

# The sirex wood wasp in Australian radiata pine plantations

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## Summary

This paper examines the essentials of the biology, impact and control of the European tree-killing wood wasp *Sirex noctilio*, which was found established in exotic *Pinus radiata* plantations in Australia about 1950-51. The wasp, with its pathogenic symbiont *Amylostereum areolatum*, has severely damaged some unthinned pine stands of intermediate-age, and valuable shelterbelts on farmland in Tasmania and Victoria. One-year life cycles are predominant, but three-month cycles and two or three-year cycles are also known. Emergence of adults, followed by attack on pine, occurs mostly between mid and late summer, when soil moisture levels, growth rates and tolerance of pine to pests and diseases are low. Various volatile substances produced by phloem/cambium tissues of stems and large branches, are important in the attraction of the pest. Susceptible trees are normally physiologically stressed, and attack on them is associated with a reinforcement of stress due to mucus injection, and a subsequent insect-pathogen development phase in the wood.

In Tasmanian plantations, the introduced ichneumonid, ibaliid and stephanid parasitoids, and the parasitic nematode *Deladenus siricidicola*, have been effective control agents, though some outbreaks have collapsed even without natural enemies. In some parts of Victoria, where droughts are frequent and summer temperatures are high, an ecological balance between host and parasite populations may occur only after an unacceptably high level of tree mortality in stands that have remained unthinned due to unfavourable markets and unavailability of funds for sanitation felling. For such stands, a control strategy is being devised that will combine the effects of established biological control agents and minimum, selective non-commercial thinning, with the strategic placement of groups of trap trees, which have been predisposed to *S. noctilio* attack by injection with herbicide during spring.

## Introduction

The European wood wasp *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) is ranked among the more serious destructive pests of planted Californian radiata pine (*Pinus radiata* D. Don), in south-eastern Australia. Fortunately, few severe outbreaks have occurred so far in the ecologically simple and thus theoretically high-risk pine monocultures. This may be a reflection of the success of the pest management strategy that has been operating in pine in recent years (Neumann 1979). Nevertheless, the authors have some reservations about the future capacity of the forest services to prevent occasional major outbreaks of *S. noctilio*. If the current Australian forest policy to enlarge radiata pine areas to over 1 million ha by the year 2010 (Australian Forestry Council 1974) is pursued, increasingly heavy demands will be placed on the already limited monetary and staff resources available for effective surveillance of plantations and for implementation of preventative or curative controls.

The object of this paper is to provide foresters with an overview of the *S. noctilio* problem, by highlighting the main features of the pest with respect to its distribution, biology, destructiveness and control in pine plantations of south-eastern Australia. The data presented is largely a review of the literature, combined with the authors' own unpublished early findings in Victoria.

## Distribution

*Sirex noctilio* was accidentally introduced into south-eastern Australia from New Zealand, and was first detected in Tasmania about 1950-51 (Gilbert and Miller 1952), and a decade later in Victoria (Irvine 1962). Since then the insect has spread within these two States, and into New South Wales near Albury and South Australia near Mt. Gambier. It seems inevitable that the pest will spread beyond its present known distribution (Figure 1), as effective geographic or climatic barriers are absent.

The pine areas in south-eastern Australia, with their dry warm summers and cool moist winters,

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are considered ally homologous region (south Turkey), where economically

## Species recognition

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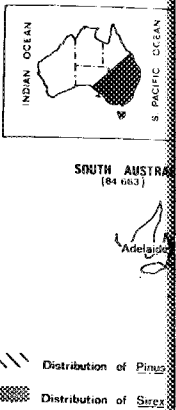


Figure 1. The known to *P. radiata* stands parentheses refer to ha within respective ritory (A.C.T.) at

a



are considered by Kirk (1976) to be bioclimatically homologous to those in the Mediterranean region (southern Europe, North Africa and Turkey), where *S. noctilio* is indigenous but economically unimportant (Hall 1968).

**Species recognition**

The male adult (Figure 2a) is metallic dark-blue, except that wings, abdominal segments III to VII, and front and mid legs are chestnut brown; the female (Figure 2b) is metallic dark-blue all

over, except for the amber-coloured wings and legs. A protective sheath, containing an ovipositor, projects 2 to 3 mm beyond the female abdomen. Antennae are setaceous and slightly pubescent, with 20 segments and a length of about 6.8 mm in the male, and 21 segments and a length of about 7.8 mm in the female; sensory patches (tyloides) are present ventrally on all flagellar segments. In both sexes the final abdominal segment (IX) terminates in a prominent spine (cercus). White-eyed forms among males and females, and sterile gynandromorphs with varying ratios of male and female structures occasionally emerge (Neumann 1970). Morphometric data for adults are shown in Table 1a.

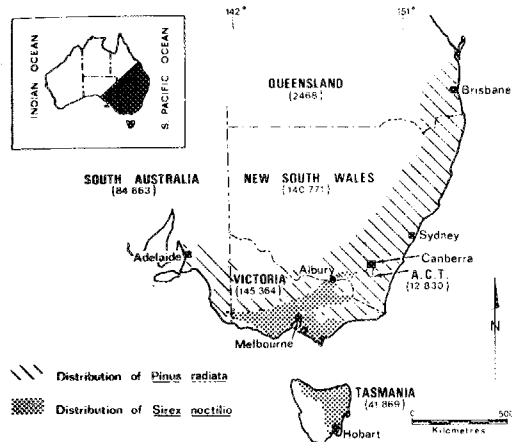


Figure 1. The known distribution of *S. noctilio* in relation to *P. radiata* stands in south-eastern Australia. Figures in parentheses refer to total commercial radiata pine areas in ha within respective States or the Australian Capital Territory (A.C.T.) at 31 March 1978 (Forestry and Timber Bureau 1979).

The egg (Figure 3a) is white, soft and smooth. Larvae (Figure 3b) are creamy-white, deeply segmented, usually distinctly S-shaped, and of near-uniform diameter. Larval antennae are one-segmented, thoracic legs are short, and the abdomen is devoid of appendages, except for a conspicuous, dark-brown sclerotised spine located distally. Three small brown sclerites are present on the ventral surface of the final abdominal segment in male larvae, as distinct from two sclerites in females (Zondag and Nuttall 1977). Prepupae and pupae (Figure 3c, d) are creamy-white, the latter gradually assuming the coloration of adults. Morphometric data for eggs, larvae and pupae are shown in Table 1 (b, c, d) respectively.

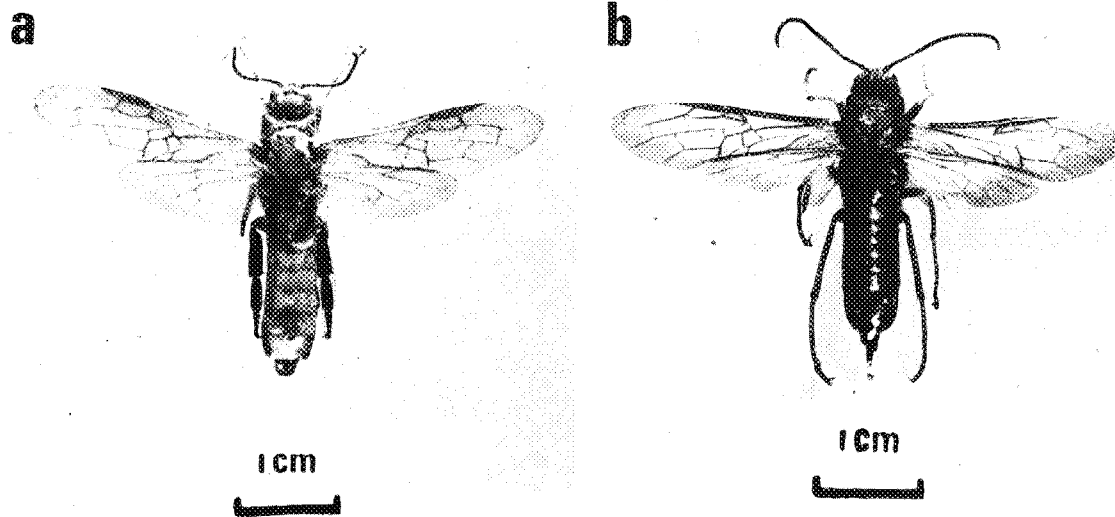


Figure 2. Adult *S. noctilio*: a, male; b, female.

