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The Sirex Wasp in Victoria

F. G. Neumann, J. L. Morey and R. J. McKimm

Edited by David Meagher

Bulletin No. 29

Lands and Forests Division

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Department of Conservation, Forests and Lands

Contents

Summary

In Victoria the sirex wasp, *Sirex noctilio* Fabricius (Hymenoptera:Siricidae), from southern Europe, is a serious pest of exotic *Pinus radiata* D. Don (radiata pine), which has been widely planted as the principal source of softwood. In the 1960s many valuable pine shelter belts on farmland were severely damaged or destroyed, and substantial tree mortality also occurred in privately-owned *P. radiata* plantations, especially in central Gippsland, east of Melbourne. The worst outbreak in government-owned plantations occurred between 1972 and 1979 in a 12 to 15-year-old plantation of 1906 ha near Delatite in east-central Victoria. In this plantation, where biocontrol agents were present, the wasp killed an average 77% of trees on 25 ha, 63% on 79 ha, 35% on 379 ha and 5% on 701 ha, whereas in 16 to 18-year-old thinned stands, tree mortality was below 27%. Only 20% (388 ha) of the plantation area remained undamaged. In the worst affected stands, the total and merchantable wood volumes were reduced by 50.4% and 48% respectively. Stocking density declined from about 1700 stems ha^{-1} to less than 420 stems ha^{-1}, which corresponds to a level approximately 62% below the prescribed stocking after a first thinning.

The sirex wasp's life cycle usually extends over a one-year period, though some individuals may pass through a three month or a two year cycle. Emergence of adults, followed by attacks on trees, occurs mostly between mid-summer and early autumn, when soil moisture levels, growth rates and resistance of pine to pests and diseases are low. Various volatiles produced by the phloem/cambium tissues of stems and large branches of living trees are important in the attraction of the wasp. Susceptible trees are usually above 12 years old, and physiologically stressed. Sirex wasp attack causes a reinforcement of stress due to the injection of phytotoxic mucus and spores of the symbiotic pathogenic basidiomycete *Amylostereum areolatum* (Fries) Boidin (commonly known as the sirex fungus) into outer sapwood during oviposition. This pathogen desiccates the wood, causes white rot, and is also a source of nutrients for the wasp's larvae. Additional degrade in the wood occurs through the tunnelling activity of the larvae, and through secondary decay fungi which enter via flight holes and render the wood unmerchantable within a year.

Since the discovery of the sirex wasp in locally produced logs near Melbourne in December 1961, it has spread to all major pine-growing regions of Victoria and beyond into south-eastern South Australia, southern New South Wales and the Australian Capital Territory. This has occurred despite a rigorous application during the 1960s of extensive search and destroy operations, the prohibition of log movements from quarantined sirex-infested properties, and periodic mill-inspections by specially trained staff, followed in the 1970s by extensive biocontrol measures. The total cost of these operations amounts to about $3 million (about $10.5 million in terms of 1984 monetary values). All State Governments (and since 1983 also the Commonwealth-administered ACT Forests) have met these costs by annual contributions approximately in proportion to the areas of *Pinus* species under cultivation. Until 1974 the Commonwealth Government also made annual allocations on a dollar for dollar basis with the states. Many private forestry organisations and local government authorities have contributed, especially during the 1960s. Funding has been progressively reduced from a peak of $315 720 in 1964-65 to $26 175 in 1984-85.

The sirex wasp is essentially a secondary opportunistic wood-boring pest. The prevention of economically important outbreaks in plantations is therefore largely a management problem that can be alleviated by routine

surveillance of plantations, the application of silvicultural measures including timely selective thinning for sustained vigour, and the early removal of multi-stemmed, unhealthy or damaged trees. Biocontrol is not required in some well-managed plantations. In fact small numbers of sirex wasp in these may be useful in killing unwanted trees between scheduled thinning treatments. However, the wasp needs to be controlled in plantations that have been damaged by protracted drought, as well as those in poor silvicultural condition because thinning has been delayed by unfavourable markets, unavailability of funds for early non-commercial thinning or other reasons. An effective multi-pronged control strategy that enables the early detection and rapid suppression of even small sirex wasp populations is now available. It combines the use of aerial reconnaissance, routine ground observations and the deployment of herbicide-injected (and hence highly susceptible) trap tree systems with the effects of biocontrol agents. Most useful among these biocontrol agents are the parasitic nematode *Deladenus siricidicola* Bedding and two parasitoids of genus *Ibalia* (Hymenoptera: Ibaliidae). The nematode is artificially inoculated into the outer sapwood of sirex-infested trap trees and significantly suppresses the fecundity of females without impairing their general vigour and sexual competitiveness. The parasitoids kill early larvae of the wasp.

Until 1983, the Forests Commission Victoria was responsible for the culturing and supply of large numbers of biocontrol agents for use in Victoria and interstate. After a restructure of government departments in 1983, this became the responsibility of the State Forests and Lands Service of the Department of Conservation Forests and Lands. In late 1985 it was transferred to the Department's Land Protection Service. In recent years the population levels of the sirex wasp have been economically unimportant, largely as a result of the effectiveness of current pest management measures. However, the insect remains a potential threat to Victoria's pine resource. Vigilance needs to continue, and preventative control measures applied, in areas where endemic populations are showing signs of build-up.

Introduction

The sirex wasp (*Sirex noctilio*), from southern Europe, was first recorded on mainland Australia near Melbourne in 1961. The wasp, and its symbiotic fungus *Amylostereum areolatum* (Fr.) Boidin, cause the death of softwood trees through a combination of a phytotoxic mucus produced by the wasp and white rot induced by the fungus. Galleries tunnelled by the wasp larvae also reduce the quality of the wood.

Considerable resources have been devoted to containing and controlling the wasp because of the threat it poses to the extensive plantations of exotic radiata pine (*Pinus radiata* D. Don) in southern Australia. A high degree of co-operation between the Commonwealth and State Governments, private forest industries and research organisations, notably the Commonwealth Scientific and Industrial Research Organisation, enabled considerable research on the wasp to be undertaken. This co-operation has probably averted a major disaster for the Australian softwood industry.

Despite these efforts, major outbreaks of the sirex wasp occurred in Victoria during the 1970s and early 1980s, and it has spread into south-eastern South Australia, New South Wales and the Australian Capital Territory. Analyses of the outbreaks helped to identify factors which made radiata pines susceptible to sirex wasp attack. This enabled plantation management measures to be formulated to reduce the likelihood of tree mortality and loss of wood production.

In addition, research conducted at the Mountain Forest Research Station near Melbourne, Victoria, enabled a number of biocontrol agents of Northern Hemisphere origin to be produced in large numbers and released to control this pest. In combination with improved forest management procedures, the applied control measures have proved to be very successful in reducing populations of sirex wasps to low, economically insignificant levels in Victoria and elsewhere.

However, because of the nature of many radiata pine plantations and the ongoing planting program in Victoria, survey and control measures need to be continued to prevent major infestations, especially following periods of severe drought.

This bulletin distils the results of 25 years of research, assessment and control of the sirex wasp in Victoria. The important historical aspects of the accidental introduction of this pest, and the subsequent organisation of research, survey and control measures, are outlined. The taxonomy and biology of the wasp, its fungal symbiont and biocontrol agents are presented in detail. The bulletin also outlines management procedures for reducing the susceptibility of plantations to sirex wasp attack, and details of the rearing and evaluation of biocontrol agents are provided.

The bulletin should be of interest to foresters, land managers, scientists, private landholders, nurserymen and others with an interest in the management of pine plantations and tree pests. A glossary is provided for those without a formal background in entomology or forestry.

1 HISTORY OF THE SIREX WASP IN VICTORIA

Accidental introduction of the sirex wasp

The sirex wasp and other species of the *Sirex*, *Urocerus* and *Xeris* genera of family Siricidae are wood-boring insects of conifers in temperate regions of the Northern Hemisphere (Europe, North-America and Asia), but none are serious primary pests of forests in those regions. Nevertheless, Australian forest authorities became increasingly concerned in the late 1940s and early 1950s about the potential threat posed by the sirex wasp and related siricids to the extensive monocultures of exotic *P. radiata* established in the southern States of Australia.

This concern arose primarily from New Zealand reports which confirmed that between 1946 and 1951 the sirex wasp had killed 20-30% of intermediate-age *P. radiata* trees in 120 000 ha of unthinned plantations following a severe drought in 1946 (Rawlings 1948, 1955), even though *P. radiata* is not a natural host of the sirex wasp. The insect had been accidentally introduced into New Zealand in about 1900, and the above observations clearly indicated that the wasp had adapted from other conifers to living *P. radiata* trees and was able to build-up large damaging populations in a region of the Southern Hemisphere where climatic conditions resembled those in parts of southern Australia. Also in the early 1950s, cargoes heavily infested by larvae and adults of siricid species began arriving at Australian sea-ports from Europe (Austria, Czechoslovakia, France, Rumania, Scandinavia, West Germany and Yugoslavia) (Cumming *et al.* 1952). Quarantine restrictions imposed by the Commonwealth Plant Quarantine Service to exclude these insects from Australia aroused much attention.

As a consequence of these developments, the Australian Commonwealth Government appointed a special committee in 1951 to examine all matters related to the importation of softwood timber infested, or likely to be infested, with the sirex wasp and other species of family Siricidae. In particular, it was to establish whether quarantine precautions being taken against siricids should be intensified, maintained or relaxed. The Committee concluded that Australian conditions were favourable to the build-up and spread of siricids and that economic loss would be caused by their introduction. It recommended that siricids be ranked as potentially serious pests of pine, that quarantine precautions at wharves with respect to the inspection of ships, timber, packing cases, crates, dunnage and prefabricated houses be intensified, and that strong quarantine action be taken to prevent the spread of siricids wherever they may become established in Australia (Cumming *et al.* 1952).

In 1952 the sirex wasp was discovered in a private *P. radiata* plantation at Pittwater near Hobart, Tasmania following its accidental introduction, probably from New Zealand (Gilbert and Miller 1952). Attempts to eradicate the pest failed, and by 1959 it had killed about 40% of slow-growing intermediate-age trees in 1 092 ha of plantation (Mucha 1967, Madden 1975). On 20 December 1961, the wasp was detected on the mainland in locally grown *P. radiata* logs at a sawmill near Melbourne (Irvine 1962). An immediate search by officers of the Forests Commission Victoria (FCV) traced the origin of the logs to a small, privately-owned plantation on a dairy farm near Woori Yallock, about 40 km east of Melbourne.

The realisation that the wasp had finally established in Victoria caused considerable concern. The insect was seen not only as a threat to the relatively new and economically viable Victorian softwood industry, but also to farmers, orchardists and park managers who relied on pine trees for year-round shade and shelter and for beautification of their properties. There was also the threat of the pest spreading to other mainland states.

Anti-sirex programs 1962-1974

Organisation and funding

Following the accidental introduction of the sirex wasp into Victoria and the insect's subsequent establishment in windbreaks and plantations, a joint approach to the Commonwealth Government was made on 15 January 1962 by the six Australian state forest services and the Commonwealth Timber Bureau to secure Commonwealth financial assistance for a national anti-sirex campaign. In early February 1962 at the Premier's Conference on financial arrangements between Commonwealth and State Governments, a National Sirex Trust Fund of $400,000 was established, to which the Commonwealth Government and the State Governments contributed on a dollar for dollar basis

At a subsequent meeting on 26 February 1962 between the Commonwealth Minister of Health and state ministers responsible for forestry matters, the decision was made to base state contributions to the fund on a proportional scale, depending on the areas of *Pinus* species under cultivation. The National Sirex Fund Committee was also established, charged with the responsibility of planning a program of activities and of authorising expenditure to achieve eradication of the sirex wasp in Australia. This Committee consisted of the permanent heads of all state forest services, the Director-General of the Forestry and Timber Bureau (FTB) (Commonwealth Department of National Development), the Chief of the Division of Entomology, Commonwealth Scientific and Industrial Research Organization (CSIRO), the Assistant Director-General (Plant Quarantine) (Commonwealth Department of Health), and a representative of private forest industries.

At later ministerial meetings, the operations of the National Sirex Fund Committee were extended by annual allocations of $400,000 on the original basis of contributions. Generous financial support for the campaign was also provided voluntarily by various local government authorities and many private forestry organisations, notably APM Forests Pty Ltd, Softwood Holdings Ltd and Southern Australia Perpetual Forests Ltd.

