FORTY YEARS OF *SIREX NOCTILIO* AND *IPS GRANDICOLLIS* IN AUSTRALIA

F. DAVID MORGAN

University of Adelaide, Waite Agricultural Research Institute,
PMB 1, Glen Osmond, South Australia 5064.

(Received for publication 5 July 1989; revision 19 December 1989)

ABSTRACT

Both *Sirex noctilio* Fabricius and *Ips grandicollis* Eichh. have been involved in serious outbreaks since their respective establishments. Some progress has been made with biological control but success in the long term may depend on attention to key silvicultural aspects of stand management.

Keywords: pest management; forest damage; *Sirex noctilio; Ips grandicollis.*

INTRODUCTION

The species *Sirex noctilio* (Siricidae) and *Ips grandicollis* (Scolytidae) are two of the more significant forest insects introduced into the Southern Hemisphere. Both are, so far, the only known species of their genera that have established and have become recognised pests of introduced conifers in the South and West Pacific sub-regions of this hemisphere. Both pests are involved in devastating outbreaks (unpubl. data) in plantations, farm woodlots, and windbreaks. These outbreaks are stimulated by the same factors: drought, overstocking of stands, poor silviculture and utilisation practices, as well as forest fires, lightning strikes, and rises in the water table leading to waterlogged root systems or "wet feet".

In direct consequence, their control, or the modification of their potential for damage, should result from a sensitive integrated programme, beginning with careful selection of planting stock and sites, including tolerance of species to critical aspects of those sites. Adequate, properly timed thinnings and forest hygiene, related to changes in availability of water in the first metre of the soil profile, are the next set of factors to be fitted to the model. Finally, biological controls or partial controls of the pests, themselves, complete a management system requiring periodic monitoring to ensure its general effectiveness. Lack of attention to these factors will lead to significant losses in the yields of forest products in plantation systems using conifers susceptible to these, and other, pests.

As both insects are actively dispersing, the boundaries shown in Fig. 1 are necessarily approximate. Key dates for *S. noctilio* are: 1952 Tasmania, 1963 Victoria, 1980 New South Wales, and 1985 South Australia. For *Ips grandicollis* they are: 1943 South Australia, 1952 Western Australia, 1980–81 Victoria, 1981–82 Queensland, and 1983 New South Wales.

Surveys for *I. grandicollis* are usually more accurate, in terms of determining its presence or absence, than they are for *S. noctilio.* This is due partly to the multivoltine life cycle for *I. grandicollis* and the more obvious symptoms of attack when it is at low

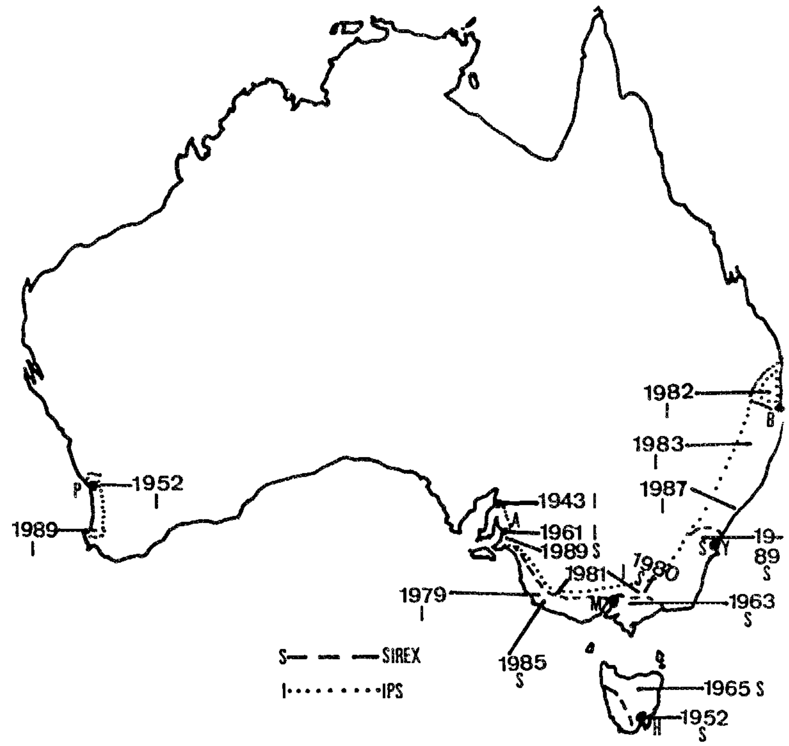

FIG. 1—The progressive distributions of *Sirex noctilio*, S, and *Ips grandicollis*, I, since their discovery in Australia. Major cities: P = Perth, A = Adelaide, M = Melbourne, H = Hobart, SY = Sydney, B = Brisbane.

population density. The woodwasp, at low population densities, is often insidious and therefore may remain undetected for several years.

