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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

J. P. Spradbery * and A. A. Kirk †
Division of Entomology, CSIRO, P.O. Box 1700, Canberra City, A.C.T. 2601, Australia

Abstract

Collections of siricid-infested coniferous trees were made in 150 localities in 19 European countries, Turkey and North Africa to obtain parasites and parasitoids of siricids for use in the biological control of *Sirex noctilio* F. in Australia. During this work, information was obtained on the distribution and biology of 8 siricid species (*S. noctilio, S. cyaneus* F., *S. juvencus* L., *Urocerus augur* (Klug), *U. gigas* (L.), *U. sah* (Mocs.), *U. fantoma* (F.), *Xeris spectrum* (L.)) and 7 parasitoids (*Rhyssa persuasoria* (L.), *R. amoena* Grav., *Pseudorhyssa maculicoxis* (Krchb.), *Megarhyssa emarginatoria* (Thnb.), *Ibalia leucospoides leucospoides* (Hochenw.), *I. rufipes drewseni* Borries, *Odontocolon geniculatum* (Krchb.)). Data are presented on distribution, flight periods and sex ratios (determined from emergence records), factors leading to the susceptibility of timber to siricid infestation and the types of timber and host tree species infested. Levels of parasitism by the various parasitoid species, determined from emergence records, are given. Localities are assigned to bioclimatic categories, and their siricid and parasitoid species are classified in relation to the climatic criteria. The ecological status of *S. noctilio* is discussed in relation to its establishment in Australia.

Introduction

Some 20 years ago the siricid woodwasp *Sirex noctilio* F. was accidentally introduced into Australia (Gilbert & Miller, 1952), where it has caused considerable damage to plantations of exotic softwoods, notably *Pinus radiata*, in Tasmania and Victoria. Nearly half a million hectares of plantations are threatened by *S. noctilio*, which is able to kill trees by injecting a symbiotic fungus, *Amylostereum areolatum*, and phytotoxic mucus into the wood.

S. noctilio is endemic to Eurasia and North Africa, although together with other siricid species it is generally considered a secondary pest of trees following primary damage by other insects and biotic factors. Rawlings and Wilson (1949) considered that *S. noctilio*, which became established in New Zealand forests in 1900 (Miller & Clark, 1935), may play a beneficial role as a natural thinning agent and, based on his own observations and previous records, Chrystal (1928) concluded that siricids act as

* Present address: CSIRO Division of Entomology, P.O. Box 6712, Boroko, Papua New Guinea.
† Present address: CSIRO Biological Control Unit, 335 Avenue Abbé Paul Parguel, 3400—Montpellier, France

indicators of pathological conditions rather than prime factors in their production. Nevertheless, widespread damage to *P. radiata* plantations has been recorded in New Zealand (Rawlings, 1948, 1953) and Tasmania (Coutts, 1965).

Because siricid larvae burrow in wood and adults are short-lived, *S. noctilio* is not amenable to conventional insecticidal control. Thus, in 1963, the Commonwealth Scientific and Industrial Research Organisation of Australia (CSIRO) established a laboratory in England to make collections of siricids and evaluate their parasites and parasitoids as biological control agents. This communication describes knowledge of the ecology of siricids and their parasitoids in Europe, North Africa and Turkey obtained from surveys and studies made in 1963–70.

Materials and methods

Surveys for siricid woodwasps, their parasites (Bedding, 1972) and parasitoids were made during 1963–70 in 19 European countries and in Turkey and North Africa. Collecting outside the British Isles was confined to late autumn and winter to ensure that material arrived in England before insect emergence. During the course of the survey, which covered 172 000 km from sea level to an altitude of 2200 m, approximately 4000 siricid-infested logs 1 m long were obtained, debarked and shipped to England.