Initially, eradication of the pest appeared to be possible, because the infested area around Melbourne was believed to be small. However, by early April 1962, survey teams of officers of the FCV, assisted by foresters and entomologists from the FTB, the New South Wales Forestry Commission, the Woods and Forests Department of South Australia, the Commonwealth Plant Quarantine Service, the Waite Agricultural Research Institute (University of Adelaide) and several private forestry organisations, had discovered two large and geographically distinct infestation areas. One was centred east of Melbourne, and the other was in central Gippsland, extending easterly from Yallourn to Sale, and southerly from Heyfield to Traralgon South (Figure 1). These observations indicated that the wasp was far more widely established than hitherto suspected, and that eradication might not be possible. As data on the ecology and control of the insect was very limited, the National Sirex Fund Committee established a Survey and Eradication (later renamed Survey and Control) Sub-Committee in 1962, headed by the Chairman of the FCV. A Research Sub-Committee chaired by the Chief of the Division of Entomology, CSIRO, was also established.

For 13 years up to 1974, the Survey and Control Sub-Committee administered a program on survey and control of the sirex wasp in Victoria, with the FCV acting as its agent. The program was essentially a 'search and destroy' operation, involving the critical examination of commercial plantations, windbreaks and isolated trees in rural areas, and the implementation of steps aimed at burning infested trees on site and thereby stopping the pest from spreading.

The Research Sub-Committee co-ordinated, over a similar period, a comprehensive research program into the biology of the sirex wasp and its control through appropriate natural enemies. Twenty-one species of parasitoid were introduced for biocontrol purposes from Europe and North America (Taylor 1976). Other research included silviculture and tree breeding, tree pathology and physiology, the ecology and behaviour of the wasp in Tasmania and overseas, nematology, biochemistry, and chemical control. The principal organisations involved in the research were the Divisions of Entomology and Building Research, CSIRO; the Forest Research Institute of the Forestry and Timber Bureau (now Division of Forest Research, CSIRO); the Waite Agricultural Research Institute, University of Adelaide; and the University of Tasmania. Several overseas institutions co-operated in the research, notably the Commonwealth Institute of Biological Control (United Kingdom) and the Forest Research Institute of the New Zealand Forest Service (Taylor 1981).

Survey and Control

In Victoria between early 1962 and mid-1972, 2-person survey teams from the FCV, each equipped with a chainsaw, binoculars, aerial

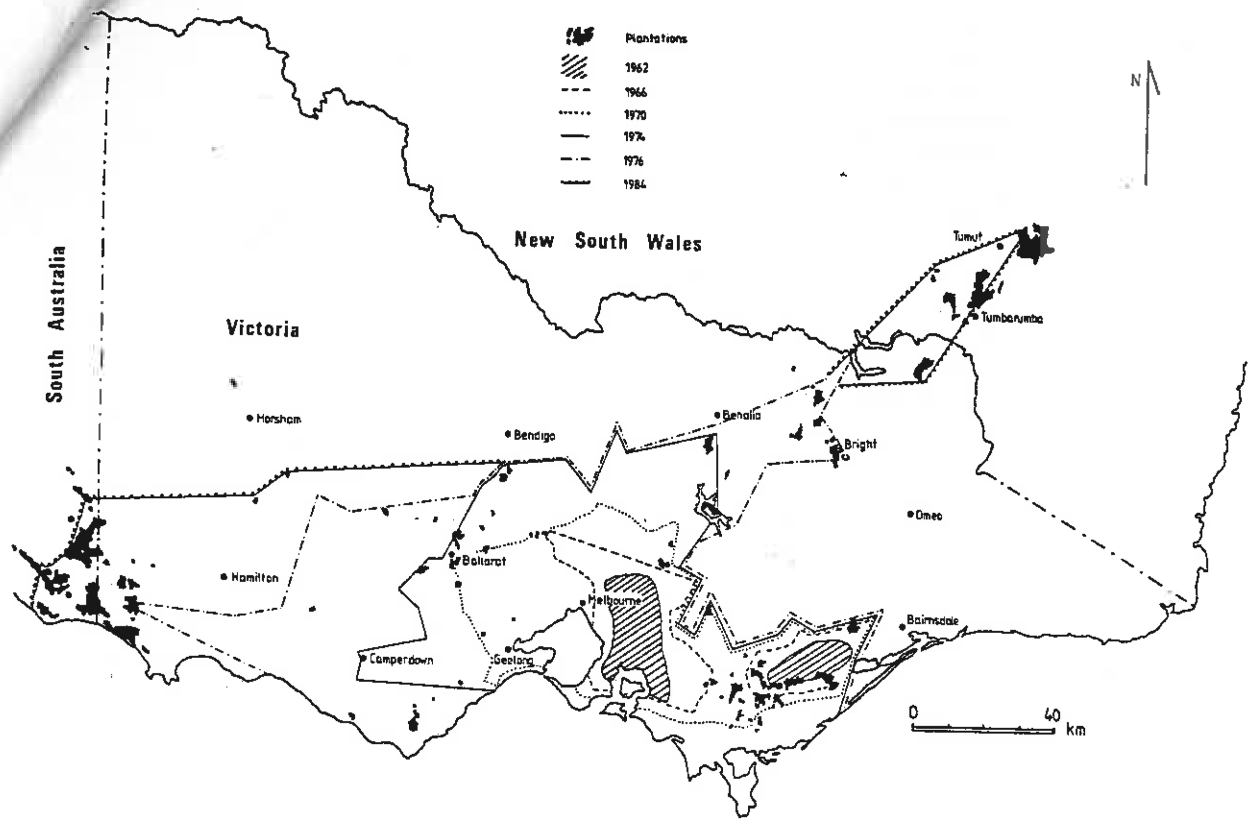


Fig. 1 *The spread of the sirex wasp (S. noctilio) over the period 1962 to 1984 in Victoria, South Australia and New South Wales. Biological control agents are now established throughout the distribution of the pest.*

photographs and county maps, systematically searched a wide range of counties in southern Victoria for infestations. To improve public awareness of the anti-sirex campaign, the survey teams travelled in vehicles painted canary-yellow to symbolise the Australian Quarantine Service and distributed appropriate literature.

For each property surveyed, the following data were recorded:

- the name of the property owner, the location and title details;
- a description of all standing coniferous trees and of trees felled since the previous inspection;
- the presence or otherwise of the sirex wasp;
- whether consent had been obtained for the destruction of infested trees, or of those suspected to contain the pest.

These survey and tree destruction activities were carried out under the QP32A provisions of the Commonwealth *Quarantine Act* 1908. All survey team leaders were appointed temporary quarantine officers by the Commonwealth Director-General of Health. Team leaders were thus empowered to order into quarantine all trees (or parts thereof) known or suspected to contain the wasp. The quarantine orders prohibited private landholders from removing pine trees from their properties without first obtaining an amendment to such orders. Amendments were issued by the Forests Commission's Forest Products Officer in appropriate cases, and the removal of trees was supervised by a softwood mill inspector trained in the detection of the pest. By the end of 1972, an area of approximately 2.5 million ha had been searched for sirex wasp infestations, and 4500 properties had been quarantined.

Both the Quarantine Act, and the Forests Regulations (1973) on diseases of trees pursuant to the Victorian *Forests Act* 1958, made it an offence for private landowners to have dead pine trees on their properties when these were located within sirex-infested areas. All destruction of dead trees was at the landowner's expense with no provision for compensation. Because of the urgency to have dying or recently dead pine trees destroyed, the National Sirex Fund Committee authorised the Forests Commission to expend money from the fund specifically for locating and burning trees infested by the sirex wasp on private land. The public co-operated well with the requirement to destroy sirex-infested trees, though some farmers

...ected to the compulsory directive to fell and ...urn dead trees which showed no symptoms of attack by the sirex wasp.

Due to rising costs associated with the labour-intensive systematic search and destruction of sirex-infested trees, and the realisation that the wasp could not be eradicated, biocontrol was adopted as the main strategy of control in 1972. This was based on the mass-breeding and subsequent release in the field of several species of wasp parasitoid and of a parasitic nematode, all of which had been successfully introduced into Australia by the CSIRO (Taylor 1967a). Greater emphasis was also placed on containing the pest within infested areas. The new measures also provided for frequent inspections of softwood mills, and the prohibition of transport of sawn pine wood to 'sirex-free' areas (unless milled to below 2.5cm thickness or kiln-dried), and of all untreated round wood. Preservative-treated round wood sawn from unhealthy trees, or recently dead trees, was not permitted to be transported outside the infested areas during the pest's pupal period between spring and autumn. The latter precaution was necessary because pupae and pharate (unemerged) adults occasionally survived pressure treatments (Neumann 1979).

Anti-sirex programs 1975-1985

Organisation and Funding

Funding by Commonwealth and State Governments for survey, research and control of the sirex wasp continued on the basis of the 1962 arrangements until 1974, when the Commonwealth Government took sole financial responsibility for the entire research program. Accordingly, the National Sirex Trust Fund was closed and the National Sirex Fund Committee and its two Sub-committees were dissolved. Subsequently, the States agreed to finance a continuing program of work relating to survey and control through a newly established State Sirex Trust Fund, without Commonwealth assistance. A new committee (the National Sirex Committee) was formed.

All sirex wasp research funded by the Commonwealth Government was terminated in 1978. However, in view of an unexpected severe outbreak of the pest in the presence of biocontrol agents in the Delatite Plantation near Mansfield during the mid 1970s, the FCV commenced a research program in 1979 aimed at improving the effectiveness of biocontrol agents. This work was completed in 1984.

In 1977, the National Sirex Committee was dissolved, and in 1978 the newly formed Forests Pests and Diseases Committee (subsequently renamed Forests and Forest Products Pests and Diseases Committee) of the Australian Forestry Council took over the administration of the State Sirex Trust Fund and the overall direction of the sirex campaign. This new Committee has been chaired since its inception by the Chief of the Division of Forest Research, CSIRO, and has included the following additional membership: ACT Forests, Commonwealth Department of Territories and Local Government; Australian Forest Development Institute; Department of Forestry, Queensland; Division of Entomology, CSIRO; Forests Department, Western Australia; Forestry Branch, Commonwealth Department of Primary Industry; Forestry Commission of New South Wales; Forestry Commission, Tasmania; Plant Quarantine Branch, Commonwealth Department of Health; State Forests and Lands Service, Department of Conservation, Forests and Lands (Victoria); and Woods and Forests Department, South Australia.

This change in the administration of the campaign was a logical step, in view of the withdrawal of CSIRO from sirex wasp research and the fact that the new Committee had been given responsibility for making arrangements with government and private organisations for funding recommended control programs on all nationally important exotic forest pests and diseases.

In 1982 the funding procedure was amended further by eliminating the State Sirex Trust Fund, and by the Victorian Department of Management and Budget providing a vote appropriation to meet costs. This change complied with the Victorian Government's objective to provide a comprehensive annual budget. Under this new scheme, Victoria is reimbursed each financial year by the other States/Territories according to the scale of contributions agreed to by the Forests and Forests Products Pests and Diseases Committee. In 1984/85 the percentage contribution rates by States/Territories to the anti-sirex campaign were: New South Wales 26.79, Victoria 22.90, Queensland 17.67, South Australia 13.61, Western Australia 9.31, Tasmania 6.86, and ACT Forests 2.86. The latter organisation commenced its contributions in 1983/84.

