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The Sirex wasp and its biological control in plantations of radiata pine variably defoliated by Dothistroma septospora in north-eastern Victoria

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Summary

The distribution and severity of pine needle blight disease (PNB), caused in spring 1989 by an outbreak of the needle cast pathogen *Dothistroma septospora*, was assessed within a 10 km radius of two study sites near Myrtleford in the Wangaratta *Pinus radiata* plantation complex of north-eastern Victoria. Areas of severe needle cast were located on colour aerial photographs in spring 1989, then checked by ground survey for the percentage of visible crowns infected. Population levels of the Sirex wasp (*Sirex noctilio*), rated in terms of the cumulative percentage tree mortality induced by the wasp since 1989, were estimated in autumn/winter 1991. Twenty-one unthinned plots, each of 400 trees aged 14-15 years, were examined for *S. noctilio* and associated symptoms of *D. septospora*. The effectiveness of parasitoids was evaluated in the laboratory by monitoring total insect emergents from 222 billets (0.8 m long), cut in winter 1991 from 100 herbicide-injected 'Sirex' trap trees. All emergents of *S. noctilio* were checked for presence of the parasitic nematode *Deladenus siricidicola*.

Sirex noctilio was most active in stands with severe *D. septospora* infection levels and large tree diameters at breast height over bark (DBHOB), as shown by positive correlations between (1) *D. septospora* infection levels and *S. noctilio* population ratings for stands of similar mean DBHOB, (2) mean DBHOB and *D. septospora* plus *S. noctilio* ratings, and (3) mean DBHOB and *S. noctilio* ratings for stands with low *D. septospora* infection levels. Unthinned plantations of intermediate age, stressed especially on the better sites from intertree competition and defoliation through severe *D. septospora* infection, are therefore highly attractive to *S. noctilio*. Prompt control of this pathogen with copper-based fungicide is therefore essential to reduce stress effects in such plantations unless thinning is imminent. Three species of parasitoid, released near Myrtleford between 1976 and 1984, collectively caused 47.9% mortality of *S. noctilio* (range 29.8 - 62.7%), with *Ibalia leucospoides* being predominant. Levels of *D. siricidicola*, introduced artificially from 1976 to 1983, were sufficient for effective sterilisation of the female *S. noctilio* population in only 20% of the study plots. Trap tree programs should therefore be intensified in all 'Sirex'-susceptible plantations affected by PNB disease to facilitate the supplementary artificial inoculation of the nematode and its natural spread.

Introduction

In Victoria, the needle cast pathogen *Dothistroma septospora* (Dorog.) Morelet, which causes pine needle blight disease (PNB), and the Sirex wasp (*Sirex noctilio* Fabricius; Hymenoptera: Siricidae), are potentially the most damaging among destructive biological agents in the extensive plantations of Radiata Pine (*Pinus radiata* D. Don) (Neumann and Marks 1990). Both agents were accidentally introduced, *D. septospora* probably around 1979 from South America via New Zealand and New South Wales (Edwards and Walker 1978, Gibson 1972, Marks 1981), and *S. noctilio* during the late 1950s from the Mediterranean region via New Zealand and Tasmania (Gilbert and Miller 1952, Irvine 1962, Neumann and Minko 1981). Outbreaks of *D. septospora* are favoured by topographic features that induce high humidity through impeded air drainage causing mists in valleys, and on some plateaus where the annual rainfall exceeds 1 100 mm (Marks *et al.* 1989). Outbreaks of *D. septospora* have so far occurred in parts of the Wodonga, Wangaratta, Benalla and Narbethong plantation complexes, and traces of the disease have been detected in the Otway Ranges south-west of Melbourne (I.W. Smith, unpubl. data). In contrast, *S. noctilio* has spread to all major pine-growing regions of the State (Neumann and Marks 1990).

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Dothistroma septospora is an airborne fungus with splash dispersed conidia. The extent of defoliation it causes depends upon host resistance, ambient air temperature, needle wetness and spore load. In Victoria, plantations up to 24 years old are susceptible (I.W. Smith, unpubl. data). In New Zealand it has been found that (1) impact on stand growth becomes economically significant when defoliation of the current year's needles is >25%, (2) 50% defoliation can cause a 50% reduction in volume increment and a 20% reduction in height growth among individual trees, (3) tree death may result from severe infection over two to three consecutive growing seasons, and (4) a high PNB disease severity rating may result in secondary attack by weaker pathogens (Whyte 1969, Woollons and Hayward 1984). In contrast, *S. noctilio* is a wood-boring and essentially 'secondary' tree-killing pest, capable of devastating commercial and amenity plantings of *P. radiata* when certain conditions, such as a protracted period of drought compounding stress among overcrowded trees, or severe inter-tree competition alone, cause a rapid rise in population level (Neumann *et al.* 1987).

As severe crown infection by *D. septospora* lowers the growth vigour of trees through premature needle fall, and as *S. noctilio* responds to conditions that are adverse to pine, there was concern that widespread massive needle-cast would cause a build-up of *S. noctilio*, thereby exacerbating the problems in severely diseased plantations (Neumann and Marks 1990). This paper reports on a study from October 1989 to March 1992 in the Wangaratta plantation complex of north-eastern Victoria, aimed at: (1) assessing the distribution and severity of PNB disease caused by an outbreak of *D. septospora* in spring 1989, (2) evaluating *S. noctilio* population levels and that of its biological control agents in diseased stands and (3) testing the likelihood of a *D. septospora*-*S. noctilio* interaction in stands of similar diameter.

