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Experimental studies on the responses of European siricid woodwasps to host trees

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SUMMARY

A study was made of the oviposition responses of the siricid woodwasps, *Sirex noctilio, S. juvencus, S. cyaneus* and *Urocerus gigas* to experimentally debilitated spruce and pine trees. Treatments included felled, fire-burned, logged and girdled trees which were treated at intervals before bioassay with cages siricid females. In comparable treatments, *S. noctilio* showed a distinct preference for pines although it was quite successful on spruce while the other siricid species displayed a preference for spruce. The *Sirex* species successfully attacked more recently treated material although *U. gigas* showed a preference for timber in a more advanced state of debility. All species showed preferences for girdled trees although other treatments were also favoured by the different siricid species. Overall, the siricids preferred the area above the girdle irrespective of tree species and there was a higher rate of eggs above the girdle in treated spruce trees. A wide range of moisture content in the timber appeared to have no effect on drilling activity or the successful development of eggs. The response of a wild population of *S. juvencus* to the treated spruce is also described. The results are discussed in relation to the ecology of Siricidae in Europe and the establishment of *S. noctilio* in Australia. It is suggested that of the species studied, only *S. noctilio* poses a serious threat to the living pine stands of Australia.

INTRODUCTION

There have been few records of siricid woodwasps causing primary damage in European forests, yet the introduced *Sirex noctilio* F. has caused wide-spread losses in the exotic radiata pine forests of New Zealand (Rawlings, 1948) and Australia (Irvine, 1962; Coutts, 1965; Mucha, 1967).

During oviposition activity, siricid woodwasps drill into timber with their ovipositor and, as well as laying eggs, inject arthrospores of a symbiotic fungus, *Amylostereum*, and a mucus secretion (Spradbery, 1977). Coutts (1969*a*, *b*) demonstrated that toxicosis results from the additive effect of the mucus secretion and symbiotic fungus. *S. noctilio* drilling activity functions to assess tress, single drills indicating a rejection response and multiple drills with eggs a favourable response (Madden, 1968, 1974). The single drill made into the timber by *Sirex* species is exploratory and contains only mucus and spores of the symbiotic fungus (Coutts, 1965). In a multiple drill (see Fig. 1), eggs are laid in one or two of the drills but the last drill made at the site contains only mucus and fungal spores (Coutts & Dolezal, 1969). The mucus conditions the tree for the developing fungus which in turn provides food for the growing siricid larvae. *Urocerus gigas* L. makes relatively long single drills with many eggs separated by fungal spores (Fig. 1). A comparison of the phytotoxicity of European siricid species confirmed that *S. noctilio* is the only species capable of killing trees but also showed that this capacity was much reduced under European conditions (Spradbery, 1973).

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This paper describes experiments made to clarify some aspects of siricid ecology in relation to host material.

MATERIAL AND METHODS

Field experiments were made in a Scots pine (*Pinus sylvestris*) plantation in Swinley Forest, Ascot, and a spruce (*Picea sitchensis*) plantation in Windsor Forest. The trees were 30–40 years old.

Tree treatments were as follows: felled trees; standing trees with a 10 cm girdle 1·5 m from ground level; trees with an area of 1 m × 50 cm of trunk burned with a blowtorch to kill the cambium; and 1 m length logs. The trees were treated at two-monthly intervals from December 1968 to August 1969.

During the flight period of *S. noctilio*, *S. juvencus* L., *S. cyaneus* F. and *U. gigas* (see Spradbery & Kirk, 1978), five females aged 1–2 days were confined to the timber using Terylene gauze netting secured to strips of foam rubber (8 × 8 cm in cross section) placed around the timber to form 50 cm long cylindrical cages. On girdled trees, cages were placed above and below the girdle. Availability of siricid females determined the numbers of treated trees bioassayed and the number of replicates. *S. noctilio* and *S. juvencus* females were also caged to living, untreated spruce and pine trees controls and oviposition activity was determined by dissecting the timber 14 months later. At the time of bioassay, wood samples were taken with a core sampler in the vicinity of the cages and the moisture content was expressed on an oven-dry weight basis.

During the winter, all timber exposed to the siricids was examined for total numbers of drill groups and at least 50 groups per replicate were dissected for number of drills per group (single, double or treble), eggs laid and early larval stages.