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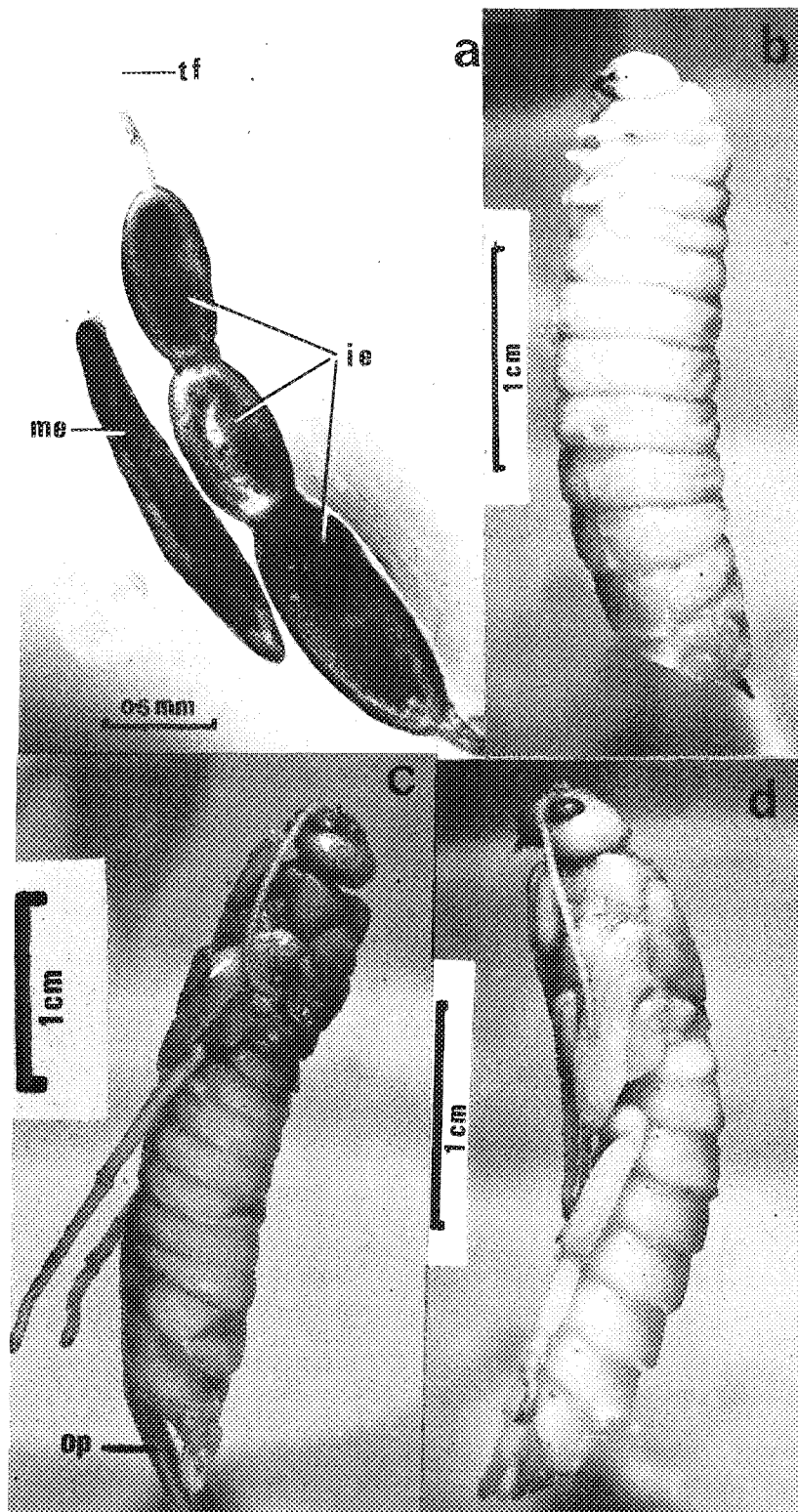


Figure 3. Immature stages of *S. noctilio*: a, mature egg (me) and an ovariole dissected from an unemerged (pharate) female, showing terminal filament (tf) and three immature eggs (ie); b, lateral view of mature larva; c and d, lateral view of a female pupa with ovipositor (op), and a male pupa, respectively.

(a) Adults

Sex

male	4
female	3

(b) Eggs

(c) Larvae

Instar<sup>1</sup>

I	
II	
III	
IV	
V	
VI	

(d) Pupae

Sex

male

female

<sup>1</sup> Standard error.

<sup>2</sup> Excluding antennae.

<sup>3</sup> Instar II to V were

Table 1. Morphometric data (mm) for *S. noctilio* from north-eastern Victoria.

## (a) Adults

Sex	Wing span (n = 100)		Body length <sup>2</sup> (n = 100)		Thoracic width (n = 40)		Tibia III length (n = 100)	
	Mean ± SE <sup>1</sup>	Range	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
male	43.87 ±0.95	14.80 62.00	25.00 ±0.54	9.30 34.90	5.43 ±0.16	1.50 6.95	5.70 ±0.11	1.90 7.90
female	39.06 ±1.06	21.40 60.00	23.19 ±0.57	12.00 34.00	5.69 ±0.15	2.20 7.20	5.96 ±0.16	3.20 9.30

## (b) Eggs

	Length (n = 53)		Width (n = 51)	
	Mean ± SE	Range	Mean ± SE	Range
	1.55 ±0.03	1.33 1.79	0.28 ±0.01	0.26 0.36

## (c) Larvae

Instar <sup>3</sup>	Number of specimens examined	Headcapsule width		Body length		Thoracic width	
		Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
I	16	0.25 ±0.04	0.20 0.33	1.06 ±0.05	0.73 1.33	0.26 ±0.04	0.20 0.37
II	8	0.50 ±0.04	0.40 0.57	1.58 ±0.07	1.47 1.93	0.55 ±0.05	0.40 0.75
III	40	1.40 ±0.03	1.00 1.70	5.70 ±0.32	3.00 9.10	1.60 ±0.03	1.10 2.00
IV	19	2.00 ±0.05	1.70 2.40	11.40 ±0.42	9.00 16.00	2.50 ±0.13	1.60 3.90
V	21	2.94 ±0.05	2.58 3.58	19.92 ±0.51	15.00 23.95	4.73 ±0.11	3.83 5.33
VI	21	3.98 ±0.07	3.50 4.60	27.17 ±0.57	23.30 33.00	6.23 ±0.15	5.33 7.40

## (d) Pupae

Sex	Body length (n = 42♂, 22♀)		Thoracic width (n = 42♂, 22♀)	
	Mean ± SE	Range	Mean ± SE	Range
male	25.41 ±1.26	7.50 34.25	5.23 ±0.29	1.50 7.35
female	25.27 ±2.39	8.20 38.40	5.90 ±0.87	1.40 7.85

<sup>1</sup> Standard error.<sup>2</sup> Excluding antennae.<sup>3</sup> Instar II to V were determined graphically from the peaks and troughs of the frequency distribution of headcapsule widths.

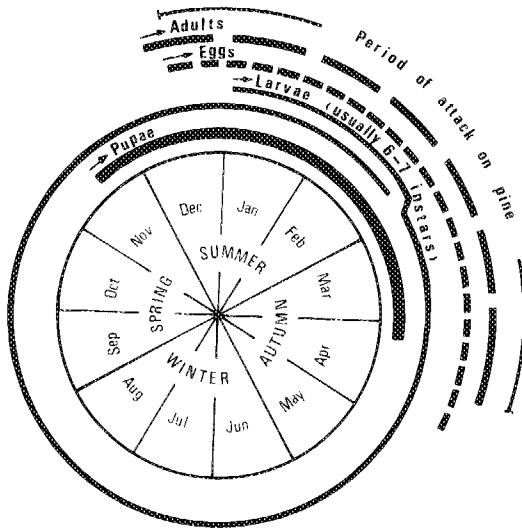


Figure 4. Annual life-cycle of *S. noctilio* in south-eastern Australia. Some individuals have shorter or longer cycles (see text).

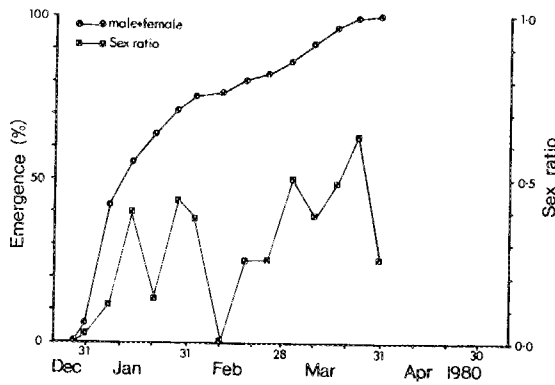


Figure 5. Mean cumulative weekly emergence and mean weekly sex ratios (proportion of females among emergents) of *S. noctilio* in north-eastern Victoria. (Means are based on 579 emergents from four separate collections of 20 billets, each 1 m long).

**Life history and symbiosis**

The life cycle of *S. noctilio* is normally completed in one year (Figure 4). In Victoria, some individuals may pass through a 2½ to 3-months cycle between summer and mid-autumn, whereas about 9% undergo a 2-year cycle. However, in the cooler Tasmanian climate, K. L. Taylor (CSIRO, pers. comm.) has found that the proportion of 2-year cycle individuals can reach 50% and that some individuals complete a 3-year cycle.

