Agricultural and Forest Entomology (2009), **11**, 283–294 DOI: 10.1111/j.1461-9563.2008.00422.x

The control of sirex wood wasp using biological control agents in Victoria, Australia

N. G. Collett and S. Elms*

*Department of Forest and Ecosystem Science, The University of Melbourne, Burnley Campus, 500 Yarra Boulevard, Richmond, Victoria 3121 and *HVP Plantations, 50 Northways Road, Churchill, Victoria 3842, Australia*

Abstract

1. The sirex woodwasp, *Sirex noctilio* has been a significant pest of radiata pine plantations in Victoria since 1961. Outbreaks are usually associated with susceptible trees being under some form of stress including the effects of drought and overcrowding.
2. This paper reviews the spread of sirex and the history and efficacy of biological control programmes implemented against sirex in Victoria from 1970 to 2006.
3. Of the numerous biological control agents released, the most effective in managing sirex have been the nematode *Beddingia siricidicola* and the parasitic wasp *Ibalia leucospoides*. Several other parasitic wasps such as *Schlettererius cinctipes* and *Megarhyssa nortoni nortoni* have also established but provide only minimal control.
4. While rates of *I. leucospoides* parasitism have improved over time, it is unlikely that this improvement will continue substantially past current levels.
5. In recent years, issues have arisen regarding a decline in the infectivity of *B. siricidicola* necessitating a re-evaluation of strategies and development of techniques to overcome this problem.
6. Ongoing research using Random Amplification of Polymorphic DNA (RAPD) testing is underway to accurately determine nematode strains and associated infectivity present in plantations in the field in order to develop management strategies to re-introduce more effective strains.

Keywords *Beddingia siricidicola*, biological control, *Ibalia leucospoides*, *Pinus radiata*, *Sirex noctilio*, *Type II population*.

Introduction

Sirex wood wasp *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) is a significant pest of introduced softwood plantations within south-eastern Australia. Native to Eurasia and northern Africa, *S. noctilio* was first detected in Tasmania in 1952 (Gilbert & Miller, 1952; Madden, 1975). From there it spread to Victoria where it was first detected in 1961 at Narbethong, approximately 70 km north east of Melbourne (Irvine, 1962; Neumann *et al.*, 1987). By 1984, Sirex had spread to and established in all pine-growing areas (consisting of predominantly *Pinus radiata* D.Don) of Victoria and adjacent plantation regions in southern New South Wales and South Australia (Neumann *et al.*, 1987). Sirex is predominantly a secondary pest in that although it is capable of attacking healthy trees, trees under stress (from drought, overcrowding, wind, and fire-damage etc.) are usually more susceptible to attack. Unthinned stands over 12 years old are most at risk (Neumann & Minko, 1981; Neumann *et al.*, 1987; Haugen *et al.*, 1990; Carnegie *et al.*, 2005).

Sirex in Australia normally has a 1-year lifecycle with females laying their eggs (along with a phytotoxic mucus and wood decaying fungus) into susceptible trees during the summer (Neumann *et al.*, 1987). By winter, the trees die and sirex adults emerge the following summer to recommence the cycle (Neumann & Minko, 1981; Neumann *et al.*, 1987). While its host range within softwood plantation species is generally broad, the preferred host species within Victoria (and southern Australia) is *P. radiata*. Within Victoria, *P. radiata*, both historically and currently, is the main softwood plantation species grown with over 210 000 ha established (National Forest Inventory, 2006).

From 1962 to 1972, attempts were made to eradicate sirex within Victoria through extensive surveillance and eradication

Correspondence: N. G. Collett. Tel: +61 3 92506839; fax: +61 3 92506886; e-mail: ncollett@unimelb.edu.au

programmes involving the quarantine of sirex-affected trees and their subsequent destruction through burning. These programmes were conducted by the then Forests Commission of Victoria under the auspices of the National Sirex Fund Committee, established by the Commonwealth Government. By 1972, however, it became clear that such methods, while slowing its spread, could not eradicate sirex. Consequently, from 1972 onwards, biocontrol was adopted as the main management strategy for sirex, in conjunction with thinning and associated silvicultural techniques (Neumann *et al.*, 1987; Bedding, 1993). Among the suite of biocontrol agents tested and subsequently introduced were *Beddingia* (formerly *Deladenus*) *siricidicola* (Bedding), a parasitic nematode which renders adult sirex sterile (Bedding, 1972; Neumann & Minko, 1981) and several species of parasitic wasps including *Ibalia leucospoides* (Hochenwarth), *Megarhyssa nortoni nortoni* (Cresson), *Schlettererius cinctipes* (Cresson), and *Rhyssa* spp. (Ichneumonidae) (Neumann *et al.*, 1987, Carnegie *et al.*, 2005). The geneus *Ibalia* is endoparasitic and lay their eggs within sirex embryos or first instar larvae whereas *Megarhyssa*, *Schlettererius*, and *Rhyssa* are ectoparasitic and lay their eggs on the surface of late instar sirex larvae (Chrystal, 1930; Neumann *et al.*, 1987).

In southern Victoria during the 1960s, many shelterbelts of *P. radiata* on farms were destroyed by sirex outbreaks and several outbreaks were recorded in *P. radiata* plantations in Central Gippsland (Neumann *et al.*, 1987). In the mid-1970s, the most significant outbreak occurred near Mansfield in central Victoria in 12–15-year-old unthinned stands. This outbreak was associated with lower than average rainfall in the area and it was estimated that $>65\%$ of trees in some stands were killed (Neumann & Minko, 1981; Neumann *et al.*, 1987). Since the early 1980s, outbreaks have tended to be small and localized in nature, mainly owing to the efficient spread of biocontrol agents coupled with improved silviculture (thinning regimes) based on the findings of numerous research and surveillance programmes in previous years (Madden, 1975; Neumann *et al.*, 1987; Haugen *et al.*, 1990; Carnegie *et al.*, 2005; Hurley *et al.*, 2007).

It is over 45 years since sirex was first detected in Victoria and it is opportune that a review of the management of this significant insect pest of *P. radiata* in Victoria is conducted, especially as the last review by Neumann *et al.* (1987) was approximately 20 years previously. Such a review is timely, especially given the establishment of sirex in recent years in *Pinus* plantations in South America (Uruguay, Argentina, Chile, Brazil), South Africa (Carnegie *et al.*, 2006; Hurley *et al.*, 2007), and more recently in North America (Hoebeke *et al.*, 2005; A. Carnegie NSW Department of Primary Industries and K. Dodds USDA Forest Service personal communication, 2007). Biocontrol of sirex coupled with other control techniques including silvicultural options is currently being undertaken in these countries.

This paper discusses the spread of sirex and the introduction of biocontrol agents and their efficacy over time in managing sirex populations together with associated management implications in Victoria. Much of the information contained within this paper has been gathered from internal government and industry commissioned scientific studies and research reports, including research study data not previously published.

Softwood plantations in Victoria

The most significant and widespread softwood plantation species in Victoria is *P. radiata* which represents over 95% of all exotic softwood plantings in the State. Prior to the mid-1990s, the significant majority of these plantations were under public ownership through government agencies such as the Forests Commission of Victoria and Department of Conservation, Forests and Lands, after which they were corporatized and then sold to a private company, HVP Plantations, (formerly Hancock Victorian Plantations Pty Limited) in 1999 which now manages over 60% (approximately 148 000 ha) of Victorian softwood plantations. The *P. radiata* plantation estate in Victoria is concentrated in five regional areas (Fig. 1).