The oviposition activity of a wild population of *S. juvencus* at the Windsor Forest site was also evaluated. All treated spruce were checked for oviposition drills and one untreated living spruce with a natural *S. juvencus* infestation was also examined.

RESULTS

Influence of moisture content

There was no correlation between the moisture content of the wood near the oviposition sites and the number of drills or proportion of single to multiple drills, number of eggs per drill or egg development. The range in moisture content was 25–255% of the dry weight with successful development of eggs occurring in timber with maximum moisture contents of 135% (*S. noctilio*) and 120% (*U. gigas*).

Tree species

The oviposition responses of caged siricid females to treated timber are given in Tables 1–5.

Treated pine trees received 29–34% of the total drills by *S. juvencus*, *S. cyaneus* and *U. gigas*, compared with 63% of the *S. noctilio* drills ($P < 0{\cdot}01$). The proportion of single, test drills made by *S. noctilio* into pine was 53% compared with 80% into spruce ($P < 0{\cdot}01$). There was no difference in the proportion of single drills made by *S. cyaneus* in response to the two tree species.

There was no statistical difference in the number of eggs per drill made by the *Sirex* species in response to treated pine and spruce but *U. gigas* laid more eggs per drill in spruce ($P < 0{\cdot}05$). A higher proportion of *S. juvencus* and *S. cyaneus* hatched successfully in spruce compared with pine ($P < 0{\cdot}01$). There was no difference in hatching of *S. noctilio* eggs attributable to tree species. *S. noctilio* did not oviposit readily in untreated spruce controls but 160 drills of which 67% were multiple drills were recorded in untreated pines. Of the drills sampled, eggs were laid

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Table 1. *The response of* Sirex noctilio *to treated timber* (*4–5 replicates per treatment*)

Treatment	Mean number of drills* per treatment	% multiple drills	Eggs per drill	% hatch of eggs	Mean no. larvae developed
A. PINE					
Girdled (above)	351	51·1	0·72	20·0	51
Girdled (below)	161	31·0	0·66	29·7	32
Felled	164	44·7	0·32	1·7	1
Logs	2	0	0·18	0	0
Fireburn	158	61·4	0·66	29·2	30
Controls	160	67·2	0·62	29·1	3
B. SPRUCE					
Girdled (above)	94	20·1	0·44	29·2	12
Girdled (below)	66	15·5	0·42	27·2	8
Felled	152	26·2	0·42	39·0	25
Fireburn	148	18·2	0·56	43·4	36
Controls	12	10·1	0·31	18·3	1

* A single, double or treble drill with a single puncture through the bark is counted as one drill.

Table 2. *The response of* Sirex juvencus *to treated timber* (*5 replicates per treatment*)

Treatment	Mean number of drills* per treatment	% multiple drills	Eggs per drill	% hatch of eggs	Mean no. larvae developed
A. PINE					
Girdled (above)	113	52·4	0·84	6·2	6
Girdled (below)	68	24·9	0·68	0	0
Felled	89	73·0	0·70	17·0	11
Logs	45	50·9	0·84	10·0	4
Controls	0	—	—	—	—
B. SPRUCE					
Girdled (above)	193	67·1	0·90	68·8	120
Girdled (below)	169	60·4	0·80	52·0	70
Felled	209	50·2	0·98	64·0	131
Logs	184	53·1	0·83	39·5	60
Fireburn	78	32·9	0·95	35·5	26
Controls	112	73·8	0·78	50·2	24

* A single, double or treble drill with a single puncture through the bark is counted as one drill.

Table 3. *The response of* Sirex cyaneus *to treated trees* (*4–5 replicates per treatment*)

Treatment	Mean number of drills* per treatment	% multiple drills	Eggs per drill	% hatch of eggs	Mean no. larvae developed
A. PINE					
Girdled (above)	55	34·3	1·40	5·4	4
Girdled (below)	28	15·9	1·45	4·3	2
B. SPRUCE					
Girdled (above)	97	47·0	1·44	51·2	72
Girdled (below)	83	15·2	1·24	21·4	22
Felled	92	12·8	1·90	53·0	93

* A single, double or treble drill with a single puncture through the bark is counted as one drill.