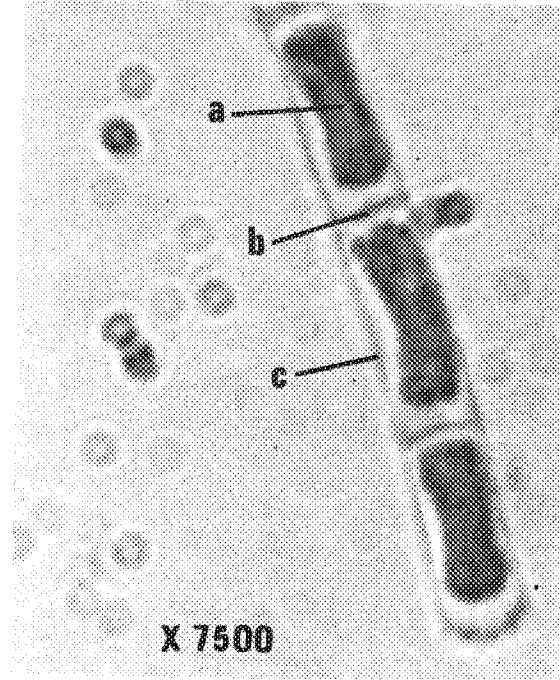


Figure 6. Arthrospores of *A. areolatum* within a parental hypha, from a culture on V8 agar. The arthrospores are multi-nucleate and homokaryotic (Gaut 1969): a. arthrospore; b. cross wall; c. parental hyphal wall.

Eggs usually hatch within 14 days between mid-summer and early autumn, though some may remain dormant for several months. Larvae generally pass through six or seven instars before pupating in outer sapwood, but K. L. Taylor (CSIRO, pers. comm.) has recorded up to 12 instars in Tasmania. Although a minimum of five moults generally appears necessary before pupation can occur, in Victoria the authors have observed the emergence after three larval moults of tiny male wasps (see the lower range of values in Table 1a) from small-diameter pine stems 2½ to 3 months after oviposition. Emergence of adults, followed by attack on pine, is usually most marked during mid-summer (Figure 5), though in Tasmania, Taylor (1978) has observed the occurrence of distinct second emergence peaks during autumn.

Dispersal occurs through several powerful flights of short duration. It usually extends over only a few kilometres per year (Zondag and Nuttall 1977; K. L. Taylor, CSIRO, pers. comm.), probably because the life span of females seldom exceeds five days and of males 12 days during warm summer weather, and less than one week for both sexes during cool autumn weather.

Emergents and/or oviposition delay.

For the purpose of both single and double drills, the one possible only colour of spores of the *tereum areolatum* (Gaut 1969) obligate symbiont. Cartwright (1969) are believed to be suitable for predisposition of trees which frequency of that in highly about mean to be much greater types, in range mucus consisting (molecular weight mixed with exogenous phenol oxidase. Crowden 1977) drill usually final drill wasp spores (Crowden) drills are more osmotic pressure.

Table 2. Drill-type

Drill
Single
Double
Treble
Quadruple

A total of 693 drills

<sup>1</sup> Estimates are based on 1974 data (Madden 1974)

<sup>2</sup> Standard error

Emergents are sexually mature, so that mating and/or oviposition usually proceed without delay.

For the purpose of oviposition, females bore both single and multiple drills about 12 mm deep into sapwood (Table 2) while stationed at the one position. Single drills generally contain only colourless phytotoxic mucus and arthrospores of the pathogenic basidiomycete *Amylostereum areolatum* (Fries) Boidin (Figure 6) (Gaut 1969, Coutts 1969a, b), which is an obligate symbiont of *S. noctilio* (Buchner 1928; Cartwright 1929, 1938; Clark 1933). Single drills are believed to be made mainly for testing the suitability of the substrate for oviposition, or for predisposing the host to subsequent attack. In trees which are tolerant to *S. noctilio*, the frequency of single drills generally far exceeds that in highly susceptible pine, so that variations about mean frequencies of single drill types can be much greater than those of multiple drill types, in randomly selected trees (Table 2). The mucus consists of protein — polysaccharides (molecular weights about  $60 \times 10^3$  to  $100 \times 10^3$ ) mixed with enzymes such as amylases, esterases, phenol oxidases, and proteolases (Fong and Crowden 1976). In multiple drill groups each drill usually contains a single egg, except the final drill which contains mucus and arthrospores (Coutts and Dolezal 1969). Single drills are mainly made at sites where the osmotic pressure (OP) of the phloem sap is high

( $> 12$  atm.), and multiple drills where OP's are low (2-8 atm.), indicating that oviposition frequency is dependent on the physiological condition of the host tree (Madden 1974).

The symbiotic pathogen *A. areolatum* reduces the moisture content of green wood to levels more favourable for egg hatching (30-70% of that of saturated wood) (Coutts 1965, Coutts and Dolezal 1965), supplies essential nutrients to larvae (Parkin 1942), causes wood decay (Gilmour 1965, King 1966), and thereby facilitates the drilling activity of larvae. In turn, female adults ensure the conservation and dispersal of the pathogen.

Female instar II larvae acquire mycelium of *A. areolatum* from infected wood (Boros 1968), and store the fungus in paired, abdominal skin-folds (hypopleural organs) (Parkin 1942). Adult females keep the fungal pathogen within paired mycangia near the base of the ovipositor (Francke-Grossmann 1957) (Figure 7a, d). In mycangia of emergents, fungal hyphae have conspicuous clamp connections, and contain numerous arthrospores, indicating that the pathogen is in an active condition during the insect's period of attack.

### Reproductive potential

Egg content (potential fecundity) increases with female size (Madden 1974). On the basis of

Table 2. Drill-type data for *S. noctilio* for mid-stem sections ( $n = 5$ ) cut from killed trees in a 16-year-old *P. radiata* plantation in north-eastern Victoria.

Drill type	Drill type frequency per 1 m section		Number of drill holes per 1 m section	Estimated number <sup>1</sup> of eggs oviposited per 1 m section
	Mean $\pm$ SE <sup>2</sup>	Mean %	Mean $\pm$ SE	Mean $\pm$ SE
Single	70.2 $\pm$ 25.6	44.9	70.2 $\pm$ 25.6	5.2 $\pm$ 2.2
Double	50.2 $\pm$ 3.0	39.7	100.0 $\pm$ 6.3	35.1 $\pm$ 2.1
Treble	12.8 $\pm$ 3.2	10.5	38.4 $\pm$ 9.6	20.4 $\pm$ 5.1
Quadruple	4.6 $\pm$ 1.2	4.2	18.4 $\pm$ 4.7	10.6 $\pm$ 2.7

A total of 693 drill groups was examined.

<sup>1</sup> Estimates are based on means of 0.04, 0.7, 1.6 and 2.3 eggs per single, double, treble and quadruple drill-types respectively (Madden 1974).

<sup>2</sup> Standard error.

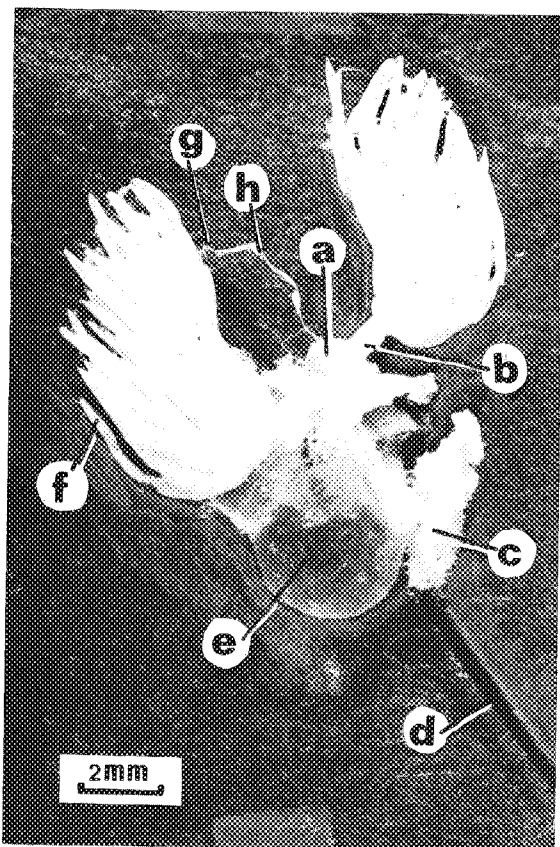


Figure 7. Aspects of the reproductive system of female *S. noctilio* showing: a. mycangium; b. lateral oviduct; c. mucus gland; d. ovipositor; e. mucus reservoir (10 to 25 mg capacity and ducted to base of ovipositor); f. mature egg within ovariole of ovary; g. nerve-cord; and h. abdominal nerve ganglion.

correlations between egg contents and female size parameters (Figure 8), the average-sized Victorian female contains about 212 eggs (range: 21 to 458,  $n = 100$ ). Taking this value for fecundity ( $F$ ) and assuming a sex ratio ( $SR$ ) of 0.25 (proportion of females in the population, calculated for 2295 emergents from caged billets over the period 1970 to 1980 in Victoria), and also assuming annual life cycles and zero mortality of life-stages, it follows that the yearly reproductive potential ( $RP$ ) per female in Victoria ( $RP = F \times SR$ ) is about 53 females.