Detection and spread of sirex in Victoria

In December 1961, Sirex was first detected in Victoria in the Central Region near Narbethong, approximately 70 km north east of Melbourne. By late 1962, it had been detected to the east of Melbourne and in the Gippsland Region's Latrobe Valley, and by 1966 had extended to plantations in the Strzelecki Ranges and Mount Macedon (Ballarat Region) (Fig. 2). By 1970, sirex had spread further into the Ballarat and Central regions, as well as to plantations adjacent to Geelong. Despite extensive attempts to eradicate it, by 1974 Sirex was approaching Delatite and Benalla in the North East region. By 1976, it was present in plantations around Bright in the North East and Dartmoor in the South West region (Fig. 2). By 1984, sirex had extended to all softwood plantation areas in Victoria and had crossed over the border into New South Wales and South Australia (Neumann *et al.*, 1987; Madden, 1988). This pattern of expansion into new areas is similar to observations made by Zondag and Nuttall (1977), with Taylor (1981) noting that adult sirex are capable of powerful flights of short duration and can move up to 30 km per year. While distances traveled by sirex in Victoria varied substantially from year to year between 1962 and 1984, based on Neumann *et al.* (1987) and Fig. 2, movement averaged 20–25 km per year. However, not all sirex movement followed the above trend, as evidenced by the rapid expansion within 2 years of sirex from the Ballarat region to Dartmoor in the South West region, a distance of over 200 km (Fig. 2). While no definitive evidence is available to explain this rapid expansion, it was possibly as a result of either (i) the transport of infested sirex material into the area or (ii) being present but remaining undetected until 1976 (F. Neumann, personal communication 2007).

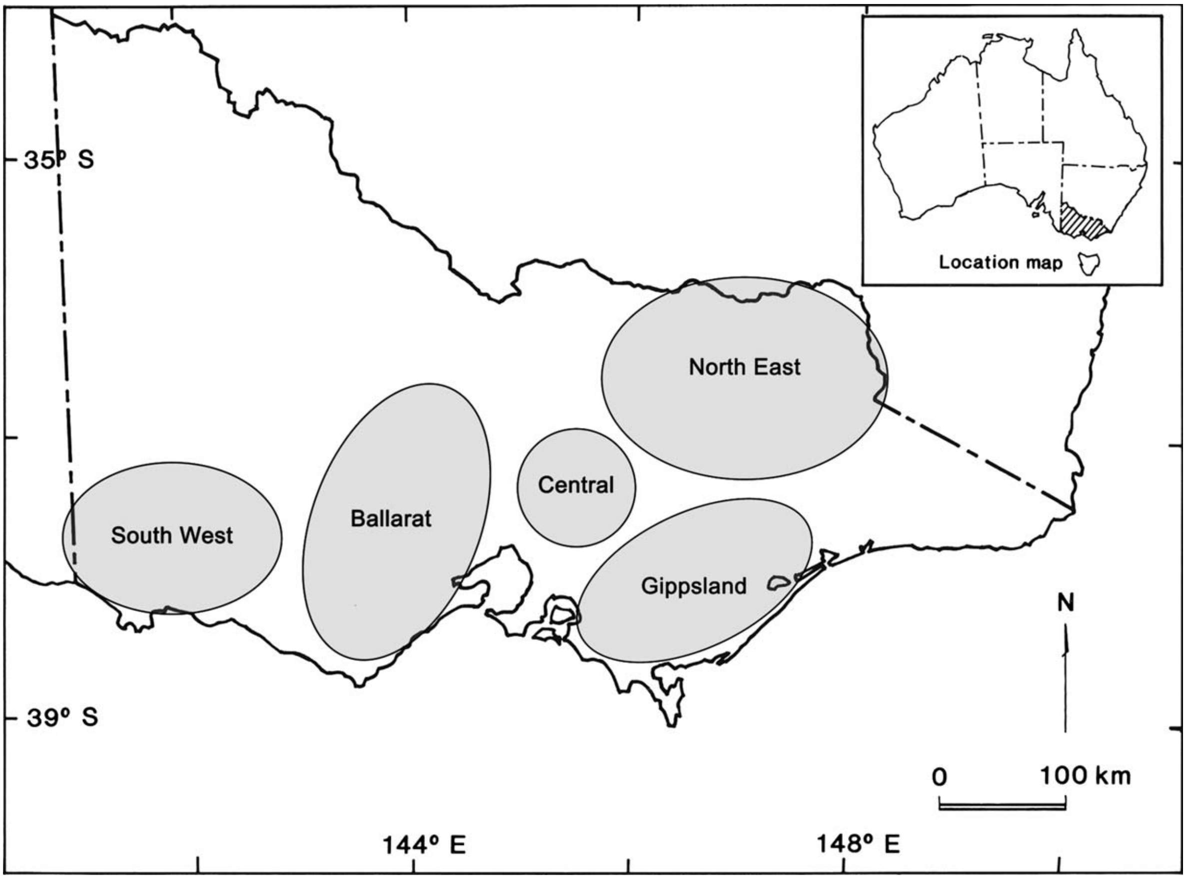

Figure 1 Location of the five major pine growing regions in Victoria, Australia.

Methodologies used for the study of sirex nematode and parasitoid populations

Within the review, reference is made to previously unpublished data concerning research and industry studies on the efficacy of field sirex nematode and parasitoid populations. The data used within the study are based on established methodologies as described in Taylor (1978), Neumann *et al.* (1987), Haugen *et al.* (1990), Neumann *et al.* (1993) and National Sirex Coordination Committee (2002) to evaluate nematode infectivity and parasitoid efficacy. The methods common to the references involve collection of sirex and parasitoid-infested billets from plantation sites which are either placed in cages, or drums with mesh covers. Subsequent insect emergents are then tallied by species and sex. Sirex are examined for evidence of nematodes by severing the abdomen and squeezing its contents on to microscopic slides to determine nematode presence or absence. The data referring to the strains and infectivity of nematode field populations are based on methodologies developed by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) on behalf of the National Sirex Coordination Committee (NSCC) involving the use of Random Amplification of Polymorphic DNA (RAPD) testing, and CO_2 to induce development of the infective form of nematode from the fungal feeding form (Calder & Bedding, 2002).

Nematode biological control release programme 1973–1985

Nematode strains selected for release

Based on the discovery that nematodes of the genus *Beddingia* (formerly *Deladenus*) have both a free-living (fungus feeding) and parasitic lifecycle, and thus were potentially suitable for use in biocontrol of sirex (Bedding & Akhurst, 1974; Bedding, 1993), extensive screening of suitable species was undertaken from the mid- to late 1960s and early 1970s. Four nematode strains, from Corsica, Greece, Hungary, and New Zealand were selected for culturing and subsequent release. Although all four strains were released in Victoria, the majority of releases were of the strain from Hungary known as Sopron Strain 198. This strain was considered superior as it tended to parasitise larger sirex (that were capable of flying longer distances) and therefore the potential for the nematode to be spread throughout the plantation estate was greater (Bedding, 1993).

Nematode inoculation programme in Victoria

The use of biocontrol agents for the management of sirex in Victoria commenced in 1973 with the first releases of parasitic