Table 4. *The response of* Urocerus gigas *to treated trees* (*4 replicates per treatment*)

Treatment	Mean number of drills per treatment	Eggs per drill	% hatch of eggs	Mean no. larvae developed
A. PINE				
Girdled (above)	181	2·05	23·0	85
Girdled (below)	144	1·23	23·6	42
Felled	63	2·13	1·4	2
Logs	97	2·20	4·7	10
B. SPRUCE				
Girdled (above)	336	2·67	35·1	315
Girdled (below)	316	2·37	19·0	147
Felled	161	4·20	92·0	622
Logs	139	4·13	92·8	533
Fireburn	351	3·95	70·9	983

Table 5. *The response of siricid woodwasps to experimentally debilitated timber*

Means of treatments	*S. noctilio**	*S. juvencus*	*S. cyaneus*	*U. gigas*
% of total drills in pine	62·6	29·2	32·4	34·2
% of total drills in spruce	37·4	70·8	67·6	65·8
Single drills as % of total drills in pine	53·2	72·6	78·2	—
Single drills as % of total drills in spruce	78·2	49·5	68·4	—
Eggs per drill in pine	0·59	0·43	1·42	1·91
Eggs per drill in spruce	0·35	0·89	1·34	2·79
% hatch of eggs in pine	20·1	7·0	4·9	13·2
% hatch of eggs in spruce	27·4	51·0	36·3	54·2
No. larvae developed in pine	37·7	5·3	3·0	34·8
No. larvae developed in spruce	20·3	81·4	62·3	520·0

* Excluding log treatments.

in 40%, of which 29% hatched. However, larval mortality was high (91%) with new wood growing over the old oviposition sites. *S. juvencus* did not drill into untreated pine controls but 112 drills were recorded in the spruce of which 73% were multiple drills. There were eggs laid in 58% of the drills and 50% had hatched. Mortality of *S. juvencus* larvae in the spruce controls was low with some larvae burrowing up to 3 cm from the oviposition site. The *S. juvencus* infested spruce showed no signs of chlorosis or any other toxic symptoms 14 months after oviposition.

Timing of treatments

There were no statistical differences in the response of siricids to trees treated at different time intervals. Nevertheless, some trends were apparent such as a decreasing proportion of *S. juvencus* multiple drills with increasing age of treated spruce and a preference by *U. gigas* for the oldest material. *S. noctilio* made more drills in pines treated 1–3 months earlier compared with timber treated 5–10 months earlier and the best hatch rate was recorded in the most recently treated material. On freshly-girdled pines, *S. noctilio* made 606 drills above the girdle compared with 34 below the girdle with the same number of drills above and below the girdle in pines 3–7 months since treatment and 468 above and 94 below the girdle in the oldest material which was 10 months since treatment.

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Mean no. larvae developed
85
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lly debilitated timber

S. cyaneus	*U. gigas*
32·4	34·2
67·6	65·8
78·2	—
68·4	—
1·42	1·91
1·34	2·79
4·9	13·2
36·3	54·2
3·0	34·8
62·3	520·0

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Response to different treatments

Treatments which stimulated the greatest response by the siricid species were as follows: *S. noctilio*, girdled pine; *S. juvencus*, logs and girdled and felled spruce; *S. cyaneus*, girdled and felled spruce; *U. gigas*, girdled and fireburned spruce. Although *S. noctilio* showed a marked preference for pine trees, pine logs stimulated virtually no drilling activity.

An analysis of variance of the siricid response to girdled trees showed that, on average, all species preferred the area above the girdle with respect to total drilling activity ($P < 0\cdot05$) and an evident but not significant trend for more eggs to be laid above the girdle, irrespective of tree species. There was a lower proportion of multiple drills made below the girdle irrespective of the siricid species. There was a higher hatch rate of eggs laid above the girdle compared with below girdle eggs in spruce ($P < 0\cdot05$) although no such difference was detected in pine.

The analysis of variance on the girdled tree data confirmed that *S. noctilio* prefers pine hosts, the other siricids prefer spruce and that the egg hatch of *S. juvencus* and *S. cyaneus* was greater in spruce than in pine. There was also a significant reaction between tree species and siricid species with respect to multiple drills such that *S. noctilio* made fewer multiple drills in spruce and *S. juvencus* fewer in pine with no significant difference in the response of *S. cyaneus* to girdled spruce and pine.