Funding of the sirex wasp survey and control program in mainland Australia has been progressively reduced from a peak of $315,720 in 1964/65 to $26,175 in 1984/85 (Figure 2). Up to mid-1985 the State Forests and Lands Service had been solely responsible for the culturing and supply of biocontrol agents of the wasp for use in Victoria and interstate, but in late 1985 this

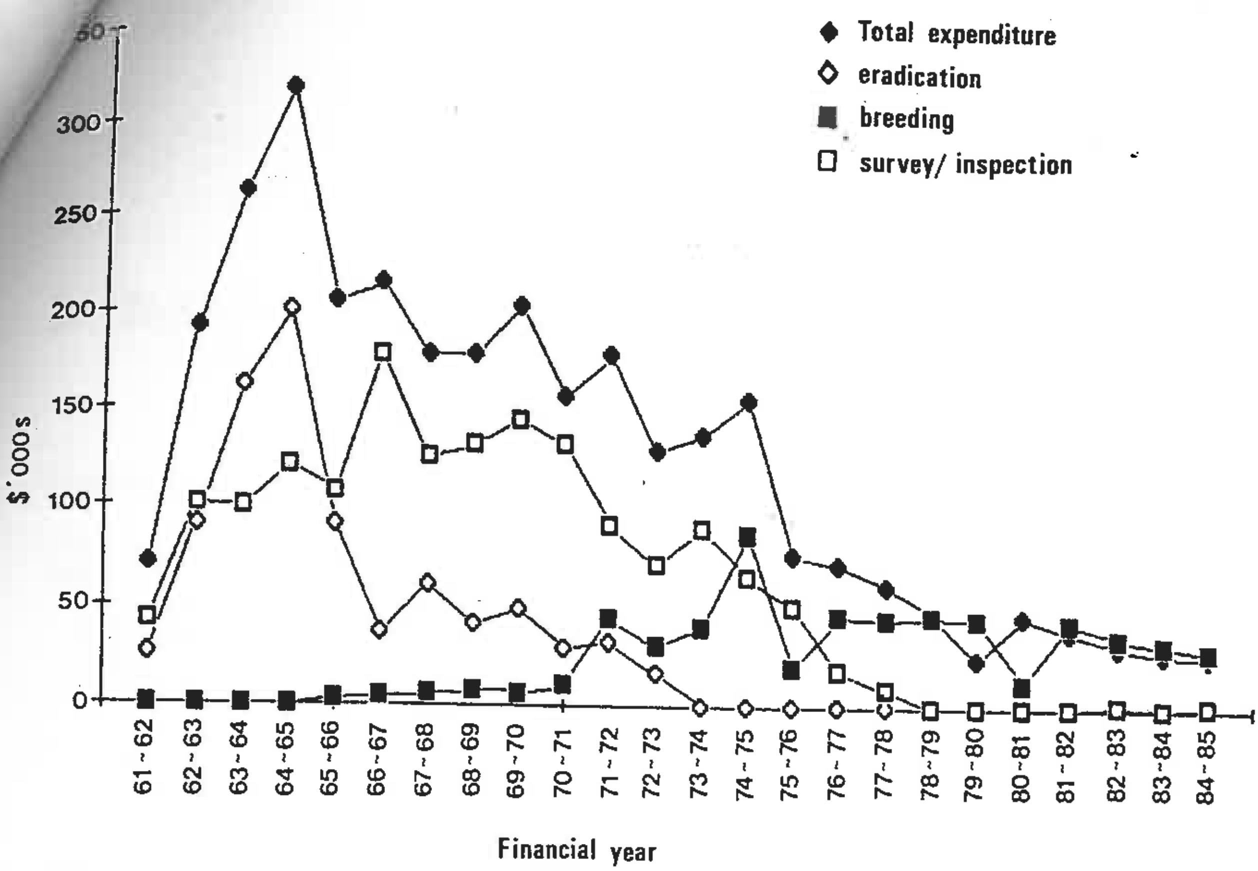


Fig. 2 *Annual costs of survey and control of the sirex wasp (S. noctilio) in mainland Australia, mainly in Victoria, over the period 1961/62 to 1984/85. The data exclude expenditure on research carried out principally by the CSIRO between 1961 and 1978, and by the Forests Commission Victoria between 1979 and 1984.*

function was transferred to the Land Protection Service of the Department. The biocontrol agents have been released mainly in Victoria, though in recent years the Australian Capital Territory, New South Wales and South Australia have been recipients.

Survey and Control

By 1974, the known sirex-infested area had increased substantially (Figure 1), and it became necessary to adopt low-cost methods for the surveillance of large areas. Visual aerial reconnaissance was phased in for detecting previously unreported dead or dying trees in plantations. For accurate delineation and evaluation of outbreak areas in plantations, aerial photography and photo interpretation followed by ground surveys were used. Vertical photography with infrared film at 1:9 000 or 1:12 000 scale was found to be satisfactory for providing both tree detail and adequate ground coverage (Ward *et al.* 1974; McKimm and Walls 1980).

Since the early 1980s, private and State-owned plantations have been checked annually for the occurence of sirex wasp by aerial reconnaissance, supplemented by routine surveillance from the ground by field staff familiar with local conditions, and by the preparation of sirex-sensitive 'trap' tree systems (see Chapter 6, 'Pest Management'). These procedures have shortened the time span between detection of the sirex wasp and action by specialists of the State Forests and Lands Service. The inspection of softwood mills has now ceased, and quarantine restrictions on private properties are no longer enforced on the grounds that the wasp is now present in all pine-growing regions of Victoria. From 1975 onward, the Forests (Part VI – Diseases of Trees) Regulations 1973, pursuant to the *Forests Act* 1958 (Vic.), have been used instead of the Quarantine Act.

2 TAXONOMY

Nomenclature and classification

The currently accepted taxonomic status of the species is:

Order: Hymenoptera;
Sub-order: Symphyta;
Family: Siricidae;
Sub-family: Siricinae;
Genus: *Sirex* Linnaeus, 1761;
Species: *noctilio* Fabricius, 1793;
Common Name: sirex wasp (CSIRO, 1980).
Previously known as the 'sirex woodwasp'.

Species recognition

The male adult is metallic dark-blue, except that wings, abdominal segments III to VII, and front and mid-legs are chestnut brown; the female is metallic dark-blue all over, except for the amber-coloured wings and legs (Plate 1). A sheath protecting an ovipositor (egg tube) projects 2 to 3 mm beyond the female abdomen. Antennae are hair-like and slightly pubescent, with 20 flagellar 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. Tyloides (sensory patches) are present ventrally on all flagellar segments. In the male, the hind legs are thick and powerful, but front and mid-legs are comparatively thin, as are all the legs of the female. The final abdominal segment of both sexes terminates in a prominent

Table 1. *Means and range (parentheses) of some morphometric measurements for larval instars I-VI and adults of the sirex wasp, collected from P. radiata host trees in north-eastern Victoria.*

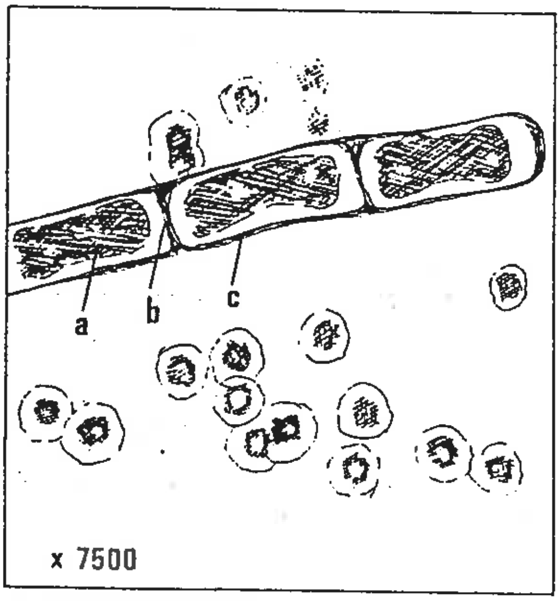
Instar	*No. of specimens examined*	*Headcapsule width (mm)*	*Body length (mm)*	*Thoracic width (mm)*	*Wing span (mm)*
I	*16*	*0.25*	*1.06*	*0.26*	–
		(0.20-0.33)	*(0.73-1.33)*	*(0.20-0.37)*	
II	*8*	*0.50*	*1.58*	*0.55*	–
		(0.40-0.57)	*(1.47-1.93)*	*(0.40-0.75)*	
III	*40*	*1.40*	*5.70*	*1.60*	–
		(1.00-1.70)	*(3.00-9.10)*	*(1.10-2.00)*	
IV	*19*	*2.00*	*11.40*	*2.50*	–
		(1.70-2.40)	*(9.00-16.00)*	*(1.60-3.90)*	
V	*21*	*2.94*	*19.92*	*4.73*	–
		(2.58-3.58)	*(15.00-23.95)*	*(3.83-5.33)*	
VI	*21*	*3.98*	*27.17*	*6.23*	–
		(3.50-4.60)	*(23.30-33.00)*	*(5.33-7.40)*	
Male pupa	*42*	–	*25.41*	*5.23*	–
			(7.50-34.25)	*(1.50-7.38)*	
Female pupa	*22*	–	*25.27*	*5.90*	–
			(8.20-38.40)	*(1.40-7.85)*	
Male adult	*100*	–	*25.00*	*5.43*[A]	*43.87*
			(9.30-34.90)	*(1.50-6.95)*	*(14.80-62.00)*
Female adult	*100*	–	*23.19*	*5.69*[A]	*39.06*
			(12.00-34.00)	*(2.20-7.20)*	*(21.40-60.00)*

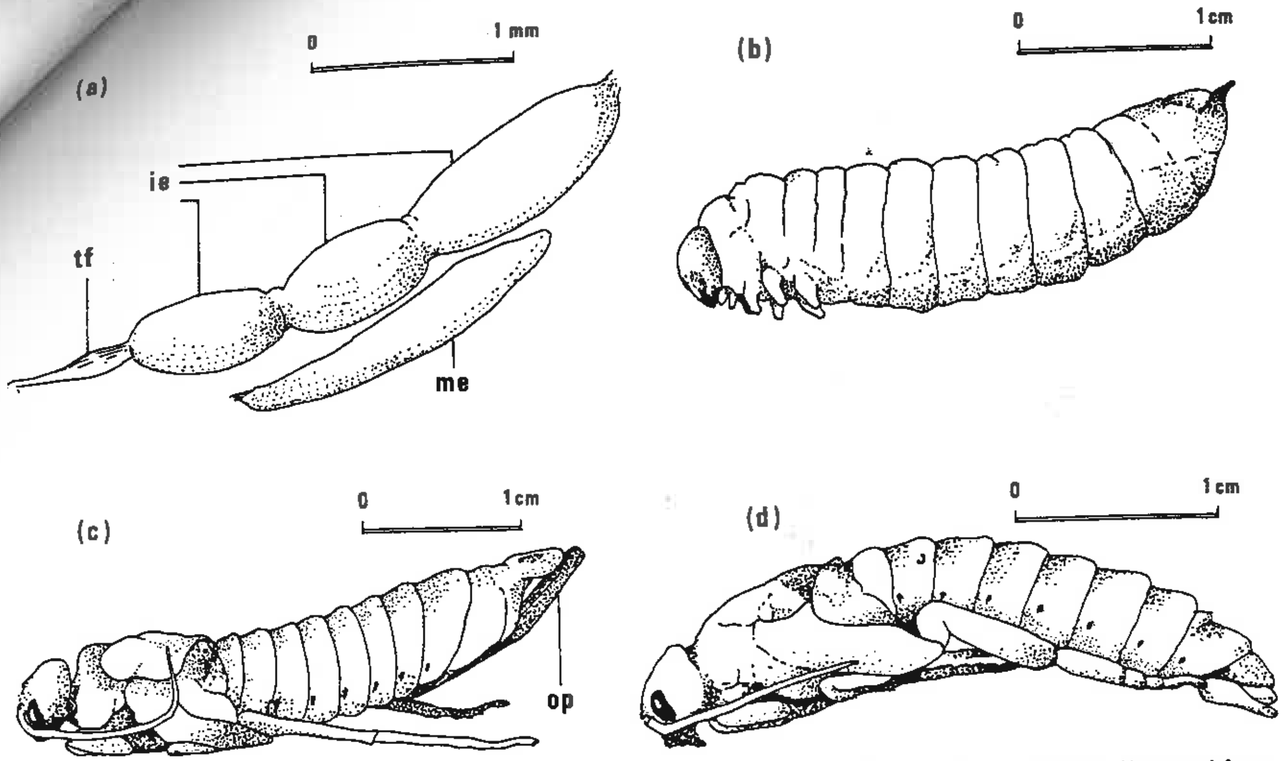
[A] *These means are based on 40 specimens.*

ADDENDA TO BULLETIN NO.30 'THE SIREX WASP IN VICTORIA'.

PLEASE PASTE THE CORRECTIONS ONTO PAGES 7 AND 11.

spine (cercus). White-eyed forms among males and females, and sterile gynandromorphs with varying ratios of male and female structures, occasionally emerge (Neumann 1970). Average dimensions of adults are shown in Table 1.
The egg (Figure 3a) is white, soft, smooth and elongate, with a mean length of 1.55 mm and width 0.28 mm (Neumann and Minko 1981).