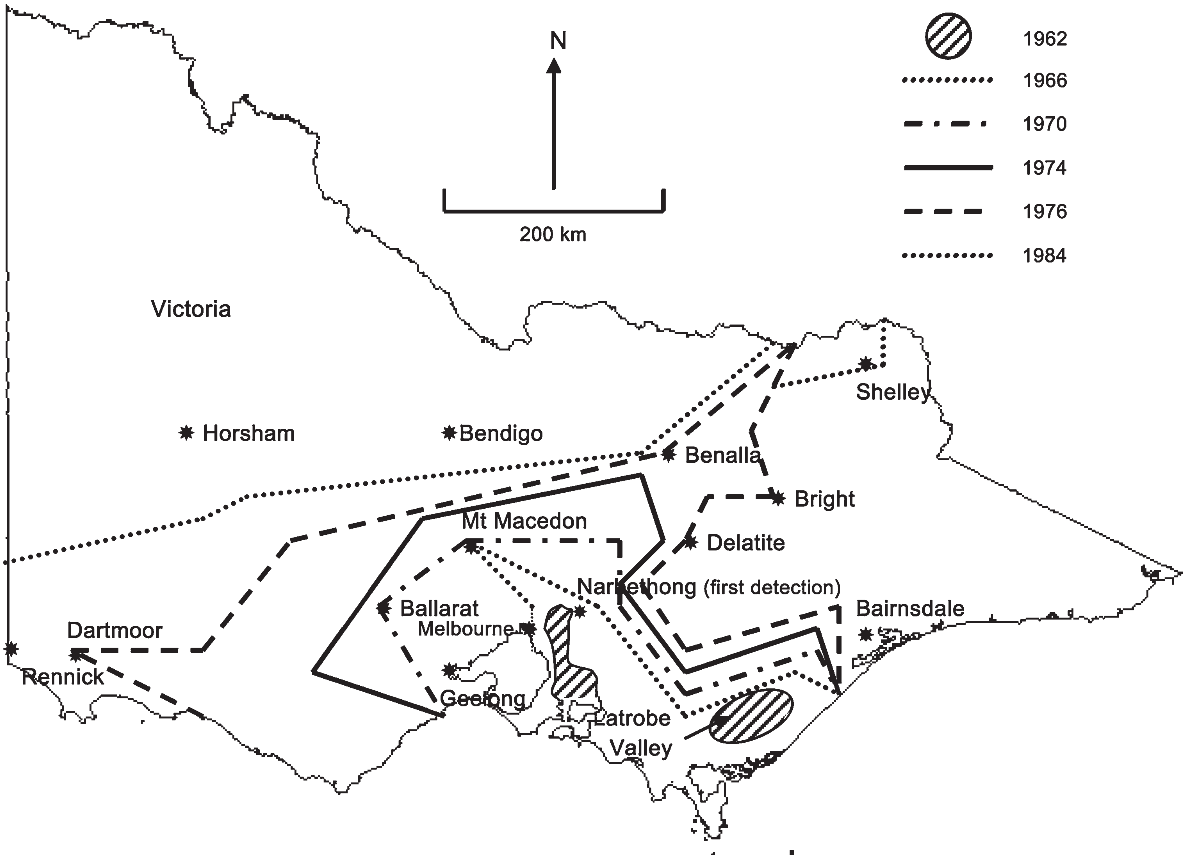

Figure 2 The spread of *Sirex noctilio* from 1962 to 1984 in Victoria (based on Neumann *et al.*, 1987).

nematodes in Gippsland, Central, and Ballarat regions reflecting the known area of activity at the time (Fig. 2). The release of nematodes follows inoculations protocols as detailed in Neumann *et al.* (1987) and updated operational worksheets produced by the National Sirex Coordination Committee (2002). These releases involved inoculations over a wide range of sites within the affected regions, with approximately 74% of the total release sites between 1973 and 1985 occurring in 1973 and 1974 (Fig. 3). Over 4500 trees and billets were inoculated, with approximately 39% of trees and 92% of billets treated in 1973 and 1974 in an attempt to saturate affected areas with the nematodes. The use of trees reflected sirex attacked trees identified in the field and inoculated on-site whereas the use of billets reflected sirex inoculated billets within insectaries and subsequently distributed to sirex-affected stands. By 1975, nematode inoculations had commenced in the North East region near Benalla and Bright. From 1982 onwards, releases were made in the North East region in the Shelley area near the New South Wales border (Fig. 2). Releases in the South West region of Victoria commenced in 1980 after sirex spread to this region. After 1975, the number of release locations and the number of trees and billets inoculated with nematodes declined in most areas. However, a significant number of trees were inoculated in the North East from 1983 to 1985 in order to increase nematode levels in a small number of specific locations around Shelley and to the north of Bright. This reduction in the number of nematode releases was as a result of the finding that nematodes were established in the sirex population to such an extent that sirex moving into new areas already contained nematodes and it was not necessary to continue nematode releases over such a wide area.

While nematode releases continued after 1985, this year marked the completion of the initial release phase aimed at introducing parasitic nematodes to new areas in Victoria. Subsequent releases in Victoria have been in response to an observed decline in nematode levels and infectivity.

Wasp parasitoid biological control release programme 1970–1986

Parasitoid species selected for release into plantations

Between 1962 and 1973, potential parasitoids of sirex were collected in the northern hemisphere (predominantly in Europe, North Africa and North America), cultured, and subsequently released in Australia (Taylor, 1976). Of the 21 species originally selected, six were subsequently reared and released on a significant scale in Victoria. These species were *I. leucospoides*, *M. nortoni nortoni*, *Schlettererius cinctipes*,

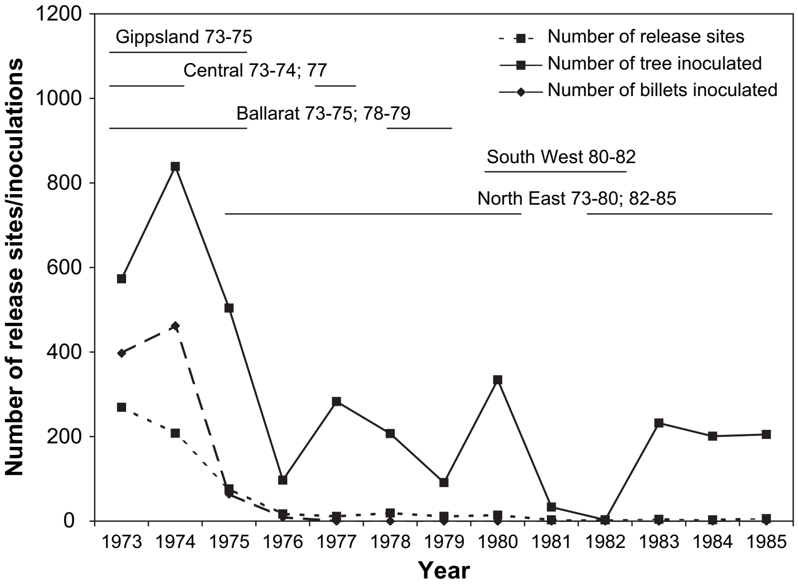

Figure 3 Sirex nematode release programme summary for Victoria 1973 to 1985 (lines indicate primary release regions for that year).

Rhyssa hoferi (Rohwer), *R. persuasoria* (L.) and *M. nortoni quebescensis* (Provancher). *Ibalia leucospoides* and *R. persuasoria* originated in Europe whereas *S. cinctipes* and *R. hoferi* originated in North America. Both *M. nortoni nortoni* and *M. nortoni quebescensis* were also sourced from North America (Taylor, 1976). Taylor (1976) questioned the validity of classifying *M. nortoni quebescensis* as a subspecies of *M. nortoni nortoni* and effectively treated them as the same species for culturing purposes. Nuttall (1989) noted some interbreeding was known to occur between *I. leucospoides* and *I. ensiger* (Norton) (native to North America), with the hybrids indistinguishable from *I. leucospoide*s. For the purposes of this paper, the two *Megarhyssa* species will be treated as one species (*M. nortoni nortoni*) as per Taylor (1976) whereas all *Ibalia* emergents will be treated as *I. leucospoides*. The selection of the six species was based on initial selections in Tasmania which found these species the easiest to culture and establish in the field. Of the other 15 species not selected, a variety of reasons were responsible for their non-establishment including decreasing females in subsequent generations, short-lived adults after emergence and failure to establish in the field (Taylor, 1976). All wasp species except *I. leucospoides* are ectoparasitic, feeding on sirex larvae that have reached an advanced stage of development, whereas *I. leucospoides* is endoparasitic, feeding on new embryos or first instar larvae (Neumann *et al.*, 1987).