A good example occurred in South Australia where the best survey data suggested that the insect was nearly 200 km south and east of where it had already been established for at least two, and probably more, generations. Hence, the data in Fig. 1 are probably inaccurate in that both pests may not be easily detected in non-plantation forests and farm trees, which they may utilise during their general dispersals, and which probably do not receive the intense attention that commercial forests do during detection surveys.

Surveys for *S. noctilio* are usually based upon aerial search for dead trees and then ground examination of them. Resin dribbles from ovipositor drills through the bark (Rawlings 1948), larvae found by chopping into boles, and evidence of adult oviposition including current selection of sites (usually February to April) and post-oviposition mortality on or at the base of trees, are some symptoms than can be recognised. During post-emergence surveys (May to October) exit holes may be seen. In most trees the population distribution is such (Fig. 2) that concentration on the mid-bole area of dead trees provides an excellent chance of finding the insects.

TILIO AND IPS
TRALIA

search Institute,
a 5064.
9 December 1989)

ave been involved in serious
has been made with biological
to key silvicultural aspects of

ps grandicollis.

llis (Scolytidae) are two of the
ern Hemisphere. Both are, so
established and have become
d West Pacific sub-regions of
g outbreaks (unpubl. data) in
tbreaks are stimulated by the
silviculture and utilisation
s in the water table leading to

ication of their potential for
amme, beginning with careful
of species to critical aspects of
st hygiene, related to changes
, are the next set of factors to
partial controls of the pests,
riodic monitoring to ensure its
vill lead to significant losses in
conifers susceptible to these,

daries shown in Fig. 1 are
952 Tasmania, 1963 Victoria,
Ips grandicollis they are: 1943
ctoria, 1981–82 Queensland,

, in terms of determining its
due partly to the multivoltine
ms of attack when it is at low

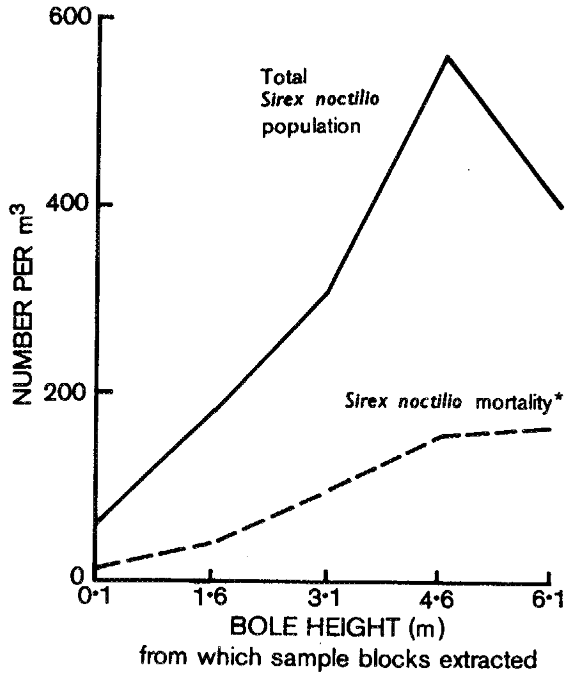

FIG. 2—Distribution of *Sirex noctilio* larvae in trees of *Pinus radiata* from 10-year-old plantations (4.6 m bole height is approximately mid-bole). Data from 43 samples at each bole site.

**Sirex noctilio* mortality 60% caused by *Rhyssa persuasoria.*

The symbiotic fungus, *Amylostereum areolatum* (Fries) Boidin, produces lenticular zones of infestation in the bark-sapwood interface. Characterised by red-brown edges and flat creamy areas between, these are easily detected by removal of the bark of attacked trees. The rapid longitudinal growth, relatively slow circumferential growth, and the ovipositional behaviour of the female woodwasp stimulate coalescence of these fungal attack areas. Despite this, the symptoms can be accurately detected by trained observers even in trees that produce no woodwasps, but which succumb to the fungus. I have used this fungal zoning as an accurate *S. noctilio* survey detection method since the late 1940s.

Presence of *I. grandicollis* is detected by accumulations of frass on logs and trees. On the latter, examinations should be concentrated on the nodes, where bark crevices are often deeper than on the internodal bark, and branches which also retain frass even after rain. Checking in the bark for adults or evidence of polygamic attack patterns (*see* Morgan 1967) will separate this species from both *Hylastes ater* (Paykull) and *Hylurgus ligniperda* (Fabricius), the other pine bark beetles present in Australia.