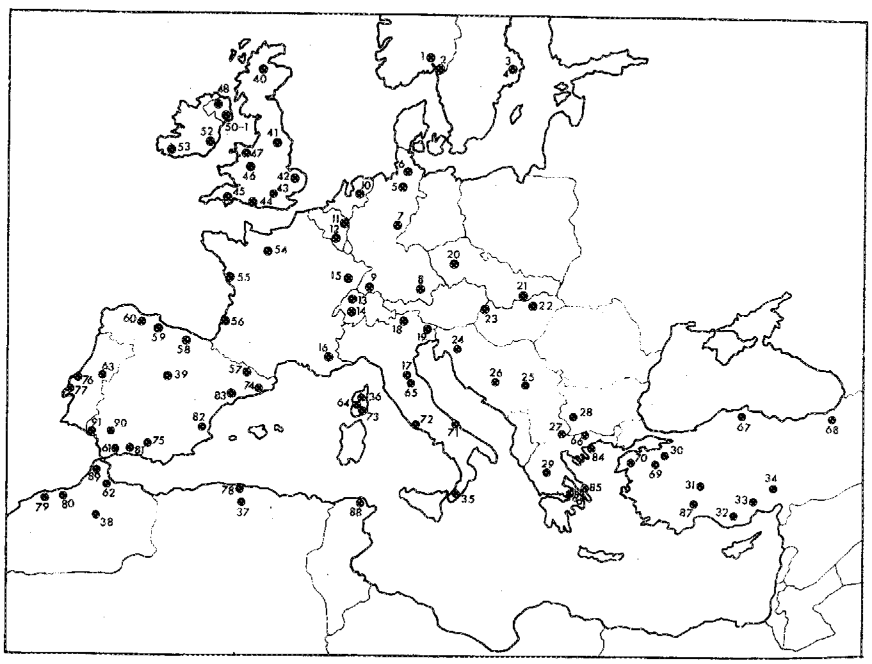

Fig. 1.—Localities in Europe, North Africa and Turkey where siricid-infested timber was collected. (Numbers refer to Appendix.)

To obtain infested material, dead, dying and damaged coniferous trees were examined for evidence of siricid activity. External signs included typically round exit holes, ovipositing siricids and their parasitoids or ovipositors of these insects embedded in timber as a result of predation or trapping by resin. Trees excavated by woodpeckers seeking siricid larvae were also sought.

Timber was sampled by cutting out pieces with an axe or sawing 10-cm discs at

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Logs lying in the forest we
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Results

The localities from whic
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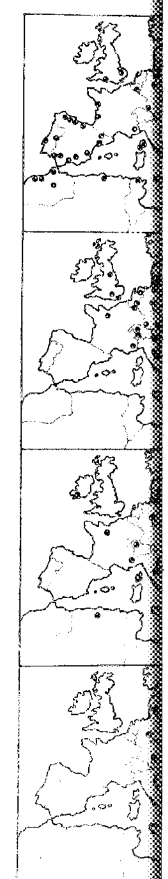

Fig. 2

2-m intervals along the trunks. These samples were examined for frass-packed galleries produced by burrowing siricid larvae, for the immature stages and for the characteristic brown staining of the timber resulting from the symbiotic fungus, *Amylostereum* sp. Logs lying in the forest were also examined for galleries and staining at the cut ends. Only timber known to contain immature siricids or their parasitoids was collected.

Infested material was classified as follows: logs (pre-cut material in forests and sawmills), dead fallen trees (including windblown trees, broken crowns, stumps and roots) and standing trees, which were further classified as dead (few red or brown leaves or none) or alive (more or less full crown of green or yellowing leaves). Further subdivisions were made in some circumstances, and details are given in the results.

The material was stored in outdoor insectaries at Silwood Park, England, according to locality of origin and tree species. Emerging insects were collected from the cages daily during the flight period.

Results

The localities from which siricid material was collected are given in Fig. 1. The distribution of siricids and their hymenopterous parasitoids, based on CSIRO surveys, is given in Fig. 2 & 3. The altitude, tree species, number of logs collected and bioclimatic designation of the localities are given in the Appendix.