#### Mortality

In the field, complete egg discharge seldom occurs and death may intervene at any life-stage prior to oviposition (Table 3). At 23 °C and 45% relative humidity, which correspond to near ideal ambient conditions for oviposition (Mad-

den 1974), Victorian females, caged with males on freshly-felled green pine, laid an average of 82.6% (range: 38.4 to 100%,  $n = 14$ ) of their estimated egg content, whereas those on three to four-week-old billets, or on seasoned pine, died without ovipositing.

The common causes of deaths of immature stages of siren are:

- (a) effective compartmentalisation (Shigo 1979) of the fungus-infected and punctured sapwood tissues containing also mucus, eggs or recently emerged larvae;
- (b) parasitism of eggs in the ovaries of pharate adults by progeny of infective stages of the nematode *Deladenus siricidicola* (Bedding 1973), or of eggs and/or young larvae by ibaliid parasitoids, or of advanced larvae by ichneumonid or stephanid parasitoids (Table 4);
- (c) starvation of larvae from lack of fungal nutrient due to antagonism by saprophytic blue-stain fungi (Coutts 1965) or toxic bacteria, or due to competition from mycetophagous stages of *D. siricidicola*; and
- (d) inability of pharate adults to emerge from host material.

Copious amounts of resin, or extreme moisture levels in wood may also cause the death of eggs or young larvae.

#### Host material and conditions for attack

*Sirex noctilio* is usually attracted to trees that are suppressed, drought-stressed, nutritionally deprived or otherwise weakened by insect and fungal defoliators. Trees damaged by wind, hail, lightning and during thinning or pruning operations, are also highly susceptible, as are green stumps, green logs and larger green logging residue.

In a 17-year-old infested and unthinned *P. radiata* plantation, the level of tree mortality (or tree susceptibility) was significantly related to stem diameter at breast height over bark (DBHOB) ( $\chi^2 = 608.29$ ,  $df = 11$ ,  $p < 0.001$ ) (Figure 9). The susceptibility threshold in terms of DBHOB was between 23 and 26 cm. Below this level, significantly more trees had died than survived ( $\chi^2 = 102.56$ ,  $df = 5$ ,  $p < 0.001$ ), and above this level, the number of survivors was significantly greater than the number of deaths ( $\chi^2 = 21.36$ ,  $df = 4$ ,  $p < 0.001$ ). Trees larger

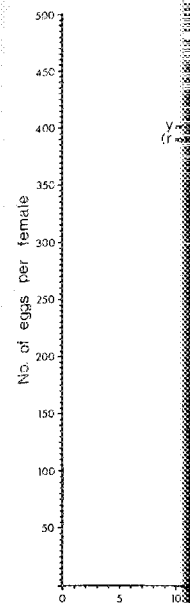


Figure 8. Relation

than 29 cm. Also, significant than single-stem *tilio* attack in 81.51,  $df = 1$ . The timing of pine material severity and p Madden (197) were immediate for 6 to 14 became susceptible and remained

Some of the v cambium tissue attraction of (Madden 1968) (1976) found aqueous volat felled *P. rad* distinct mono maining 5% at phone, isopin the alcohol tra of compounds the alcohol, at 3-carene,  $\beta$ -p drene) have e female antenn

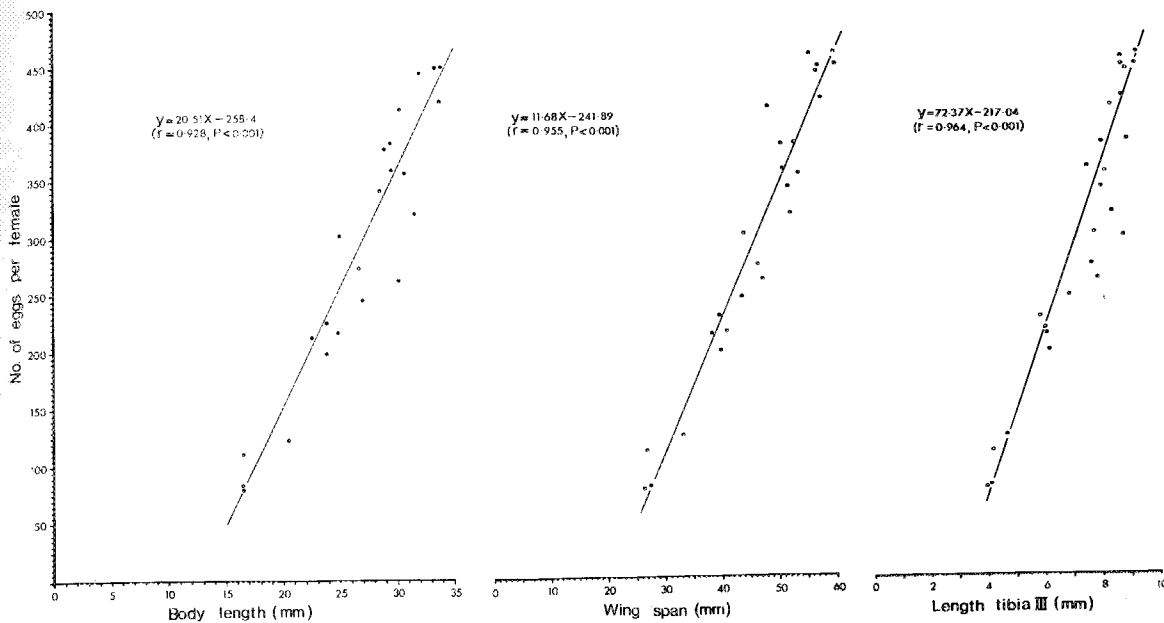


Figure 8. Relationships between potential fecundity and size parameters of female structures of *S. noctilio* from north-eastern Victoria.

than 29 cm DBHOB had remained healthy. Also, significantly more multi-stemmed trees than single-stemmed trees had died from *S. noctilio* attack in a sample of 1571 trees ( $\chi^2 = 81.51, df = 1, p < 0.001$ ).

The timing and duration of attractiveness of pine material to *S. noctilio* depends on the severity and persistence of physiological stress. Madden (1971) demonstrated that felled trees were immediately attacked and remained attractive for 6 to 14 days, whereas high-pruned trees became susceptible 9 to 12 days after treatment and remained so for several months.

Some of the volatiles produced by the phloem-cambium tissues of pine are important in the attraction of *S. noctilio* to susceptible trees (Madden 1968, 1971). Simpson and McQuilkin (1976) found that about 95% of the non-aqueous volatiles, which emanate from freshly felled *P. radiata* logs, are composed of 11 distinct monoterpene hydrocarbons, and the remaining 5% are composed of ketones (pinocamphone, isopinocamphone and camphor) and of the alcohol transpinocarveol. Of this wide range of compounds, the vapours from the ketones, the alcohol, and some monoterpenes ( $\beta$ -pinene, 3-carene,  $\beta$ -pinene, myrcene and  $\beta$ -phellandrene) have elicited the strongest responses in female antennae of *S. noctilio* (Simpson 1976),

and hence, appear to be the prime pine-produced substances capable of stimulating the nervous system of *S. noctilio*.

Simpson and McQuilkin (1976) further showed that the ketone and alcohol vapours (i.e. principally the oxygenated compounds) emitted by freshly cut *P. radiata* logs, increase from trace

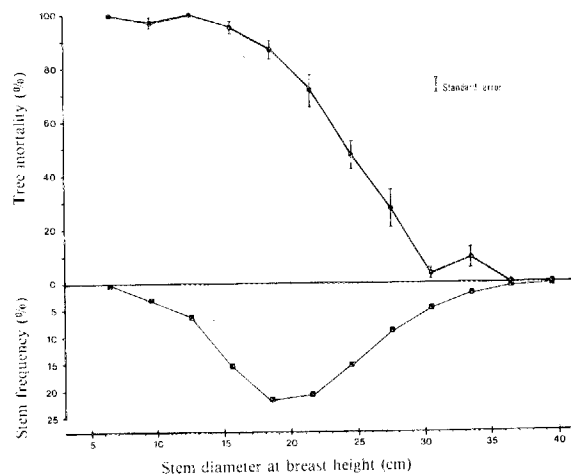


Figure 9. Tree mortality and stem frequency in relation to stem diameter at breast height over bark, in an unthinned 17-year-old stand of *P. radiata* in east-central Victoria, following the collapse of an outbreak of *S. noctilio*. (The data are based on 571 trees).