Methods

Study sites

In October 1989, two sites, each approximately 250 ha in area, were selected for study in compartments 007 and 230 of the Cropper Creek Block about 8 km south-west of Myrtleford, and in compartments 001 to 003 of the Running Creek Block about 10 km north-east of Bright. The Cropper Creek study site was adjacent to the Long Corner Creek and Hurdle Creek plantations in the north and west respectively, and to farmland in the east and south. In contrast, the Running Creek (Bright) site was surrounded by mixed species eucalypt forest in the north, south and west, and by agricultural land in the east. Both sites constituted valleys that were dissected by the Cropper and Running Creeks respectively. At the Cropper Creek site, the terrain rose steadily from 300 m to 770 m a.s.l. and at the Running Creek site from 500 m to 1 100 m. The Cropper Creek site carried 1977 plantings of *P. radiata* and the Running Creek site 1976 plantings. Both areas remained unthinned during the 2½-year study period, so that stocking approximated 1700 trees ha^{-1}.

From February 1976 to January 1984, the former Forests Commission Victoria (now the Department of Conservation and Natural Resources (CNR)) introduced six species of biological control agent into unthinned plantations of intermediate age at several localities near Myrtleford and Bright for control of *S. noctilio* (Appendix I). The predominant parasitoid released was *Ibalia leucospoides* Hochenwarth (Ibaliidae) (7 468 specimens), followed by *Megarhyssa nortoni* (Cresson) (Ichneumonidae) (736), *Schlettererius cinctipes* Cresson (Stephanidae) (400) and the ichneumonids *Rhyssa persuasoria* Linnaeus and *R. hoferi* Rohwer (collectively 364 specimens). The parasitic nematode *Deladenus siricidicola* Bedding (Neotylenchidae), which sterilises adult female but not male *S. noctilio* (Bedding 1972, Bedding and Akhurst 1974), had been inoculated into 255 tree stems and 5 billets (Appendix I). The shortest distance between the release/inoculation localities and the two study sites is approximately 10 km.

Survey of PNB disease and S. noctilio

Plantations at the study sites, and within a 10 km range, were surveyed for incidence and severity of PNB disease during the outbreak in spring 1989. A two-person survey team scanned the periphery of each compartment from positions along roadsides, and assessed disease severity by estimating the percentage of visible tree crowns infected by *D. septospora* on a 0-6 scale (0 = nil infection, 1 = trace to 5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95% and 6 = >95%) (Marks and Hepworth 1986). In variously defoliated stands, infection severity was expressed in terms of the sum total of the percentage infection among needles and the percentage of cast needles. Where shading had killed the lower foliage, only the level of disease in the unsuppressed crown portions was assessed (Kershaw *et al.* 1982). Spot examinations were used to confirm the presence of PNB disease, particularly in stands where

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needle yellows (*Cyclaneusma* spp.) (Di Cosmo *et al.* 1983) were prolific and masked *D. septospora* symptoms. Whole trees were examined closely at specific inspection points selected within each compartment on the basis of topographic features considered to provide a range of possible PNB disease severity ratings. Where PNB severity ratings were low around inspection points of greatest disease hazard (e.g. within moist valleys and on plateaus) the whole compartment was ranked as 'low' for disease level. The PNB ratings (0-6) were then plotted onto CNR compartment maps of 1:10 000 scale. The survey results were further refined by interpreting images on colour aerial photographs taken at about 3 330 m a.s.l. on a 1:15 000 scale on 22 November 1989 (Woodgate *et al.* 1990).

Population levels of *S. noctilio*, rated in terms of the cumulative percentage tree mortality induced by the wasp, were assessed between late autumn (May) and early winter (June) 1991, i.e. about 1½ years after the PNB epidemic of 1989. At the Cropper Creek study site, 13 plots of 400 trees (20 rows x 20 trees), 0.5 km apart, were surveyed. Nine of the plots were located in post-canopy closure stands and four in pre-canopy closure stands. At the Running Creek site, eight plots of 400 trees were examined exclusively in post-canopy closure stands, as no pre-canopy closure stands of 1976 origin were present. Each of the 8 400 trees in the survey was scanned with 8 x binoculars where necessary, and assessed according to the following criteria:

(a) healthy, unaffected by *D. septospora* or *S. noctilio*;

(b) as above but with traces to <25 % *D. septospora* infection levels;

(c) dead-topped, upper crown dying or recently dead, lower crown healthy or with traces to <25% *D. septospora* infection levels, no evidence of *S. noctilio*;

(d) dying with chlorotic crown and wilting terminal shoots, or recently dead with copper-brown needles and sapwood surface dry and non-resinous; no flight holes, but evidence of *S. noctilio* symptoms caused by adult females of the 1990-91 generation;

(e) dead with no foliage, fresh flight holes from the 1990-91 *S. noctilio* generation visible on trunk;

(f) dead with no foliage, old flight holes from the 1989-90 *S. noctilio* generation visible on trunk, bark often cracked and sapwood generally blue-stained or showing decay symptoms; and

(g) dead with symptoms as in (f), but no *S. noctilio* flight holes visible.

The diameter at breast height over bark (DBHOB) of 40 trees was measured in the two innermost rows of each of the 21 study plots (a 10% sample). These data were used for regression analyses of relationships between mean DBHOB and PNB severity and *S. noctilio* population ratings. The 10% sample approach was adopted because a survey of three randomly selected study plots, each of 400 trees, in the post-canopy closure stands had indicated that the means of DBHOB and the sample variances for total trees in each of the plots did not differ significantly from those obtained in the same plots for samples of 40 trees located in the two innermost rows or other combinations of two rows (For sample variances, $F_{(0.05)}$ 399, 39 ranged from 1.15 – 1.37).

Assessment of biological control

The extent of parasitism among *S. noctilio* in stands severely infected by *D. septospora* was studied by establishing five 'Sirex' trap tree plots of 10 trees each during mid-November 1990 at both study sites where PNB disease severity ratings were a high 5-6. The plots were located at 0.5 km intervals about four trees in from major access roads. The trees were injected basally with 20% w/v dicamba[1] herbicide into the outer sapwood at a rate of 2 ml (= 0.4 g a.i.) per 10 cm of circumference (Neumann *et al.* 1982). During winter 1991, all dead trees were felled, measured for DBHOB and length, and then examined for the presence of *S. noctilio* larval galleries by cross-cutting stems at about 1.8 m intervals. Infested billets were end-coated with timber sealer to slow down drying effects that could be adverse to the parasitic nematode. The billets were then stacked about 15 cm above the ground until retrieved from the field during mid-November 1991 for laboratory studies.

