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Studies with *Sirex noctilio* (hymenoptera: siricidae) and its parasites that illustrate the importance of evaluating biological control attempts

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SUMMARY

Populations of *Sirex noctilio* F. declined in the 2-3 years following release of insect parasitoids in two small Tasmanian plantations of *Pinus radiata*. Evaluation studies have shown that the host population was declining rapidly before the natural enemies could have caused any significant degree of control.

Although it has been demonstrated at another site in Tasmania that the parasitoids played a significant role in controlling *S. noctilio*, the present study emphasizes the need for planned sampling to evaluate the results of any biological control attempt.

RÉSUMÉ

Au cours des 2-3 ans qui ont suivi les lâchers de parasitoïdes, les populations de *Sirex noctilio* F. ont diminué dans 2 petits peuplements de *Pinus radiata* en Tasmanie. Des études quantitatives ont montré toutefois que la population-hôte diminuait rapidement avant même que les ennemis naturels aient pu engendrer un degré significatif de parasitisme. Dans un autre site de Tasmanie, les parasitoïdes ont, en revanche, joué un rôle régulateur important en limitant *S. noctilio*. Le présent travail souligne la nécessité d'établir un programme d'échantillonnage permettant de déterminer le succès de toute tentative de lutte biologique.

INTRODUCTION

In recent years many authors have emphasized the importance of evaluating the effectiveness of natural enemies in biological control attempts. DeBach & Huffaker (1971) recommended techniques "to exclude the possible contributing or compensatory effects of other environmental parameters such as weather, competitors, or genetic variation, etc., so as to evaluate the actual total regulatory effect brought about essentially by the action of natural enemies".

"Other environmental parameters" are probably more important when evaluating biological control attempts against *Sirex noctilio* F. than they are for many other insects. This is because the successful invasion of trees by *S. noctilio* and its symbiotic fungus is closely linked to the physiological condition of the tree. Many factors control this, such as climatic variations, fire, and mechanical damage (Madden, 1971) all of which contribute in some way to water stress (Madden, 1974). In addition, when the siricid invades any plantation the most susceptible trees are killed first. In an analysis of the initial outbreak of *Sirex noctilio* F. in Tasmania, Madden (1975) showed that after annual tree mortality reached a peak in 1959 it declined sharply, as did the numbers of *S. noctilio*. He stated that "a consequence of the thinning

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effect of *Sirex* in killing susceptible trees was an increase in vigour of the remaining trees accompanied by an increase in the proportion of trees possessing natural resistance as reflected in an increased number of unsuccessful attacks and a decreasing survival of the insect within the tree". Another consequence is that the size of *S. noctilio* individuals emerging decreases with increasing resistance of the trees. Smaller females lay fewer eggs (MADDEN, 1974), so this means that each succeeding generation tends to have a lower reproductive potential.

The population of *S. noctilio* in a plantation over a series of years is thus seriously affected by changes in the availability of susceptible hosts. These changes greatly complicate the evaluation of introduced natural enemies of the woodwasp. Such changes in tree availability were taken into consideration when the success of the insect parasitoids introduced to Australia to control *S. noctilio* was evaluated in a plantation of *Pinus radiata* D. Don at Pittwater, near Hobart, Tasmania (TAYLOR, 1978). The results showed that there was a marked decrease in the numbers of *S. noctilio* relative to those of its parasitoids in the trees killed by the pest and that this was accompanied by a significant reduction in the total population of *S. noctilio*. It was shown that the joint action of two rhyssine species, *Megarhyssa nortoni* (Cresson) and *Rhyssa persuasoria* (L.) was mainly responsible.

Changes in the relative numbers of *S. noctilio* and its parasitoid species emerging over a period of 5-6 years from trees killed at 2 small plantations elsewhere in Tasmania suggested that the rhyssines were also responsible for reducing those populations of the host insect. This paper presents evidence that other factors were mainly responsible for those reductions.

MATERIALS AND METHODS

STUDY AREAS

The two plantations in which these studies were carried out were small woodlots. One (1.42 ha) was located on a farm near Campania, about 25 km NNW of Hobart Airport, and the other (0.81 ha) was a school plantation at Bracknell, about 30 km SW of Launceston. The Campania block carried 1,600 sixteen year old trees while at Bracknell 560 trees 13 to 16 years old were planted adjacent to a block of 220 larger trees a few years older.