**Table 3.** Some life table data for *S. noctilio* assessed from a sample of five 1 m long mid-stem sections, each section randomly selected from 20 recently killed *P. radiata* trees, in a 16-year-old unthinned plantation in north-eastern Victoria.

No. of eggs laid by parental females <sup>1</sup>	No. of instar I larvae <sup>2</sup>	No. of adult progeny			No. of parasitoid emergents <sup>3</sup>			Ratio of parasitoid to host emergents <sup>4</sup> (%)	Mortality (%) of:			
		Male	Female	Total	Male	Female	Total		Eggs and instar I larvae	Eggs and larvae, due to parasitoids alone	Larvae (> instar I), pupae, pharate adults	Total
356	245	137	50	187	18	24	42	22.5	31.2	11.8	16.3	47.5

<sup>1</sup> Estimated using Madden's (1974) 'drill type-egg number' conversion factors, and on the following tally of drill types: 322 single, 264 double, 75 treble, 21 quadruple, 1 quintuple and 1 sextuple.

<sup>2</sup> Assessed by tallying number of galleries associated with oviposition drills.

<sup>3</sup> Exclusively *Ibalia leucospoides* (see Table 5); nematode parasites were not encountered in this study.

<sup>4</sup> This is the commonly used measure of the extent of biological control by parasitoids, and may considerably overestimate mortality due to parasitoids, as shown here.

amounts to about 1% of total volatiles, within three weeks of felling. In contrast, they found practically no change in the composition and rate of emission of monoterpene volatiles from fresh logs over the same period. Metabolic change in living woody tissues therefore seems to be a necessary requisite for increased emission of oxygenated volatiles, whereas any rise in monoterpene vapour levels may be solely due to greater bark permeability (Madden 1977a). It is unclear whether the oxygenated compounds (that are being synthesised in increasing amounts during the period when the attractiveness of pine to *S. noctilio* is diminishing) act as repellents or as chemical agents capable of neutralising the effects of attractant monoterpenes.

#### Pathogenic mechanism

Trees become predisposed to *S. noctilio* attack when they are damaged and/or become physiologically stressed by factors such as wind, hail, lightning, man's activities, defoliators, drought and inter-tree competition. Predisposed trees are usually characterised by:

- low mitotic rate in stem cambia, but above-average transpiration and respiration rates;
- high water tension in vascular systems, associated with low cell turgor and resin pressures in wood;
- stem phloem that is nutritionally deprived, partially dehydrated and partially aerated, and with sap of low osmotic pressure (< 8 atm.); and

(d) above-average bark permeability associated with high rates of emission of attractant pine volatiles;

(Coutts 1969; Titze and Mucha 1965; Coutts and Dolezal 1966; Madden 1968, 1971, 1974, 1977a).

Stress conditions in predisposed trees are reinforced, when *S. noctilio* females inject toxic mucus (derived from a reservoir (Figure 7e)) into the outer sapwood (Figure 10). This mucus is usually rapidly translocated into foliage, where it elicits a complex syndrome of reactions adverse to the trees, for example:

- cessation of mitoses and hence, of growth;
- increased enzyme activity associated with the conversion of foliar starch reserves to soluble sugars;
- a rise in respiratory activity which results in the rapid depletion of soluble sugar levels; and
- the breakdown of chlorophyll followed by the collapse of vascular tissues, causing chlorosis, wilting and premature needle fall;

(Coutts 1969 a, b, 1970; Fong and Crowden 1973; Spradbery 1973).

In the stem phloem and outer sapwood of predisposed and mucus-stressed trees, conditions are usually favourable for germination and growth of *A. areolatum* (King 1966; Boros 1968; Coutts 1969a; Titze and Turnbull 1970; Kile and Turnbull 1974). Subsequent growth of this pathogen leads to death of cells in the phloem,

**Table 4.**

Species

*Deladenus*  
Bedding (B)

*Ibalia leuco-*  
(Hochenwa)  
(Ibaliidae)

*Megarhyssa*  
*nortoni*  
(Cresson)  
(Ichneumon)

*Rhyssa pers-*  
(Linnaeus)  
(Ichneumon)

*Schlettereriu-*  
(Cresson)  
(Stephanidae)

cambium  
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In the outer  
increased  
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associated  
insect-path

Table 4. The more promising, established biological control agents being used against *S. noctilio* in Australian *P. radiata* plantations.

Species	Mode of action	Comments
<i>Deladenus siricidicola</i> Bedding (Neotylenchidae)	Nematode parasite; sterilises host females by destroying eggs in ovaries prior to emergence; male hosts are also parasitised but not sterilised; may compete with host larvae for fungal food causing starvation of host larvae or a reduction in size of host adults	From Europe (Hungary), New Zealand; females dimorphic; free-living, short mycetophagous life-cycles and long entomophagous cycles; dispersal slow, and is dependent on female hosts injecting nymphal stages into trees during oviposition; very effective in Tasmania and Victoria (Akhurst 1975; Bedding 1968, 1973; Bedding and Akhurst 1974; Zondag (1962)
<i>Ibaltia leucospoides</i> (Hochenwarth) (Ibaltidae)	Wasp parasitoid with short ovipositor; causes the death of eggs and/or of young host larvae; endoparasitic until larval instar II of host, then ectoparasitic on dead host larvae	From Europe (England and continent), Turkey; life-cycle usually in near-synchrony with that of host; dispersal is rapid and over long distances; most effective parasitoid in Victoria; works well in warm areas as egg hatching is not delayed (Chrystal 1930; Taylor 1967a, 1976, 1978)
<i>Megarhyssa nortoni</i> nortoni (Cresson) (Ichneumonidae)	Wasp parasitoid with long ovipositor; paralyses advanced host larvae, oviposits on them, and young larvae feed ectoparasitically on hosts	From U.S.A., Canada; life-cycle either of 3 months duration between spring and summer, or annual with emergence in early spring; second most commonly released parasitoid in Victoria; very effective in Tasmania (Taylor 1967a, b, 1976, 1978, 1980)
<i>Rhyssa persuarsoria</i> (Linnaeus) (Ichneumonidae)	As above	From Europe (England, Spain), Turkey, U.S.A., Canada, Morocco, Japan; life-cycles as above; appears to require cool shaded conditions; more effective in Tasmania than in Victoria (Hocking 1967a, b; Morgan and Stewart 1966; Taylor 1967a, 1976, 1978, 1980)
<i>Schlettererius cinctipes</i> (Cresson) (Stephanidae)	Wasp parasitoid with long ovipositor killing advanced host larvae	From U.S.A., New Mexico; life-cycles as above, but emergence occurs well after that of <i>Megarhyssa</i> and <i>Rhyssa</i> , hence is complementary to them. Seems more suitable for Tasmanian than Victorian conditions (Taylor 1967b, 1976)

cambium and rays, and to wood desiccation ahead of the mycelium. Hyphae invade water-conducting and supporting tracheids via pits, or by dissolving cell walls at points of contact (King 1966). Within tracheids, fungal spread is significantly faster along the wood grain than in both radial and tangential directions across the grain (Coutts 1965).

In the outer sapwood around oviposition drills, increased levels of infection create conditions conducive to hatching of eggs and subsequent growth of larvae, and hence lead to events associated with the advanced stages of the insect-pathogen development phase (Figure 10).

As a result of these events, the roots of the tree become starved and its water relations break down completely and irreversibly. After tree death, significant wood degrade occurs as a result of advancing dry rot and larval drilling activity. Finally, the disintegration of the host tree occurs and is brought about by the action of principally saprophytic fungi, insects (including termites), and weather factors.

