THE SIREX-AMYLOSTEREUM-PINUS ASSOCIATION

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The associations between Sirex woodwasps, their Amylostereum fungal symbionts, and the Pinus trees which together they may damage or kill, have been of interest for nearly 50 years. There is much to delight the biologist investigating the ecological and physiological interactions of these organisms or discovering and using a range of insect and nematode parasites to control Sirex populations. A great amount of scientifically rewarding research has been conducted on these topics, but what is not so clear to a reviewer is just how economically profitable it has been.

In most parts of the world Sirex woodwasps are regarded as pests of secondary importance, causing relatively minor defects in timber, the losses from which are small in relation to total volume of timber produced (48, 80). Infestations of Pinus radiata in England, France, Italy, Spain, and Portugal are low and insignificant (54); in conifers in Germany (100) and Belgium (121) they are viewed with greater concern. In the USA, Japan, and Korea, Sirex appears important only in areas of damage to forests through fire, windthrow, or other insects, and where there is delay in salvage logging (48). Only in New Zealand and Australia has Sirex been consistently viewed as a major pest of Pinus trees.

Sirex noctilio was accidentally introduced to New Zealand before 1900, probably in timber from Europe (50, 79, 92) but did not reach epidemic proportions until after a severe drought in 1946–1948. Between 1946 and 1951 about 30% of Pinus radiata trees over about 300,000 acres were killed (50, 95, 97). Mortality was confined mostly to trees in grossly overstocked stands which were thus beneficially thinned (97). Improvements in silvicultural practice and the introduction of parasites of S. noctilio now keep Sirex populations in New Zealand at a level which is no longer a serious forestry problem (42). In 1950–1951, S. noctilio reached Tasmania (49) where it devastated plantations of P. radiata near Hobart, killing about half of the trees (35, 52). In 1961 it was discovered in Victoria (61) on the mainland of
Australia, and has spread progressively in that state (48). Its establishment in Australia was viewed with great concern because in periods of prolonged drought, which are frequent, plantations might be practically wiped out (10). A National Sirex Fund was established in 1962 to finance survey, research, and eradication work in an attempt to prevent further spread of the pest to other Australian states; annual expenditure on these problems exceeded $A400,000 in 1968 (80). In fairly heavily affected stands of P. radiata in Australia it is generally accepted that about 10% absolute loss in volume production may be caused (52) by Sirex in an average climate. On balance it would seem that Sirex infestations may be trifling, beneficial, or devastating depending very much upon climatic and silvicultural factors in particular places.

SIREX

The genus Sirex comprises about 18 to 23 species of woodwasps (6, 15) indigenous to the northern hemisphere (5, 15, 56, 69) and distributed through North America, Europe, North Africa, the USSR, India, Japan, and China (15, 80). In the southern hemisphere, siricids have occasionally been intercepted in imported timber but only S. noctilio has become firmly established; it is widespread on P. radiata in New Zealand, occurs in Tasmania and Victoria, and has once been recorded from South Africa (80). South America is apparently free of Sirex (5, 48).

Sirex noctilio and S. juvencus were probably of Eurasian origin, and S. cyaneus and S. areolatum of Neoeartic origin (80), but all four of these major Sirex species are now widespread in North America, Europe, and Asia. Disagreement on Sirex taxonomy, however, makes caution necessary in assessing distribution records. Early reports from New Zealand incorrectly identified S. noctilio as S. juvencus (30), while in North America there apparently has been confusion between S. cyaneus and S. juvencus (5, 9, 15, 48, 56, 62, 67, 68, 78, 98). Some Sirex species are separated on biometric or color differences which may be only of geographical significance (16).

While some other siricids are able to attack hardwoods, Sirex species are restricted to conifers (5, 15) with species of Pinus as the major hosts. Of the 23 species of Pinus listed in the literature as hosts of Sirex, P. radiata is by far the most prominent.