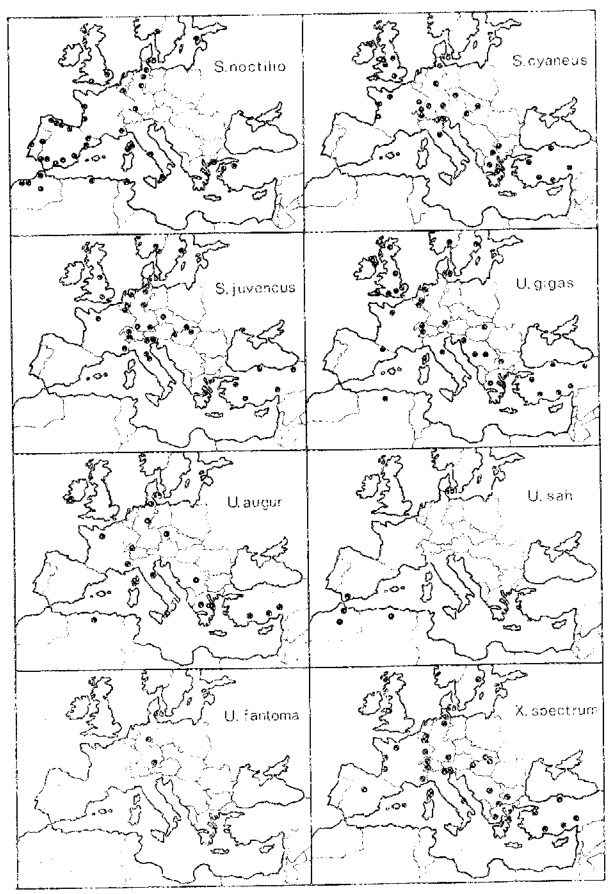

Fig. 2.—Distribution of siricid woodwasps.

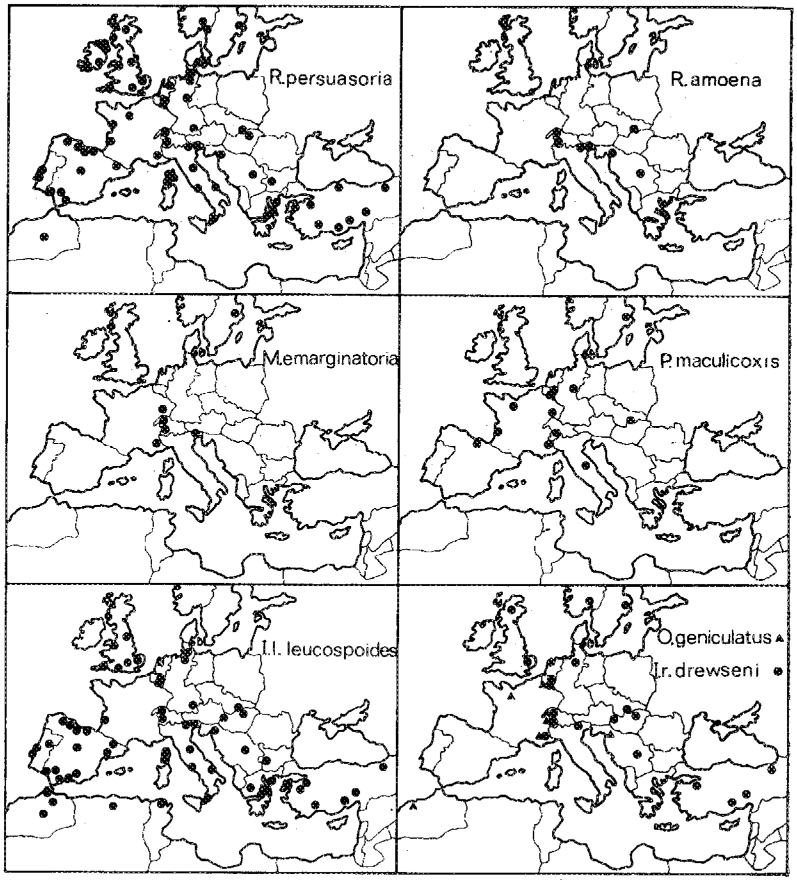

Fig. 3.—Distribution of parasitoids of siricid woodwasps.

TABLE I. *Sex ratios of siricids and their associated parasitoids*

Species	Number of adults	Number of females:males
Siricids		
S. noctilio	9052	1:1·82
S. cyaneus	7122	1:1·49
S. juvencus	13230	1:1·99
U. gigas	7333	1:2·11
U. augur (Klug)	959	1:1·72
U. sah (Mocsary)	69	1:0
U. fantoma (F.)	54	1:0·80
X. spectrum	6205	1:1·50
Parasitoids		
R. persuasoria (L.)	7857	1:2·89
R. amoena	191	1:1·01
M. emarginatoria	152	1:1·08
P. maculicoxis (Kriechbaumer)	494	1:1·81
I. l. leucospoides (Hochenwarth)	6470	1:1·15
I. rufipes drewseni (Borries)	669	1:1·03
O. geniculatum (Kriechbaumer)	384	1:2·43