Field exposure of billets enabled checking the study sites for the presence of *M. nortoni*. This parasitoid emerges and oviposits into late-instar larvae of *S. noctilio* during spring ('one-year life-cycle' generation) and again from mid- to late-

(1) 3,6 - dichloro - 2 - methoxybenzoic acid.

summer ('short 3-4 month life-cycle' generation) (Neumann *et al.* 1987). In Victoria, short generations of *M. nortoni* are only effective against 'two-year life-cycle' generations of *S. noctilio*, as by mid- to late summer, 'one-year cycle' generations of the pest have largely emerged, and their progeny, then present in the form of eggs and small early-instar larvae just below the bark, are not susceptible to *M. nortoni*.

In the laboratory, the 1.8 m long billets were cross-cut into 222 billets of 0.8 m length and placed vertically, on a trap-tree plot basis, into 200*l* steel drums covered by fine-mesh nylon. Emerged insects were collected 3-4 times per week, cooled for about 15 minutes at 3-4° C, and then counted by species and sex. The ovaries and testes of all *S. noctilio* specimens were checked at 10-20 x magnification for the presence of *D. siricidicola* nymphs.

After insect emergence, all billets from plots that had attracted *M. nortoni* (as evidenced by the appearance of its 'short-life-cycle' generation during summer) were cross-cut into 30 cm lengths, split open and checked for unemerged insects, and in particular for larvae of the 'one-year life-cycle' generation of *M. nortoni* expected to emerge in spring 1992. The latter undergoes 12-months of development because diapause supervenes at the larval stage. In Victoria, the ratio of 'short-life-cycle' to 'one-year life-cycle' generations of *M. nortoni*, as observed over 16 generations in the insectary, has averaged 0.84 (F. G. Neumann, unpubl. data).

For each trap-tree plot, the mean percentage mortality of *S. noctilio* per billet due to all species of parasitoid (Sm), and the mean percentage sterility among female *S. noctilio* per billet due to infection of the ovaries by nematodes (Ss), were determined by substituting in the formulae:

$$Sm = [100\,P\,(S + P)^{-1}]n^{-1}$$

where P = no. of parasitoids (all species) and S = no. of *S. noctilio* specimens from n billets, and

$$Ss = (100\,FT^{-1})\,n^{-1}$$

where F = no. of sterilized female *S. noctilio* and T = total no. of female *S. noctilio* from n billets.

Analysis of PNB – 'Sirex' – DBHOB relationships

Regression analysis of the data on PNB disease severity and *S. noctilio* population ratings from study plots with statistically similar mean DBHOBs was used for testing the possibility of a link between severe PNB occurrence and *S. noctilio* build-up. This approach eliminated the effects of inter-tree competition on the distribution and abundance of *S. noctilio*. Regression analyses were also used for testing the relationships between (1) mean DBHOB and the combined ratings of PNB disease severity and *S. noctilio* levels for the 21 plots assessed, (2) mean DBHOB and PNB disease ratings for these plots, and (3) mean DBHOB and *S. noctilio* ratings for plots with low PNB disease occurrence.

Results

Distribution and severity of PNB disease

The Cropper Creek study site, located within the Emu and Meriang CNR plantation management blocks, was about 5 km north and west of the Abbeyard and Nug Nug blocks respectively. High levels of PNB disease occurred in all four blocks, but the disease was most widespread (3 690 ha) in the Merriang block (Table 1). In total, 740 ha of these four blocks had incurred >25% crown infection, and 505 ha of this area had >50% infection. However, complete defoliation (except for expanding shoots of the current year's growth) was recorded in only 75 ha of the Emu and Merriang blocks. At the Cropper Creek study site itself, PNB disease severity ratings varied from 1 to 6 (Table 2), with ratings 3-6 confined to the lower elevations of around 430m a.s.l., and ratings 1-3 between this elevation and approximately 600 m.

The Running Creek study site, located in parts of the Havilah and Running Creek (Bright) CNR management blocks, was within a 10 km range of the Porepunkah block to the west, and the Bright and Freeburgh blocks to the south-west. In these five blocks, a total of 500 ha had incurred >25% crown infection, but PNB disease severity ratings 5-6 appeared restricted to the Havilah and Running Creek blocks (Table 1). At the Running Creek study site, PNB severity ratings again ranged from 1-6 (Table 2); ratings 3-6 occurred at 500–550 m a.s.l. and the lower ratings above these elevations.

In the 21 study plots at the Cropper Creek and Running Creek sites, the mean stem diameters of trees assessed in autumn/winter 1991 for tree health conditions (Table 2), were positively correlated to the PNB disease severity ratings assessed in October 1989. The curve of best fit was a third-order polynomial (Figure 1a). In unthinned stands of intermediate age, PNB severity was therefore

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maximal in areas where trees had grown at a fast rate. These areas were of a high site quality, and thus more crowded and poorly ventilated. They provided conditions conducive to disease development (Marks and Hepworth 1986, Marks and Smith 1987).

The trees with crowns damaged during the disease outbreak in spring 1989 had regenerated their foliage within the 1½ years following the epidemic. Infection levels had remained very low during 1990 and 1991, as indicated during winter 1991 by the high percentage of healthy trees (88.6-97.3%) with slight to moderate 'old' PNB disease symptoms of 1989 origin throughout the 21 study plots (Table 2). Unthinned *P. radiata* stands of intermediate-age are therefore capable of rapid recovery from severe crown damage, provided there is no recurrence of severe PNB disease in subsequent years.

Table 1. Areas of *Pinus radiata* affected by pine needle blight disease (PNB) at the study sites and within a 10 km radius, as assessed in October 1989 in the Wangaratta plantation complex, north-eastern Victoria.