THE WOODWASPS - SIRICOIDEA

The three families comprising this super-family of the Order Hymenoptera all have indigenous representatives in the Australia sub-region of the world (Maa 1949; Morgan 1968), e.g., *Guiglia* spp. (Orussidae), *Austrocyrta* spp. (Xiphidryiidae), and

Eriotremex spp. Siricidae). While the former are considered to be parasitoids of woodboring insects (Riek 1955; Baker 1972), the latter two groups are typical woodwasps, those studied depending upon symbiotic fungi for food and development (Buchner 1965; Francke-Grossman 1939, 1957; Parkin 1941; King 1966; Gaut 1969).

Most woodwasp species produce glandular secretions both in female larvae (Rawlings 1951) and in adult female mycangia (Parkin 1942). These secretions are critical components of the continuing association between insect and fungus (Francke-Grossman 1957; Talbot 1977; Spradbery 1973; Stillwell 1966). The most recent reviews of these relationships are by Madden & Coutts (1979) and Madden (1988).

Adult insect, fungal symbiont, and insectan secretions are actively involved in a mutualism which results in the development of a medium in trees which permits eggs to develop, larvae to grow and mature, and females to re-infest themselves and continue the cycle. In the process of this cycle, host trees are partially or wholly killed (Morgan 1968; Coutts 1969; Fong & Crowden 1973; Spradbery 1973) and the symbiotic fungi may cause decay and deterioration of the infested wood (Stillwell 1960).

In certain areas of the Holarctic, localised outbreaks of damage by siricids have been recorded (Keen 1952 for California; Baker 1972, Stillwell 1960, 1966 for Eastern North America; Chrystal 1928 for Europe). Most of these records have derived from moribund trees, logs, and timber. None has involved the change from secondary to primary pest status as has occurred with *S. noctilio* in Australasia.

SIREX NOCTILIO

Estimated to have established in New Zealand about 1900 (Miller & Clark 1935), this woodwasp was responsible for a minor outbreak in duneland plantations of *Pinus radiata* D. Don near the township of Foxton 100 km north of Wellington. Though the cause of this was not clear, one stimulus could have been thinning of stands with much slash left on the forest floor (A.F. Clark pers. comm.), providing breeding material for a resident population without most of its insect and nematode enemies from the lands of its origin. About 25 years later, *S. noctilio* was involved in outbreaks (Rawling 1955) that destroyed an estimated 30% of 120 000 ha of pine plantations within a land area that exceeded 20 000 km². The most seriously affected stands lost about 90% of their growing stock. These series of outbreaks were caused by poor forest management leading to overstocked stands subjected to drought. Once the woodwasp had reached near potential population densities, it became a primary insect pest (*see* Rawlings 1948; Jackson 1955).

It emerged as a pest in Australia in sand dune plantations of *P. radiata* near Hobart, Tasmania, in 1952 (Gilbert & Miller 1952) where some 40% of trees in certain age-classes over an area of 1100 ha were destroyed by 1958 (Madden 1975). Subsequent outbreaks have been recorded in Victoria (Neumann *et al.* 1987) and South Australia (Woods and Forests Department 1988).

Its biology, behaviour, and control have been intensively studied and documented (Rawlings 1948, 1955; Morgan & Stewart 1966; Horwood *et al.* 1970; Taylor 1978, 1981), with a recent review by Madden (1988). These aspects need no reiteration.

Modern population control is dominated by the establishment and distribution of Zondag's nematode (Zondag 1969, 1971; Bedding & Akhurst 1974), with variable assistance from rhyssine and ibaliid parasitoids (Zondag 1971; Taylor 1981).

The basic model (Table 1) illustrates the dynamics of this type of biological control. A key feature of it is an expected large decrease in fecundity from a mean potential 240 or a mean actual fecundity of about 160 (Table 1) to about 14. The partial life tables of the model, though the components will vary from generation to generation, show that for successful biological control each hundred eggs laid must result in no more than about four adults if the sex ratio is 7:1. Should the sex ratio change in favour of females, as it does in low population densities, then compensating mortality is critical to continued effective control of this pest.