At the beginning of the study, *Ibalia leucospoides* Hochenwarth had already become established at both sites by natural migration. The only other parasitoid released at Campania was *M. nortoni* (24 females in the 1968-1969 season). At Bracknell, during 1968, 1969 and 1970, additional stocks of *I. leucospoides* were released, with over 300 females of *M. nortoni* and 150 females of *R. persuasoria* (Taylor, 1976). The parasitic nematode, *Deladenus siricidicola* Bedding, was not present at either site throughout the study.

SAMPLING

Trees. As each plantation was small, all trees killed or partly infested each year were readily located and identified.

Adult insects. The duration of development of *S. noctilio* in pine trees, from egg laying until the emergence of adults may take 1, 2 or even 3 seasons. Furthermore, the parasitoids attack either early instar larvae in the first year, or late instar larvae in subsequent years. Most of the progeny of those species attacking late instar larvae emerge one year later, so the duration of emergence of adult insects from one year's initial *Sirex* attack extends over at least the next two years. TAYLOR (1978) for a study at Pittwater, described how the species of insects emerging from a tree killed by *S. noctilio* one year, can be sampled by moving emergence cages sequentially over the next 2 years. Estimates were made from the derived data of the numbers of the siricid and of each of its parasitoids, summed over both seasons, which emerged from 2 such cages at varying heights on each tree. By felling dead trees the total number of insects emerging from the whole tree were estimated from samples of the emergence holes at intervals of about 60 cm over the full length of the trunk.

The same emergence cage technique was used in the present study, but an estimate of total insects was not made. At Campania, 2 cages were fixed on each tree. The number of trees sampled varied over the years of observation from 8 to 24, depending on the number of trees available and their suitability for fixing cages. At Bracknell, however, only 1 cage was fixed on each of 10 trees, except in 1971 when only 8 trees were available.

Estimating populations

At both sites, cages were fixed only on trees which were completely killed in the preceding season, and which were classified suitable for the development of *S. noctilio*. Some of the remaining trees (infested in the same season) were directly comparable with these; others although still suitable, were smaller, larger, or only partly killed (*e. g.* one of two leaders). Some of the trees for various reasons proved unsuitable for the development of siricid larvae.

It was not feasible at these two sites to take samples for emergence along the full length of the trunk as was done at Pittwater (Taylor, 1978). For each year the mean number of insects per cage at Campania and Bracknell (from table II) was converted to a mean number of insects per tree by use of the ratio, insects per cage: insects per tree, obtained from the Pittwater data.

For unsampled trees classed as "suitable" for *S. noctilio*, an estimate was made, on the basis of surface area of the bark, of the siricid numbers each would support as compared with the mean numbers in the sampled trees (*i. e.* with cages fixed). Estimates were made of the siricid numbers in trees only partly killed, or unsuitable, and these were expressed as a fraction of the numbers in the average suitable tree. In this way the total trees infested, in whole or in part, each year were converted to a number of "tree equivalents" (table I).

The product of the mean number of insects per tree and the number of "tree equivalents" (as defined above, see table I), for each year represented, provided an index of the total population in the study areas.

The relative numbers of each insect species in the trees killed each year were calculated by the method used in the Pittwater study (Taylor, 1978).

RESULTS

Tree mortality

The numbers of trees killed or partly killed, and the estimated "tree equivalents", at the 2 plantations are given in table I.

It is apparent that the number of trees killed each year by *S. noctilio* was initially relatively low, but reached a peak at Campania in 1967 and at Bracknell in 1968, after which the numbers killed declined markedly.

At both sites many trees were unsuccessfully attacked by *S. noctilio*, and the proportion of these (of the total attacked) was greatest over the period from 1967-1969 inclusive.

Insect populations

Table II gives details of the number of cages fixed each year at each of the two plantations, the total numbers of insects emerging into the cages, and the breakdown of those totals representing *S. noctilio* and each of its parasitoids.

These figures show that although more trees were killed at Campania in 1967, the number of insects *per cage* was only about one-third the number per cage in the trees killed in 1968. Consequently the number of insects in the wood was greatest in the trees killed in 1968, as it was at Bracknell.

TABLE I

Numbers of trees killed annually in the Campania and Bracknell plantations 1965-1973.

Year	Whole trees	Parts	Tree equi-valents	No. of trees fitted with 2 cages	Whole trees	Parts	Tree equi-valents	No. of trees fitted with 1 cage
1965	21	2 (*)	18	8	9	—	12	—
1966	27	—	23	16	15	—	19	—
1967	125	6	96	24	16	8 (*)	29	10
1968	70	7	54	24	86	14	95	10
1969	45	12	38	18	37	—	40	10
1970	17	1	15	10	10	1	10	10
1971	15	2	13	9	8	—	8	8
1972	23	2	17	10	(thinned, no trees killed)			
1973	10	4	11	10				

(*) Partially killed.