Plantation block	Area (ha) by PNB severity rating[3]: 1	2	3	4	5	6	Total
Abbeyard	0	225	0	0	0	0	225
Emu[1]	1 060	135	190	160	120	65	1 730
Merriang[1]	3 490	60	45	20	65	10	3 690
Nug Nug	45	0	0	65	0	0	110
Total	4 595	420	235	245	185	75	5 755
Bright	1 695	0	0	0	0	0	1 695
Freeburgh	75	0	0	0	0	0	75
Havilah[2]	920	115	100	120	10	0	1 265
Porepunkah	345	15	15	5	0	0	380
Running Creek[2]	110	20	20	40	165	25	380
Total	3 145	170	135	165	175	25	2 100
Grand total	**7 740**	**590**	**370**	**410**	**360**	**100**	**7 855**

[1] The Cropper Creek study site was located within these two blocks.
[2] The Running Creek study site was located within these two blocks.
[3] Rating 1 = trace to 5% crown infection, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95% and 6 = >95%.

Sirex population levels and biological control

Trees successfully attacked by *S. noctilio* appeared to be randomly distributed within study plots and a near exponential increase in population levels had occurred between generations (Figure 2). At both study sites during the 1991 assessment, the percentage of trees dying (or of recent deaths) from *S. noctilio* attack was maximal in plots with high PNB disease ratings and minimal in those with low ratings (Table 2). In plots with very low PNB ratings (≤2.5), the means of DBHOB were positively correlated to the corresponding *S. noctilio* ratings, expressed as the cumulative percentage tree mortality associated with *S. noctilio* attack (Figure 1b). The pest had therefore responded to increased levels of crowding in unthinned stands that had been relatively free of PNB disease. The low incidence of dead-topping among trees at both study sites (Table 2) suggested that there was no link between this disorder and either the occurrence of PNB disease or *S. noctilio* attacks.

Table 2. The condition of 8 400 *Pinus radiata* trees (20 rows x 20 trees x 21 plots) as assessed at the study sites during autumn/winter 1991 in north-eastern Victoria.

Study site (year of planting)	PNB severity rating in October 1989[1]	No. of plots	Mean DBHOB[2] (cm)	Proportion (%) of trees assessed in the following health categories: Healthy with nil or slight to moderate 'old' PNB symptoms of 1989 origin	Dead-topped	Dying or recently dead from 'Sirex' attack in summer 1990/91[3] (C)	Dead with 1990/91 'Sirex' flight holes(4) (DR)	Dead with 1989/90 'Sirex' flight holes(4) (DO)	Dead without 'Sirex' symptoms	Cumulative tree mortality (%) from 'Sirex' attack (C+DR+DO)
Cropper Creek (1977)	5-6	5	21.5	88.6	0.1	5.4	1.2	0.7	4.1	7.3
	3-4	5	16.1	97.3	0.9	0.4	0.1	0.1	1.3	0.6
	1-2	3	12.8	96.1	2.5	0.5	0.2	0.2	0.6	0.3
Running Creek (1976)	5-6	4	20.2	90.1	0.3	6.2	0.1	0.0	3.4	6.3
	3-4	3	16.8	95.9	0.7	2.0	0.1	0.0	1.3	2.1
	1-2	1	18.8	97.0	1.0	1.5	0.0	0.0	0.5	1.5

[1] Rating 1 = trace to 5% crown affected by pine needle blight disease, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95%, and 6 = >95%.
[2] DBHOB = diameter of stem at breast height (1.3m) over bark.
[3] These trees contained larvae of the 1991-92 'Sirex' generation.
[4] The 1990/91 flight holes were left by adult emergents of the 1990-91 'Sirex' generation, and the 1989/90 flight holes by the 1989-90 generation; the current 1991-92 generation had not yet produced flight holes at the time of the survey.

Each of the 10 trap-tree plots attracted *S. noctilio*, but the proportion of trees successfully infested was higher at the Cropper Creek site (50-80%) than at the Running Creek site (20-50%) (Table 3). The *S. noctilio* population in the Cropper Creek plantation was therefore assumed larger than at Running Creek. This was supported by the finding that three generations of *S. noctilio* were evident at the Cropper Creek study site since summer 1989/90 compared with two generations at Running Creek since summer 1990/91 (Table 2).

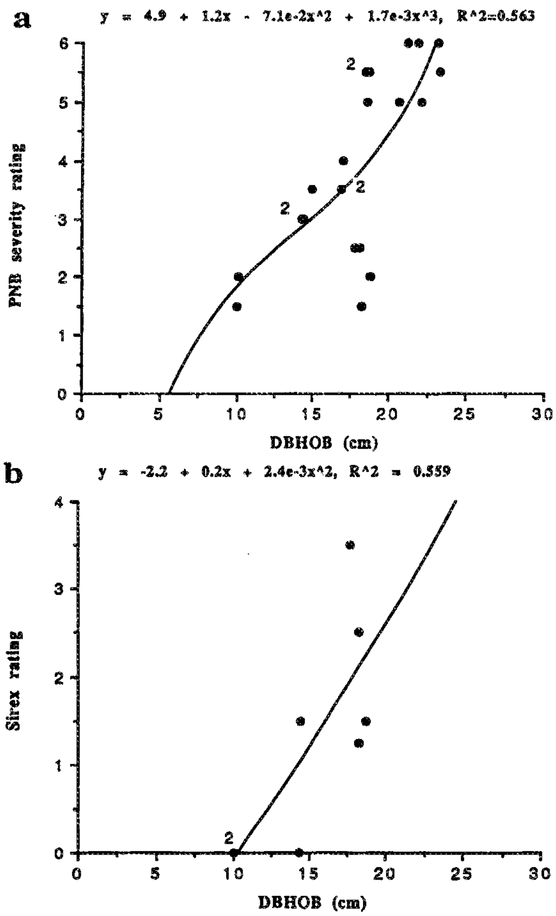

Figure 1. Relationships between mean tree diameter at breast height over bark (DBHOB) and (a) severity rating for pine needle blight disease (PNB) (o = nil to 6 = >96% crown infection), as assessed in October 1989 for 21 plots each of 400 trees, and (b) *Sirex noctilio* rating in terms of the cumulative percentage tree mortality caused by this pest, as assessed during autumn/winter 1991 for eight plots each of 400 trees with <25% of crown affected by PNB disease, at the two study sites in north-eastern Victoria. Coincidental points on the graphs are marked with the digit 2.