SIREX ANATOMY RELATED TO CARRYING OF THE FUNGAL SYMBIONT

In all species of Sirex yet investigated the adult females carry a symbiotic fungus in a pair of small invaginated intersegmental sacs protruding into the body and connecting by ducts with the anterior end of the ovipositor (7, 12, 13, 17, 18, 31, 45, 89). The fungus is present in wasps newly emerged from pupae (7, 45, 50). Older females, just before oviposition, contain in their intersegmental sacs large amounts of mycelium (7, 45) and of mycelium fragmented into oidia or arthrospores (7, 31, 45, 46, 50, 88, 89) consisting of one to four short clamped cells (47, 48, 65, 113). During oviposition, the host female becomes an arthropore sac. It is transmitted to the host via the hypodermis and secreted by the ovipositor sheath. The fungus is transmitted from the host to the parasite via the ovipositor sheath. It is necessary to take the parasite sheath into the host

FUNGI

Mistletoe, arthropore spore, and parasitic fungus.
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Female Sirex larvae, from second instars onwards (7), carry the fungus in hypopleural organs situated on both sides of the body in deep skin folds between the first and second abdominal segments (88, 89, 93). These organs contain coils or oidia of the fungus in a waxy matrix (7, 46, 50) formed in a series of pits. With each molt the cuticular layers of the hypopleural organs are shed and the newly formed organs become longer and more pitted (7). During molting, septa of the pits collapse and expose the contents, from which individual wax packets containing the fungus can be removed (7, 46).

It is not certain how the fungus is acquired by the female larvae and eventually transmitted to the adult females. When the body of the tunneling larva elongates, the hypopleural organs become exposed and scraps of fungus are caught on cuticular spines (80); thus the hypopleural organs could become infected by fungus scraped from the wall of the tunnel. Possibly secretions from the organ are able to direct growth of the hyphae into the pits. Although larvae feed on mycelium (17, 45, 89) and on wood decayed by the fungus (17, 89) they apparently digest extra-intestinally (80), and mycelium is absent from the larval gut (7) despite a report to the contrary (31). The fungus has been reported as absent from the pupal stage (50, 88, 89), or present in the form of a few strands of clamped mycelium in late-stage female pupae (18). It is almost certainly acquired anew by the intersegmental uces of young adult females. The fungus may perhaps grow directly from the walls of larval tunnels into the intersegmental uces (89). More probably it is acquired from wax packets shed from hypopleural organs and taken up into the ovipositor by reflex movements of the ovipositor stylets against one another (46), damaging the wax packets and liberating some of the fungus. While it has been suggested that wax packets may be taken directly into the intersegmental uces (46), Boros (7) found no trace of them in the uces and considered that the packets could pass along the ovipositor only where the first and second pairs of valvulae slide against one another, but would be stranded where they diverge. At this point the ducts of the oil sac and mucus and club glands open into the ovipositor. The wax is soluble in mixed oil and mucus secretions (7). These substances may (7) or may not (38) stimulate growth of the fungus markedly, and it appears that the club gland secretion stimulates growth (119). Thus these secretions may act as attractants and stimulants to the fungus at the site where hyphae could grow up the ovipositor and into the intersegmental uces (7). The source of the fungus could be from the pupal tunnel (14) or from the wax packets (7, 46). Stillwell (112) was able to infect intersegmental uces with fungus taken from hypopleural organs; this suggests that secretions of the larval and adult female organs are similar both chemically and in their effects on the fungus.

FUNGI CONCERNED IN THE ASSOCIATION

Misdetermination of both the siricids and their symbiotic fungi has often led to disagreement on the identity of the fungus in association with a particular Sirex species.
In England, Cartwright (18) determined the symbiont of *Urocerus gigas* as *Stereum sanguinolentum*, and that of *Sirex cyanus* as closely resembling but not identical with this species. Several subsequent authors (11, 23, 25, 26, 55, 89) have adopted the names *S. sanguinolentum*, or *Stereum* sp. (90) for the fungal symbionts of both of these siricids. Cartwright’s cultures were used for comparison with the symbiont of *S. noctilio* in New Zealand (31) and thus it was identified at first as *Stereum sanguinolentum*. In Cartwright’s own description of the fungus he mentions the presence of “cystidia with crystalline incrustations” though these are never present in *S. sanguinolentum*. One of his original subcultures from *U. gigas* was studied by Stillwell (112) and by Gaut (48); both determined the fungus as *Amylostereum chailletii* (= *Stereum chailletii*).