Figs. 3a-d *Immature stages of the sirex wasp (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) lateral view of a female pupa with ovipositor (op); and (d) lateral view of a male pupa.*

The egg (Figure 3a) is white, soft, smooth and spine (cercus). White-eyed forms among males and females, and sterile gynandromorphs with varying ratios of male and female structures, occasionally emerge (Neumann 1970). Average dimensions of adults are shown in Table 1. elongate, with a mean length of 1.55 mm and width 0.28 mm (Neumann and Minko 1981). Egg length increases with female size. Regression equations describing relationships between mean egg length per female (y) and length of tibia III (x_1), body length (x_2) and wing span (x_3) for 10 females from north-eastern Victoria are respectively:
$y = 0.040x_1 + 1.249$ ($r = 0.865$, $P<0.01$);
$y = 0.011x_2 + 1.232$ ($r = 0.859$, $P<0.01$); and
$y = 0.006x_3 + 1.258$ ($r = 0.860$, $P<0.01$).

Larvae (Figure 3b) are creamy-white, deeply segmented, usually distinctly S-shaped, and of near-uniform diameter. Antennae are one-segmented, thoracic legs are short, and the abdomen is equipped with a conspicuous dark-brown to black sclerotic spine located distally. It is believed that this spine is used by the larvae for compressing frass (mixture of faeces, chewed wood and excretions) behind it during tunnelling activity through the wood, or it may be used for providing terminal support. Imprints of this single spine in tightly packed frass within galleries can be an important diagnostic feature in old timber suspected to have contained the wasp. The sexes of larvae are differentiated by the presence of three small brown sclerites on the ventral surface of the final abdominal segment in males and by two sclerites in females (Zondag and Nuttall 1977).

Prepupae and pupae (Figures 3c, d) are creamy white, the latter gradually assuming the colouration of adults. Average dimensions of pupae are shown in Table 1.

3 BIOLOGY

Life history and behaviour

In Victoria, the life cycle of the sirex wasp is normally completed in one year (Figure 4), though some individuals may pass through a 2 ½ to 3-months cycle between summer and mid-autumn, and about 9% undergo a 2-year cycle.

Eggs usually hatch within 14 days of oviposition between mid summer and early autumn, though some may remain dormant for several months.

Larvae construct galleries that are oriented principally along the wood grain. The galleries are sickle-shaped in longitudinal section and near circular in cross-section. A complete gallery, extending from the initial oviposition puncture to the flight hole, can measure between 5 and 26 cm in length, and vary from an initial width of about 0.3mm to a final width of between 3.5 and 9 mm (see Plate 3d, e).

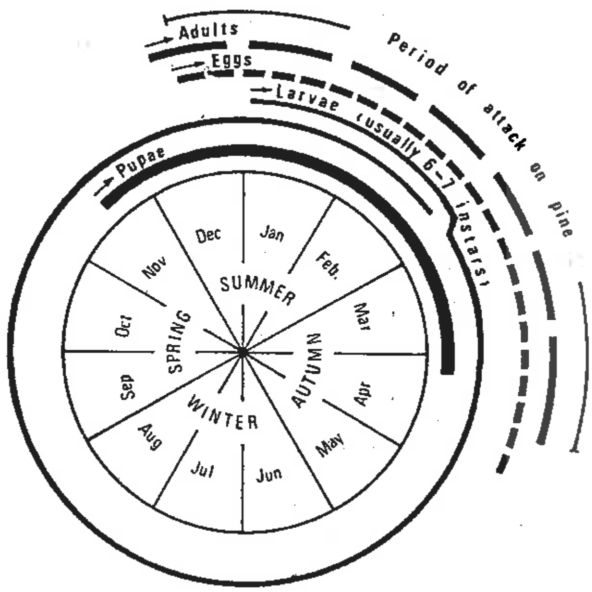


Fig. 4 *Annual life cycle of the sirex wasp (S. noctilio) in Victoria. Some individuals have shorter or longer cycles (see text) (After Neumann and Minko 1981).*

Six or sometimes seven larval instars usually develop before pupation in outer sapwood. Taylor (1981) has recorded up to 12 instars in the cooler Tasmanian climate, suggesting that the rate of larval development is dependent upon ambient temperature. In Victoria a minimum of five moults generally appears necessary before pupation can occur, though the senior author has observed the emergence after only three larval moults of tiny male wasps from small-diameter pine stems 2 ½ to 3 months after oviposition (see the lower range of values in Table 1).

Emergence of adults is usually most marked during mid summer (Figure 5), but the pattern and duration of emergence can vary considerably in different climates. A second emergence peak, associated to some extent with short-life-cycle individuals, occasionally occurs during autumn. Dispersal is through several powerful flights of short duration. In New Zealand and Tasmania it has extended over several kilometres per year (Zondag and Nuttall 1977; Taylor 1981), and up to 30 kilometres per year have been recorded in south-western Victoria. The female life span seldom exceeds five days and that of males 12 days during warm summer weather, and about two weeks for both sexes during cool autumn weather.

Emergents are sexually mature, so that mating followed by attack on pine hosts proceeds without delay. Mating appears to be initiated by female wasps when in close proximity to males in tree crowns (Morgan and Stewart 1966), though in the Mountain Forest Research Station insectary at Sherbrooke near Melbourne, mating occurs prolifically in the free space above pine billets of 1.8 m length stacked vertically side by side. Males respond to female signals by fluttering their wings and playing on the body of females with their front legs and antennae. Receptive females come

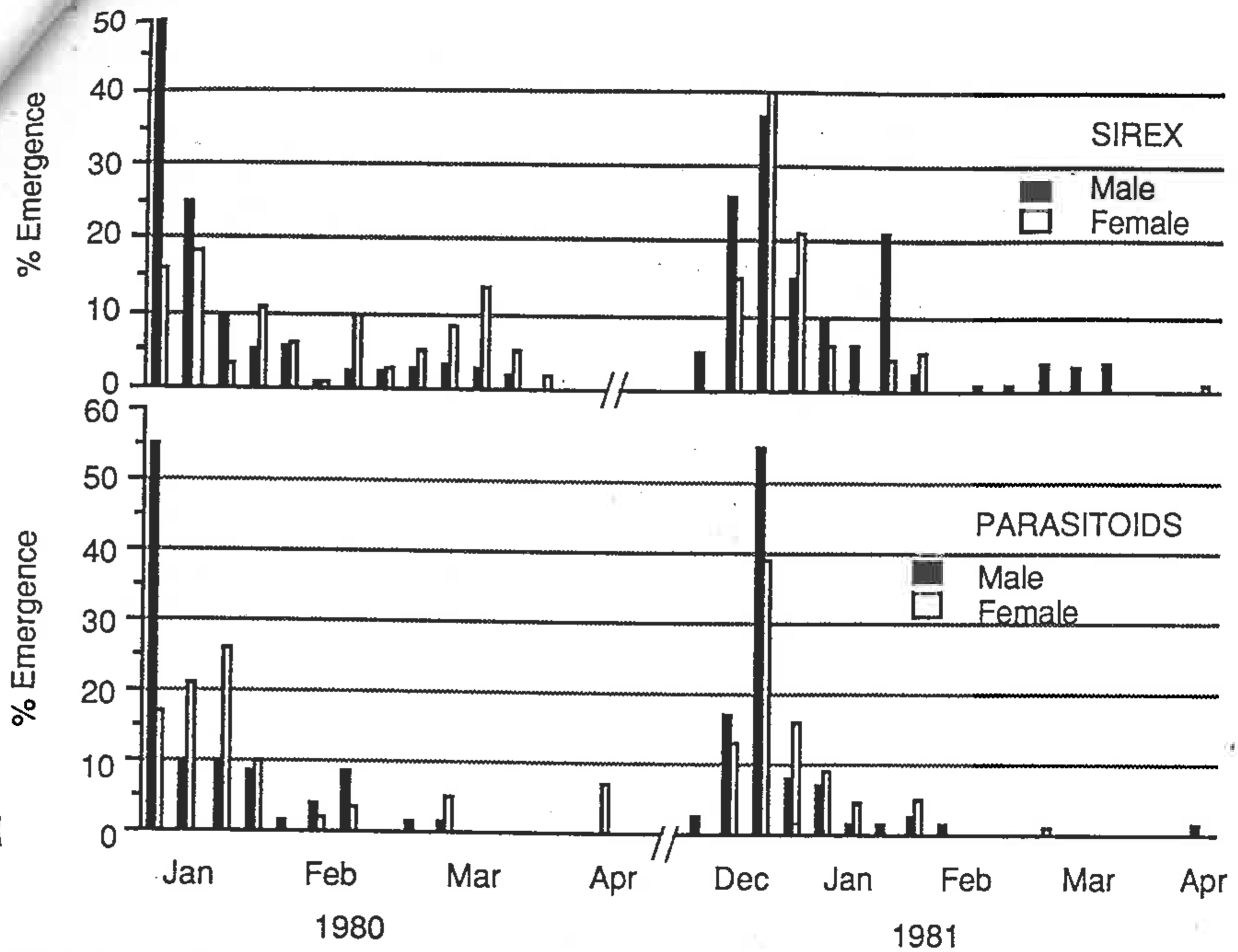


Fig. 5 *Mean weekly emergence of the sirex wasp (S. noctilio) and of the pool of parasitoids (Ibalia spp. and Megarhyssa spp.) from caged host material placed within a pine plantation during 1980 and 1981 in north-eastern Victoria (The data are based on 1557 sirex wasp and 518 parasitoid emergents. Bar graphs are independent, and originate at the base line for each sex).*

to rest and copulation occurs. Temperatures above 21°C and sunny conditions appear important in stimulating copulation, as is a preponderance of male over female wasps. The latter requirement has prevailed in most plantations in Victoria.

Egg laying

Oviposition (egg laying) usually begins near the base of the tree. The female subsequently works up the stem to below the top and then gradually returns to the base. Females bore both single and multiple drills about 12 mm deep into sapwood while stationed at the one position on the bark surface (Table 2, Plate 4a). Single drills are generally injected only with colourless phytotoxic mucus and arthrospores of the mildly pathogenic sirex fungus (Talbot 1964; King 1966; Gaut 1969; Coutts 1969a, b), and are made mainly for testing the suitability of the substrate for oviposition, or for predisposing trees to successful attack. In multiple drill groups, the early drills usually contain a single egg each, and the final drill contains mucus and arthrospores (Coutts and Dolezal 1969). Single drills are mainly made at sites where the osmotic pressure of the phloem sap is high (>1210 kPa), and multiple drills where osmotic pressures are low (200 kPa-810 kPa), indicating that oviposition frequency is dependent on the physiological condition of the tree host (Madden 1974).