Table 6. *Response of wild* Sirex juvencus *to experimentally debilitated spruce*

Treatment	No. trees treated	No. trees infested	Total drills	% multiple drills	Eggs per drill	% egg development
Girdled (above)	17	11	284	53·5	0·58	15·2
Girdled (below)	17	10	460	60·2	0·81	53·0
Felled	10	8	2328	60·3	0·72	84·3
Logs	9	0	0	—	—	—
Fireburn	9	6	283	59·4	0·46	76·7

There was a positive linear correlation for each siricid species between the number of drills per treatment and the number of eggs per drill, (*S. noctilio*, $r = 0\cdot3705$; *S. juvencus*, $r = 0\cdot3488$; *S. cyaneus*, $r = 0\cdot3642$; *U. gigas*, $r = 0\cdot3608$). In *U. gigas* there was a positive correlation between egg hatch and the number of eggs per drill ($r = 0\cdot6875$) but no such correlation was demonstrated for the other species.

The response of wild *S. juvencus* to the treated spruce is summarised in Table 6. The most attractive treatment was felled timber which accounted for 69% of all drills. Large numbers of drills were also recorded on girdled trees which were attacked predominantly below the girdle. There was no indication that oviposition had caused chlorosis in the leaves, even though the egg development and hatch were generally good. No logs were attacked. There was a positive linear correlation between total drills per tree and the proportion of eggs which hatched ($r = 0\cdot775$, $P < 0\cdot001$).

In an untreated living spruce attacked by wild *S. juvencus* a year earlier, 200 drills were recorded in a 30-cm length of stem of which 88% were multiple drills. There were eggs in 58% of the drills and 44% had hatched. The larvae were 6–14 mm in length and were developing normally. Since oviposition, the wood of the current year had grown over the drill holes and there was little evidence of drilling activity at the wood surface. The foliage appeared normal and there was no evidence of toxicosis.

DISCUSSION

European siricid woodwasps attack a wide range of conifer species, utilising dead, damaged and living trees in a variety of situations, although an analysis of field-collected material has shown some ecological preferences by the different siricid species (Spradbery & Kirk, 1978). For example, *S. noctilio* was reared almost exclusively from pines (99%), all other siricids being found predominantly in other conifer genera. The response of *S. noctilio* reported here demonstrates a preference for pine, the number of drills and proportion of multiple drills being considerably more in pine than in spruce under comparable conditions. Of the other species, *S. cyaneus* was the only one infesting pine trees in the field but at a very low level (Spradbery & Kirk, 1978). In the present study, 32% of *S. cyaneus* drills were made into pine, although the proportion of multiple drills and eggs per drill in the two tree species did not differ. However, egg hatch and development of *S. cyaneus* larvae in pine trees was very poor. Chrystal (1928) observed that *S. cyaneus* was confined to larch in a mixed larch/Scots pine forest at Oxford although both *S. cyaneus* and *U. gigas* have been recorded from pine by Chrystal (1928) and Evans (1922). *S. juvencus* did not drill when caged to untreated pines and only 19% of the total drills were made in response to treated pine.

In the field, *S. noctilio* was only rarely found in severely debilitated timber such as logs and windthrows while *U gigas* invariably infested physiologically inert timber (Spradbery & Kirk, 1978). The present study underlines these preferences, especially with respect to the low oviposition response by *S. noctilio* to pine logs. Felled and logged spruce were highly favoured by *U. gigas* with regard to the numbers of eggs per drill and also egg hatch. In Tasmania, the attractiveness of freshly-cut logs to *S. noctilio* was brief with a maximum response occurring 5–8 days after felling (Madden, 1971). Although felled pine trees in our experiments stimulated a high level of drilling by *S. noctilio*, the number of eggs per drill and percentage hatch were very low. In Madden's (1971) study, felled trees elicited a peak response by wild *S. noctilio* on days 5–7 but they remained attractive for up to 3 wk after felling.

When pine trees were ring-girdled in Tasmania, they became attractive to wild *S. noctilio* after 9–12 days and, for 6–7 wk after treatment, attack was confined many to the region below the girdle (Madden, 1971). In our study, responses to the region above and below the girdle were reversed even in the case of *S. noctilio* oviposition on freshly girdled pines in which many more drills were recorded above the girdle. Wild *S. juvencus* showed a preference for felled trees although girdled trees stimulated much drilling activity especially in the region below the girdle.