Rawlings (92) recorded that the symbiont of *S. noctilio* in New Zealand might be a species of *Stereum* but was not *S. sanguinolentum*, while Orman (87), using fructifications developed in culture on woodblocks, considered that it was a species of *Pentaphora*. Talbot (113) studied the fungus from *S. noctilio*, including Orman’s cultures, and determined it as a species of *Amylostereum*. This designation was used by many authors pending specific determination. On the basis of comparison by gel electrophoresis it was suggested (65) that the fungus was a strain of *Amylostereum chailletii*. However, the definitive work on determination of this species by its morphology, by electrophoresis and by interfertility tests, was reported by Gaut (47, 48); the species with *S. noctilio* in Australia and New Zealand is in fact *Amylostereum areolatum*.

It was suggested (45) that *S. sanguinolentum* and *S. chailletii* may be associated in Germany with *Sirex juvencus* and *S. noctilio*, but Gaut (48) regards both woodwasps in Germany as carrying *A. areolatum*.

Stillwell (111) reported on the frequent association in Canada of *S. sanguinolentum* and *A. chailletii* with *Sirex* in living fir trees, but later (112) showed that the fungus isolated from *S. juvencus* and two species of *Urocerus* was *A. chailletii*. Gaut (48) found that *S. cyanus* and *S. juvencus* from Canada both carried *A. chailletii*, but also presented evidence suggesting that the specimen of woodwasp which he received, determined in Canada as *S. juvencus*, was really *S. cyanus*.

Interest in the specificity of the relationship between *Sirex* and fungus species started when Francke-Grosmann (45) concluded that “different wasp species are not always associated with the same fungal species, but with the individual species one fungus would seem to be the dominant one” and that “individual wasp species have not adapted themselves to one particular fungus.” This view is almost certainly incorrect, as shown by Gaut (48) who examined 75 cultures from ten siricid species distributed over North America, England, Europe, Asia, Australia, and New Zealand. With only one exception, that of *S. juvencus* in Canada, each insect species, wherever it occurred geographically, always carried the same species of fungus. It is almost certain that the insect-fungus relationship is species-specific, irrespective of geographical distribution. The anomalous position of *S. juvencus* in Canada is probably due to misidentification of the wasp; the wasp from which the culture was made was identified by F. D. Morgan as *S. cyanus* (48), not *S. juvencus*. If so, the identification of its symbiont as *A. chailletii* would agree with other isolates from

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**PHYSIOLOGY**

*Sirex noctilio* and *S. radiata* are noted for their method of attack. The wasps exude a substance that considerably reinforces the gallery, making it a formidable barrier to predators.
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S. cyanus It is not clear whether S. juvencus is established anywhere in North America. According to various authors (9, 56, 78) S. cyanus occurs in North America but S. juvencus does not. Benson (5) suggested that typical S. juvencus does not occur in North America, but that an atypical form is present. This first record of S. juvencus in North America was considered dubious by Benson himself, yet subsequent records of this species in checklists (15, 62, 67–69, 98) are probably repetitions of Benson’s record. Gaut’s (48) evidence for species-specificity is so clear that one must conclude that in some instances Sirex taxonomy, particularly that of S. juvencus and S. californicus, should be reinvestigated. His evidence suggests that S. juvencus does not occur in North America and that S. californicus may more correctly be regarded as a subspecies of S. cyanus than of S. juvencus.

Gaut (47, 48) found that Amylostereum areolatum is carried by S. juvencus, S. noctilio, and S. nitobei, while A. chaillietii is the symbiont of S. cyanus, S. imperialis, S. areolatus, S. californicus, Urocerus gigas, U. augur augur, and U. augur sa.