Parasitoid release programme in Victoria

From 1970 to 1986, five wasp species (*I. leucospoides*, *M. nortoni nortoni*, *S. chlettererius cinctipes*, *Rhyssa hoferi*, and *Rhyssa persuasoria),* totaling 224 088 individuals, were released across more than 1044 locations in Victoria (Tables 1 and 2). *Ibalia leucospoides* represented the largest numbers released with 84.4% of the total parasitoid release. The first releases of wasp parasitoids occurred in 1970 with releases of *I. leucospoides* and *M. nortoni nortoni*. These two parasitoids continued to be released until 1986, with a total of 189 095 *I. leucospoides* released at more than 470 sites and 26 680 *M. nortoni nortoni* released at more than 382 sites (Table 1). *Schlettererius cinctipes* was released over 7 years from 1971 to 1977, with 1052 individuals released at 36 sites (Table 1). Releases in Gippsland occurred from 1971 to 1973, Ballarat from 1972 to 1977 and North East Victoria in 1972 and 1975 to 1977. A single release was conducted in Central region in 1977 (Table 1).

Rhyssa hoferi and *R. persuasoria* releases occurred from 1971 to 1985 (excepting 1976) and 1971 to 1986 (excepting 1974 and 1984), respectively (Table 2). *Rhyssa hoferi* had 1650 individuals released at 25 sites while *R. persuasoria* had 5611 released at 131 sites (Table 2). Releases of both *Rhyssa* species followed the spread of sirex, with earlier releases in Gippsland and Ballarat regions, whereas later releases reflected the move of sirex into the North East and South West regions (Table 2). *Rhyssa persuasoria* was released at a single site at the southern extremity of the Northeast region in 1975, 2 years earlier than *R. hoferi*, but in very low numbers (<15 individuals).

The pattern of parasitoid releases broadly follows the spread of sirex throughout Victoria, with initial releases occurring in Gippsland followed by Ballarat, then in North East and South West Victoria in the late 1970s and early 1980s as sirex moved into these regions (Neumann *et al.*, 1987) (Fig. 2, Table 1). While substantial releases occurred, the number of individuals released often varied between sites and regions. Of note is the large number of *I. leucospoides* and *M. nortoni nortoni* released in 1985 and 1986 at the conclusion of the wasp biocontrol breeding programme. There have been no further releases in Victoria since 1986. These releases reflected the final liberations of wasp breeding stock currently held at the time rather than a response to an increased requirement for these species in managing sirex field populations (F. Neumann, personal communication 2007). Of note

Table 1 Sirex wasp parasitoid release programme summary for Victoria, 1970 to 1986 for the wasp species *Ibalia leucospoides*, *Schletterius cinctipes*, and *Megarhyssa nortoni nortoni*

	Ibalia leucospoides				*Schletterius cinctipes*				*Megarhyssa nortoni nortoni*			
Year	Number of release sites	Total male	Total female	Primary release region(s)[a]	Number of release sites	Total male	Total female	Primary release region(s)	Number of release sites	Total male	Total female	Primary release region(s)
1970	unkn	5322	5634	B, G	—[b]	—	—	—	unkn	3233	2336	B, G
1971	unkn	4876	7315	B, G	2	40	55	G	15	316	428	B, G
1972	41	6298	5698	C, B, G	9	25	195	G, B, NE	49	735	1715	B, G, C
1973	51	7161	6547	B, G	6	0	125	B, G	48	1135	1583	B, G, C
1974	45	12 141	10 276	B, G	4	28	39	B	24	712	604	B, G, C
1975	58	6193	4592	B, G	9	71	278	B, NE	51	1336	1895	B, G, NE
1976	50	10 859	9521	B, G, NE	2	13	29	B, NE	39	1400	1293	B, G, NE
1977	39	4602	4854	B, G, NE	4	24	130	B, NE, C	40	925	1332	B, NE, SW
1978	57	8421	7446	B, NE, SW	—	—	—	—	32	1063	1052	NE, SW
1979	37	12 943	10 493	B, NE, SW	—	—	—	—	24	817	293	C, NE
1980	26	4878	3386	B, NE, SW	—	—	—	—	22	350	355	NE, SW
1981	15	4463	2791	NE, SW	—	—	—	—	3	22	77	NE, SW
1982	10	1624	1547	NE, SW	—	—	—	—	5	69	167	NE, SW
1983	15	3681	2550	NE, SW	—	—	—	—	9	251	292	NE
1984	5	432	588	NE, SW	—	—	—	—	1	8	8	SW
1985	7	1193	645	NE, SW	—	—	—	—	9	308	241	NE
1986	14	2685	2118	NE, SW	—	—	—	—	11	163	166	NE
Total	470	103 094	86 001		36	201	851		382	12 843	13 837	

[a]Region(s) where majority of releases for that year occurred (G = Gippsland, SW = South West, B = Ballarat, C = Central, NE = North East).

[b]Indicates no parasitoids released for that year.

too are the small numbers of *R. hoferi* and *S. cinctipes* released owing to problems of both maintaining viable cultures in the breeding insectary and recovering breeding stock from previous field releases (Neumann *et al.*, 1987; F. Neumann, personal communication 2007).

Efficacy of the nematode in controlling sirex

Early releases and efficacy in outbreak situations

The first nematode releases (comprising four distinct strains from Corsica, Greece, Hungary, and New Zealand) occurred in 1973 in the Gippsland, Ballarat, and Central regions (Figs 1, 3). The majority of releases were of the Hungary Sopron 198 Strain. No data are available from the 1970s and 1980s apart from some research data from north east Victoria in 1980/81 (Neumann *et al.*, 1987) on the efficacy of the nematodes in managing sirex populations, but the literature and anecdotal evidence suggests that levels of parasitism of nearly 100% were initially achieved in the field (Bedding & Akhurst, 1974; Bedding, 1993). This level of parasitism was, in part, as a result of a combination of coordinated releases within known existing areas of sirex activity and continued releases into areas of new sirex activity.

Despite initial successes in controlling sirex, an increasing number of dead trees as a result of sirex attack were recorded in 1976 at Delatite Plantation in North East Victoria. The attack reached a peak in the summer of 1976/77 with over 1000 ha of plantation suffering varying degrees of sirex attack. Damage ranged from light (<5% of trees killed), to severe (over 77% of trees killed) (McKimm & Walls, 1980; Neumann *et al.*, 1987). Investigations into the causes of this outbreak highlighted the positive interaction between the sirex lifecycle and drier than average conditions prevailing in the area during 1975/76. Further investigation established that while initially nematodes established successfully in the area, no additional inoculations were conducted in the early stages of the outbreak. It was erroneously assumed that the initial inoculations would adequately control sirex and this event highlighted the need for widespread coordinated inoculations early in sirex outbreak situations.

The importance of coordinating nematode inoculation with observations of increasing sirex tree mortality was further highlighted in the 'Green Triangle' region of South east South Australia and western Victoria where a sirex outbreak commencing in 1987 and lasting 3 years saw over 5 million tree deaths in a managed plantation estate from sirex attack with a value of $10–12 million lost (Haugen, 1990; Haugen & Underdown, 1990; Haugen *et al.*, 1990). A review of the situation in the region found that inoculations were conducted on a relatively small scale and were scattered over a wide area (Haugen & Underdown, 1990). The Green Triangle and Delatite outbreaks highlighted the necessity of monitoring sirex populations in situations where prolonged warmer than average climatic conditions and delayed thinning schedules created conditions favourable for outbreaks to occur. Further highlighted was conducting significant nematode inoculation operations over as wide an area as possible if sirex

Table 2 Sirex wasp parasitoid release programme summary for Victoria, 1970 to 1986 for the wasp species *Rhyssa hoferi* and *Rhyssa persuasoria*

Year	*Rhyssa hoferi* Number of release sites	Total male	Total female	Primary release region(s)[a]	*Rhyssa persuasoria* Number of release sites	Total male	Total female	Primary release region(s)
1970	—[b]	—	—	—	—	—	—	—
1971	unkn	55	141	B, G	3	134	108	G, C
1972	unkn	25	268	B, G	28	407	464	C, B
1973	unkn	—	55	B, G	12	157	547	B, G
1974	unkn	48	107	B, G	—	—	—	—
1975	unkn	64	239	B, G	24	35	724	G, B, NE
1976	—	—	—	—	11	264	235	C, B
1977	7	58	98	C, G, NE	13	292	385	G, B, NE
1978	3	30	40	NE	9	124	163	NE, SW
1979	1	3	5	NE	4	206	164	NE, SW
1980	2	33	41	NE	7	132	159	NE, SW
1981	4	32	85	NE, SW	3	70	59	NE, SW
1982	1	14	18	SW	2	105	182	NE
1983	3	48	48	NE, SW	5	206	144	NE
1984	1	2	6	NE	—	—	—	—
1985	3	32	55	NE	1	25	18	NE
1986	—	—	—	—	9	63	39	C, SW
Total	25	444	1206		131	2220	3391	

[a]Region(s) where majority of releases for that year occurred (G = Gippsland, SW = South West, B = Ballarat, C = Central, NE = North East).
[b]Indicates no parasitoids released for that year.

populations approach outbreak levels, rather than at a small, localize level so as to enhance the more rapid spread of the nematode.