Among the criteria used to gauge the suitability of timber to siricids was the viability of eggs. The comparatively low hatch rate in pines might reflect unsuitable conditions for the development of the symbiotic fungus which causes local drying out around the drills with subsequent hatching of the eggs (Coutts & Dolezal, 1965; 1969) although siricid eggs laid in late summer or early autumn may overwinter and hatch in the early spring (Chrystal, 1928; Spradbery, 1970). Nevertheless, the relatively low hatch of *S. juvencus*, *S. cyaneus* and *U. gigas* in pine suggest that these species and their symbionts are better adapted to spruce hosts. There was no difference in the viability of *S. noctilio* eggs in pine and spruce.

This study has demonstrated differences in the response of *Sirex* species to different types of material and the timing of treatment compared to *U. gigas*. In spite of similarities in oviposition behaviour among the *Sirex* species, *S. noctilio* was distinguished by its preference for pine and for the most recently treated and hence least physiologically debilitated trees. It appears, therefore, that *S. noctilio* is the only European siricid posing a serious threat to Australia's living stands of *Pinus radiata* although the other siricid species could cause mechanical damage to felled or damaged conifers in some circumstances.

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REFERENCES

CHRYSTAL, R. N. (1928). The *Sirex* woodwasps and their importance in forestry. *Bulletin of Entomological Research* **19**, 219–247.

COUTTS, M. P. (1965). *Sirex noctilio* and the physiology of *Pinus radiata*. *Bulletin of Forestry and Timber Bureau*, No. 41.

COUTTS, M. P. (1969*a*). The mechanism of pathogenicity of *Sirex noctilio* on *Pinus radiata*. I. Effects of the symbiotic fungus *Amylostereum* sp. (Thelophoraceae). *Australian Journal of Biological Sciences* **22**, 915–924.

COUTTS, M. P. (1969*b*). The mechanism of pathogenicity of *Sirex noctilio* on *Pinus radiata*. II. Effects of *S. noctilio* mucus. *Australian Journal of Biological Sciences* **22**, 1153–1161.

COUTTS, M. P. & DOLEZAL, J. E. (1965). *Sirex noctilio* and its associated fungus, and some aspects of wood moisture content. *Australian Forest Research* **1**, 3–13.

COUTTS, M. P. & DOLEZAL, J. E. (1969). Emplacement of fungal spores by the woodwasps, *Sirex noctilio*, during oviposition. *Forest Science* **15**, 412–416.

EVANS, W. (1922). Notes on the woodwasps (*Sirex*) occurring in Scotland with special reference to their present day distribution. *Scottish Naturalist* 175–189.

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

MADDEN, J. L. (1968). Physiological aspects of host tree favourability for the woodwasps *Sirex noctilio* F. *Proceedings of the Ecological Society of Australia* **3**, 147–149.

MADDEN, J. L. (1971). Some treatments which render Monterey pine (*Pinus radiata*) attractive to the wood wasp *Sirex noctilio* F. *Bulletin of Entomological Research* **60**, 467–472.

MADDEN, J. L. (1974). Oviposition behaviour of the woodwasp, *Sirex noctilio* F. *Australian Journal of Zoology* **22**, 341–351.

MUCHA, S. (1967). The establishment and spread of *Sirex noctilio* F. in Tasmania from 1950 to 1964. *Australian Forest Research* **3**, 3–23.

RAWLINGS, G. B. (1948). Recent observations of the *Sirex noctilio* populations in *Pinus radiata* forests in New Zealand. *New Zealand Journal of Forestry* **5**, 1–11.

SPRADBERY, J. P. (1970). The biology of *Ibalia drewseni* Borries (Hymenoptera: Ibaliidae), a parasite of siricid woodwasps. *Proceedings of the Royal Entomological Society, London* (*A*) **45**, 104–113.

SPRADBERY, J. P. (1973). A comparative study of the phytotoxic effects of siricid woodwasps on conifers. *Annals of Applied Biology* **75**, 309–320.

SPRADBERY, J. P. (1977). The oviposition biology of siricid woodwasps in Europe. *Ecological Entomology* **2**, 225–230.

SPRADBERY, J. P. & KIRK, A. A. (1978). Aspects of the ecology of siricid woodwasps (Hymenoptera: Siricidae) in Europe, North Africa and Turkey with special reference to the biological control of *Sirex noctilio* F. in Australia. *Bulletin of Entomological Research* **68**, 341–359.

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