Reproductive potential

Egg content (potential fecundity) increases with female size (Madden 1974). On the basis of correlations between egg contents and female size parameters (Figure 6), the average-sized female in Victoria contains about 212 eggs (range: 21-458, n = 100). Taking this mean value for fecundity (F), and assuming a sex ratio (SR) of 0.25 (proportion of females in the population, calculated for 3648 emergents from caged billets over the period 1970 to 1981), and also assuming annual life cycles and zero mortality of life-stages,

Table 2. *Drill-type data (mean ± standard error) for the sirex wasp (S. noctilio) assessed for billets of 2 m length randomly selected from killed trees in a P. radiata plantation of intermediate-age in north-eastern Victoria.*

Year of S. noctilio attack	*No. of billets examined*	*Drill-type frequency per billet:*				*Total no. of drill holes per billet*	*Estimated no. of eggs oviposited per billet*[B]
		Single	*Double*	*Treble*	*Quadruple*[A]		
1980	*19*[C]	*18.3*	*25.6*	*12.6*	*2.6*	*119.3*	*45.4*
		±2.7	*±5.9*	*±2.9*	*±0.4*	*±27.4*	*±10.4*
	24[D]	*31.4*	*40.8*	*21.3*	*3.8*	*192.5*	*71.8*
		±5.7	*±8.9*	*±4.6*	*±0.8*	*±42.0*	*±15.7*
1981	*30*[D]	*181.0*	*109.0*	*46.8*	*11.2*	*584.5*	*184.1*
		±25.1	*±9.6*	*±4.3*	*±1.6*	*±51.0*	*±14.4*

[A] *Pooled with the low number of quintuple types detected.*
[B] *Estimates are based on means of 0.04, 0.7, 1.6 and 2.3 eggs per single, double, treble and quadruple drill-type respectively (Madden 1974).*
[C] *Billets free of the parasitic nematode Deladenus siricidicola.*
[D] *Billets naturally infected with D. siricidicola nematodes by nematode-sterilised S. noctilio during oviposition activity. No nematode-free billets were found in 1981.*

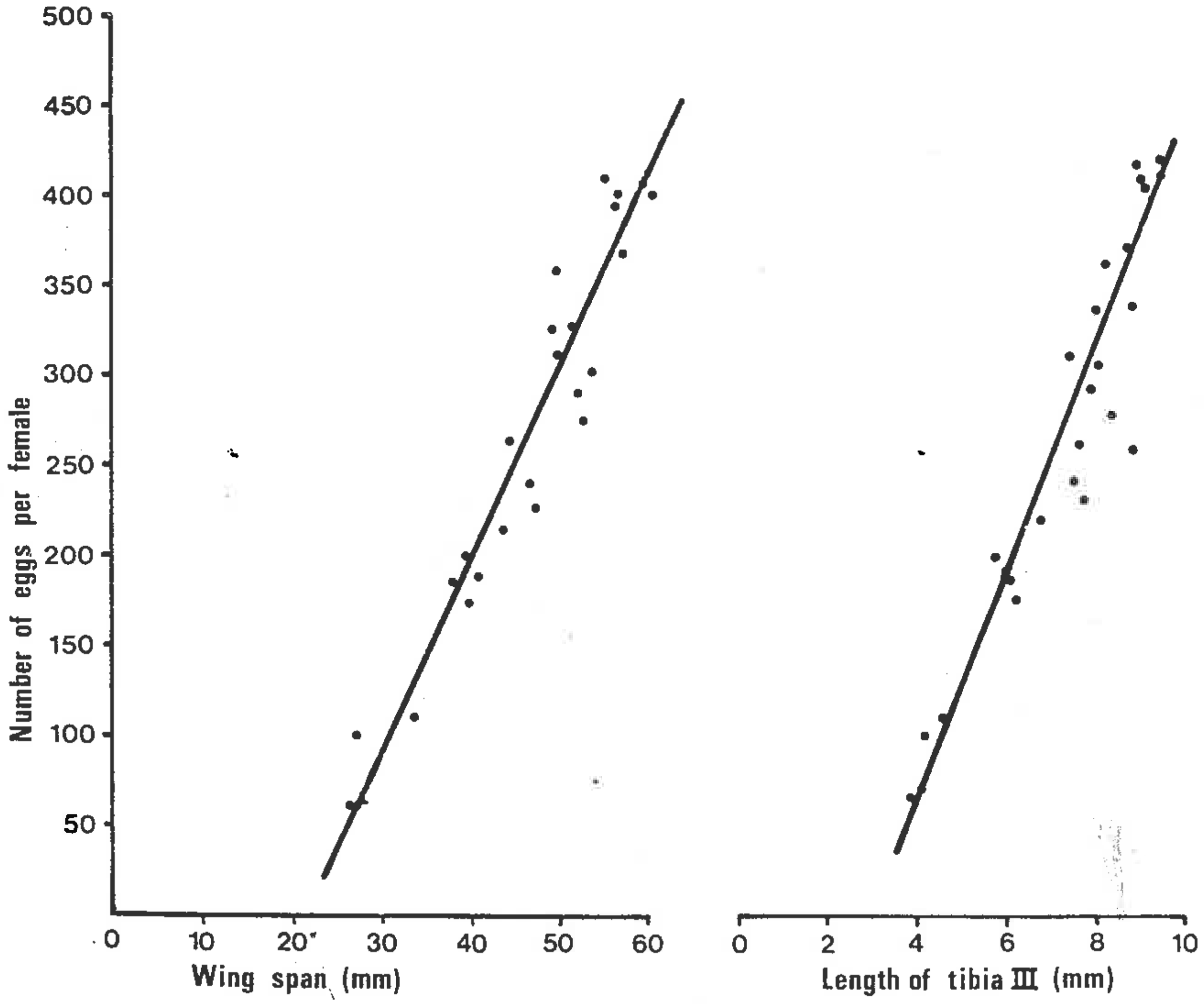


Fig. 6 *Relationships between potential fecundity and size parameters of female sirex wasps (S. noctilio) collected in north-eastern Victoria.*

It follows that in Victoria the annual reproductive potential (RP) per fertilised female (RP = F×SR) is about 53 females. Sex determination in the wasp (as in all Hymenoptera) is by male haploidy and female diploidy, so that males arise from unfertilised eggs and are hence fatherless. Stray virgin females may therefore oviposit and produce only a male population with no capacity to survive. Such short-lived infestations, which have been associated with tree deaths, have been recorded in several Victorian plantations.

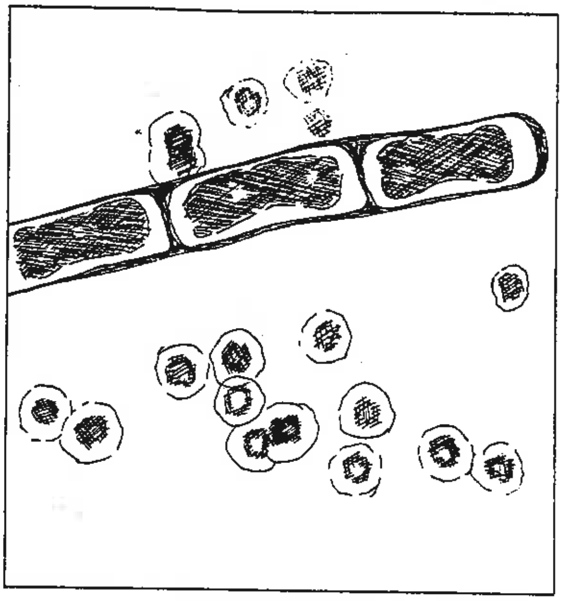


Fig. 7 *Arthrospores of the sirex fungus (A. areolatum) within a parental hypha, from a culture on V_8 agar. The arthrospores are multinucleate and homokaryotic (Gaut 1969): (a) arthrospore; (b) crosswall; (c) parental hyphal wall.*

Mortality

In the field, the females seldom discharge their full complement of eggs, and death may intervene at any stage of the life cycle. At 23°C and 45% relative humidity, which correspond to near ideal ambient conditions for oviposition (Madden 1974), females from Victoria exposed to males on freshly-felled green pine material laid an average of 82.6% (range 38.4-100%, n = 114) of their estimated egg content, whereas those on three to four-week-old pine billets, or on seasoned pine, died without ovipositing. In addition, not all eggs that are oviposited are viable, and some become non-viable during incubation (Table 3).

Common causes of sirex wasp decline in Victorian plantations are:

- effective compartmentalisation (Shigo 1979) in the host tree of sapwood tissues containing the sirex fungus, phytotoxic mucus, eggs or early instar larvae;
- lethal or sterilising effects of introduced biocontrol agents;
- effective isolation of the nutritive sirex fungus by fungistatic polyphenol barriers resulting in starvation of larvae;
- starvation of larvae from lack of nutrients as a result of antagonism between saprophytic blue-stain fungi and the sirex fungus (Coutts 1965; King 1966);
- inability of pharate adults to emerge from host material;
- predation by birds or small mammals on ovipositing females; and
- copious amounts of resin, very high moisture levels, or the effects of entomophagous fungi.

Table 3. *Estimates of egg mortality (mean ± standard error) for the sirex wasp (S. noctilio), assessed in autumn 1981 from a random sample of 40 billets 1 m in length derived from sirex-killed trees in a 17-year-old unthinned P. radiata plantation in north-eastern Victoria.*

No. of adult emergents per billet		*Estimated no. of eggs laid by parental females*	*No. of instar 1 larval galleries*	*Proportion of non-viable eggs*
Male	*Female*	*per billet*[A]	*per billet*[B]	*per billet*[C] *(%)*
20.6 ± 3.2	*7.4 ± 1.0*	*59.3 ± 7.3*	*43.6 ± 5.1*	*27.9 ± 3.7*

[A] *Estimated by using Madden's (1974) 'drill type-egg numbers' conversion factors, and on the following means for drill-types per billet: 25 singles, 34 doubles, 17 trebles, and 3 quadruples and quintuples.*
[B] *Assessed by tallying numbers of galleries associated with oviposition drills.*

[C] *Assessed using the formula* $Me = \frac{1}{n}\sum_{i}^{n} 100(E_i - G_i)E_i^{-1}$,

where Me = mean percentage egg mortality per billet; E = estimated no. of eggs oviposited per billet, G = no. of instar I larval galleries per billet, and n = number of billets (Neumann and Morey 1984).

...ationship with fungal symbiont

The sirex wasp has co-evolved with the sirex fungus (Figure 7) into a symbiotic association, in which insect and fungal pathogen are mutually interdependent for survival (Büchner 1928; Cartwright 1929, 1938; Clark 1933). Thus the sirex wasp cannot act alone, and as a result, interactions between it and its obligate fungal symbiont and tree hosts are complex.

The sirex fungus 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), and causes dry white rot of the wood (Gilmour 1965; King 1966), thereby facilitating the tunnelling activity of larvae. In turn, female adults ensure the conservation and dispersal of the sirex fungus by placing its arthrospores into the sapwood of susceptible hosts during oviposition.

Instar II larvae of prospective females acquire mycelium of the sirex fungus from infected wood (Boros 1968) and store the fungus in paired abdominal skinfolds (hypopleural organs) (Parkin 1942) until these are discarded during metamorphosis. Pharate adult females re-acquire the mycelium of the fungus and keep it within paired mycangia near the base of the ovipositor (Büchner 1928) (Figure 8). Within the mycangia of wasp emergents, fungal hyphae have conspicuous clamp connections and contain numerous arthrospores, indicating that the sirex fungus is in an active condition during the insect's period of attack.

The phytotoxic mucus injected into the outer sapwood appears to stimulate the germination and early growth of the sirex fungus (King 1966; Boros 1968; Titze and Turnbull 1970; Kile and Turnbull 1974). The mucus, which is synthesised within paired internal secretory glands and stored in a 10-25 mg capacity reservoir (Coutts 1969b) ducted to the base of the ovipositor (Figure 8; c, d, e), consists of protein – polysaccharides (molecular weights about 60×10^3 to 100×10^3) mixed with enzymes such as amylases, esterases, phenol oxidases, and proteolases (Fong and Crowden 1976).

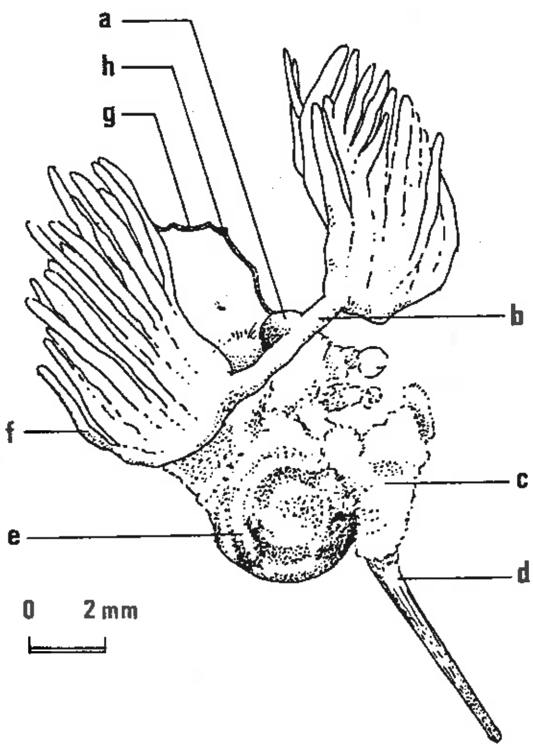


Fig. 8 *Aspects of the reproductive system of the female sirex wasp (S. Noctilio): (a) mycangium; (b) lateral oviduct; (c) mucus gland; (d) ovipositor; (e) mucus reservoir; (f) mature egg within ovariole; (g) nerve-cord; and (h) abdominal nerve ganglion (After Neumann and Minko 1981).*

4 CONDITIONS, MECHANISM AND SYMPTOMS OF ATTACK

Effect of tree condition on susceptibility

The sirex wasp is attracted to trees that are suppressed, drought-stressed, nutritionally deprived or otherwise weakened by insect or fungal defoliators. Trees damaged by wind, hail, lightning, snow and by thinning or high-pruning operations are also highly susceptible, as are green logs and large diameter green slash. Trees and logs of these categories are described as being in the 'predisposition phase'.