Table 3. Trap-tree plot data as assessed during autumn/winter 1991 at the two study sites in north-eastern Victoria.

Study site	Trap-tree plot No [1]	Proportion of dead trees[2] (%)	DBHOB (cm) Mean ± se	Height (m) Mean ± se	Proportion of trees with 'Sirex' (%)
Cropper Creek	1	60.0	13.1 ± 0.6	16.5 ± 0.5	60.0
	2	80.0	16.0 ± 1.1	17.1 ± 0.7	80.0
	3	80.0	12.7 ± 1.3	14.8 ± 1.0	70.0
	4	80.0	14.9 ± 1.5	15.3 ± 1.0	70.0
	5	90.0	16.4 ± 1.0	16.2 ± 0.8	50.0
Running Creek	6	90.0	17.8 ± 0.8	16.3 ± 0.6	50.0
	7	70.0	20.1 ± 1.1	15.7 ± 1.6	30.0
	8	90.0	21.2 ± 1.0	17.8 ± 0.9	50.0
	9	60.0	20.1 + 0.8	15.8 ± 0.6	20.0
	10	70.0	16.1 ± 1.2	14.8 ± 1.1	30.0

[1] Each plot consisted of 10 trees, thus a total of 100 trees were sampled.
[2] The trees had been injected with 20% dicamba herbicide during mid-November 1990 at the rate of 2 ml concentrate per 10 cm of circumference.

In the laboratory, 222 'Sirex'-infested 0.8 m long billets, derived from trap trees, produced a total of 3 738 insects between 1 December 1991 and 12 March 1992, a mean of 16.8 specimens per billet. Most emergents were *S. noctilio* (1 900 specimens), followed by the parasitoids *I. leucospoides* (1 735), *S. cinctipes* (67) and *M. nortoni* (36) (Table 4). Emergence of *S. cinctipes* occurred from 3 December to 6 January, and that of *M. nortoni* ('short-life-cycle' generation only) from 20 to 24 December. In contrast, *I. leucospoides* emerged in synchrony with *S. noctilio* throughout the 102-day emergence period, which peaked during the final week of December. Fifty per cent of total insects had emerged by 2 January, just 32 days after emergence had commenced. At the completion of emergence, 55 billets (suspected to contain larvae of one-year life-cycle *M. nortoni*) split and checked for living and dead specimens of all four species, contained 13 healthy larvae plus 5 dead adults of *S. noctilio*, 4 dead adult *I. leucospoides*, and 15 healthy larvae plus 1 dead adult of *M. nortoni*. Insect mortality during metamorphosis from the larval to the adult stage was therefore very low (0.18 specimens per billet), and the life-cycle of *S. noctilio* was almost exclusively of one-year duration. The low incidence of one-year life-cycle *M. nortoni* (0.27 specimens per billet) meant that the ratio of 'short-life-cycle' to 'one-year cycle' generations (2.4) was higher than previously recorded (0.84).

The mean number of *S. noctilio* and parasitoid (= parasitized *S. noctilio*) emergents per 0.8 m billet for trap-tree plots at Cropper Creek and Running Creek (Table 5) averaged 19.3 and 11.20

respectively, a mean difference of 8.1 that was significant (P<0.05). This result supported the earlier finding, based on the proportion of 'Sirex'-infested trap trees, that levels of *S. noctilio* were higher at Cropper Creek. The low sex-ratios for *S. noctilio* at half of the 10 trap-tree plots, indicating a preponderance of males over females (Table 5), suggested that most *S. noctilio* eggs at these plots had not been fertilised during the 1990/91 flight season, as sex in Hymenoptera is controlled by haploidy (producing males) and diploidy (females) (Naumann 1991). In contrast, the near 50% sex-ratios among parasitoids at 90% of trap-tree plots indicated a much greater degree of egg fertilisation than among the *S. noctilio* populations.

Table 4. Cumulative insect emergence over time by species and sex as assessed in the laboratory from 222 billets of 0.8 m length derived from 10 'Sirex' trap-tree plots at the two study sites in north-eastern Victoria.

Date	No. of days	Insect species[1]: *Sn*		*Il*		*Sc*		*Mn*		All species (%)
		Female	Male	Female	Male	Female	Male	Female	Male	
1.12.91	0	0	0	0	0	0	0	0	0	0
3.12	2	38	73	4	15	0	0	0	0	3.5
5.12	4	72	128	6	27	2	8	0	0	6.5
6.12	5	87	166	7	44	2	8	0	0	8.4
9.12	8	116	252	21	80	6	13	0	0	13.1
11.12	10	116	265	21	92	6	13	0	0	13.7
16.12	15	168	343	42	141	10	13	0	0	19.2
20.12	19	205	372	81	170	10	13	0	0	22.8
24.12	23	241	535	119	221	24	33	18	18	32.3
30.12	29	315	737	207	318	27	37	18	18	44.9
2.01.92	32	371	831	242	370	27	38	18	18	51.2
6.01	36	396	913	270	431	29	38	18	18	56.5
9.01	39	404	958	287	471	29	38	18	18	59.5
13.01	43	498	1 054	377	565	29	38	18	18	69.5
20.01	50	542	1 132	514	713	29	38	18	18	80.4
24.01	54	558	1 167	597	792	29	38	18	18	86.1
28.01	58	582	1 199	665	834	29	38	18	18	90.5
3.02	64	594	1 220	705	872	29	38	18	18	93.5
7.02	68	599	1 225	747	886	29	38	18	18	95.2
17.02	78	604	1 238	774	911	29	38	18	18	97.1
6.03	96	607	1 260	794	923	29	38	18	18	98.6
12.03	102	623	1 277	801	934	29	38	18	18	100.0

[1] *Sn* = *Sirex noctilio*, *Il* = *Ibalia leucospoides*, *Sc* = *Schletterius cinctipes* and *Mn* = *Megarhyssa nortoni*.