TABLE 1–Partial life tables for *Sirex noctilio* without and with parasitoids and parasites

Stage	Without*			With		
	Number	Loss	Causal agents	Number	Loss	Causal agents
Egg	100	10	Natural infertility	100	92	*Deladenus* + *Ibalia* + infertility
Larva I	90	17	Fungal pathogens	8	2	Parasitoids (Rhyssines)
Larvae II to prepupa	73	0		6	1	Rhyssines
Pupa	73	5	? *Beauvaria* sp. + Pyemotidae	5	1	Pathogens
Adult	68			4		
Generation II eggs†	1600			90		

* Data from Gippsland, Victoria, before biological controls were established.
† Based on sex ratio of 7:1 and a fecundity rating of 160.
Note: The 2-year life-cycle has been included in the 1-year cycle for convenience.

The balance between control and population increase is, therefore, a fragile one and points to the need not only to monitor field populations from time to time but also to practise good forest management to provide additional pressure on the ability of the pest to break the control imposed.

Significant losses of trees, particularly in unthinned stands at Delatite in Victoria, occurred from 1970 to 1979 despite the presence of *Deladenus siricidicola* Bedding and several parasitoids (McKimm & Walls 1980). Obviously the forest susceptibility dominated the unknown level of control of *S. noctilio* reached by the mid-1970s (*see* Table 2 for comparisons between losses at Delatite and in planned thinnings of similar stands in Gippsland).

IPS GRANDICOLLIS

The introduced five-spined engraver originated in eastern North America and is presumed to have reached Australia in crate or dunnage timbers through Port Pirie (Morgan 1967). It was first found in a plantation of *Pinus nigra calabrica* (= *P. laricio*) at Wirrabara in 1943 (D.C. Swan unpubl. data) but it was already well established and

TABLE 2–Comparative *Sirex noctilio*-associated deaths in Gippsland tree farms of APM Forests Pty Ltd heavily thinned at age 9 years and regularly thereafter as a woodwasp control system, and unthinned stands of *Pinus radiata* at Delatite about 120 km north of Traralgon

Period of *S. noctilio* activity	Place	Stems per hectare		
		Established	After first thinning	Loss to *S. noctilio*
1962–69	Gippsland	~1700	~850	<1*
1972–79	Delatite	~1700	~1700†	>370‡

* Data from APM Forests Pty Ltd records
† Unthinned, but probably somewhat less than 1700 stems/ha had survived before *S. noctilio* attack began.
‡ 5% to 77% of trees were killed by *S. noctilio* over 1084 ha (Neumann *et al.* 1987)

was in outbreak population density. In 1952 it was also identified from pine populations some 40 km north of Perth (Rimes 1959).

While in Western Australia its distribution remained similar to that recorded by Rimes (1959) for more than 20 years, in South Australia it dispersed southward to the central forest region in the Mount Lofty Ranges and was established in all pine plantations by 1962 (Morgan 1967). A quarantine on the movement of material from this region to the south-eastern forests of the "Green Triangle" (the pine plantations in south-eastern South Australia and south-western Victoria) saw a delay in its dispersal further afield. In 1979 it was first recorded near Mt Gambier (Woods and Forests Department 1980) and reached western and north-eastern Victoria by 1982 (Neumann & Morey 1984).

With the help of the timber trade it reached Queensland in peeler logs by 1982 and dispersed into northern New South Wales by 1983 (Eldridge 1983). Like *S. noctilio*, this small beetle has a capacity to establish quickly in reasonable sites where suitable conifer hosts are present. Windbreaks, isolated trees, farm woodlots, and plantations may be utilised, along with log and slash dumps near sawmills and pulp and paper mills.

The factors that predispose host trees to attack by *I. grandicollis* are the same as those for the woodwasp.

The biology and the behaviour of *I. grandicollis* in mainland Australia have been presented in detail by various authors (Rimes 1959; Morgan 1967; Witanachchi & Morgan 1981; Neumann & Morey 1984; Lawson 1989). Attempted biological control as a component of integrated control is proceeding (Lawson 1989) (*see also* Table 3).

TABLE 3–Parasitoids and predators of scolytids introduced into Australia as a biological control component in the integrated control of *Ips grandicollis*

Species	Family	Control type	Establishment status	Preliminary control assessment (1988)
Roptrocerus xylophagorum	Pteromalidae	Parasitoid	Widespread	25%
Dendrosoter sulcatus	Braconidae	Parasitoid	Doubtful*	–
Thanasimus dubius	Cleridae	Predator	Doubtful*	–
Temnochila virescens	Trogossitidae	Predator	Doubtful*	–

* Breeding in field release sites recorded.