In an infested 17-year-old unthinned *P. radiata* plantation near Mansfield in east-central Victoria, the level of tree mortality (or tree susceptibility) was significantly ($P > 0.001$) related to stem diameter at breast height over bark (DBHOB) (Figure 9). The susceptibility threshold in terms of DBHOB was between 23 and 26 cm. Below 23 cm DBHOB, significantly more trees had been killed than survived ($P > 0.001$). Above 26 cm DBHOB, the number of survivors was significantly greater than the number of deaths

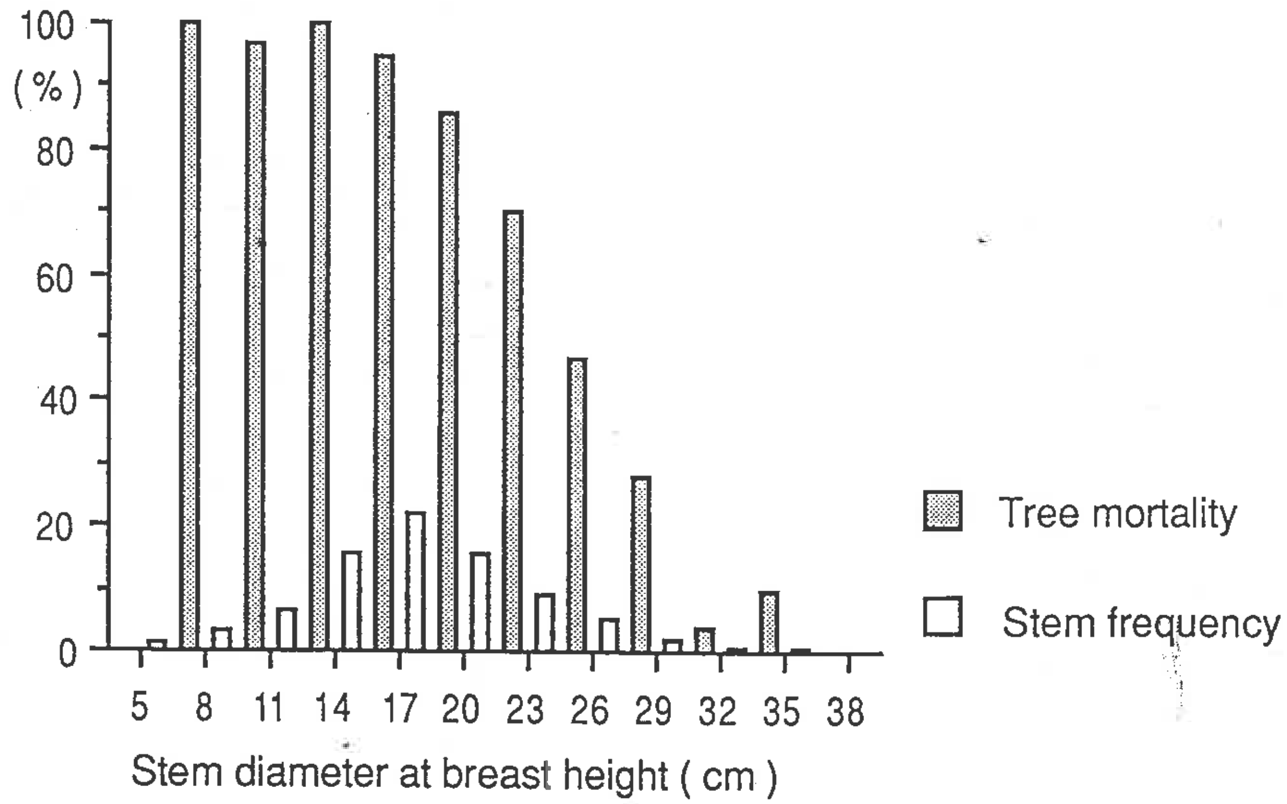


Fig. 9 *Tree mortality and stem frequency relative to stem diameter at breast height over bark, in an unthinned 17-year-old stand of P. radiata in east-central Victoria, following the collapse of an outbreak of the sirex wasp (S. noctilio) (The data are based on 1571 trees).*

	Number of trees:		
Tree shape	Killed	Healthy	Total
Single-stemmed	680 (61%)	434 (39%)	1114
Multi-stemmed	386 (84%)	71 (16%)	457

Table 4. Tally of killed and healthy P. radiata trees among single and multi-stemmed categories within 1 ha of an unthinned 17-year-old stand in east-central Victoria, following an outbreak of the sirex wasp (S. noctilio).

($P > 0.001$). Trees larger than 35 cm DBHOB remained healthy. Also, multi-stemmed trees were significantly more susceptible to death from sirex wasp attack than single-stemmed trees ($P < 0.001$) (Table 4).

The timing and duration of attractiveness of trees or material of pine to the wasp 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 material are important in the attraction of the wasp (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, isopinacamphone and camphor) and the alcohol *trans*-pinocarveol. Of this wide range of compounds, the vapours from the ketones, the alcohol, and about half of the monoterpene compounds have elicited the strongest responses in female antennae of the sirex wasp (Simpson 1976), and hence appear to be the prime pine-produced substances capable of stimulating the nervous system of the wasp.

Simpson and McQuilkin (1976) further showed that the ketone and alcohol vapours emitted by freshly cut *P. radiata* logs increase from trace amounts to approximately 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 green logs over the same period. Metabolic change in living woody tissue therefore seems to be a necessary requisite for increased emission of ketone and alcohol volatiles, whereas any rise in monoterpene vapour levels may be due solely to greater bark permeability (Madden 1977a). The ketone and alcohol compounds are being synthesised in increasing amounts during the period when the attractiveness of pine to the wasp is diminishing. However, it is not clear whether they act as repellents or as chemical agents capable of neutralising the effects of attractant monoterpenes.

Pathogenic mechanism of attack

The principal physiological, entomological and pathological events associated with sirex wasp attack can be described in terms of an initial 'predisposition phase', followed by a 'stress reinforcement phase' and a 'sirex fungus – wasp development phase'. These phases need to occur consecutively if tree death and substantial wood degrade are to follow.

Trees enter the predisposition phase when they are damaged or physiologically stressed by environmental factors or by man's activities. Predisposed trees usually have:

- a low rate of mitotic cell division in stem cambia, but above-average transpiration and respiration rates;
- a high water tension (due to moisture stress) in vascular systems, associated with low cell turgor and low resin pressures in wood;
- stem phloem that is nutritionally deprived, partially dehydrated and partially aerated, and with sap of low osmotic pressure ($\leqq$ 800 kPa); and
- above-average bark permeability associated with high rates of emission of attractant pine volatiles (Coutts 1969a, b; Titze and Mucha 1965; Coutts and Dolezal 1966; Madden 1968, 1971, 1974, 1977a).

The stress reinforcement phase is initiated when females inject phytotoxic mucus into the outer sapwood of trees (Figure 10). This mucus is usually rapidly translocated into foliage, where it elicits a complex syndrome of adverse reactions such as:

- a cessation of mitosis 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
- a breakdown of chlorophyll followed by the collapse of water-conducting vascular tissues, causing chlorosis, wilting and premature needle fall (Coutts 1969a, 1969b, 1970; Fong and Crowden 1973; Spradbery 1973).

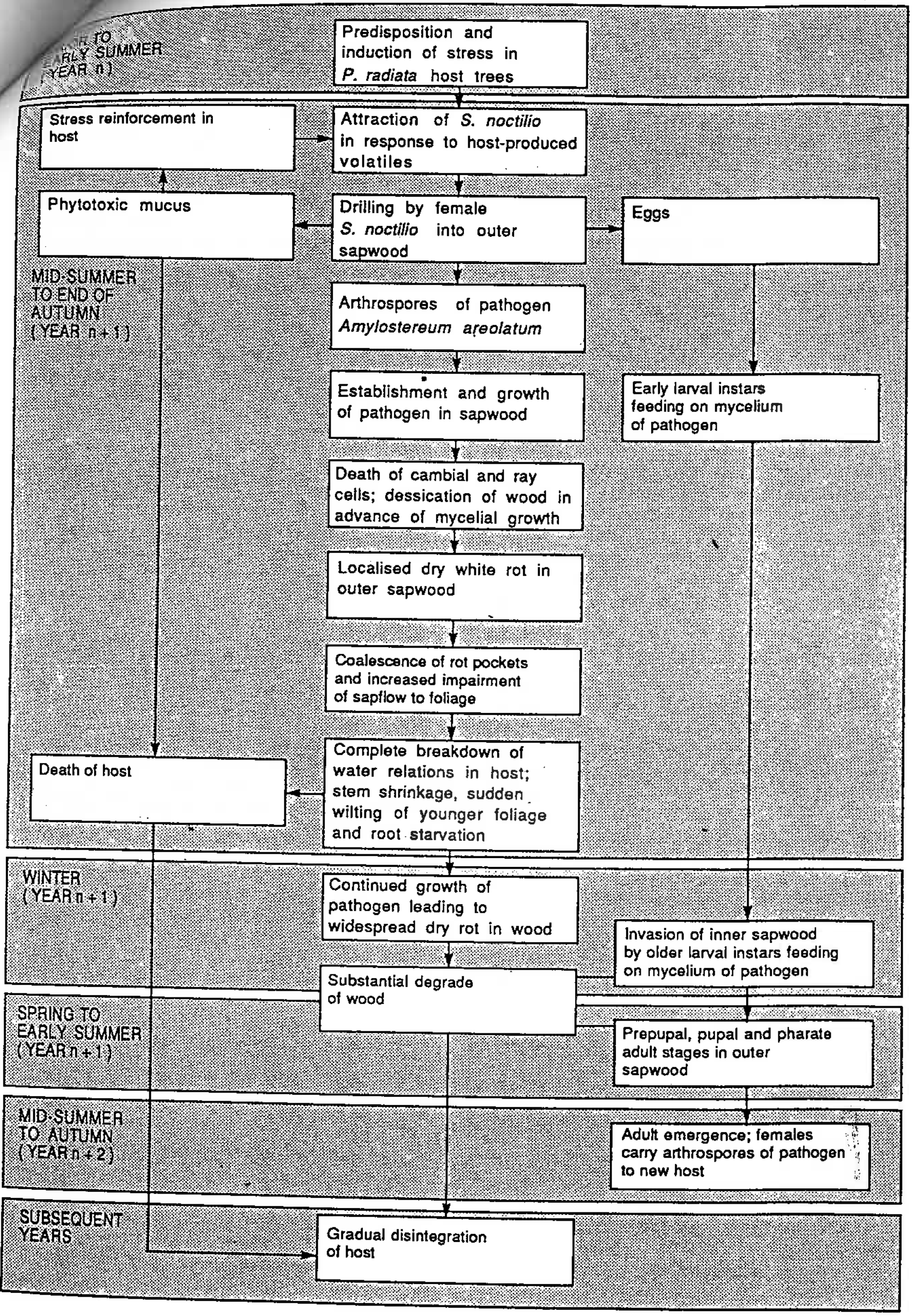


Fig. 10 *A summary of physiological, entomological and pathological events associated with attack by the sirex wasp (S. noctilio) on P. radiata trees (After Neumann and Minko 1981).*

... stem phloem and outer sapwood of predisposed and mucus-stressed trees, conditions are usually favourable for the initiation of the sirex fungus – wasp development phase (Figure 10) (Coutts 1969a; Titze and Turnbull 1970; Kile and Turnbull 1974). Subsequent growth of the sirex fungus leads to death of cells in the phloem, cambium and rays, and to desiccation of the wood ahead of the fungal mycelium. Hyphae invade water-conducting and supporting tracheids via pits, or by dissolving cell walls at points of contact (King 1966) (Plates 2a-c). The sirex fungus spreads significantly faster along the wood grain than in either radial or tangential directions across the grain (Coutts 1965). In the outer sapwood of a tree stem, increased levels of infection around oviposition drills create conditions conducive to the hatching of eggs and subsequent growth of sirex wasp larvae. The roots of the tree become starved as the destruction of phloem tissues proceeds and the water movements within the tree break down completely and irreversibly. After tree death, significant wood degrade occurs as a result of advancing dry rot and drilling activity by sirex wasp larvae. Finally, the disintegration of the host tree is brought about by the action of saprophytic decay fungi, weather factors, and other insects such as termites (Plates 3a-c).