TABLE II

Summed emergence over 3 years of Sirex noctilio *and its parasitoids into cages on trees killed in each year 1966-1973.*

Year tree killed (*)	Campania					Bracknell				
	No. of cages	Total insects (**)	Proportion of each species (%)			No. of cages	Total insects	Proportion of each species (%)		
			S. noctilio	*I. leucospoides*	*M. nortoni* (1)			*S. noctilio*	*I. leucospoides*	Rhyssines (1)
66	32	1,783	87.9	12.1	—	10	841	84.3	8.9	6.9
67	48	1,622	89.6	10.4	—	10	897	79.0	19.5	1.5
68	48	4,512	85.7	14.3	—	10	1,075	81.4	4.8	13.8
69	36	1,564	64.8	15.0	20.2	10	711	71.5	12.2	16.3
70	20	1,054	34.8	9.4	55.8	8	387	42.6	3.1	54.3
71	18	663	12.2	3.0	84.8					
72	20	225	37.3	9.3	53.3					
73	20	270	36.3	11.1	52.6					

(*) Trees are killed in Summer and Autumn of each year quoted.
(**) The total emergence occurs during the following two seasons.
(1) *M. nortoni* liberated Spring 1968 at Campania, 1967 at Bracknell.
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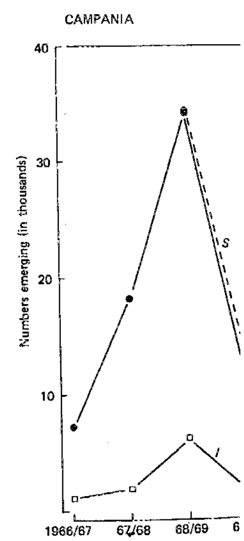

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The insects within the trees killed in any one year (table II) actually emerge during the two seasons following successful oviposition on the trees by *S. noctilio*. The estimated numbers of each species actually emerging in successive seasons from all trees can be calculated from the estimated total population of all species present in the trees successfully attacked each year. Figures 1 and 2 represent those emerging each season at Campania and Bracknell respectively. At both sites the numbers of siricids emerging reached a peak in the 1968-1969 season and then declined sharply.

At Campania the numbers of *M. nortoni* relative to those of the host increased rapidly until 1971 and then declined to a lower level (table II). At Bracknell the numbers of both rhyssine species, in relation to those of *S. noctilio*, increased more gradually and were still rising when sampling ceased. At both sites these increases took place *after* the host populations began to decline (fig. 1, 2).

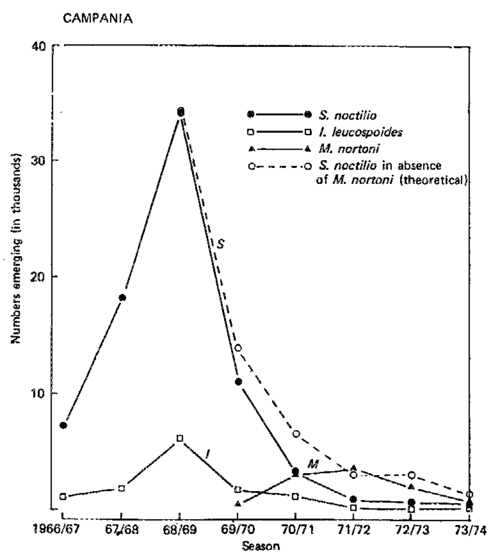

FIG. 1. — Estimated numbers of each species emerging each active season (Spring, Summer and Autumn) from all trees killed by *S. noctilio* at Campania, 1966-1967 to 1973-1974.