Like many Scolytids, *I. grandicollis* has a feeding phase and, after becoming satiated, enters a breeding phase (Morgan 1967). Adults feed extensively in the breeding galleries where they developed and mating occurs before emergence, the females being able to attack and breed in suitable material without another feeding phase (Witanachchi 1980).

Surveys (Table 4) have related planting sites to tree mortality associated with infestation by this bark beetle. They demonstrate that the depths to which roots can penetrate and the moisture contents of soil down the profile are critical to survival of trees during droughts. The picture does not alter much where precipitation is higher (1.8 times) than where these data were obtained (*see* notes Table 4).

TABLE 4–*Ips grandicollis*-associated deaths of 12-year-old *Pinus radiata* in Bundaleer Forest Reserve, South Australia, in the drought years 1967–68, related to maximum root penetration and profile soil moisture contents.

Depth of root penetration (mm)	Soil moisture content in summer (gravimetric %)	Percentage trees dead (*I. grandicollis*-associated)
100	Trace	100
450	1	100
600	4	0
850	8	0
1000	10	0

Note: (a) Soils are red-brown clay loams over marl, which prevents *P. radiata* root penetration.
(b) These data have been confirmed for Mt Crawford forest reserve with precipitation averages about 1.8 times that at Bundaleer.

These data for both *S. noctilio* and *I. grandicollis* may now be used to derive a pest management system for both.

PEST MANAGEMENT PROPOSALS AND UNDERLYING REASONS FOR THEM

Experience since 1965, that is after *Deladenus siricidicola* was included in biological controls, has shown that, in the vanguard of *S. noctilio* dispersal, most adults are not infected by the nematode. This suggests that infected adults, under field conditions, are not as dispersive as non-infected ones. Are infected individuals adversely affected by the nematode? This question begs an answer as we, at present, must introduce the nematode wherever *S. noctilio* establishes to ensure a reasonably rapid development of this control component. Australian evidence suggests that natural dispersal of the nematodes could lag behind the woodwasp by up to 10 years, but with man's assistance good field infestations may be achieved in from 2 to 5 years (*see* Zondag 1971; Bedding & Akhurst 1974; Neumann *et al.* 1987).

The amount of water available per tree is apparently the critical factor in successful attack by both *S. noctilio* and *I. grandicollis* (*see* Morgan 1967; Madden 1988. Moreover, it is the amount of water available from spring to autumn that is vital. Severe drought effects during the period January through March when both *S. noctilio* and *I. grandicollis* are exerting most attack pressure on trees usually result in varying degrees of tree mortality, dependent upon the level of strees which is the major stimulus to *S. noctilio* and *I. grandicollis* population growth rates that leads to their change from secondary to primary pest status.

The pest management model (Table 5), based upon experience in eastern Victoria for *S. noctilio* (Table 2) and in the Wirrabara/Bundaleer Forest Reserves of South Australia for *I. grandicollis* (Table 4), does not depend upon a biological control component (Tables 1 and 3) for its success, but the latter components, once established, may influence the frequency of the silvicultural components fundamental to its long-term effectiveness.

The cardinal rules are:

(i) Monitor stands for stress symptoms.

(ii) First thinnings for *S. noctilio* and *I. grandicollis* control must be much heavier than would be usual without their presence.

Note: It is the first thinning that is most important in terms of both timing and stems removed.

(iii) Hygiene must be high, leaving little breeding material for pest population build-ups in all slash but particularly after the first thinning and after clear-felling.

TABLE 5–Proposed pest management plan for control of *Sirex noctilio* and *Ips grandicollis* in plantations of susceptible conifers

Part 1: Site selection

Mean daily temperature (range)	Soil types (without deleterious toxins)	Aspect (slope)	Precipitation (annual)
10°–25°C	Sandy to clay loams	<40°	>600 mm

Part 2: Plant selection, based on parental history

Progeny of elite seed orchard parents
with good root/crown ratios,
desirable growth characteristics for intended end-product,
tolerance to pathogens and pests demonstrated by survival through infestations,
and an ability to respond rapidly to thinning operations.