Problems with nematode strain efficacy

It was during the 1987 Green Triangle outbreak in South Australia that the first indications emerged of a decline in the levels of nematode parasitism of sirex. It was noted that while initial nematode inoculations early in the 1970s resulted in parasitism levels approaching 100% (Bedding & Akhurst, 1974; Bedding, 1993), inoculations conducted during the Green Triangle outbreak resulted in parasitism levels of less than 20% (Bedding, 1993; Haugen & Underdown, 1993). Subsequent investigation found the cause of this loss of infectivity was as a result of repeated re-culturing of nematodes on fungus in the laboratory without the intervention of a parasitic cycle. This resulted in selection favouring the fungal feeding form of the nematode at the expense of the parasitic form and an associated decline in the overall ability of the nematode to adequately keep sirex populations under effective control (Bedding & Iede, 2005).

The ramifications of this decline in nematode infectivity for Victoria were especially serious as this so-called ‘defective’ nematode strain had been released in Victoria for many years prior to 1987. This meant that in an outbreak situation, as many as four to five times more nematode releases were required to achieve the same result as earlier, when the strain was more effective. Furthermore, it meant that there was the potential for greater tree mortality to occur before effective control of sirex was achieved (Bedding, 1993). Consequently, in the late 1980s, an immediate halt was placed on the culturing and liberation of the defective strain. This was followed by the re-isolation of a more effective strain (‘Kamona’ from Kamona in Tasmania, the site of the first nematode releases in Australia in 1970) which still had parasitism levels >80%. This strain has been re-released from the early 1990s onwards with revised management practices to eliminate the potential for loss of infectivity from repeated re-culturing. These practices include nematode storage in liquid nitrogen and annual re-culturing from new stock.

In order to determine how widespread the defective strain was and to monitor the re-introduction of the more effective Kamona strain, studies commissioned by the NSCC were undertaken from 1997 onwards by CSIRO to determine nematode strains present in field sirex populations using RAPD testing. Results for Victoria showed that (i) no Kamona strain nematodes were recovered from field populations despite releases over a 5-year period, and (ii) the presence of several ‘other’ strains (different from the defective and Kamona strains) were found to predominate in Victorian sirex populations (Table 3). These ‘other’ strains are considered most likely to be the result of the defective strain interbreeding with the earlier original releases of nematodes from Corsica, Hungary, New Zealand, and Greece in the early 1970s. The mean infectivity of the ‘other’ strains (based on tests conducted from 1997 to 2006) was 54.7, 59.2, 38.8, and 55.9% in Gippsland, South West, Ballarat, and North East regions, respectively (Table 3). It could be concluded that these ‘other’ strains provide an adequate level of control in Victorian plantations, albeit significantly lower than the original Soporan strain. However, the relatively lower infectivity from Ballarat is of concern (Table 3).

Table 3 Sirex nematode infectivity and strain data based on test results for all pine growing regions in Victoria from 1997–2002 and 2004–2006

Region[a]	Mean infectivity % (±SE)[b]	Strain of nematode present
Gippsland (*n* = 14)[c]	54.7 ± 10.3	Other/Defective
South West (*n* = 5)	59.2 ± 3.6	Other
Ballarat (*n* = 6)	38.8 ± 7.2	Other
North East (*n* = 13)	55.9 ± 8.9	Other
Total all regions (*n* = 38)	53.2 ± 5.0	
	83.4 ± 5.8	Kamona[d] (*n* = 5)
	7.9 ± 0.1	Defective[d] (*n* = 4)

[a] No results available for Central Region.
[b] SE, standard error.
[c] *n* = number of infectivity tests conducted.
[d] Kamona and Defective strain used as baseline tests of superior/inferior infectivity levels.

Sirex emergence sex-ratios and nematode infectivity

Emergence data gathered since 1998 shows that on a regional and statewide basis, approximately two-thirds of sirex emergents are male and one-third female (Table 4). As sex determination in sirex is by male haploidy and female diploidy (Neumann *et al.*, 1987), males only originate from unfertilized eggs. Unfertilized stray females therefore only produce male sirex which have no capacity to spread nematodes (Neumann *et al.*, 1987). Therefore, in order for nematodes to effectively control sirex populations, it is important that nematode infection of female sirex is at a level sufficient to ensure nematode populations persist in the field and thus prevent outbreaks from occurring. Infectivity data gathered on a regional and statewide basis since 1998 indicates that for North East, Ballarat, and Gippsland areas, the percentage of total male and female emergents infected with nematodes was 17, 18, and 39% (Table 4). Current management practices state that should >10% of total sirex sampled from trap trees be infected with nematodes, additional inoculations are not required (Haugen *et al.*, 1990; National Sirex Coordination Committee, 2002). Based on this 10% threshold, North East, Ballarat, and Gippsland regions achieve these 10% criteria for both total male and female nematode-infected sirex and nematode-infected females as a percentage of female emergents (Table 4). This emphasis on nematode-infected female emergents is important as it is the females who subsequently spread the nematodes. However, it should be noted that these data are based on a pool of regional and statewide data whereas infection data at a more local stand level can vary from these percentages expressed.

Efficacy of parasitic wasps in controlling sirex

Success and efficacy of released parasitoid species

Of the wasp species released between 1970 and 1986 in Victoria, three species (*I. leucospoides*, *S. cinctipes*, and *M. nortoni nortoni*) have successfully established in *P. radiata* plantations whereas two (*Rhyssa hoferi* and *R. persuasoria*) failed to establish in the field. While the two *Rhyssa* species bred satisfactorily in the insectary, they did not establish successfully in the field. While the causes for this are not fully understood, Neumann *et al.* (1987) suggests they may include factors such as prevailing climatic conditions, synchronicity of lifecycles, and diminished ability to seek out sirex in the field.

By far the most successful wasp parasitoid species to establish in Victoria has been *I. leucospoides*. Approximately 95% of parasitoid emergents recovered in Victoria are *I. leucospoides*, with *S. cinctipes* and *M. nortoni nortoni* representing the remaining 5% of parasitoids recovered. *Ibalia leucospoides* has a univoltine lifecycle which closely follows the sirex lifecycle. It attacks sirex embryos or first instar larvae soon after they are laid. Parasitoid emergence data (predominantly reflecting *I. leucospoides* emergence) gathered at 10-year intervals since 1971 reflects a generally increasing trend (apart from short-term declines in 1978/79, 1982/83 and 2000/01) from initial mean parasitism rates of 5.6% in 1971/72, to 28.5% in 1981/82, 46.1% in 1991/92 and 52.8% in 2001/02 (Fig. 4). Since 1998, parasitism rates (predominantly *I. leucospoides*) in the North East, Ballarat, and Gippsland regions were 48, 60, and 57%, respectively (Table 5). In terms of percentage male and female parasitoid emergence, the pooled regional mean levels were 46 and

Table 4 Summary of total sirex nematode infection data expressed as a percentage based on emergence data collected from 0.8 m billets obtained from sirex attacked *Pinus radiata* at various sites across Victoria from 1998/99 to 2005/06

Region[a] (No. sites/billets/total sirex emergents)	Male sirex as % of total sirex emergents	Female sirex as % of total sirex emergents	Nematode infected of total sirex emergents	Nematode infected female sirex as % of total sirex emergents
North East (102/464/2286)	66	34	17	15
Ballarat (40/195/572)	69	31	18	13
Gippsland (43/270/1508)	65	35	39	34
Statewide (all regions) (185/929/4366)	66	34	25	21

[a] Insufficient data available for South West and Central regions.