These fungus species were determined by anastomosis, dikaryotization, and inter-
fertility tests and by starch gel electrophoresis of proteins in culture. It was shown
that A. areolatum produces arthrospores in culture while A. chaillietii does not. This
simple feature could be useful in Sirex taxonomy; a woodwasp whose fungal symbiont produced arthrospores in culture could not, for example, be S. cyanus (48).

Gaut (48) also posed the question whether the fungal symbiont may influence the
antenna color of the insect, which is the chief character used to distinguish S. 
juvencus and S. cyanus. This could be tested by investigating the ability of larvae
to feed and grow on the Amylostereum species with which they are not normally
associated.

Gaut (48) found that isolates of A. areolatum from the same geographical region
had identical protein and enzyme patterns. The Australasian isolates of A. areola-
tum corresponded closely in pattern with isolates from Belgium and Switzerland.
The sample was not large enough, however, to get conclusive results from this novel
way of tracing geographical origins of introduced fungal species. Others have also
suggested that S. noctilio reached New Zealand from Europe (50, 79, 92).

The only other known species of Amylostereum, A. laevigatum, has not been
recorded as a Sirex symbiont. This is explained (48) on the grounds that the two
principal hosts of A. laevigatum are Juniperus and Taxus, both with very tough
 durable wood which is possibly unsuitable for Sirex development. Cupressus is a
host of both Sirex and A. laevigatum, but all three are not known to occur together
anywhere in the world (48).

PHYSIOLOGY OF THE ASSOCIATION

Sirex noctilio in Australasia is attracted initially to physiologically stressed Pinus
radiata trees (71). When trees are girdled, lopped, or felled, the timing and duration
of attacks are correlated with the amount of stress undergone (72). Injured trees
exuding resin are particularly attractive to S. noctilio (35, 50, 92, 118); the resin
produced in oviposition holes attracts further waves of attacks as also does the
reinforcement of tree stress induced by injection of Sirex mucus into the tree (71).
Resin, however, is a residue of variable composition associated with the production of volatiles from essential pine oils and related compounds from the bark-phloem of the stem. These volatiles, formed when supply of soluble solids is limiting, are the specific Sirex attractants (71). They are numerous and of several different classes of chemical compounds: monoterpenes, hydrocarbons, alcohols, aldehydes, ketones, acetates, phenols, and ethers (103-105). Paradoxically, a high resin content in the trees is regarded as important in restricting growth of the fungus A. areolatum at a later stage in the association (35, 41), and it may also depress the survival rate of Sirex larvae (39). Where the osmotic pressure of phloem sap is very high, exceeding 16 atm, as in dominant or healthy trees, the site is usually rejected for ovipositioning by S. noctilio (73).

Resistance of P. radiata trees to attack by S. noctilio is related to their ability to obtain adequate soil moisture (28) and to the moisture content of the wood. The optimum moisture content for egg laying is relatively low, 40-75% over dry weight (82). Dominant trees with a high moisture content tend to be rejected by Sirex (35), and the survival rate of larvae in such trees is often low (39). Amylostereum areolatum, deposited with the S. noctilio eggs, spreads only slowly in wood with a moisture content of about 70% of saturation or greater (35, 39). As the fungus grows, it reduces the moisture content of the wood locally (11, 38, 39, 50, 64, 92) with the result that the eggs hatch and the larvae bores in relatively dry wood (39). The moisture content of heavily infested wood averages about 35% over dry weight (31). Eggs and young larvae become desiccated in wood with moisture content below 20% dry weight, but fairly mature larvae can survive in very dry wood (39).

The larvae of Sirex species are able to live and grow for at least three months on pure cultures of the symbiont fungus (17); they are at least in part mycetophagous (17, 45, 89). Digestive juices of the larvae are able to destroy the fungal hyphae in wood (45), and it has been suggested that the fungus is digested extra-intestinally by saliva discharged into the cupped mandibles from distended salivary reservoirs in S. noctilio (80).