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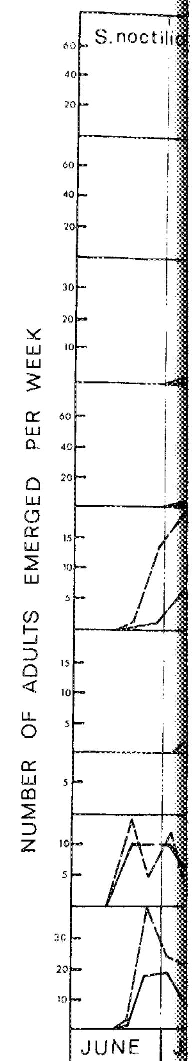

Fig. 4.—Emerge

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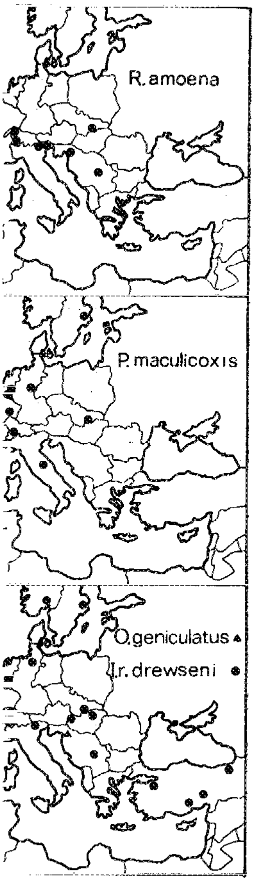

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iated parasitoids

Number of females:males
1:1·82
1:1·49
1:1·99
1:2·11
1:1·72
1:0
1:0·80
1:1·50
1:2·89
1:1·01
1:1·08
1:1·81
1:1·15
1:1·03
1:2·43

The periods of emergence of the siricid and parasitoid species, based on emergence records at Silwood Park, are given in Fig. 4 & 5. In most species, the males started to emerge before the females. The sex ratios are given in Table I. Total siricid emergence

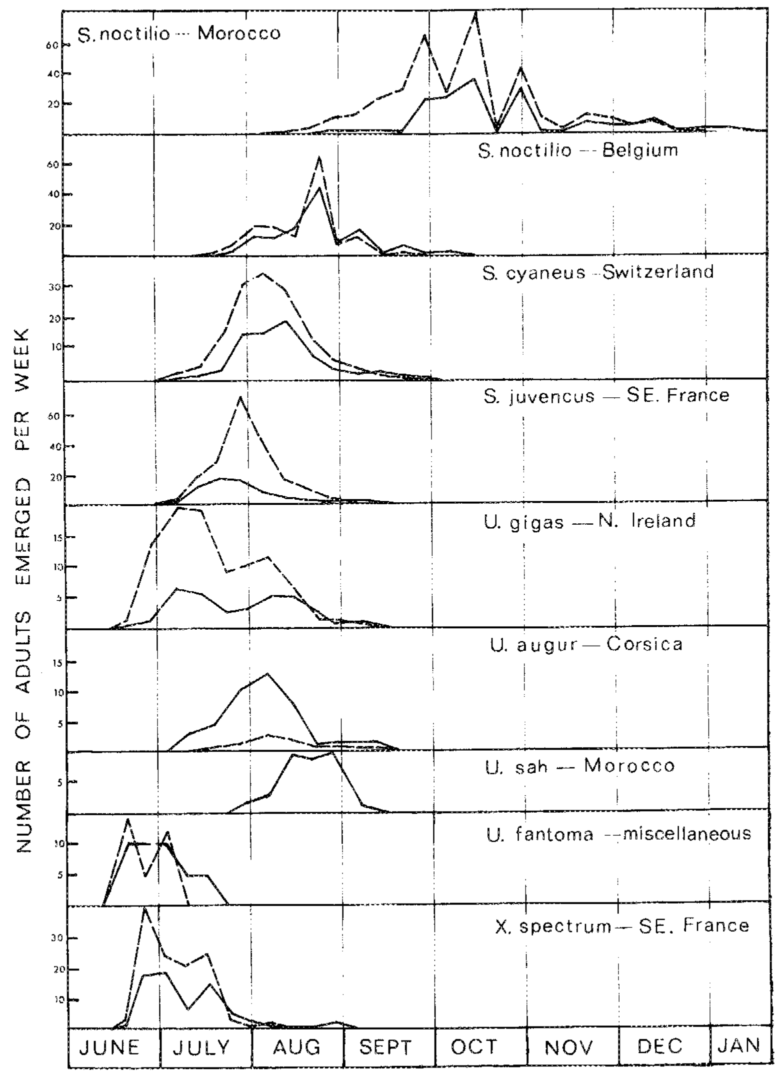

Fig. 4.—Emergence records of siricid woodwasps (based on emergence at Silwood Park insectaries).

and the proportion of each species emerging from the same material in successive years is given in Table II.