Table 5. Emergence data for *Sirex noctilio* and its parasitoids, and biological control effects due to parasitoids and the parasitic nematode *Deladenus sincidicola*, as assessed for the study sites during summer/autumn 1992.

Trap-tree plot No.[1]	No. of 0.8 m billets	Mean no. of 'Sirex' emergents per billet		Sex-ratio[2] of 'Sirex' (%)	Mean no. of parasitoid emergents[3] per billet		Sex-ratio[2] of parasitoids (%)	Mean no. of total insects [4] per billet	Mean mortality of Sirex' due to total[4] parasitoids per billet (%)	Proportion of total 'Sirex infected by the nematode	Proportion of female 'Sirex'[5] infected by the nematode (%)
		Female	Male		Female	Male					
1	27	2.0	5.5	26.7	5.6	6.1	47.9	19.1	61.1	52.7	37.7
2	38	2.9	7.7	27.4	4.0	5.6	41.7	21.3	47.6	0.0	0.0
3	37	3.4	8.9	27.6	5.0	5.7	46.7	23.0	46.7	0.2	2.7
4	30	1.9	4.9	27.9	5.3	4.3	55.2	16.6	58.5	0.5	0.0
5	22	4.3	4.1	51.2	2.9	4.3	40.3	16.2	46.7	0.0	0.0
6	22	1.1	1.5	42.3	1.8	2.5	41.9	7.0	62.7	0.0	0.0
7	12	3.3	4.5	42.3	1.8	1.8	50.0	11.4	31.6	0.0	0.0
8	16	4.7	8.3	36.2	2.6	2.9	47.3	18.4	29.8	3.4	5.3
9	6	5.0	4.8	51.0	4.0	4.2	48.8	18.0	45.4	1.7	0.0
10	12	1.3	1.8	41.9	0.8	2.1	27.6	5.9	49.3	13.9	0.0

[1] Plots 1-5 were located at the Cropper Creek study site, and plots 6-10 at the Running Creek site.
[2] Sex ratio = proportion of females in the population.
[3] *Ibalia leucospoides*, *Schletterius cinctipes* and *Megarhyssa nortoni* which emerged in the ratio of 40:9:1 (Cropper Creek) and 15:1:0 (Running Creek) (Table 5).
[4] Includes total no. of emergents plus total no. of unemerged *S. noctilio* and parasitoid specimens recovered from 55 billets.
[5] Only female *S. noctilio* are considered as these alone become sterilised and transmit the nematode between 'Sirex' generations.

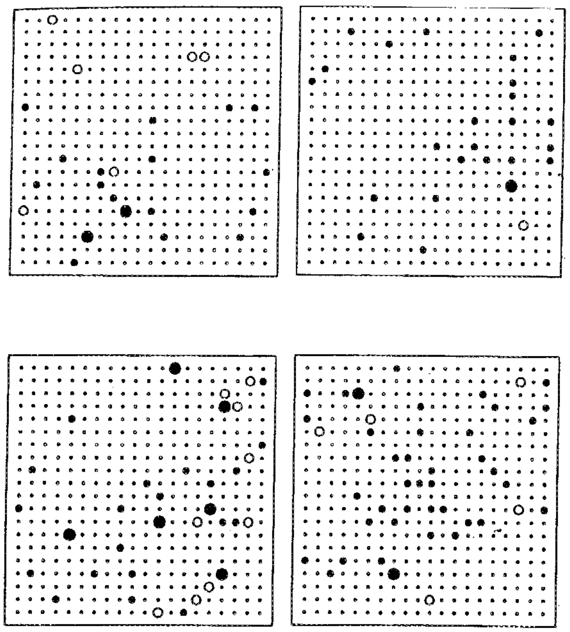

Figure 2. Distribution of *Pinus radiata* trees killed by three generations of *Sirex noctilio* in four study plots severely defoliated in October 1989 by *Dothistroma septospora* at the Cropper Creek study site, north-eastern Victoria. Symbols: small dots = healthy trees, second smallest dots = chlorotic or recently dead trees containing the 1991-92 *S. noctilio* generation, but attacked by adult females of the 1990-91 *S. noctilio* generation; hollow circles = dead trees, devoid of foliage and with fresh exit holes, killed by the 1989-90 *S. noctilio* generation; and largest dots = dead trees with 'old' exit holes, cracked bark and blue stained sapwood, killed by the 1988-89 *S. noctilio* generation.

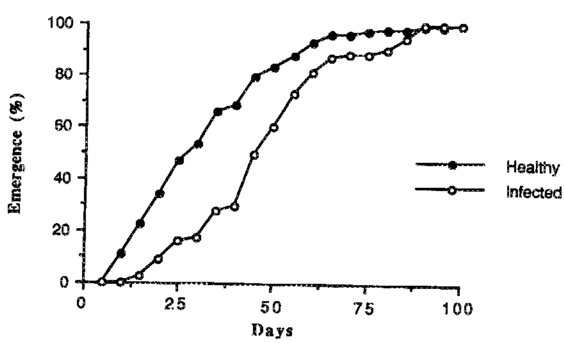

Figure 3. Cumulative emergence (%) over time in the laboratory of healthy individuals of *Sirex noctilio*, and of those infected by the parasitic nematode *Deladenus siricidicola*. The graphs are based on a total of 320 healthy and 123 infected specimens of both sexes.