Part 3: Silviculture

Site qualities (grouped)	Original stand densities (stems/ha)	Thinnings I: Age (yr)	Thinnings I: Residual stand (stems/ha)	II: Age (yr)	II: Residual stand (stems/ha)	III: Age (yr)	III: Residual stand (stems/ha)	IV: Age (yr)	IV: Residual stand (stems/ha)
I and II	1500	6–8	900	11–12	650	16–18	400	25	200
III and IV	1200	8–9	800	11–12	650	16–18	400	25	200
V to VII	900	8–9	700	13–15	450	18–20	300	26	200

Part 4: Hygiene

	Thinnings I	II	III	IV
Utilisation to: 100 mm diam.	———	———	———	——→
Major product: wood chips, round and sawlogs	———	———	———	——→

GENERAL DISCUSSION

Sirex noctilio

Localised outbreaks of this woodwasp, with severe damage to stands, still occur despite the general success of biological control based upon the nematode *Deladenus siricidicola* and the parasitoids *Megarhyssa* spp., *Rhyssa persuasoria persuasoria* L., and *Ibalia leucospoides* Hochenwarth. The latest region so affected is in the pine plantations of South Australia where silviculture of plantings from 1972 to 1974 was inadequate to cope with the droughts of the mid-1980s and extensive bushfires (1983) which together apparently weakened the trees over hundreds of hectares. The increased susceptibility of such affected trees to the woodwasp (Rawlings 1948, 1955) led to the current problems of control of the insect there.

Of concern is the discovery of a non-sterilising form of *D. siricidicola* in New Zealand. Its spread has not been monitored to date (R. Zondag pers. comm.). Small loci of tree mortality associated with *S. noctilio* infestations in New Zealand are being treated by releases of adult *Megarhyssa nortoni nortoni* (Cresson). Several factors emerge from these events. Firstly, the woodwasp, still well under control on a national basis using the biological techniques available (Zondag 1971), has the ability to develop small outbreak loci with a frequency that, to me, is disturbing. Secondly, the population densities are such that parasitoids are common enough to be able to be collected in sufficient numbers to be used in applied controls of the woodwasp. Thirdly, it seems that such controls should not be applied without some monitoring of these outbreak loci to determine what effects these controls are having on the other biotic agencies present therein.

These problems, as yet considered minor by forest entomologists in New Zealand, are nevertheless apparent in the control system for *S. noctilio* which is depended upon by forest owners of the South Pacific region. It is appropriate, therefore, to realise that silvicultural systems are available if, in future, the parasite and parasitoid control system for this woodwasp should break down.

The descriptive model presented as Table 5 is based on conservative components. For example, *P. radiata* grows in a wider range of temperatures and soil types than presented here and tolerates much higher precipitation than the model suggests. The problem in presenting such a model is that one cannot complicate it by listing all the variations possible in any site possibly suitable for *P. radiata*, when deficiency in one component is offset by variation of another. In other words, permutations on the basic theme are possible.

The pest management plan presented is, therefore, merely an indication that viable alternatives to the biological control of the woodwasp (and of the bark beetle, if one is developed) may be derived from sound techniques already embraced in good silviculture for the pest-susceptible trees one wishes to grow in forest communities. An integrated control for both pests in pine plantations is possible.

Ips grandicollis

Outbreaks of this bark beetle have, so far, not been observed in their various developmental stages in New Zealand or in the eastern states of Australia. The earliest outbreaks, probably stimulated by drought and also by bushfires in some sites, occurred in the northern forest reserves, Wirrabara and Bundaleer, in both 1958–60 and 1967–68. Severe losses ranging from 15% to 100% of certain sites in some stands occurred.

A further factor modified the utilisation of some stands at both reserves. In 1933 plantings, the forester decided to remove 66% of the desired volume in a first thinning in early summer 1959–60 and then salvage the trees attacked by *I. grandicollis* in an early autumn second thinning. He removed approximately 90 000 cubic feet (2549 m^3) in the first and 40 000 cubic feet (1133 m^3) from attacked trees in the second thinning in autumn. Both thinning and salvage resulted in the total yield desired (A.H. Cole pers. comm.).

The latest outbreak devastated stands of *P. radiata* in the Rainbow River plantations of the Department of Conservation and Land Management of Western Australia. I surveyed these for introduced parasitoids and predators of the bark beetle in 1987. The stimuli involved in this outbreak were drought and wind breakage after violent storms. The oldest stands were about 17 years from planting and 50% to 100% of those examined had been killed. The parasitoid *Roptrocerus xylophagorum* was well established in these and other plantations where releases had been made in this State over 5 years.

In north-eastern New South Wales, the bark beetle became established in 1983 (Eldridge 1983) apparently dispersing from infestations to the north of Brisbane where it was well established by 1982 (R. Wylie pers. comm.). I surveyed the plantations near Casino in 1986 and evidence for the establishment of *R. xylophagorum* and *Dendrosoter sulcatus* was obtained.

More recently Stone & Simpson (pers. comm.) have collection data for these two parasitoids and for *Temnochila virescens* (*see* Table 3). The braconid *D. sulcatus* was also found in the Mt Gambier region of South Australia in 1986. While establishments are claimed for *R. xylophagorum* over all release sites in mainland Australia, the other species are still listed as doubtful until confirmed.