Consequently, predisposed trees die because of the effects of the phytotoxic mucus and the sirex fungus; both factors were shown by Coutts (1969b) to be lethal to radiata pine in combination. The wood-boring larvae take no part in killing the tree, and merely degrade the wood. In Victoria sirex wasp attacks peak between mid-summer and mid-autumn when soil moisture is generally limited and when growth rates and the carbohydrate levels in the phloem sap of pine trees are declining rapidly to a minimum (Fielding 1966; Madden 1977b). Thus inoculation of phytotoxic mucus and arthrospores of the sirex fungus occurs at a time when the tree's resistance to pests and disease is low, so that the attacked tree dies fairly rapidly. In Victoria, this occurs between six weeks and several months after attack.

Symptoms

External symptoms of sirex wasp attack are: progressive and irreversible needle chlorosis (yellowing) terminating in distinct copper-brown discolourations; sudden wilting of old foliage and then of current generation foliage; heavy needle fall with the onset of warmer weather in spring; and finally, death and decay (Plates 3a, b). Numerous resin blobs and, sometimes, small resin flows are visible on the bark surfaces of stems. In the outer sapwood distinct narrow bands of brownish fungal staining can be observed, mainly along the grain. Single or multiple oviposition drills of approximately 0.14 mm diameter, and dry non-resinous phloem and outer sapwood, are also symptomatic of sirex wasp attack.

The nature of the larval galleries, with their increasing diameter over length, their orientation principally along the wood grain and their tightly packed granular frass contents are indicators of sirex wasp attack (Plates 3d, e). So too are circular flight holes (mean diameter 5.57 mm, range 3.3-7.3, $n = 100$), and hollow pupal chambers in the outer sapwood.

Resistance of trees to attack

Trees which are best able to resist sirex wasp attack appear to be those that have sustained no physical injury and have consistently grown vigorously on good sites in well-managed stands, producing sustained patterns of relatively wide growth-rings. The resistance capacity may also have a genetic basis, because the foliage of some *P. radiata* clones is not adversely affected by phytotoxic mucus (Coutts 1969b; Kile *et al.* 1974). In addition, wasp development can fail in some trees, yet be successful in nearby trees of similar size. Resistance mechanisms involve a rapid and extensive resin flow into wasp-induced lesions; effective isolation of infected wood by fungistatic polyphenol barriers; early fall of needles carrying high loads of phytotoxic mucus; and growth of new functional tissues of phloem, cambium and xylem around lesions.

Drilling by female sirex wasps is usually sparse in trees that are unattractive and resistant, so that the loads of eggs, of mucus and of the sirex fungus remain low. The inhibitory effects of resin on the sirex fungus may be both physical and chemical in origin; thus, resin may engulf and kill the mycelium, and resin volatiles (especially α- and β- pinenes) may effectively check fungal growth (Kile and Turnbull 1974). In tissues around lesions, the synthesis of fungistatic polyphenols seems to be triggered by rising levels of ethylene (Shain and Hillis 1972), produced when soluble carbohydrates are abundant (Hillis 1962). The polyphenols, comprised mainly of pinosylvin and pinosylvin mono-methyl ether (Hillis and Inoue 1968), become concentrated around the margins of resin-impregnated lesions, which are thereby encapsuled and checked (Coutts and Dolezal 1966).

5 EPIDEMIOLOGY AND DAMAGE CAPACITY (CASE HISTORY)

Background

In southern Victoria during the 1960s, many valuable pine shelterbelts on farmland were destroyed by the wasp. Substantial tree mortality has also occurred in privately-owned *P. radiata* plantations in various localities of Central Gippsland, south-eastern Victoria (Table 5).

A protracted severe outbreak of the sirex wasp during the 1970s in the 1906 ha Delatite Plantation near Mansfield in east-central Victoria afforded an opportunity to study outbreak development and decline (epidemiology) and the damage caused by this pest in a Victorian commercial *P. radiata* plantation (Figure 11). This plantation had been established between 1959 and 1968 on cleared land that contained remnants of the original dry sclerophyll forest of predominantly *Eucalyptus polyanthemos* Schauer (red box), *E. macrorhyncha* F. Muell. ex Benth. (red stringybark), *E. melliodora* A. Cunn. ex Schauer (yellow box), *E. camaldulensis* Dehnh. (river red gum) and *E. goniocalyx* F. Muell. ex Miq. (long-leaf box)†. The soils are Ordovician or Silurian clay loams. There is a 10° northerly aspect, the average annual rainfall is 934 mm, and the mean

†Nomenclature after Willis (1972).

Table 5. *Tree mortality induced by the sirex wasp (S. noctilio), and expenditure for control by felling and burning during the 1960s in P. radiata plantations owned by APM Forests Pty. Ltd. in Central Gippsland, Victoria.*

Emergence season	*Locality*	*Total no. of sirex-killed trees detected*	*Control costs in year of emergence ($)*	*Control costs in real terms based on 1984 values ($)*[A]
1962-63	*Longford*	*526*	*45 154*	*205 472*
1963-64	*Longford, Stockdale*	*188*	*35 492*	*160 400*
1964-65	*Longford, Flynn, Silver Creek*	*633*	*33 550*	*145 788*
1965-66	*Longford, Flynn, Maryvale*	*1 032*	*8 883*	*37 252*
1966-67	*Longford, Flynn, Maryvale*	*2 571*	*13 664*	*55 745*
1967-68	*Longford, Glencoe, Maryvale, Boola, Silver Creek, Flynn*	*3 081*	*13 623*	*53 639*
1968-69	*Longford, Glencoe, Maryvale, Boola*	*2 447*	*4 490*	*17 252*
Totals		*10 478*	*154 856*	*675 548*

Source: APM Forests Pty. Ltd. (unpublished data).
[A] *The 1984 monetary values have been computed by considering annual movements in the CPI as in Figure 2.*

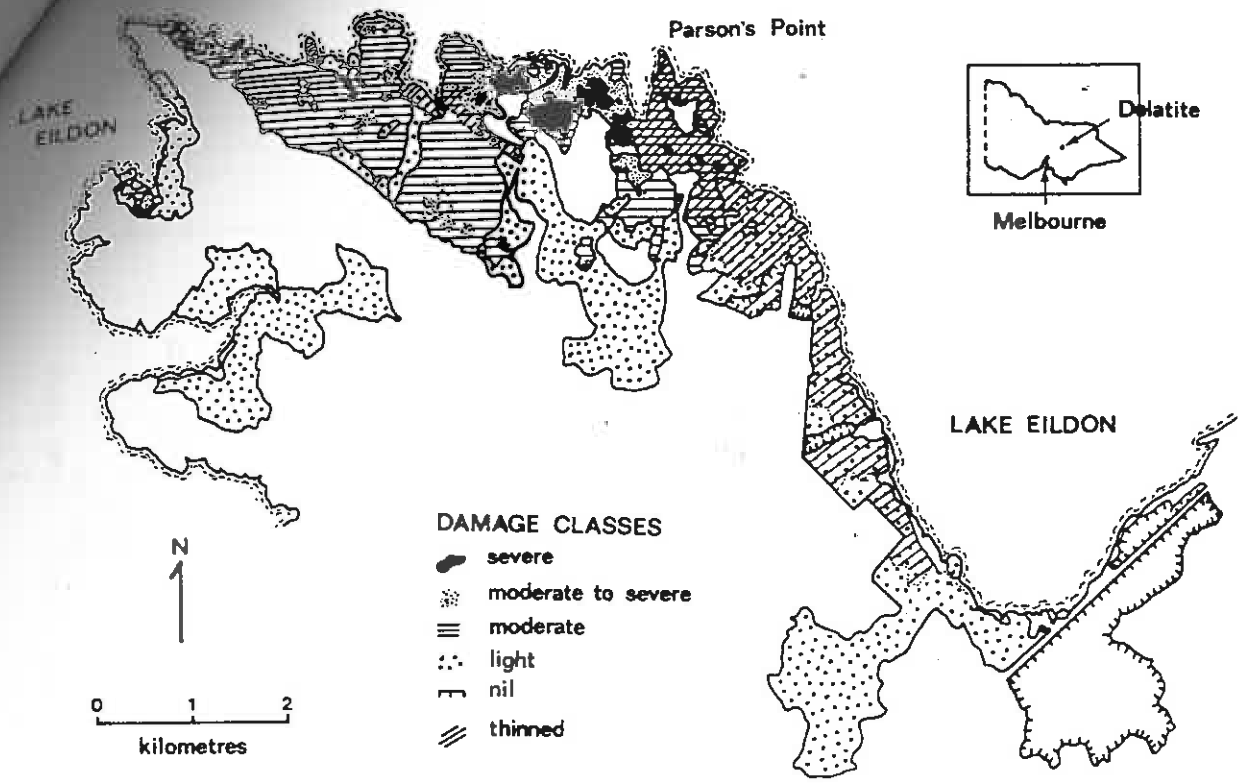


Fig. 11 *Delatite Plantation in east-central Victoria, showing areas of different damage classes in thinned and unthinned stands of P. radiata as assessed in 1979.*

daily maximum and minimum temperatures average 27.7°C and 12.2°C during summer and 12.2°C and 3.9°C during winter.

The trees had been planted at a spacing of 2.4 m × 2.4 m, providing an initial stocking density of about 1700 stems ha^{-1}. Out-row thinning (one row in three) was applied at about 14 years, mainly to stands planted between 1959 and 1961. These operations were suspended in 1975 due to poor demand for small-diameter round timber, so that by 1979, approximately 82% (1572 ha) of the plantation, all of which was at a sirex-susceptible age, had remained unthinned (McKimm and Walls 1980).

Outbreak history

A female adult sirex wasp was discovered fortuitously in water by a fisherman near the Delatite Plantation in January 1972. A subsequent intensive ground survey established that there were only two trees with emergence holes from the 1971-72 flight season, and 10 trees containing the immature progeny of the initial parental population. Sirex-specific wasp parasitoids were introduced into the plantation during the 1972/73 sirex wasp flight season and also a parasitic nematode in mid 1975. Because these biocontrol agents were subsequently found established in the plantation, it was thought that the population of the pest would remain at a low uneconomic level. However in autumn 1976, an increasing number of dead trees riddled by sirex wasp flight holes was detected, especially in the older unthinned stands. This indicated an intensification of the wasp problem, which reached a peak by the end of the 1976/77 flight season in both unthinned and thinned stands, but subsequently declined to negligible levels in 1979 (McKimm and Walls 1980).