Consequently, predisposed trees die because of the effects of the phytotoxic mucus and the pathogen, although these factors were shown by Coutts (1969b) to be lethal to pine only in combination. The wood-boring larvae take no part

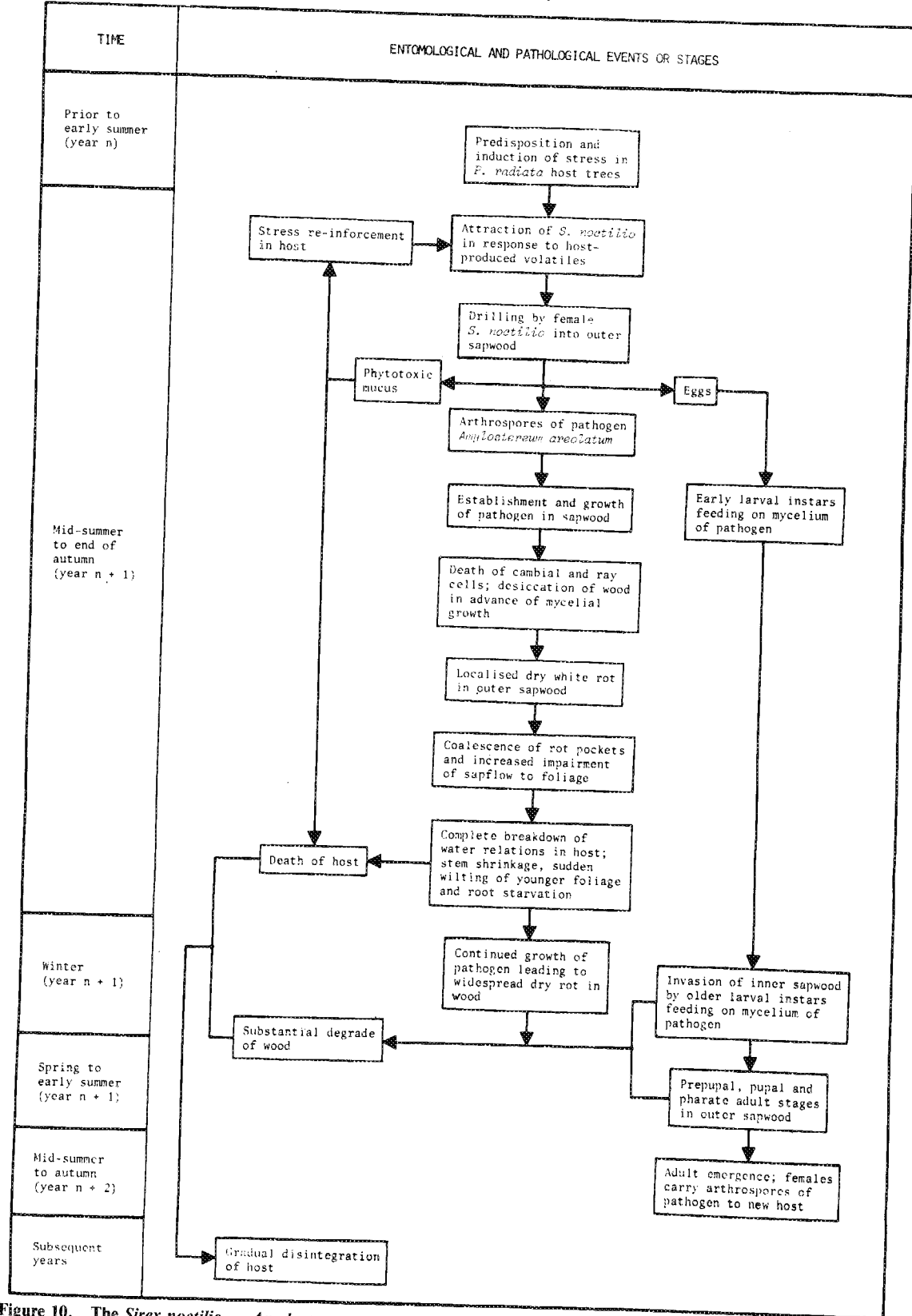


Figure 10. The *Sirex noctilio* — *Amylostereum areolatum* development phase in wood of *P. radiata* hosts in south-eastern Australia. (The time scale refers to the predominantly annual life cycle).

Figure 11. transverse section of a tree showing a vertical puncture to the wood.

in killing the tree. In south-eastern Australia, the most common time for attack is in autumn, i.e. generally between October and December. *P. radiata*, as a result of its phloem sap being rich in tannins and other compounds, has low to medium susceptibility to attack. This may explain why it is not killed within 6 to 12 months.

Attack symptoms of *S. noctilio* on *P. radiata* are: stem shrinkage, sudden wilting of younger foliage and root starvation.

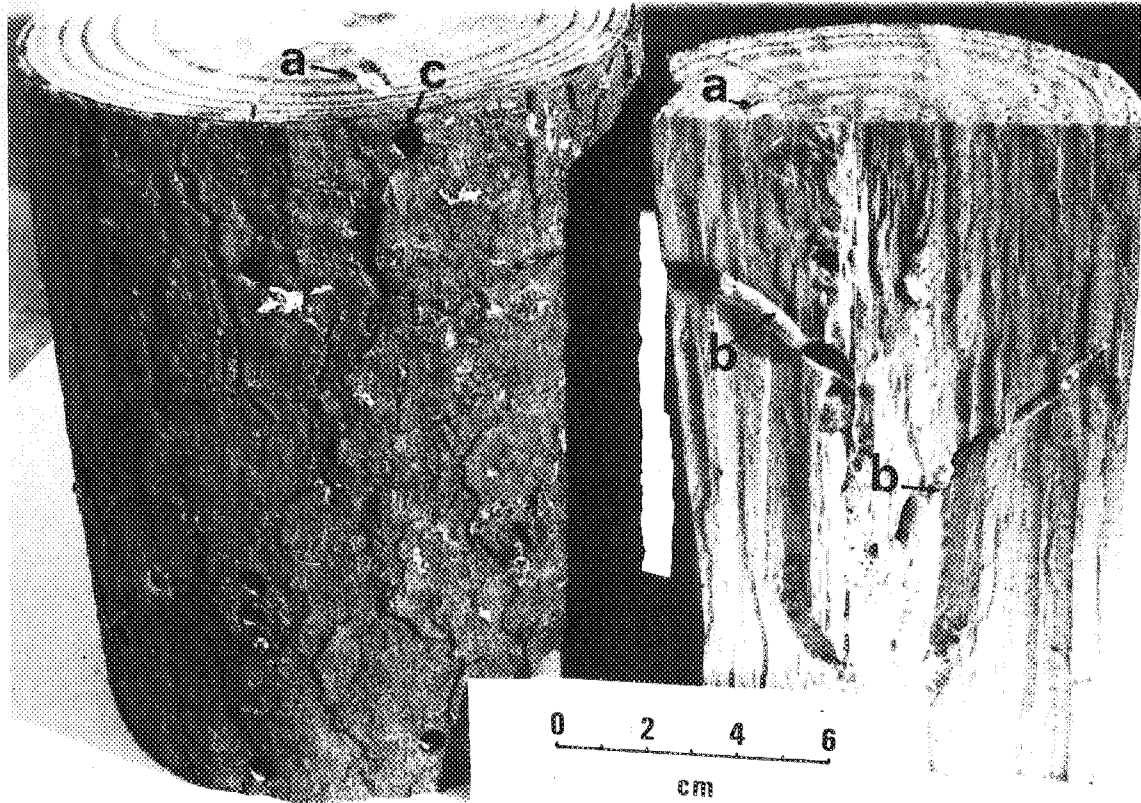


Figure 11. Typical wood degrade and damage symptoms in *P. radiata* due to attack by *S. noctilio*: a. larval gallery in transverse section; b. larval galleries in radial section; c. flight-hole. (A complete gallery, extending from the initial oviposition puncture to the flight hole, can measure between 50 and 260 mm in length, and vary from an initial width of about 0.3 mm to a final 3.5 to 9 mm).

in killing the tree, and merely damage the wood. In south-eastern Australia, *S. noctilio* attacks are most marked between mid-summer and mid-autumn, i.e. over a period when soil moisture is generally limiting, and when growth rates of *P. radiata*, as well as the carbohydrate levels in phloem sap, are declining rapidly to a minimum (Fielding 1966; Madden 1977b). Thus, the inoculation by *S. noctilio* of pine with toxic mucus and arthrospores occurs at a time when the host has low tolerance to pests and diseases. This may explain the rapid death of pine (in Victoria within 6 to 8 weeks) following *S. noctilio* attack.

**Attack symptoms**

Features symptomatic of *S. noctilio* attack on pine are: progressive and irreversible needle

chlorosis terminating in distinct copper-brown discolorations; sudden wilting of old foliage and then of the current season's foliage; and heavy needle fall with the onset of warmer weather in spring. Other symptoms include: numerous resin blobs and, sometimes, small resin flows on outer bark surfaces; distinct narrow bands of greyish-brown fungal staining, principally along the grain in the outer sapwood; single or multiple oviposition drills each of approximately 0.14 mm diameter; and dry non-resinous phloem and outer sapwood. The shape and orientation of the larval galleries, which contain tightly packed granular frass, and of the empty pupal chambers in the outer sapwood are also diagnostic, as are the circular flight holes (diameter  $5.57 \pm 0.11$  mm, range 3.25-7.25, n = 100) which occur on stems and larger branches (Figure 11).

