks, reduced growth and the resistance and death of forest trees.

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DYNAMICS OF FOREST INSECT POPULATIONS

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