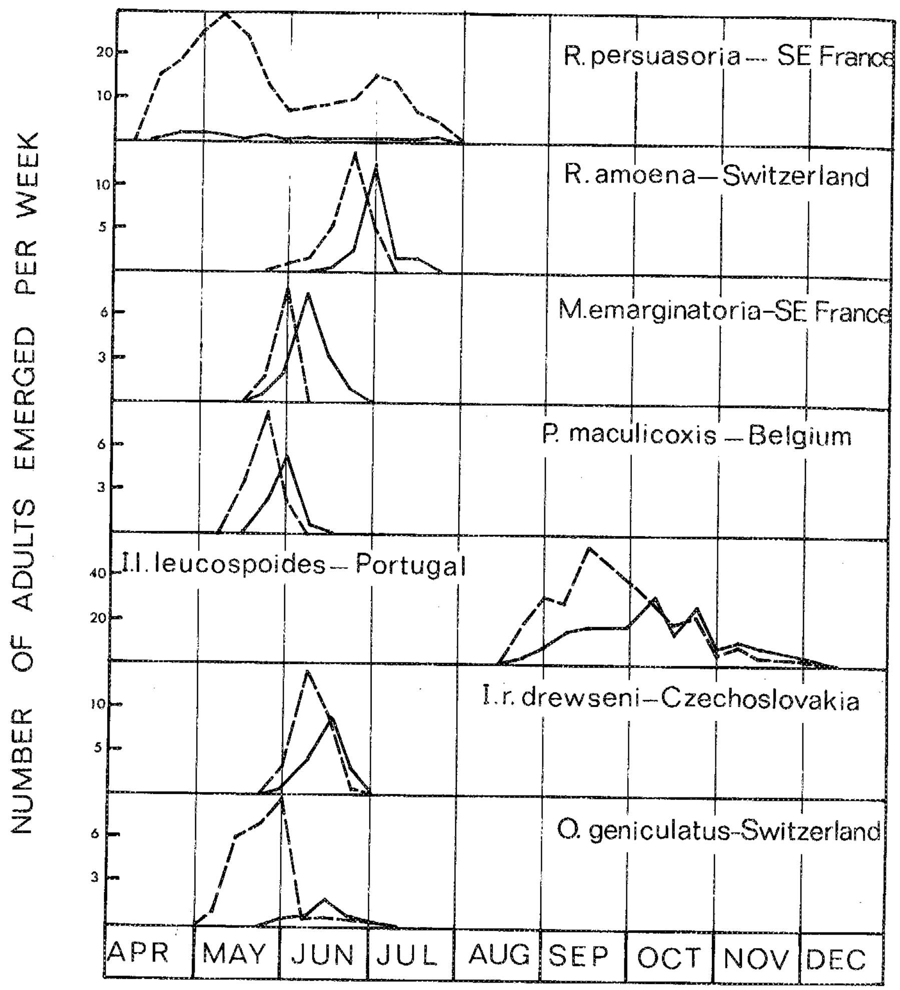

Fig. 5.—Emergence of parasitoids of siricid woodwasps in Silwood Park insectaries.

TABLE II. *Emergence of siricids in successive years after log collection*

Species	Total emerged	Emergence per year (%) 1	2	3	4
S. noctilio	6195	98·34 (6)	1·62 (6)	0·04 (5)	0 (1)
S. cyaneus	6629	97·45 (6)	2·45 (6)	0·10 (5)	0 (1)
S. juvencus	12097	88·80 (6)	11·15 (6)	0·05 (5)	0 (1)
U. gigas	4530	75·90 (6)	22·56 (6)	1·04 (5)	0·50 (1)
U. augur	752	90·20 (5)	8·70 (5)	1·10 (5)	0 (1)
U. sah	48	98·80 (2)	1·20 (2)	0 (2)	—
U. fantoma	55	92·20 (3)	7·80 (3)	0 (3)	0 (1)
X. spectrum	5797	84·20 (6)	13·60 (6)	2·20 (5)	0 (1)