The Amylostereum symbiont benefits from its association with Sirex by being placed in the wood of a suitable host without having to penetrate any protective tissues (7, 45), and its growth may be stimulated by glandular secretions from the insects (7, 119). With this efficient means of dispersal the production of fruitbodies becomes almost superfluous (45). In fact, fruit bodies of A. areolatum have never been found in nature in Australia and New Zealand, although isolates have not lost the ability to produce fruit bodies in culture (45, 65, 87, 92, 113). Species of Amylostereum cause a white-rot of Pinus wood, destroying both cellulose and lignin (45, 50, 65, 92) and possibly rendering the wood more digestible for Sirex larvae (17, 89), though they do not actually ingest wood (80).

Spread of A. areolatum in P. radiata wood is restricted by the formation of polyphenols and resins near the oviposition holes as a reaction of the tree to attack (39, 40, 41, 57, 63, 102). Polyphenols are formed from stored or translocated carbohydrates which are most readily available in vigorous trees (41, 57). Polyphenols, as stilbenes, form in the sapwood after infection, appear to restrict the spread of the fungus, and disorganize the Pinus ray cells in advance of the hyphae.

(57, 65). Polyphenolic trees that recover which is toxic

Amylostereum in four months but not sapling attack by Sirex fungus, A. areolatum. A. areolatum is off supply of is eventually dry restriction of changes that (36).

Cowen (37) systemic toxic (38), the rapid such changes leaves—when stem bark, immature was followed resembling P. radiata fungus nor the leaf is lethal (38, 39), subsequently crown, the death (38). The response (44) in which some of the leaves of the tree. A be gained by in a 100 ppm S. noctilio in changes in the but its insignificance the cycles of damage is higher degree insufficient to

CONTROL

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Species of *Sirex* are able to digest the fungal hyphae in the fungus or the mucus alone is capable of killing the tree but that the combination is lethal (38, 108). Mucus is thought to condition the tree (38, 44); the fungus subsequently kills it by invasion of the sapwood and cutting of the sap flow to the crown, the death of the tree being preceded by a sudden increase in leaf water deficit (38). The responses of the tree to mucus are interpreted as a hypersensitive reaction (44) in which premature senescence and shedding of foliage, the tree removes some of the mucus toxin; such a reaction is but one aspect of the total resistance of the tree. A good indication of the relative susceptibilities of trees to mucus may be gained by a “mucus test” (8) in which green twigs are cut and placed for 45 days in a 100 ppm aqueous solution of the mucus. Spradbery (108) has shown that only *S. noctilio* mucus, of seven siricids investigated, produced rapid physiological changes in the host *Pinus*. He attributes the importance of *S. noctilio* in Australia but its insignificance in the northern hemisphere to differences in these regions in the cycles of insect emergence and tree growth. In addition, the higher incidence of damage in Tasmania as compared with Europe has been attributed (57) to a higher degree of water stress; when water content decreases rapidly there would be insufficient time for protective substances to be formed.

**CONTROL**

Many workers (23, 24, 28, 30, 31, 35, 52, 97) have stressed the value of improving silvicultural practices as a means of controlling *S. noctilio* attacks on *P. radiata* in Australia and New Zealand, since the attacks occur most on weakened, suppressed,
overcrowded, fire-damaged, or drought-stricken trees (30, 50, 54, 71, 79, 82, 85, 92, 117), or those weakened by other insect pests (30, 55, 79, 91). These measures aim to make the host trees unsuitable for initial attacks by the woodwasps.

Dominance, or tree vigor, is probably an expression of the tree genotype modified by a wide range of phenotypic characteristics induced by the environment (117). *Pinus radiata* trees of outstanding vigor are rare in Australian plantations, about one in 60 acres (33), but a long-term project for breeding trees resistant to the effects of *Sirex* attack has been planned (33, 34). It is noted that, as dominant *P. radiata* trees produce more ethylene after injury or *S. noctilio* attack than do suppressed ones, this may be a suitable indicator of the degree of resistance and, if heritable, may be of use in breeding programs (102).

Birds normally have little effect in controlling *Sirex* populations (55) but may be important in some areas (28, 43, 76, 99).