This paper has provided data and records indicating that the woodwasp and the bark beetle have a number of biotic characteristics sufficiently similar from a plantation ecology viewpoint to warrant the development of a pest management system for them. Although a silvicultural system was used by A.P.M. Forests in Gippsland with some success during the 1960s and 1970s, the bark beetle was not present in these areas until the mid-1980s.

The pest management system proposed (Table 5) has yet to be tested for forests containing both pests, but the data and reports presented offer encouragement to do this research. It may, however, be delayed by the possible success of the biological controls currently being developed for both insects. The problem with the woodwasp nematode in New Zealand may stimulate further research into silvicultural means of control for *S. noctilio* and any deficiencies in the biological control system for *I. grandicollis* will emphasise the need to reconsider silviculture as the basis for its control in the future.

REFERENCES

BAKER, W.L. 1972: Eastern forest insects. *U.S. Department of Agriculture Miscellaneous Publication No. 1175:* 465-7.

BEDDING, R.A.; AKHURST, R.J. 1974: Use of the nematode *Deladenus siricidicola* in the biological control of *Sirex noctilio* in Australia. *Journal of the Australian Entomological Society 13:* 129-35.

BUCHNER, P. 1965: Siricids. Pp. 83-92 *in* "Endosymbiosis of Animals with Plant Micro-organisms". J. Wiley and Sons, New York. 909 p.

CHRYSTAL, R.N. 1928: Sirex woodwasps and their importance in forestry. *Bulletin of Entomological Research 19:* 219-47.

COUTTS, M.P. 1969: The mechanism of pathenogenicity of *Sirex noctilio* on *Pinus radiata.* I. The effects of the symbiotic fungus, *Amylostereum* sp. (Thelephoraceae). *Australian Journal of Biological Science 22:* 915-24.

ELDRIDGE, R.H. 1983: Introduced pine bark beetles in New South Wales. *Forestry Commission of N.S.W., Forest Protection Series 5.*

FONG, L.K.; CROWDEN, R.K. 1973: Physiological effect of mucus from the woodwasp *Sirex noctilio* F. on the foliage of *Pinus radiata* D. Don. *Australian Journal of Biological Science 26:* 365-78.

FRANCKE-GROSSMAN, J. 1939: Uber das Zusammenleben von Holzwespen (Siricinae) mit Pilzen. *Zeitschrift fur Angewandte Entomologie 25:* 647-80.

——— 1957: Uber das schiksal des siricidenpilze wahrend der metamorphose. *Wanderversammel. Deutsch. ent. 8:* 37-43.

GAUT, I.P.C. 1969: Identity of the fungal symbiont of *Sirex noctilio. Australian Journal of Biological Science 22:* 905-14.

GILBERT, J.M.; MILLER, L.W. 1952: An outbreak of *Sirex noctilio* in Tasmania. *Australian Journal of Forestry 16:* 63-9.

HORWOOD, D.W.; MORGAN, F.D.; STEWART, N.C. 1970: Effectiveness of contact insecticides against the woodwasp *Sirex noctilio. Australian Forestry 34:* 49-59.

JACKSON, D.S. 1955: The *Pinus radiata – Sirex noctilio* relationship at Rotoehu Forest, New Zealand. *New Zealand Journal of Forestry 7:* 26-40.

KEEN, F.P. 1952: Insect enemies of western forests. *U.S. Department of Agriculture Miscellaneous Pulication No. 273:* 200-1.

KING, J.M. 1966: Some aspects of the biology of the fungal symbiont of *Sirex noctilio. Australian Journal of Botany 14:* 25-30.

LAWSON, S.A. 1989: Studies on two predators and a parasitoid of *Ips grandicollis* Eichh. the five-spined engraver beetle in South Australia. M.Ag.Sc. Thesis, University of Adelaide.

McKIMM, R.J.; WALLS, J.W. 1980: A survey of damage caused by the Sirex woodwasp in the radiata pine plantation of Delatite, northeastern Victoria between 1972 and 1978. *Forestry Commission of Victoria 28:* 3-12.

MAA, T.C. 1949: A synopsis of Asiatic Siricoidea with notes on certain exotic and fossil forms. *Notes. ent. China 13:* 76-163.

MADDEN, J.L. 1975: An analysis of the outbreak of the woodwasp *Sirex noctilio* (Hymenoptera: Siricidae) in *Pinus radiata. Bulletin of Entomological Research 65:* 491-500.