The extent of biological control of *S. noctilio*, in terms of the proportion killed by parasitoids alone (predominantly *I. leucospoides*), averaged 47.9% per trap-tree plot, and ranged from 29.8% to 62.7% (Table 5). Examinations of ovaries and testes of *S. noctilio* emergents also indicated the presence of the parasitic nematode *D. siricidicola*. It was detected at 60% of trap-trees plots, but only trap-tree plots 1 and 10 had adequate levels for effective biological control (≥10% nematode infection among total *S. noctilio*), requiring no additional artificial inoculation to boost nematode numbers (Haugen *et al.* 1990) (Table 5). The distribution of the nematode was therefore clumped,

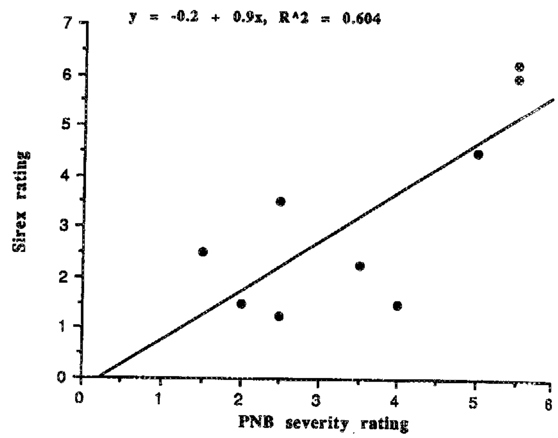

Figure 4. Relationship between pine needle blight disease (PNB) severity ratings and *Sirex noctilio* ratings (expressed as the cumulative percentage tree mortality from *S. noctilio* attack) in nine study plots, each of 400 trees, of similar mean DBHOB.

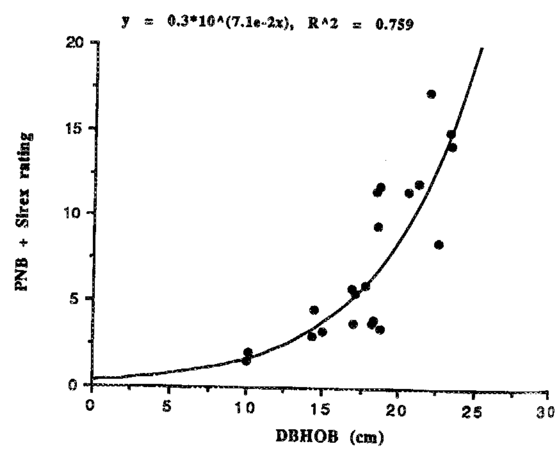

Figure 5. Relationship between mean diameter at breast height over bark and pine needle blight disease (PNB) severity plus *S. noctilio* ratings in the 21 study plots.

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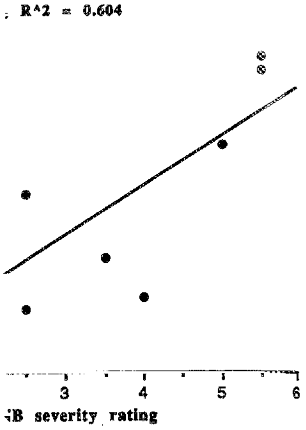

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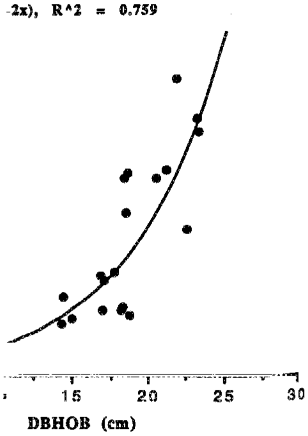

tween mean diameter at breast k and pine needle blight disease lus *S. noctilio* ratings in the 21

and its effectiveness limited across the study sites during 1990-91. Nematode-infected *S. noctilio* emerged at a slower rate than healthy individuals (Figure 3).

Relationship between PNB disease severity and 'Sirex' population ratings

An analysis of variance, carried out on the 21 sets of DBHOB of 40 trees from the innermost rows of the study plots, showed that trees in nine of the plots had statistically similar mean DBHOBs, which averaged 18.4 cm and ranged from 17.0 to 20.6 cm. For these nine plots there was a positive linear correlation between PNB disease severity ratings (scale 0-6) and *S. noctilio* ratings, expressed as the cumulative percentage tree mortality from *S. noctilio* attack (Figure 4). This relationship indicated the possibility of an interaction between *D. septospora* infection and subsequent attack by *S. noctilio* independent of crowding effects between trees in unthinned plantations of intermediate age. An exponential relationship was also demonstrated between DBHOB and PNB severity plus *S. noctilio* ratings with a threshold of 15 cm DBHOB above which the gradient of the curve became very steep (Figure 5). Unthinned stands of trees with mean DBHOB ≥15 cm are therefore expected to deteriorate more rapidly from the combined effects of PNB disease and *S. noctilio* attack than those below this threshold diameter.

Discussion

The study showed that unthinned plantations of *P. radiata*, variably defoliated by *D. septospora* during spring 1989 when aged 12-13 years, were associated with varying levels of *S. noctilio*. In subsequent years, crown recovery by trees, through the production of new needles, was generally very effective except for trees killed by *S. noctilio*. A positive correlation was demonstrated between PNB disease severity and *S. noctilio* population ratings for stands of similar DBHOB, thereby indicating the possibility of a link between *D. septospora* infection and *S. noctilio* levels independent of the effects of intertree competition (Figure 4). Mean DBHOB and PNB severity ratings were also positively correlated, implying that disease severity tends to be more marked in crowded than uncrowded plantations. These findings were consistent with the observed build-up of *S. noctilio* since summer 1989/90 in stands with high PNB disease ratings and high mean DBHOB.