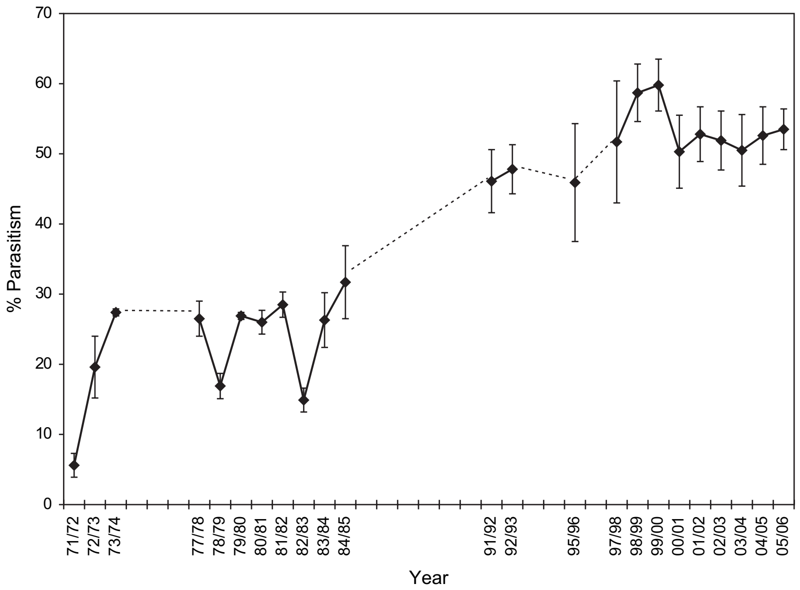

Figure 4 Percentage parasitism of *Sirex noctilio* by *Ibalia leucospoidesacross* Victoria from 1971 to 2006 (s.e. indicated by error bars).

54%, respectively, which were relatively consistent across all three regions (Table 5).

In 2001, studies were conducted by CSIRO using RAPD DNA testing procedures to determine whether there were any distinct variations in *I. leucospoides* genetic strains in field populations. Initial results showed distinct polymorphisms between *I. leucospoides* from different regions although no information was available on their parasitism levels (NSCC, unpublished data). Further studies are required to determine if there is a link between genetic strains and parasitism efficacy allowing in the future for potential selection of *I. leucospoides* with superior parasitism ability for release in plantations.

Discussion

It is timely that a review is conducted of the efficacy of sirex biocontrol agents in Victoria, Australia given that over 35 years has elapsed since their initial release and changes in efficacy have been observed over that time to both the nematodes and the parasitoid *I. leucospoides*. Furthermore, as sirex has not yet reached Queensland and Western Australia, and given its recent detection and establishment in the United States and Canada, potential lessons regarding the introduction and management of biocontrol agents should be highlighted.

Despite Victoria's small area relative to Australia as a whole, the extensive movement of goods including timber products and packaging within the state and the ability of sirex to fly considerable distances (Zondag & Nuttall, 1977; Taylor, 1981), it took over 22 years for sirex to spread throughout the Victoria softwood resource. Although the exact reasons for this relatively slow spread are uncertain, it could be attributed to factors such as the non-contiguous nature of the softwood plantation estate in Victoria, its lifecycle of one generation per year and the significant efforts in the 1960s and early 1970s in attempting to eradicate sirex in combination with the increased introduction of biocontrol agents from 1970 onwards. The slow spread in Victoria is also reflected in New South Wales where movement of sirex from the southern to northern areas of the state has taken over 20 years (Carnegie *et al.*, 2005).

Of the various control agents released, the nematode *Beddingia siricidicola* remains the primary agent used against sirex, with several parasitic wasp species (particularly

Table 5 Summary of total wasp parasitoid[a] emergence data expressed as a percentage based on emergence data collected from 0.8-m billets obtained from parasitized sirex attacked *Pinus radiata* at various sites across Victoria from 1998/99 to 2005/06

Region[b] (no.sites/billets/total parasitoid emergents)	Parasitism %	Male emergence as % of total parasitoid emergents	Female emergence as % of total parasitoid emergents
North East (102/464/2130)	48	47	53
Ballarat (40/195/873)	60	44	56
Gippsland (43/270/2006)	57	47	53
Statewide (all regions) (185/929/5009)	53	46	54

[a] Pool of total emergents for all parasitoid species.

[b] Insufficient data available for South West and Central regions.

I. leucospoides) being considered secondary agents owing to their inability to control sirex populations adequately in outbreak situations. Most nematode releases occurred in the first 3 years of the release programme from 1973 to 1975. Subsequent releases occurred as sirex moved into new areas. The pattern of release reflected the expected ability for the nematode to move with sirex populations and to require only additional 'top-ups' as it established in new areas. The release programme was generally similar to that later proposed by Shea and Possingham (2000) who advocate 'mixed' biocontrol release programmes which encourage varying release intensities and locations in order to improve chances of achieving optimal establishment. This release programme appeared to suit situations such as at Delatite in the 1970s where tree stress was minimal. However, when conditions changed to encourage a rapid increase in sirex numbers, it proved inadequate in preventing the outbreak from occurring. In such situations and as shown by the Green Triangle outbreak in the 1980s, early signs of pending outbreaks require coordinated additional releases of nematodes in susceptible stands to prevent or minimize outbreak impacts, as well as coordinated surveillance programmes to provide early warning of outbreaks. This highlights the ongoing revision of biocontrol strategies to continue to achieve desired outcomes (Memmott *et al.*, 1996).

The main wasp parasitoids released were *I. leucospoides* and *M. nortoni nortoni*. These species were the most successful within insectary breeding programmes and in establishing populations in the field. Of these, the most successful was *I. leucospoides*, with approximately 95% of total sirex mortality caused by parasitoids owing to this species. This corresponds closely to New South Wales and South Australian data which also show *I. leucospoides* responsible for approximately 99% of sirex mortality as a result of parasitoids (Haugen, 1990; Carnegie *et al.*, 2005). Possible factors contributing to the success of this species include the fact that the original populations released in Victoria were sourced from Mediterranean and southern European climates similar to those in Victorian pine growing regions (Taylor, 1976). These areas overlapped with the native range of sirex and thus, natural selection may have ensured strains suited to parasitize sirex. Studies by Fry (1981) noted an improvement of *I. leucospoides* parasitism of sirex from 12% in 1970 to 32% in 1973 based on studies in small plantation plots in the Gippsland region. Similar results also occurred across the entire Gippsland region over the same period (F. Neumann, personal communication 2007). Although the reasons for this increase in parasitism are uncertain, a possible reason for it occurring early in the release programme is that it may reflect increased numbers of *I. leucospoides* being released in a small area early in the programme. From 1973 onwards to the completion of the release programme in 1986, parasitism showed little improvement above 32%. A review by Crowder (2007) noted that in 63% of cases where a pest was targeted with a parasitoid, increased release rates did not significantly affect pest mortality or the rate of parasitism. Factors such as prey availability, settlement rates, fecundity, dispersal and the method, and timing of release appear to play a greater role. Studies by Collier and van Steenwyk (2004) showed similar ecological factors could limit control efficacy in the release period and shortly thereafter.