Number of years' data in parentheses

Factors affecting the susceptibility of trees to siricid attack

Tree species from which siricids and parasitoids emerged, are given in Table III. The numbers of logs, siricids and parasitoids from timber classified as windblown, felled,

TABLE III. *Percentage emergence of siricids and their parasitoids from various host trees*

Host tree species	*S. noctilio*	*S. cyaneus*	*S. juvencus*	*U. gigas*	*U. augur*	*U. sah*	*U. fantoma*	*X. spectrum*	*R. persuasoria*	*R. amoena*	*P. maculicoxis*	*M. marginatoria*	*I. l. leucospoides*	*I. r. drewseni*	*O. geniculatum*
Abies alba	0·01	67·1	19·9	39·2	74·0	0	19·2	63·6	31·0	56·1	54·8	38·9	30·9	34·3	74·2
A. borisii-regis	0	0·7	0·03	0·8	5·6	0	0	4·8	0·09	0	0	0	1·4	0	0
A. bornmuelleriana	0	4·6	0·5	7·8	0	0	0	0·4	2·8	0	0	0	0·1	0	0
A. cilicia	0·04	10·2	0·09	2·5	15·9	0	0	10·9	3·9	0	4·0	0	9·0	1·8	0
A. equi-trojan	0	0	0	0·04	0	0	0	0·02	0	0	0	0	0	0	0
A. grandis	0	0	0	0·5	0	0	0	0	0·6	0	0	0	0	0	0
A. nobilis	0	3·0	0	26·6	0·7	0	0	0	6·2	0	0	0	0·03	0	0
A. pinsapo	0	0	0	0	0	84·5	0	0	0·2	0	0	0	5·0	0	0
TOTAL %	0·05	85·6	20·5	77·4	96·2	84·5	19·2	79·7	44·8	56·1	58·8	38·9	46·4	36·1	74·2
Cedrus atlantica	0	0	0	0·08	0	15·5	0	0	1·2	0	0	0	0·3	0	0
Larix decidua	0	0·1	0·1	3·0	0	0	0	0·05	1·0	0	0	0	0·07	0	0
Picea abies	0·7	12·0	69·2	6·4	3·1	0	80·8	19·0	26·6	43·9	11·0	61·1	13·3	45·5	12·3
P. orientalis	0	0	9·7	2·0	0	0	0	0·03	5·4	0	0	0	3·4	2·1	0
P. sitchensis	0·1	0·8	0·6	10·3	0	0	0	0·8	3·2	0	1·3	0	0·9	0·4	0
TOTAL %	0·8	12·9	79·6	18·7	3·1	15·5	80·8	19·9	37·4	43·9	12·3	61·1	18·0	48·0	12·3
Pinus brutia	10·9	0	0	0	0	0	0	0	2·9	0	0	0	1·6	3·6	0
P. halepensis	17·5	0	0	0	0	0	0	0	0·6	0	0	0	0·7	0	0
P. nigra	4·5	1·0	0·07	0·06	0	0	0	0	1·4	0	3·0	0	8·3	0·3	0
P. pinaster	45·3	0·2	0	0	0	0	0	0·3	2·8	0	0·3	0	8·3	0·4	0
P. pinea	2·7	0·3	0	0	0	0	0	0	0·2	0	0	0	2·5	0	0
P. radiata	6·0	0·4	0·04	0	0	0	0	0	2·0	0	0	0	6·7	0·3	0
P. sylvestris	12·1	0·08	0	0·08	0·7	0	0	0·08	7·1	0	25·6	0	7·4	11·1	13·5
TOTAL %	99·0	2·0	0·1	0·1	0·7	0	0	0·4	17·0	0	28·9	0	35·5	15·7	13·5
Pseudotsuga macrocarpa	0	0	0	0·8	0	0	0	0	0·5	0	0	0	0	0	0
TOTAL wasps	8265	2493	6687	5272	862	71	26	3973	5637	264	301	18	2890	279	325

etc. are given in Table IV and the proportion of the siricid species emerging from fallen and standing timber is summarised in Table V.