——— 1988: Sirex in Australasia. Chapter 20 *in* Berryman, A.A. (Ed.) "Dynamics of Forest Insect Populations". Plenum Press, New York and London. 603 p.

MADDEN, J.L.; COUTTS, M.P. 1979: Role of fungi in the biology and ecology of woodwasps (Hymenoptera: Siricidae). Pp. 165-74 *in* Batra, L.R. (Ed.) "Insect-Fungus Symbiosis". J. Wiley and Sons, New York. 276 p.

MILLER, D.; CLARK, A.F. 1935: *Sirex noctilio* (Hym.) and its parasites in New Zealand. *Bulletin of Entomological Research 26:* 149-54.

MORGAN, F. David 1967: *Ips grandicollis* in South Australia. *Australian Forestry 31:* 137-55.

——— 1968: Bionomics of Siricidae. *Annual Review of Entomology 13:* 239-56.

MORGAN, F. David; STEWART, N.C. 1966: The biology and behaviour of the woodwasp *Sirex noctilio* (F.) in New Zealand. *Transactions of the Royal Society of New Zealand 7(14):* 195–204.

NEUMANN, F.G.; MOREY, J.L. 1984: Influence of natural enemies on the Sirex woodwasp in herbicide-treated trees of radiata pine in northeastern Victoria. *Australian Forestry 47:* 218–24.

NEUMANN, F.G.; MOREY, J.L.; McKIMM, R.J. 1987: The Sirex wasp in Victoria. *Conservation, Forests and Lands Department, Melbourne, Bulletin 29.*

PARKIN, E.A. 1941: Symbiosis in larval Siricidae. *Nature 147:* 329.

——— 1942: Symbiosis and Siricid woodwasps. *Annals of Applied Biology 29:* 268–74.

RAWLINGS, G.B. 1948: Recent observations on the *Sirex noctilio* population in *Pinus radiata* forests in New Zealand. *New Zealand Journal of Forestry 5(11):* 411–21.

——— 1951: The establishment of *Ibalia leucospoides* in New Zealand. *Forest Research Notes 1(3):* 1–14.

——— 1955: Epidemics in *Pinus radiata* forests in New Zealand. *New Zealand Journal of Forestry 7:* 53–8.

RIEK, E.F. 1955: The Australian sawflies of the family Orussidae (Hymenoptera : Symphyta). *Australian Journal of Zoology 3:* 99–105.

RIMES, G.D. 1959: The bark beetle in Western Australian pine forests. *Journal of Agriculture of Western Australia 8:* 2–4.

SPRADBERY, J.P. 1973: A comparative study of the phytotoxic effects of Siricids on conifers. *Annals of Applied Biology 75:* 309–20.

STILLWELL, M.A. 1960: Decay associated with woodwasps in balsam fir weakened by insect attack. *Forest Science 6:* 225–31.

——— 1966: Woodwasps in conifers and the associated fungus *Stereum chailletii* in eastern Canada. *Forest Science 12(1):* 121–8.

TALBOT, P.H.B. 1977: The *Sirex–Amylostereum–Pinus* association. *Annual Review of Phytopathology 15:* 41–54.

TAYLOR, K.L. 1978: Evaluation of insect parasitoids to control *Sirex noctilio* (Hymenoptera : Siricidae) in Tasmania. *Oecologia (Berlin) 32:* 1–10.

——— 1981: The Sirex woodwasp: Ecology and control of an introduced forest insect. Pp. 231–48 *in* Kitching, R.L.; Jones, R.E. (Ed.) "The Ecology of Pests — Some Australian Case Histories". CSIRO, Melbourne.

WITANACHCHI, J.P. 1980: Evidence for pre-emergence mating among mature progeny of *Ips grandicollis* Eichh. *Journal of the Australian Entomological Society 19:* 93–100.

WITANACHCHI, J.P.; MORGAN, F.D. 1981: Behaviour of the bark beetle *Ips grandicollis* Eichh. during host selection. *Physiological Entomology 6:* 219–23.

WOODS AND FORESTS DEPARTMENT 1980: *Annual Report 1979–80.* Woods and Forests Department of South Australia.

——— 1988: *Annual Report 1987–88.* Woods and Forests Department of South Australia.

ZONDAG, R. 1969: A nematode infection of *Sirex noctilio* (F.) in New Zealand. *New Zealand Journal of Science 12:* 732–7.

——— 1971: Control of *Sirex noctilio* with *Deladenus siricidicola* Bedding. *New Zealand Journal of Forestry Science 1:* 5–14.