The importation of insect parasites of *S. noctilio* to New Zealand was suggested (26, 28, 86, 116) after it had been shown (22) that *Rhyssa persuasoria* has a very long ovipositor capable of reaching *Sirex* larvae in their tunnels. Proposals also to introduce *Ibalia leucospoides* (24) to New Zealand were made because the larval tunnels of *S. noctilio* are deeper than those of *S. juvencus* in Europe, where *R. persuasoria* was an effective parasite. Control with *Rhyssa* began in New Zealand in 1928 (29, 79, 81). As there was evidence of competition for *Sirex* larvae between *Rhyssa* and *Ibalia*, it was suggested that they should be liberated in different parts of New Zealand (25). *Rhyssa*, however, was considered insufficient by itself to control *S. noctilio* (30); one reason may be that it is not effective at locating its host (81). Later work (55) has shown that the percentage of parasitism is higher when both *Rhyssa* and *Ibalia* are used together. By 1944 *R. persuasoria* had multiplied and spread "remarkably" (19); rearing and liberation in new locations were continued and control of *S. noctilio* was reported as "satisfactory" (20, 21). This, however, was immediately before the major outbreaks of *Sirex* in 1946–1948, an indication that control was not as satisfactory as it might have seemed.

*Ibalia leucospoides* was also established in New Zealand (93, 94) and Tasmania (114, 122, 125). In Tasmania there was no definite and immediate indication of the success of *Rhyssa* and *Ibalia* in biological control (114), although they became well established and had spread. Later introductions of insect parasites of siricids to Australia and New Zealand include other species of *Ibalia* (107) and *Rhyssa* (127), *Schlettererius cinctipes* (115), and *Megarhysa* sp. (15, 70). Indigenous insect parasites of *Sirex noctilio* include *Ceronotus tasmaniensis* in Tasmania (59) and *Guignia schaunslandi* in New Zealand (51, 96).

Some of the most promising biological control work stems from the discovery of nematodes causing parasitic castration of *S. noctilio* in New Zealand (32, 123–126). Two species of the nematode, *Deladenus wilsoni* and *D. siricidicola* (2), were recovered from *S. noctilio* in New Zealand, from *S. cyaneus*, *S. juvencus*, other siricids, and *Ibalia leucospoides* from Europe, and from two species of *Rhyssa* introduced to Tasmania from India and Europe (1, 58). The nematodes can be cultured on *Amylostereum* (1). Larvae of the nematodes become released into the hemocoel of the host *Sirex*, migrating to the testes or eggs and sterilizing both sexes of the
woodwasp. The larvae do not interfere with oviposition but are deposited into fresh timber along with *Sirex amylostereum*. In both these species of *Deladenus* the females are strongly dimorphic (2, 126). One form is free-living and feeds and reproduces on *Amylostereum* in coniferous timber; the other form is parasitic and penetrates the host insect larva, reproducing in its hemocoel (2). Four species of *Sirex* and two associated insect parasites of *Sirex* were shown to be parasitized by *Deladenus* (3).

*Deladenus siricidicola* was reared and released in large numbers in Tasmania and Victoria in 1970–1971 (4) with encouraging results; by 1972, 92% of *Sirex*-infested trees in the release area and 37% of infested trees in the whole forest contained the nematode. Clearly these nematodes show great promise in biological control of *Sirex nocillo* (125); but they also attack the insect parasites of *Sirex*, namely species of *Ibitia* and *Rhysta*. A recent evaluation (77) estimates that 85% of a tested *Sirex* population was affected by insect or nematode parasites three years after their introduction and that thereafter an ecological balance was established; the most effective parasites were *Ibitia leucospoides* and *D. siricidicola*.

In Germany a cytoplasmic polyhedrosis virus has been found probably responsible for the death of larvae and adults of *S. juvencus*, *S. nocillo*, and other siricids (66, 101). Its use as a possible biological control merits investigation.