Of particular, however, interest is the substantial improvement in parasitism levels observed from 1991/92 onwards compared with the period prior to the last releases in 1986. Studies by Amarasekare (2000) indicate the possibility that competition between competing parasitoid species in the initial release phase may have limited the potential of *I. leucospoides* to achieve higher levels of parasitism until the other parasitoid species declined. Such factors as genetic selection for greater *I. leucospoides* parasitism ability over time may also be involved. However, the potential for future increases in *I. leucospoides* parasitism rates is doubtful based both on field observations showing a stabilizing in rates since 2000 and studies by Fernandez-Arhex and Corley (2005) indicating *I. leucospoides* shows a type III population functional response (i.e. low early age survival offset by production of numerous young). However, this response was probably as a consequence of host discovery inefficiencies at low host densities and that a type II population response (i.e. decline is exponential with the death rate similar for every population) was more likely under realistic conditions (Fernandez-Arhex & Corley, 2003, 2005)).

It is interesting to note that levels of *I. leucospoides* parasitism now observed in the field are similar to those achieved under ideal conditions within insectary-rearing cultures maintained in Victoria between 1972 and 1984 [i.e. 55% (range: 42–73%) (Morey, 1985)]. This may reflect a possible interaction between nematode efficacy and *I. leucospoides* parasitism and, as the nematode has become less effective, *I. leucospoides* has been able to express its 'normal' rates of parasitism. However, such observations are purely speculative and based on general observations only. The possibility of such an interaction occurring would require more study, potentially using comparisons between sirex parasitized by wasps and nematodes within the same trees over time to determine if such a link exists and if so, the mechanisms of any possible population interactions.

Despite *M. nortoni nortoni* being recovered in sufficient quantities in the field for further rearing and release programmes, it accounts for less than 5% of sirex mortality in the field indicating its general unsuitability as an effective sirex biocontrol agent in Victoria (Taylor, 1976). However, it may be more suited to the cooler pine growing regions (Neumann *et al.*, 1987; Murphy, 1998) given its recovery is usually from these regions of Victoria (such as Ballarat), coupled with its predominance in Tasmania (Taylor, 1976, 1978). Of the other introduced wasp parasitoids, both *Rhyssa* species failed to establish in the field because of problems involved with maintaining viable insectary cultures. However, *S. cinctipes*, despite being released in small numbers as a result of culturing problems, did establish successfully in the field. However, as $<5\%$ of sirex parasitism involves *S. cinctipes*, this species makes a negligible contribution to management of sirex in Victoria.

The most significant issue threatening the effectiveness of ongoing biocontrol success is the range of nematode strains present in Victoria, their variable infectivity, and their potential to impact adversely on future sirex outbreaks. Despite the Kamona strain having been released since the early 1990s, subsequent tests have not recovered it from field populations, which indicates it has failed to effectively establish in the field and replace the defective/other strains. This is in contrast to New South Wales where the defective strain was released only in southern region of the state, but subsequent releases of the Kamona strain in this region appears to have replaced the defective strain (Carnegie *et al.*, 2005). However, any direct comparison should be cautioned as in New South Wales, the release of Kamona in the southern regions in 1990 after inoculations with the defective strain from 1980 occurred over a far shorter timeframe than in Victoria, potentially giving a greater chance for the Kamona strain to predominate. Laboratory studies indicate that for the defective/other strain to be replaced by the Kamona strain, the defective/other and Kamona strain must cross-breed several times (Bedding & Iede, 2005). While it is suggested that the Kamona strain be used to, in effect 'flood out' the less effective strains, significant problems are associated with this. The difficulties of achieving the level of cross-breeding required (without the defective/other strain intervening) at any point coupled with the significant logistical effort and associated cost ensures the problem of replacing current field strains with the Kamona strain will remain for the foreseeable future. However, improvements in plantation management (specifically timely thinning) coupled with current adequate levels of nematode infectivity in field populations provided by the 'other' strains should assist in reducing the potential for sirex outbreaks until methodologies are developed to introduce the Kamona strain at levels sufficient to replace the defective/other strains. The further development of the RAPD testing currently in use, not only for identifying strains of nematodes present but to potentially replace costly and time-consuming plate tests to evaluate nematode infectivity, should also assist greatly in developing management procedures to improve nematode infectivity in softwood plantations.

Aside from biocontrol, a significant factor in reducing the ongoing impact of sirex on Victorian plantations has been the increased establishment of pulp and paper industries as the emerging resource has matured. This has provided a market for thinnings and improved the health of stands in the sirex-susceptible 10–20 year age group by removing suppressed trees from stands and reducing competition. Wang (1998) notes that silvicultural methods (i.e. thinning) for sirex control are indeed more cost effective than biocontrol if a commercial early first thinning is feasible. Where commercial early first thinning is not feasible, biological control is a better choice in terms of relative profitability. Detailed plantation health surveillance programmes conducted within Victorian softwood plantations since 2001 have also reflected a very low incidence of sirex-related tree mortality reflecting not only the contribution of biocontrol measures, but also the substantial improvements in stand health as a result of timely thinning and stand hygiene measures since the mid-1990s. It is not possible to determine with any accuracy whether the low incidence of sirex-related tree mortality in recent years reflects more on improving silvicultural methods (i.e. thinning) increasing stand health in comparison to the ongoing effects of biocontrol. However, Haugen and Underdown (1990) observed that during the outbreaks in the Green Triangle, significant areas of radiata pine subsequently attacked by sirex were well overdue for first thinning. Furthermore, flights over affected stands during the outbreaks showed thinned areas directly adjacent to sirex-attacked stands suffering minimal sirex attack to trees only along the outer boundaries of plantations (F.G. Neumann, personal communication 2008). Given the drought conditions experienced in Victoria over the past 10 years coupled with the loss of efficacy within nematode field populations, it is reasonable to conclude that improved stand management through the timely implementation of thinning has reduced sirex attacks substantially.

Biological control of sirex using nematode and wasp parasitoids commenced in Victoria in the early 1970s and has proved highly successful in managing sirex populations thereby saving the softwood industry many millions of dollars in lost production in the ensuing years. Similar success has been observed elsewhere in New South Wales and Brazil with biocontrol measures proving successful in reducing the efficacy of sirex (Carnegie *et al.*, 2005; Carnegie *et al.*, 2006) although South Africa has experienced disappointing results in terms of nematode parasitism levels in plantations (Hurley *et al.*, 2007). However, even with the extensive research and monitoring of sirex and its associated biological control agents that has occurred over the years, issues concerning the loss of nematode infectivity potential in field populations are reminders that constant monitoring, surveillance, and ongoing review is required to ensure biocontrol agents retain their optimal efficacy. Ongoing research coupled with improved stand hygiene and thinning schedules should also assist in preventing Sirex populations reaching outbreak levels in the future.

Acknowledgements

The authors wish to acknowledge the assistance of the National Sirex Coordination Committee for their help in providing data and advice and HVP Plantations for additional data supplied. Many thanks to Dr Charlma Phillips, Dr Kevin J. Dodds, and the reviewers for reviewing the manuscript and providing very helpful critical feedback.

References

Amarasekare, P. (2000) Coexistence of competing parasitoids on a patchily distributed host local vs spatial mechanisms. *Ecology*, **81**, 1286–1296.

Bedding, R.A. (1972) Biology of *Deladenus siricidicola* (Neotylenchidae) an entomophagous nematode parasitic in siricid woodwasps. *Nematologica*, **18**, 482–493.

Bedding, R.A. (1993) Biological control of *Sirex noctilio* using the nematode *Deladenus siricidicola*. *Nematodes and the Biological Control of Insect Pests* (ed. by R. A. Bedding, R. J. Akhurst and H. K. Kaya), pp. 11–20. CSIRO Publications, East Melbourne.

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**, 129–135.

Bedding, R.A. & Iede, E.T. (2005) Application of *Beddingia siricidicola* for Sirex wasp Control. *Nematodes as Biological Control Agents* (ed. by P. S. Grewal, R. Ehlers and D. I. Shapiro-IIan), pp. 385–399. CAB International, London.

