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

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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 Neoarctic 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 mucus (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

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oviposition, mucus and oidia adhere to the eggs (17, 18, 45, 50, 89) and mycelium develops in the wood surrounding oviposition holes and larval tunnels (17, 18, 45, 65, 89).

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 sacs of young adult females. The fungus may perhaps grow directly from the walls of larval tunnels into the intersegmental sacs (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 sacs (46), Boros (7) found no trace of them in the sacs 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 sacs (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 sacs 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 cyaneus* 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 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 *Peniophora*. 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. cyaneus* 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. cyaneus*.

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 misdetermination of the wasp; the wasp from which the culture was made was identified by F. D. Morgan as *S. cyaneus* (48), not *S. juvencus*. If so, the identification of its symbiont as *A. chailletii* would agree with other isolates from

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S. cyaneus It is not clear whether *S. juvencus* is established anywhere in North America. According to various authors (9, 56, 78) *S. cyaneus* 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. cyaneus* than of *S. juvencus*.

Gaut (47, 48) found that *Amylostereum areolatum* is carried by *S. juvencus, S. noctilio,* and *S. nitobei,* while *A. chailletii* is the symbiont of *S. cyaneus, S. imperialis, S. areolatus, S. californicus, Urocerus gigas, U. augur augur,* and *U. augur sah.* 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. aerolatum* produces arthrospores in culture while *A. chailletii* 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. cyaneus* (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. cyaneus.* 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. areolatum* 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: monoterpene 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% oven 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 bore in relatively dry wood (39). The moisture content of heavily infested wood averages about 35% oven 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

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(57, 65). Polyphenols increase greatly in amount in affected sapwood of *P. radiata* trees that recover from attack by *S. noctilio*, the major polyphenol being pinosylvin, which is toxic to *A. areolatum* (57).

Amylostereum areolatum grows fairly slowly in *P. radiata* wood, e.g. 50 mm in four months (120). By itself the fungus can kill young *P. radiata* seedlings in vitro, but not saplings or larger trees in the field (120). The killing of *P. radiata* trees after attack by *Sirex noctilio* was long attributed to pathogenic effects of the associated fungus, *A. areolatum*, with the suggestion that the fungus acts primarily by cutting off supply of sap to the crown (92). Although the fungus does spread slowly and eventually dries the wood so much as to render it nonconducting (35, 39), this restriction of sap flow is gradual and cannot explain the marked physiological changes that occur in the tree within the first two weeks after attack by *S. noctilio* (36).

Coutts (37) inoculated sapwood of *P. radiata* with *A. areolatum* and detected no systemic toxic effects. However, when he injected mucus secretions from *S. noctilio* (38), the rapid early physiological changes typical of *Sirex* attack were induced. Such changes included increase in stem respiration, accumulation of starch in the leaves—which has subsequently been denied (44)—and decrease of starch in the stem bark, implying that translocation of the photosynthate was inhibited (38). This was followed by yellowing, wilting, and abscission of much of the foliage, symptoms resembling premature senescence, and by increased susceptibility to the effects of *Amylostereum* which is weakly pathogenic (38). The view is taken that neither the fungus nor 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, by 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 Australasia 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 *Megarhyssa* sp. (15, 70). Indigenous insect parasites of *Sirex noctilio* include *Certonotus tasmaniensis* in Tasmania (59) and *Guiglia schauinslandi* 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

en trees (30, 50, 54, 71, 79, 82, 85, 92,
: (30, 55, 79, 91). These measures aim
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woodwasp. The larvae do not interfere with oviposition but are deposited into fresh timber along with *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 noctilio* (125); but they also attack the insect parasites of *Sirex*, namely species of *Ibalia* and *Rhyssa*. 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 *Ibalia 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. noctilio*, 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 luretraps 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. noctilio* (83). Lure-trees sprayed with Imidan® were attacked by *S. noctilio* 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. noctilio*; 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. noctilio* without inhibiting growth of *Amylostereum areolatum* in the oviposition sites (84). Bidrin was superior and completely controlled egghatching 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 Melprex®, Carbam®, 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),

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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