In areas of low *Sirex* density, girdled and pruned trees may be used to divert much natural attack by *Sirex* to specific trees which can then be destroyed before the next flight season (75). Such trees may also be used as lure traps sprayed or implanted with insecticide (83). Trees implanted with Bidrin® organophosphate insecticide were cheap to establish and operate, and were successful in forests with low density of *S. nocillo* (83). Lure-trees sprayed with Imidan® were attacked by *S. nocillo* with significantly reduced emergence, life span, and egg hatching (83). In Serbia, trap-logs sprayed with 2% BHC (1, 2, 3, 4, 5, 6-hexachlorocyclohexane) and 2% malathion, or 2% BHC in diesel oil, gave 95–100% protection against several siricid species after three years, but this was considered an uneconomical control measure (53).

Horwood, Morgan & Stewart (60) tested 40 contact insecticides (chlorinated hydrocarbons, organophosphates, and carbamates) against *S. nocillo*; seven organophosphates and one carbamate were effective. Some of these sprayed on bark significantly reduced longevity of ovipositing woodwasps and the level of egg laying, and the effect persisted for several weeks. Bidrin and Phosphamidon® implanted in holes bored around the tree trunks were temporarily toxic to the trees but decreased longevity and fecundity of *S. nocillo* without inhibiting growth of *Amylostereum areolatum* in the oviposition sites (84). Bidrin was superior and completely controlled egg hatching and development to third larval instars.

As *Sirex* larvae are at least partly mycetophagous (7, 45, 89), control of *Amylostereum* symbionts by antibiotics or fungicides would appear to offer a way of controlling *Sirex* infestations. However, the antibiotic Actidione® and the systemic fungicides Melprof®, Carbarn®, and Wepsyn® gave disappointing results (110) when sprayed on the base of the tree or injected into the bole. Basal sprays did not diffuse sufficiently into the wood to inhibit fungal growth, while bole injection resulted in spiral translocation with no lateral movement of the chemical in the wood of *Pinus radiata*. In addition, as *Amylostereum* volatiles (119), possibly acetaldehyde (70),

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en trees (30, 50, 54, 71, 79, 82, 85, 92, 93, 55, 79, 91). These measures aim attacks by the woodwasps.

pression of the tree genotype modified by the environment (117). Rare in Australian plantations, about 5% of breeding trees resistant to the effects is noted that, as dominant *P. radiata S. nocillo* attack than do suppressed degree of resistance and, if heritable, the growing *Sirex* populations (55) but may be

occasio to New Zealand was suggested (8) that *Rhysida persusoria* has a very high that *S. juvencus* in Europe, where R. n. with *Rhysida* began in New Zealand competition for *Sirex* larvae between 1 should be liberated in different parts 2 is considered insufficient by itself to 3 it is not effective at locating its host tage of parasitism is higher when y 1944 R. persusoria had multiplied eration in new locations were contin- satisfactory" (20, 21). This, however, of *Sirex* in 1946–1948, an indication th have seemed.

New Zealand (93, 94) and Tasmania y in the immediate indication of the nals of *Ibitia* (107) and *Rhysida* (127), sp. (15, 70). Indigenous insect parasites in Tasmania (59) and Guiglia
are the principal attractants whereby the parasites *Ibalia*, *Rhyssa*, and *Megarhyssa* locate their *Sirex* hosts in wood (70, 81, 106, 107, 109), the elimination of the fungus by chemical control, if feasible, would destroy some of the usefulness of these parasites in biological control. Another attractant of *Rhyssa* and *Megarhyssa* is a species of yeast, *Saccharomyces*, found in *Sirex noctilio* oviposition holes and larval tunnels (74).

CONCLUSION

Considerable progress has been made in specifying the organisms which may be involved at times in the *Sirex-Amylostereum-Pinus* association, in understanding their complicated web of relationships, in elucidating how they interact physiologically, and in suggesting ways in which the ecological balance can be swung in favor of maintaining healthy *Pinus* trees.

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sites *Italia*, *Rhysa*, and *Megaloryssa* (17, 109), the elimination of the fungus or some of the usefulness of these wasp *Italia juvencus* is a 

ifying the organisms which may be *Pinus* association, in understanding 

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