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### Host tolerance

Generally, trees which are best able to tolerate *S. noctilio* attack are healthy and undamaged, and have consistently grown vigorously on good sites in well managed stands, as shown by sustained patterns of relatively wide growth-rings. Host-tolerance capacity may also have a genetic basis, as the foliage of some *P. radiata* clones is not adversely affected by phytotoxic mucus (Coutts 1969b; Kile *et al.* 1974), and *S. noctilio* development can fail in some trees, yet be successful in nearby trees of similar size and age. The screening of *P. radiata* trees in seed orchards for mucus resistance, and the subsequent culling of mucus-sensitive clones should be an important aspect of preventative control in the future.

Tolerance mechanisms seem to involve processes such as:

- rapid and extensive resin flow into sirenx-induced lesions;
- effective isolation of infected wood by fungistatic polyphenol barriers;
- early abscission of older needles carrying high loads of phytotoxic mucus; and
- growth of new functional tissues of phloem, cambium and xylem around lesions.

### Destructive potential

In New Zealand between 1946 and 1951, 20 to 33% of intermediate-age *P. radiata* trees were killed by *S. noctilio* in 120 000 ha of overcrowded plantations, following a severe drought in 1946 (Rawlings 1948, 1955, N.Z. For. Serv. 1974). In Tasmania, at Pittwater near Hobart, *S. noctilio* killed about 40% of slow-growing intermediate-age *P. radiata* trees in a 1092 ha plantation between 1952 and 1959 (Madden 1975), but elsewhere, tree mortality has remained low (K. L. Taylor, CSIRO pers. comm.).

The destructive potential of *S. noctilio* may be substantially greater in mainland Australia than in Tasmania (or New Zealand) because, on the mainland, droughts are more severe and frequent, summer temperatures are higher, and first thinnings are behind schedule in a greater number of plantations. In southern Victoria many valuable shelterbelts on farmland have been destroyed, especially during the 1960s. At

Delatite in east-central Victoria, about 25% of a 1906 ha plantation has been severely damaged. Unthinned stands of intermediate age incurred over 70 per cent tree mortality and merchantable volumes were substantially reduced over a seven year period, even in the presence of natural enemies (Table 5). Surviving trees were unevenly distributed and about one-third of these will need to be felled to prevent stagnation and resurgence of the pest during the second half of the projected 40-year rotation (Figure 12). Final stocking density is expected to be around 300 trees/ha, which corresponds to the usually acceptable level for the final crop. Surviving trees are also vulnerable to damage by wind and fire, particularly during the early post-epidemic period. The eventual harvesting of mature trees may be difficult and costly due to the likely presence of intermediate-age natural regeneration in clearings.

### Pest management

Usually outbreaks of *S. noctilio* only occur when conditions are adverse for pine, implying that the insect is essentially a secondary pest. The eradication of *S. noctilio* in large well-managed plantations is therefore neither feasible nor necessary, because they provide environments capable of supporting only small populations of the pest. Localised 'flare-ups' of *S. noctilio* may occasionally occur, but in the absence of suitable hosts these outbreaks usually decline naturally, after causing only minor damage. Small populations of *S. noctilio* may even be useful in well-managed stands, because they may aid the natural propagation and spread of biological control agents (Table 5), and cause the death of a few scattered unwanted trees between scheduled thinning treatments. In New Zealand, *S. noctilio* has been of minor importance to forestry since the 1950s due to the practice of good standards of silviculture and the maintenance of introduced sirenx-specific parasitoids and of the nematode parasite *D. siricidicola* in plantations (N.Z. For. Serv. 1974).

Unfortunately, large areas of 15 to 18-year-old plantations with high stocking densities of between 1770 and 2400 trees/ha occur in some major Australian pine-growing regions, such as north-eastern Victoria. In these regions, approximately 30% of stands grow on high quality sites which are capable of producing 28 m tall trees at

age 20 years. Lack of functional markets. A large number of trees with tolerance to occasional deficiencies in physiological processes. Some areas show a decrease in stand density of *S. noctilio* over time. (J. Wall)

Loss of control. Delayed first thinning on the better sites. Additional delayed thinning therefore required.

One solution is to overcrowd the stand. Control of the pest (Taylor 1967) is to work satisfactorily. *S. noctilio* populations rapidly to a biological control agent in Victoria, but always seem to cause damage in pine

Table 5. The distribution of *S. noctilio* in pine plantations.

No. of plots	Plot area (ha)
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3	0.2
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Stand factors: (years) = 24.2

<sup>1</sup> Diameter at breast height

<sup>2</sup> Standard error

<sup>3</sup> Functions used: section per tree =  $2.73 \times 10^{-5}$

about 25% of a severely damaged. The age incurred and merchantable volume over a seven year period were unevenly distributed. Most of these will stagnate and in the second half of the century (Figure 12). Final volume will be around 300 m<sup>3</sup> per ha, the usually achieved volume. Surviving trees will be lost to wind and fire, and a post-epidemic decline in the number of mature trees will lead to the likely natural regenera-

age 20 years. Thinning has been delayed due to lack of funds for sanitation-felling, and lack of markets. Therefore, these plantations contain large numbers of suppressed trees, with a low tolerance rating for *S. noctilio*. The effects of occasional severe droughts and of nutritional deficiencies may compound the problem of physiological stress from over-crowding, in some areas. Furthermore, the range of susceptible tree sizes in terms of DBHOB appears to increase in stands following sustained attack by *S. noctilio* over several generations (R. McKimm and J. Walls, For. Comm. Vic., pers. comm.).

Loss of crown and windthrow may follow delayed first-thinning (Lewis 1963), particularly on the better sites, and retained trees can suffer additional damage from sun scorch. After delayed thinning treatments plantations may therefore remain favourable habitats for *S. noctilio*.

One solution to the problem of *S. noctilio* in overcrowded stands was thought to be biological control using introduced natural enemies of the pest (Table 4) (Bedding and Akhurst 1974, Taylor 1967a, 1976, 1978). This strategy seems to work satisfactorily in Tasmania, where *S. noctilio* populations have occasionally declined rapidly to very low levels even without effective biological control (Taylor 1980). However, in Victoria, parasitoids and nematodes do not always seem capable of preventing substantial damage in plantations (Table 5).

Current research into siren suppression within crowded plantations in Victoria aims at formulating a control prescription that will combine the effects of established biological control agents (Table 6) and of minimal non-commercial thinning with the strategic placement on a grid pattern of groups of trees artificially made attractive and susceptible to *S. noctilio* by injection of the sapwood with herbicide during spring (summer injections are less effective). A number of herbicides appear suitable for this purpose (Table 7). In operational practice, it is intended to fell the herbicide-treated 'trap' trees after the flight season, and inject them with a preparation of nematodes in gelatin (Bedding and Akhurst 1974) at a rate of four or five 1 ml shots of 2500 nematodes per 1 m of stem, to ensure that siren females become sterilised prior to emergence. As sterile nematode-infected siren female adults introduce nematodes into trees during oviposition drilling activity, it is expected that nematode-infected female emergents from 'trap' trees will bring about a more rapid spread of the highly effective, but usually slowly dispersing nematodes, and thus contribute to an early collapse of *S. noctilio* populations in susceptible plantations. The 'trap' trees are also expected to be useful in the early detection of new occurrences of *S. noctilio* and for the annual monitoring of the relative population levels of the pest and of its natural enemies within their known distribution.

Table 5. The destructive potential of *S. noctilio* in the presence of natural enemies (ibaliid and ichneumonid parasitoids and nematode parasites) in an unthinned, 17-year-old stand of *P. radiata*, in east-central Victoria.

No. of plots	Plot size (ha)	No. trees per plot	Percentage of total trees (Mean ± SE <sup>2</sup> )			Percentage of dead trees (Mean ± SE) with:		Percentage reduction in volume per plot due to Siren (Mean ± SE):	
			Healthy	Dying	Dead	Exit holes	Nil exit holes	Total volume <sup>3</sup>	Merchantable volume <sup>3</sup>
3	0.25	400	28.42 ±0.87	0.50 ±0.25	71.08 ±1.08	96.93 ±0.82	3.07 ±0.82	50.38 ±2.54	48.10 ±2.82

Stand factors: mean stand top height = 22.1 m (n = 50); mean DBHOB<sup>1</sup> = 21.3 cm; site index (stand top height at age 20 years) = 24.2 m.

<sup>1</sup> Diameter at breast height over bark (1.30 m).

<sup>2</sup> Standard error.

<sup>3</sup> Functions used for computation of total volume under bark per tree (Vt) and merchantable volume to 10 cm under bark section per tree (Vm) were, respectively:  $V_t (m^3) = 2.71 \times 10^{-5} D^2 H - 1.325 \times 10^{-4} H^2 + 405 \times 10^{-2}$ , and  $V_m (m^3) = 2.73 \times 10^{-5} D^2 H - 1.370 \times 10^{-4} H^2 + 1.719 \times 10^{-2}$ , where D = DBHOB (cm) and H = stand top height (m).