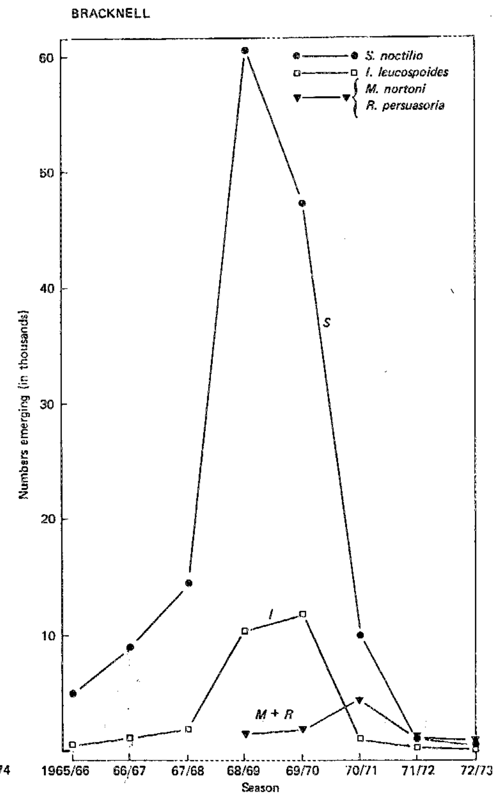

FIG. 2. — Estimated numbers of each species emerging each active season from all trees killed by *S. noctilio* at Bracknell, 1965-1966 to 1972-1973.

DISCUSSION

It is significant that at both sites the total population of *S. noctilio* reached a peak in the 1968-1969 season. In the Summer of 1966-1967 at these two sites (and at others in Tasmania where *S. noctilio* was established) the rainfall was well below average for 3-4 months, so that the climate became "temporarily mediterranean" (KIRK, 1974). Rainfall in the Summer of 1967-1968 was also below average, though less so than in the previous year. A marked increase in the number of susceptible trees and in the degree of susceptibility, in 1966-1967, due to water stress, would undoubtedly have favoured an increase in successful oviposition by *S. noctilio*, and the resulting higher population would tend to be maintained in the following Summer when the trees were again moderately stressed. In 1969-1970 and the following two Summers rainfall was above or close to average, so that the surviving trees should not have been under stress.

Figures 1 and 2 leave no doubt that at both sites the population of *S. noctilio* had already declined to a low level before the parasitoids could have made any significant impact. It is clear (fig. 1) that there would have been a steep decline in the host population at Campania after 1968-1969 even if *M. nortoni* had not been introduced. However, it is also clear that *M. nortoni* was partly responsible for the decline in 1970-1971; and that subsequently it was destroying a substantial part of each generation of *S. noctilio*. The changes which would have occurred in the host population at Campania without the intervention of *M. nortoni* can be represented by the dotted line in figure 1. This is obtained by converting the numbers of *M. nortoni* emerging in seasons *n* (*i. e.* the non-diapausing fraction) and $n + 1$ to numbers of *S. noctilio*, which, if unparasitized, would have emerged in season *n*.

At Bracknell, the marked decline in the total population of *S. noctilio* in 1970-1971 (fig. 2) also coincides with an increase (though disproportionate) in the relative numbers of the rhyssine parasitoids in the 1971 trees (table II).

Although the evaluation studies at Pittwater (TAYLOR, 1978) showed a similar decline in the population of *S. noctilio* from 1968-1969, there was in that case a corresponding increase in the numbers of the rhyssines (fig. 3). The rhyssines were

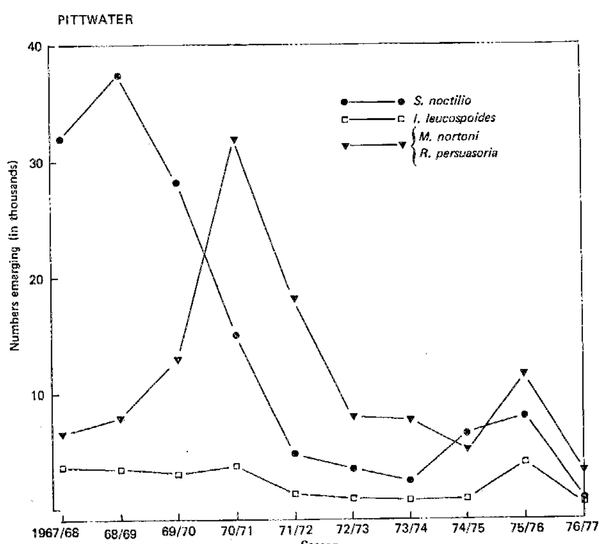

FIG. 3. — Estimated numbers of each species emerging each active season from all trees killed by *S. uoctilio* at Pittwater, 1967-1968 to 1976-1977.

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established earlier there than at Bracknell or Campania. Also the Pittwater trees were younger, and the study extended over a longer period, so that the role of the parasitoids was not obscured so much by the effect of other factors on the host population.

The results at Campania and Bracknell support the remarks of DEBACH & HUFFAKER (1971) and other authors concerning the need for evaluation of biological control attempts. At these 2 sites, without any evaluation, it would probably have been assumed that the parasitoids had achieved a high degree of success.

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