Unthinned plantations of intermediate age, stressed through substantial needle cast caused by *D. septospora* infection, therefore appear to be highly favoured habitats for *S. noctilio*. This situation is enhanced when inter-tree competition imposes additional stress on trees, as indicated by the finding of a positive correlation between mean DBHOB and *S. noctilio* population levels for stands with low PNB disease severity ratings, and of an exponential relationship between mean DBHOB and PNB severity plus *S. noctilio* ratings (Figure 5). Outbreaks of PNB disease in unthinned plantations of intermediate age should therefore be promptly controlled with copper-based fungicide (Whyte 1976) unless thinning has been scheduled in the immediate future. Priority for control should be given to the higher site quality stands, as in these the combined adverse effects of *D. septospora* and *S. noctilio* on plantation health are likely to be most pronounced.

The observation that the Cropper Creek study site had attracted greater populations of *S. noctilio* and of its parasitoids than the Running Creek site (Tables 3 and 5) is probably associated with the latter site being largely surrounded by native forest that is less readily accessible to the insects than the pine plantation and farmland areas around Cropper Creek. As *M. nortoni* was not detected at the Running Creek site, it appeared that this comparatively large parasitoid is less capable of dispersal through native forest than the smaller sized *S. noctilio*, *I. leucospoides* and *S. cinctipes*. The preponderance of the 'short life-cycle' generation of *M. nortoni* at the Cropper Creek site, and the shortage of late-instar larval 'Sirex' host material during summer, also suggested that *M. nortoni* faced considerable difficulties as a biological control agent during 1991-92. Another possible negative for *M. nortoni* is that it might be a hyperparasite of *I. leucospoides* and *S. cinctipes*.

The extent of biological control among the 1991-92 *S. noctilio* generation from the effects of total parasitoids ranged from 29.8 to 62.7% (Table 5), with a mean of 47.9% of *S. noctilio* being killed. This high level of biological control was unprecedented as 1982 records for the Myrtleford area had indicated only 24.4 to 33.8% parasitism (Neumann and Morey 1984), and for other Victorian plantation areas 12.7 to 28.9% (Neumann *et al.* 1987).

Of the five parasitoid species introduced near Myrtleford between 1976 and 1984 (Appendix I) only *I. leucospoides*, *S. cinctipes* and *M. nortoni* were recovered from the trap-tree plots. These species had not been field-released since 1984, and the nearest release site was approximately 10 km away from both the Cropper Creek and Running Creek study sites. The parasitoids had therefore self-propagated and had spread to new plantation areas (like Cropper and Running Creek) after these had been invaded by *S. noctilio* within the last decade. The high degree of parasitism recorded at the study sites suggested that self-propagated field populations of parasitoids might be more effective than recently released laboratory-cultured populations on which the 1982 estimates of parasitism were largely based.

However, only *I. leucospoides* performed well, as *S. cinctipes* and *M. nortoni* collectively caused only 3.16% mortality among *S. noctilio* during 1991-92, and both *R. hoferi* and *R. persuasoria* had failed altogether. *Ibalia leucospoides* was therefore the major mortality factor of *S. noctilio* during 1991-92. This confirmed the conclusion by Neumann and Morey (1984) that among the available species of introduced parasitoid, only *I. leucospoides* is an effective contributor to control of *S. noctilio* in north-eastern Victoria.

The parasitic nematode *D. siricidicola* had been artificially inoculated into trees and billets in plantations near Myrtleford and Bright over the period 1976-1983 (Appendix I) at localities at least 10 km away from the Cropper Creek and Running Creek study sites. The clumped distribution of this parasite at the study sites suggested that individual nematode-infected female *S. noctilio* spread more slowly to new areas than healthy females. The slower rate of emergence of infected *S. noctilio* (Figure 3) supports this view, as the dispersal of late emergents is likely to be impeded by less favourable cool weather.

The spread of the nematode, which is totally dependent on the movement of infected female *S. noctilio*, must therefore be artificially assisted. Past experience has shown that this can best be achieved by establishing, at regular intervals, plots of herbicide-injected 'Sirex' trap trees that provide (1) highly attractive foci for both infected and healthy *S. noctilio* within susceptible plantations, and (2) readily available pine material for supplementary artificial inoculation of the nematode (Neumann *et al.* 1982, Neumann *et al.* 1989). Trap tree programs should therefore be intensified in all 'Sirex'-susceptible plantations that have been severely defoliated by *D. septospora*.

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Appendix I. History of parasitoid releases by species, and of inoculations of a parasitic nematode[1], for biological control of *Sirex noctilio* prior to the present study in *Pinus radiata* plantations near Myrtleford and Bright, north-eastern Victoria.

Year	*Il*[2]			*Mn*[2]			*Sc*[2]			*R*[2]			Inoculations	
	No. of sites	Female	Male	No. of sites	Female	Male	No. of sites	Female	Male	No. of sites	Female	Male	No. of sites	No. of items[4]
1976	0	0	0	1	57	55	0	0	0	0	0	0	1	5
1977	2	326	296	2	83	61	1	94	76	0	0	0	1	12
1978	7	783	1 126	3	148	147	3	102	79	1	28	29	1	14
1979	2	1 108	978	0	0	0	0	0	0	0	0	0	1	10
1980	4	518	730	2	59	43	0	0	0	1	20	27	*[3]	196
1981	4	514	1 089	1	57	26	0	0	0	2	49	54	*[3]	0
1982	0	0	0	0	0	0	0	0	0	2	59	86	0	0
1983	0	0	0	0	0	0	0	0		0	0	0	1	23
1984	0	0	0	0	0	0	1	28	21	1	4	8	0	0
Total		**3 249**	**4 219**		**404**	**332**		**224**	**176**		**160**	**204**		**260**

[1] *Deladenus siricidicola.*
[2] *Il* = *Ibalia leucospoides*, *Mn* = *Megarhyssa nortoni*, *Sc* = *Schletterius cinctipes*, *R* = *Rhyssa hoferi* and *R. persuasoria* (in the ratio of 1:30).
[3] Various unspecified localities.
[4] All items were trees except for 5 billets in 1976.