*S. noctilio* only occur in pine, implying a secondary pest. In large well-managed stands neither feasibility nor profitability provide enough incentive for silviculture, only small 'flare-ups' of the pest occur, but in the early stages usually only minor damage. *S. noctilio* may occur in stands, because of propagation and dispersal (Table 5), and caused unwanted damage. In the case of minor infestations due to the silviculture and siren-specific parasite *D.* For. Serv.

to 18-year-old stands. In some regions, such as the south-eastern regions, approximately 10 m tall trees at

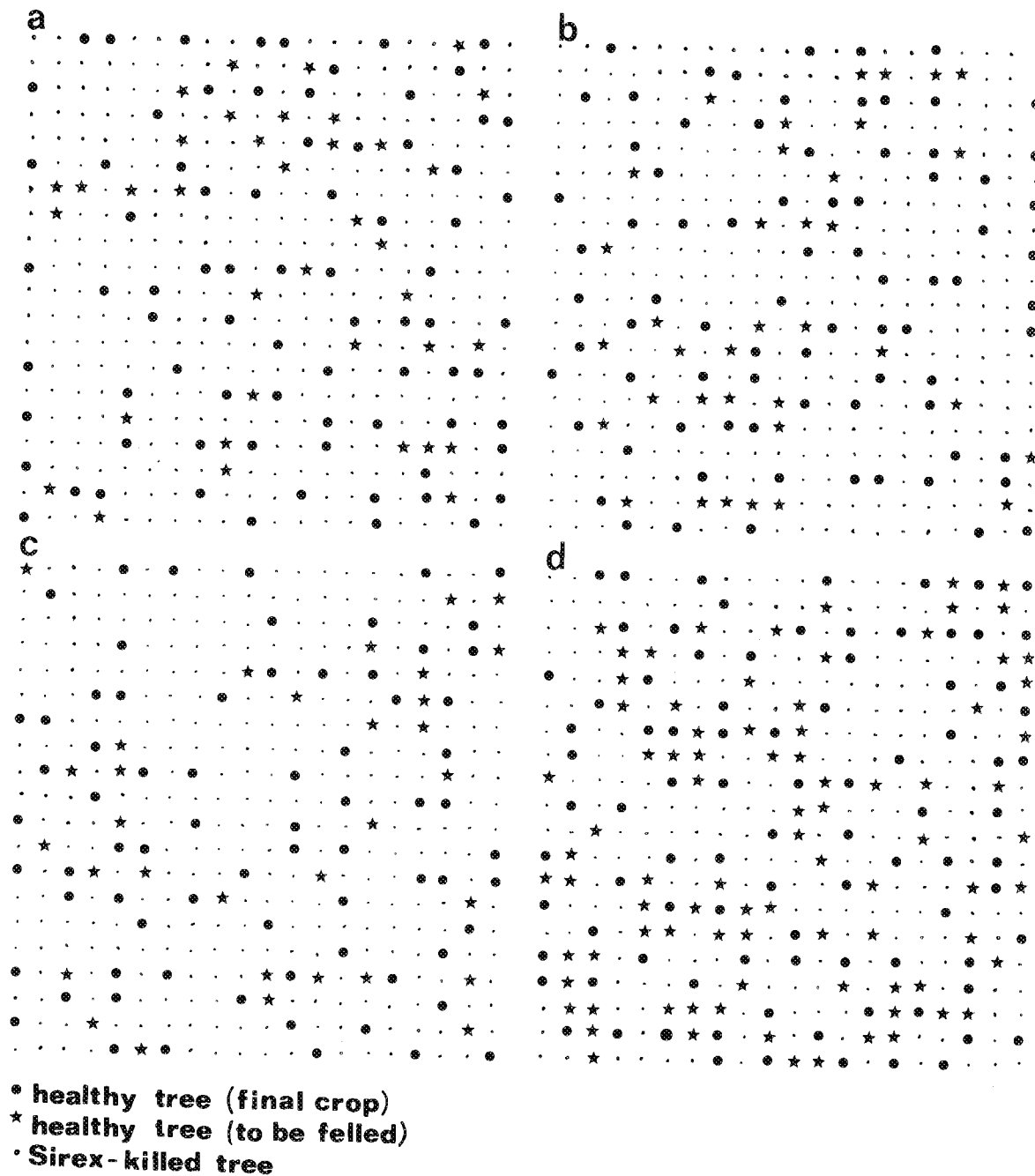


Figure 12. The distribution of healthy and sirenx-killed trees in four 0.25 ha plots (a, b, c, d) located in an unthinned 17-year-old *P. radiata* plantation, in east-central Victoria.

Also shown are the positions of trees that need to be felled to prevent competition between final crop trees. Over the study area, *S. noctilio* has declined to negligible levels as a result of greater tolerance of surviving trees to the pest and biological control.

Table 6.

Year	Male
1970	5322
1971	4876
1972	5398
1973	7161
1974	7017
1975	6193
1976	10859
1977	4602
1978	8421
1979	12923
1980	4878
Total	77650

<sup>1</sup> Species are: A

<sup>2</sup> *Deladenus siri*

<sup>3</sup> Short life cycle

Table 7. Frequency around circumference

Tree age (years)	No. of trees per hectare
16	
14	
12	
10	
8	
Total	

A total of 400 trees frequent in herb

that trees aged 1

Active ingredient

2,4-D (800 g L<sup>-1</sup>)

chloro-2-methyl

isopropanol am

Table 6. Summary of the biological control program against *S. noctilio* in Victoria for the period 1970 to 1980.

Year	No. of specimens released of species:								Totals (all species)		No. of items injected with nematodes <sup>2</sup>	
	A <sup>1</sup>		B <sup>1</sup>		C <sup>1</sup>		D <sup>1</sup>		Male	Female	Trees	Billets (1 m)
	Male	Female	Male	Female	Male	Female	Male	Female				
1970	5322	5654	3193	2316	884	721	—	—	9399	8691	—	—
1971	4876	7315	313	420	134	108	55	141	5378	7984	—	—
1972	5398	4991	531	1646	408	483	25	268	6362	7388	—	—
1973	7161	6547	1121	1516	34	218	—	55	8316	8336	573	400
1974	7017	6164	593	553	—	—	48	107	7658	6824	839	493
1975	6193	4592	1217	1774	5	724	64	239	7479	7329	504	64
1976	10859	9521	1319	1183	270	245	—	—	12448	9648	97	9
1977	4602	4854	862	1197	209	269	24	130	5697	6450	283	—
1978	8421	7446	1063	1052	129	153	—	—	9613	8651	207	—
1979	12923	10493	—	—	173	123	3	5	13099	10621	91	—
1980	4878	3386	113 <sup>3</sup>	73 <sup>3</sup>	—	—	—	—	4991	3459	334	—
Total	77650	70963	10325	11730	2246	3044	219	945	90440	86682	2928	966

<sup>1</sup> Species are: A, *Ibalia leucospoides*; B, *Megarhyssa nortoni nortoni*; C, *Rhyssa persuasoria*; D, *Schlettererius cinctipes*.

<sup>2</sup> *Deladenus siricidicola*.

<sup>3</sup> Short life cycle individuals only.

Table 7. Frequencies of *S. noctilio* infestation in trees injected with herbicides during the previous spring (1 ml a.i. every 10 cm around circumference, into sapwood at base) compared with frequency of infestation in untreated, windthrown and healthy control trees.

Tree age (years)	No. trees per treatment	Herbicide-treated trees						Windthrown trees	Controls	Total
		2,4-D	Dicamba	MCPA	Picloram	Glyphosate	Amitrole			
16	10	10	8	8	7	9	0	8	0	50
14	10	5	5	2	1	4	0	1	0	18
12	10	2	2	3	0	1	0	0	0	8
10	10	3	0	4	4	0	0	0	0	11
8	10	2	3	1	4	0	0	0	0	10
Total		22	18	18	16	14	0	9	0	97

A total of 400 trees was examined. An analysis of variance showed that the occurrence of *S. noctilio* was significantly more frequent in herbicide-treated trees (except for those treated with Amitrole) than in windthrown or control trees ( $p < 0.01$ ), and that trees aged 16 years were significantly more susceptible to attack than younger trees ( $p < 0.001$ ).

Active ingredients of herbicides (parentheses):

2,4-D (800 g L<sup>-1</sup> of the ethyl ester); Dicamba (200 g L<sup>-1</sup> of 3,6-dichloro-2-methoxybenzoic acid); MCPA (250 g L<sup>-1</sup> of chloro-2-methylphenoxyacetic acid); Picloram (50 g L<sup>-1</sup> of tri-isopropanol amine salt) + 2,4-D (200 g L<sup>-1</sup> as the tri-isopropanol amine salt); Glyphosate (360 g L<sup>-1</sup> N (phosphonomethyl) glycine); Amitrole (250 g L<sup>-1</sup> 3-amino-1,2,4-triazole).

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