Calder, J. & Bedding, R. (2002) *Standard Operating Procedures (SOP's) for Production, Experimentation and Quality Assurance Testing of the Sirex Nematode, Beddingia siricidiola*. CSIRO/National Sirex Coordination Committee, Canberra.

Carnegie, A.J., Eldridge, R.H. & Waterson, D.G. (2005) History and management of Sirex wood wasp in pine plantations in New South Wales, Australia. *New Zealand Journal of Forestry Science*, **35**, 3–24.

Carnegie, A.J., Matsuki, M., Haugen, D.A. *et al*. (2006). Predicting the potential distribution of *Sirex noctilio* (Hymenoptera: Siricidae), a significant exotic pest of *Pinus* plantations. *Annals of Forest Science*, **63**, 119–128.

Chrystal, R.N. (1930) Studies of the Sirex parasites. The biology and post-embryonic development of *Ibalia leucospoides* Hochenw. (Hymenoptera-Cynipoidea). *Oxford Forestry Memoirs*, **11**, 63.

Collier, T. & van Steenwyk, R. (2004) A critical evaluation of augmentative biological control. *Biological Control*, **31**, 245–256.

Crowder, D.W. (2007) Impact of release rates on the effectiveness of augmentative biological control agents. *Journal of Insect Science*, **7**, 1–11.

Fernandez-Arhex, V. & Corley, J.C. (2003) The functional response of parasitoids and its implications for biological control. *Biocontrol Science and Technology*, **13**, 403–413.

Fernandez-Arhex, V. & Corley, J.C. (2005) The functional response of *Ibalia leucospoides* (Hymenoptera: Ibaliidae), a parasitoid of *Sirex noctilio* (Hymenopetra: Siricidae). *Biocontrol Science and Technology*, **15**, 207–212.

Fry, B.D. (1981) *Sirex noctilio and its biological control within a radiata pine plantation in Mirboo North District of South-Central Victoria*. Dip For (Vic.) Thesis, Forests Commission of Victoria, Melbourne.

Gilbert, J.M. & Miller, L.W. (1952) An outbreak of *Sirex noctilio* F. in Tasmania. *Australian Forestry*, **16**, 63–69.

Haugen, D.A. (1990) Control procedures for *Sirex noctilio* in the Green Triangle: review from detection to severe outbreak (1977–87). *Australian Forestry*, **53**, 24–32.

Haugen, D.A. & Underdown, M.G. (1990) *Sirex noctilio* control program in response to the 1987 Green Triangle outbreak. *Australian Forestry*, **53**, 33–40.

Haugen, D.A. & Underdown, M.G. (1993) Reduced parasitism of *Sirex noctilio* in radiata pines inoculated with the nematode *Beddingia siricidicola* during 1974–1989. *Australian Forestry*, **56**, 45–48.

Haugen, D.A., Bedding, R.A., Underdown, M.G. & Neumann, F.G. (1990) National strategy for control of *Sirex noctilio* in Australia. Special Liftout Section No. 13. *Australian Forest Grower*, **13**, 1–8.

Hoebeke, E.R., Haugen, D.A. & Haack, R.A. (2005) *Sirex noctilio*: discovery of a Palearctic siricid woodwasp in New York. *Newsletter of the Michigan Entomological Society*, **50**, 24–25.

Hurley, B.P., Slippers, B. & Wingfield, M.J. (2007) A comparison of control results for the alien invasive woodwasp, *Sirex noctilio*, in the southern hemisphere. *Agricultural and Forest Entomology*, **9**, 159–171.

Irvine, C.J. (1962) Forest and timber insects in Victoria. *Victoria's Resources*, **4**, 40–43.

Madden, J.L. (1975) An analysis of an outbreak of the woodwasp, *Sirex noctilio* F. (Hymenoptera, Siricidae), in *Pinus radiata*. *Bulletin of Entomological Research*, **65**, 491–500.

Madden, J.L. (1988) *Sirex* in Australasia. *Dynamics of Forest Insect Populations* (ed. by A. A. Berryman), pp. 407–429. Plenum Pub. Corp., New York.

McKimm, R.J. & Walls, J.W. (1980) *A Survey of Damage Caused by the Sirex Woodwasp in the Radiate Pine Plantation at Delatite, North-Eastern Victoria, Between 1972 and 1979*. Forests Commission Victoria Research Branch Report No. 156. Forests Commission, Victoria, Melbourne.

Memmott, J., Fowler, S.V., Harman, H.M. & Hayes, L.M. (1996) How best to release a biological control agent. *Proceedings of the IX International Symposium on Biological Control of Weeds* (ed. by V. C. Moran and J. H. Hoffmann), pp. 291–296. University of Cape Town, Cape Town.

Morey, J.L. (1985) *Biological Aspects, Breeding, Liberation and Evaluation of Natural Enemies of the Sirex Woodwasp in Victoria*. Department of Conservation, Forests and Lands, State Forests and Lands Service Research Branch Report No. 303. Department of Conservation, Forests and Lands, Melbourne.

Murphy, S.T. (1998) Indigenous Siricid spp. Parasitoid communities and principal biological control agents of *Sirex noctilio* in Australasia: a review. *Proceedings of a Conference: Training in the Control of Sirex noctilio by the Use of Natural Enemies,* USDA Forest Service FHTET 98–13 (ed. by E. T. Iede, E. Schaitza, S. Penteado, R. C. Reardon and S. T. Murphy), pp. 31–36. Forest Health Technology Enterprise Team Morgantown, West Virginia.

National Forest Inventory (2006) *National Plantation Inventory 2006*. Bureau of Resource Sciences, Canberra.

National Sirex Coordination Committee (2002) *National Sirex Control Strategy Operations Worksheets October 2002*. National Sirex Committee, Melbourne.

Neumann, F.G. & Minko, G. (1981) The sirex wood wasp in Australian radiata pine plantations. *Australian Forestry*, **44**, 46–63.

Neumann, F.G., Morey, J.L. & McKimm, R.J. (1987) *The Sirex Wasp in Victoria. Bulletin No. 29*, Lands and Forest Division, Department of Conservation, Forests and Lands, Melbourne.

Neumann, F.G., Collett, N.G. & Smith, I.W. (1993) The Sirex wasp and its biological control in plantations of radiata pine variably defoliated by *Dothistroma septospora* in north-eastern Victoria. *Australian Forestry*, **56**, 129–139.

Nuttall, M.J. (1989) *Sirex noctilio* F., Sirex wood wasp (Hymenoptera: Siricidae). *Review of Biological Control of Invertebrate Pests and Weeds in New Zealand From 1874 to 1986*, Technical Communication No. 10 (ed. by P. J. Cameron, R. L. Hill, J. Bain and W. P. Thomas), pp. 296–306. CAB International Institute of Biological Control, Wallingford.

Shea, K. & Possingham, H.P. (2000) Optimal release strategies for biological control agents: an application of stochastic dynamic programming to population management. *Journal of Applied Ecology*, **37**, 77–86.

Taylor, K.L. (1976) The introduction and establishment of insect parasitoids to control *Sirex noctilio* in Australia. *Entomophaga*, **21**, 429–440.

Taylor, K.L. (1978) Evaluation of the Insect Parasitoids of *Sirex noctilio* (Hymenoptera: Siricidae) in Tasmania. *Oecologia*, **32**, 1–10.

Taylor, K.L. (1981) The Sirex woodwasp, ecology and control of an introduced forest insect. *The Ecology of Pests* (ed. by R. L. Kitching and R. E. Jones), pp. 231–248. CSIRO, Melbourne.

Wang, G. (1998) *An economic evaluation of pest management in some Australian forests*. M. For. Sci (Vic.) Thesis, The University of Melbourne, Melbourne.

Zondag, R. & Nuttall, M.J. (1977) *Sirex noctilio Fabricius (Hymenoptera: Siricidae)*. Forest and Timber Insects in New Zealand, No. 20. Forest Research Institute, New Zealand Forest Service, Rotorua.

Accepted 26 August 2008