Monthly rainfall data for 1971-79, recorded at nearby Lake Eildon for specific ecological periods of the wasp's life cycle (Figure 12), suggests that the sudden substantial rise in sirex wasp activity in autumn 1975, followed by peak activity two years later, was associated with drought-induced tree stress. The much lower than average rainfall recorded during the attack period between January and April in both 1975 and 1976 probably resulted in a substantial reduction of the already depressed levels of tree resistance normally prevailing at that time of year against attack. The continuation of drought conditions over a 6-month period until November 1976, followed by another eight months of below-average rainfall

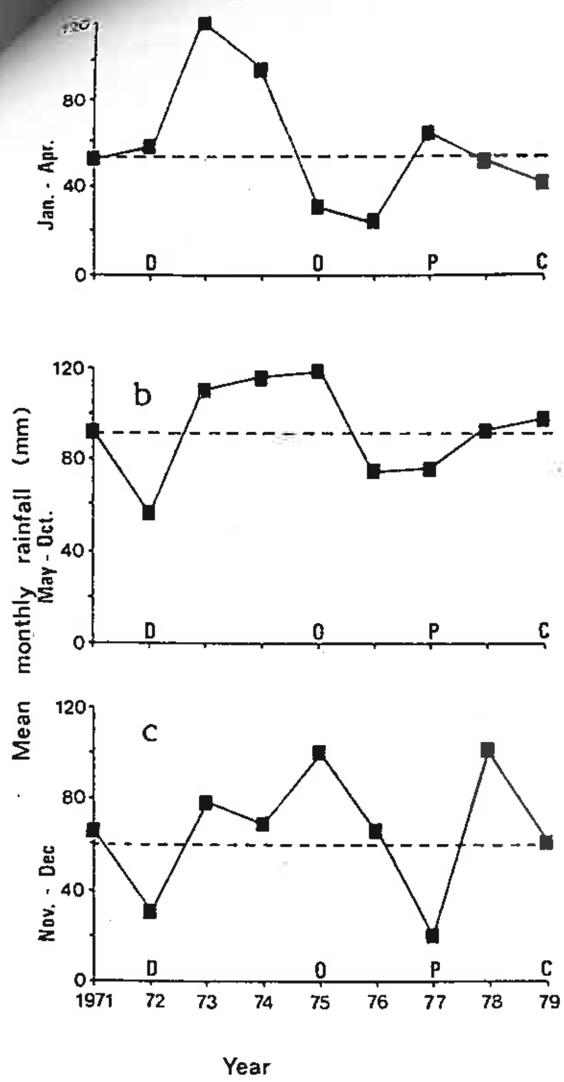


Fig. 12 *Mean monthly rainfall (■——■) at Lake Eildon near Delatite between 1971 and 1979 compared with the 20-year-mean monthly averages (– – –) for each of the following ecological periods pertaining to the sirex wasp (S. noctilio): (a) the principal flight and attack period (4 months, January-April); (b) the principal larval period within host trees (6 months, May-October); and (c) the principal late instar larval, pupal and pharate adult period within host trees (2 months, November-December). Symbols: D = year of sirex wasp detection; O = year of outbreak release; P = peak outbreak year; C = year of population collapse.*

in 1977, undoubtedly worsened existing moisture stress in trees, lowered their resistance even further and allowed a rapid build-up of sirex wasp populations in the plantation.

The decline in sirex wasp populations during 1978 and their collapse in 1979 was probably due to the effects of several factors including; a return to near-average or better rainfall levels; a substantial increase in the proportion of large-diameter and more resistant trees among the residual tree populations; and an increase in nematode-induced sterility among adult female wasps.

Extent of damage

Until 1979, in unthinned stands aged between 12 and 15 years, an average of 77% of trees were killed on 25 ha of plantation (severe damage class), 63% on 79 ha (moderate to severe damage class), 35% on 379 ha (moderate damage class) and 5% on 701 ha (light damage class);

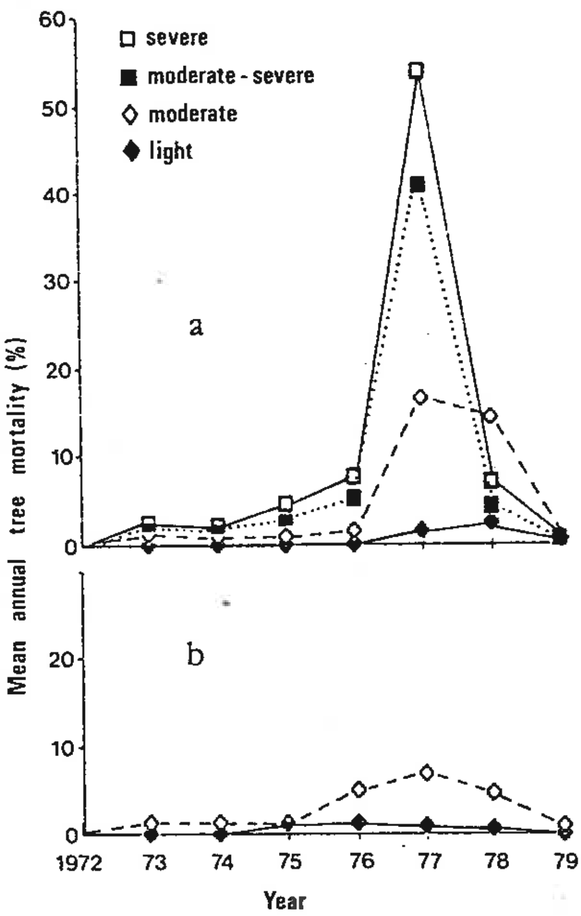


Fig. 13 *Mean annual tree mortality due to sirex wasp (S. noctilio) attack between 1972 and 1979, categorised by damage classes in (a) unthinned and (b) thinned stands of P. radiata in the Delatite Plantation, east-central Victoria. The means are based on an assessment of 10 plots each containing 30 trees per damage class. The damage classes refer to cumulative percentages of killed trees since 1972 as follows: severe >65% trees killed; moderate to severe 40-64%; moderate 15-39%; and light 1-14%.*

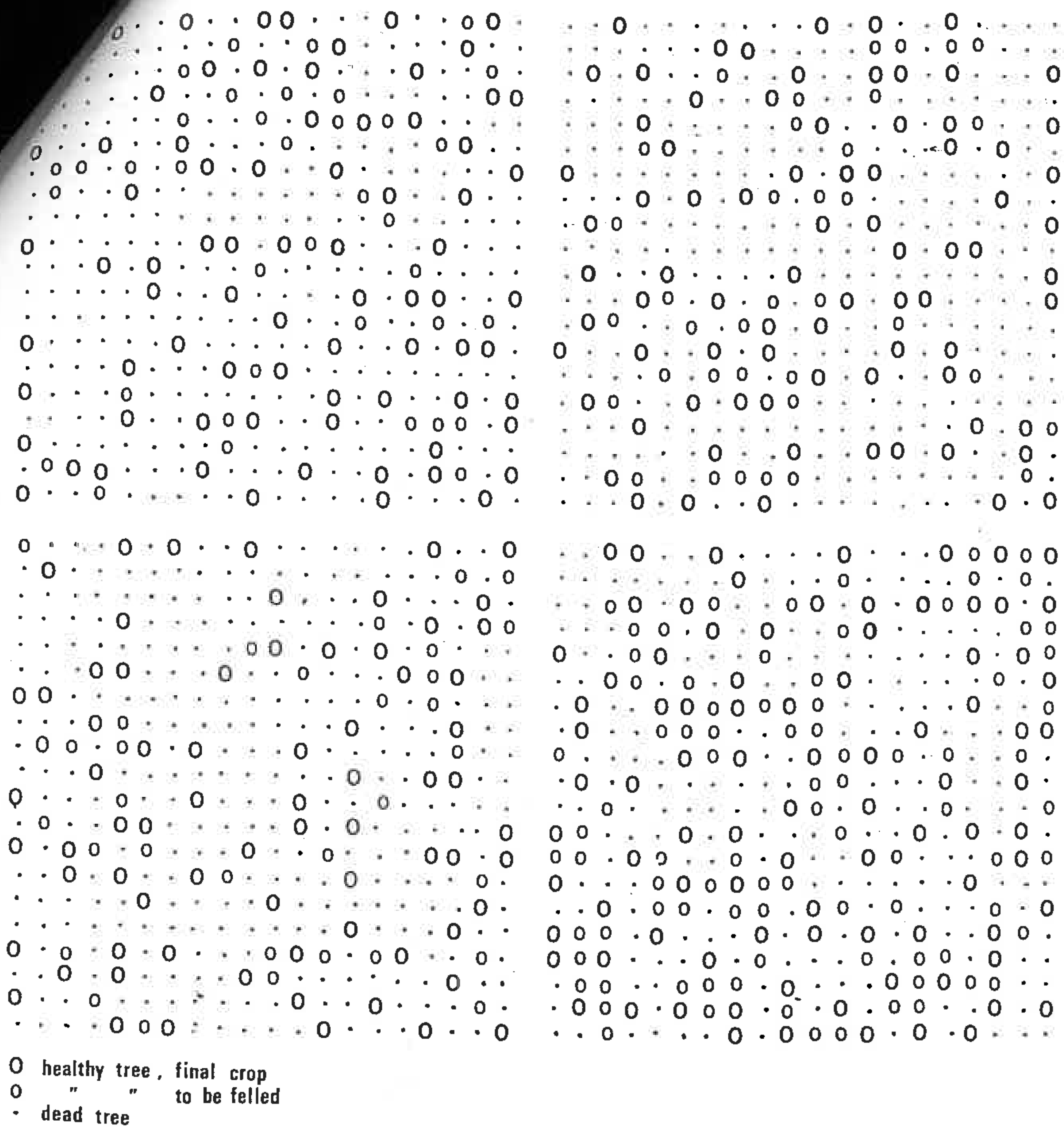


Fig. 14 *The distribution of healthy and killed trees in four 0.25 ha plots located in severely damaged, unthinned 17-year-old stands at the end of the sirex wasp outbreak in 1979 in Delatite Plantation, east-central Victoria. Also shown are the positions of trees that need to be felled to prevent competition between final crop trees (After Neumann and Minko 1981).*

approximately 390 ha of the 10 and 11-year-old unthinned stands remained uninfested. In the thinned stands, aged 16 to 18 years, 26% of trees were killed on 78 ha (moderate damage class) and 5% on 256 ha (light damage class) after 1975. Thus, severe damage or moderate to severe damage due to attack by the sirex wasp did not occur in the thinned stands. Only 20% (388 ha) of the entire plantation remained free from damage, all of which had been planted in 1967 and 1968.

Figure 13 shows that in both unthinned and thinned stands, tree losses rose sharply in 1976, peaked in 1977 and then declined to negligible levels in 1979. In the worst affected stands, the sirex wasp had reduced stocking to less than 420 stems ha^{-1}. Surviving trees were unevenly distributed, and about one third of these needed to be felled to prevent inter-tree competition (Figure 14). With this subsequent thinning, the final stocking density was expected to be about

...le 6. *Stem diameters for P. radiata trees killed by S. noctilio compared with healthy trees in various damage ...asses within thinned and unthinned stands in the Delatite Plantation (After McKimm and Walls 1980).*

Silvi-cultural treatment	*Damage class (cumulative % of trees killed since 1972)*	*Mean DBHOB^A (cm) for 300 trees per damage class in:* 1977		1978		1979	
		Killed	*Healthy*	*Killed*	*Healthy*	*Killed*	*Healthy*
Unthinned	*Severe (>65%)*	18.9	21.6	—	—	—	—
	Moderate to severe (40-64%)	18.4	21.2	18.3	21.2	—	—
	Moderate (15-39%)	16.6	20.5	16.0	21.0	—	—
	Light (1-14%)^B	14.3	18.0	16.3	19.7	17.4	21.3
Thinned	*Moderate (15-39%)*	19.8	23.1	19.3	24.9	—	—
	Light (1-14%)^B	18.2	21.8	20.8	23.9	21.7	25.3

^A DBHOB, stem diameter at breast height (1.30 m) over bark.
^B Trees in the light damage class in both unthinned and thinned stands were of younger age and hence of smaller average diameter than those in the higher damage class.

the 280 stems ha^{-1} usually aimed at in Victoria during a second thinning before age 20 years.

The surviving trees were vulnerable to damage by wind and fire, particularly during the early post-outbreak period. Also, the eventual harvesting of mature trees (usually at age 40 years) was expected to be difficult and costly, due to the likely presence of intermediate-age natural regeneration in clearings. Thus, the ultimate effect of the sirex wasp on stocking in severely damaged stands may be greater than is indicated here (McKimm and Walls 1980, Neumann and Minko 1981).

The cumulative tree losses incurred in the moderately damaged unthinned stands (35% on 379 ha) were probably due to large wasp populations combined with a high proportion of susceptible trees, especially in 1977 and 1978. The stocking density had been reduced to 1100 stems ha^{-1}, a level that corresponds approximately to the prescribed stocking after a first thinning.

The thinning achieved as a consequence of wasp attack was selective; the smaller trees were preferentially killed ($P < 0.05$) irrespective of the level of damage, the year of attack or the silvicultural treatment imposed (Table 6). The range of susceptible tree sizes increased progressively whenever an attack was sustained over several years. Up to 1979 the cumulative loss in merchantable wood volume (to 10 cm under bark small-end diameter) was approximately 35 500 m^3 in unthinned stands and 2500 m^3 in thinned stands. These losses were equivalent to 12% of the total 1979 merchantable wood volume in the entire plantation (McKimm and Walls 1980). However in the worst affected stands, total wood volume and merchantable volume were reduced by 50.4% and 48.1% respectively (Neumann and Minko 1981).