TABLE IV. *Siricid and parasitoid emergence from tree material of different types (1963–66)*

Source	No. logs collected	Total no. siricids emerged	No. parasites emerged: Ichneumonidae	No. parasites emerged: Ibaliidae	No. siricids and parasitoids per log
Windblown	95	1253	259	137	17·3
Logs	220	1071	166	112	6·1
Dead, standing	343	3682	787	282	13·9
Damaged live trees	91	285	77	0	4·0
Detached crowns	38	75	5	0	2·1
TOTAL	787	6366	1294	531	10·4

TABLE V. *Percentage of each siricid species emerging from fallen or standing timber* *

Species	Fallen	Standing
S. noctilio	0	100·0
S. cyaneus	24·3	75·7
S. juvencus	56·9	43·1
U. gigas	83·5	16·5
U. augur	88·7	11·3
U. sah	41·2	58·8
U. fantoma	8·2	91·8
X. spectrum	18·1	81·9

*Fallen material includes windblown trees, crowns, stumps and roots.

There were two examples of natural infestations of living pine by *S. noctilio* in England. One tree (*P. radiata*) with a full crown of green leaves was found on 1 October in Wareham, Dorset, with heavy resin flow from several oviposition punctures in the trunk. In a 10-cm length of stem, there were 35 oviposition holes with first- to third-instar larvae present. In the other case, in Thetford Chase, Norfolk, a *S. noctilio* female was observed ovipositing in a living *P. sylvestris* on 9 October. Live pines infested by *S. noctilio* were also recorded in Belgium, Corsica, Spain, Algeria and Morocco. Most of these trees were examined some months after the initial attack, and the leaves were yellow-green and twisted, with resin streaming from the oviposition drills. The majority of living trees attacked by *S. noctilio* were classed as suppressed, with sparse crowns. Of 3078 logs collected, 408 (13·2%) were derived from pine trees that were alive at the time of attack.

The numbers of insects that emerged per log from windblown and standing trees were similar (Table IV). Material that was small in volume and liable to drying out (*e.g.*, crowns) or where the infested area was strictly limited (*e.g.*, damaged areas of living trees) had considerably smaller populations of siricids. The number of infested logs per windblown tree was relatively low, but the logs were generally more heavily populated than logs from standing timber, in which siricids were more evenly distributed throughout the length of the stem. In Switzerland, 28 300 cm^3 (1 ft^3) at the base of a windblown tree contained 83 mature siricid larvae. At Ballykelly, N. Ireland, 60 infested logs of *Abies nobilis* were estimated to contain 6500 larvae (Kirk, 1975).

A sitka spruce (*Picea sitchensis*) forest in Windsor, Berkshire, England, was surveyed to determine the proportion of trees attacked by siricids. The area was 161·5 ha (399 acres), with current and old infestations of *S. juvencus* L. *Urocerus gigas* (L.) was also present but in relatively small numbers. There were 122 dead trees, of which 43 were fallen and 79 still standing. The fallen trees were virtually all windblown. There were 7 (16%) infested fallen trees and 44 (56%) infested standing trees; 42% of all dead trees had been attacked. Dead trees with a diameter at breast height (DBH) of less than 13 cm were not infested; 11% of those between 13 and 16 cm were infested, as were 48% of dead trees with a DBH in excess of 16 cm. The infestation levels, as measured by number of flight holes, are summarised in Table VI.

TABLE VI. Sirex juvencus *infestation throughout length of trees in a sample of trees from a site at Windsor, England (10 trees per group)*

Height of stem from base (cm)	Flight holes per 90-cm sample of stem (%)			
	Standing trees		Fallen trees	
	mean	s.e.	mean	s.e.
0–90	28·2	1·041	16·0	1·898
91–180	21·3	0·651	21·0	2·921
181–270	16·7	0·630	14·4	1·824
271–360	13·4	0·630	25·2	0·825
361–450	9·6	0·483	22·0	0·987
451–540	7·0	0·650	9·6	1·414
541–630	5·0	0·358	2·5	0·707
mean number of flight holes per tree	387·6		130·0	

In standing trees, the population of siricids decreased with height of tree and decrease in diameter of stem. The flight holes in fallen trees were uniformly distributed along the length of the trunk with no bias towards the butt end. Populations of siricids in the standing trees were nearly three times greater than those in windblown timber.

Biotic factors sometimes reduced the susceptibility or attractiveness of trees to siricid attack. For example, some fungi, such as blue-stain of pine and *Trichoderma*, inhibited oviposition, and the fungal symbionts associated with certain wood beetles (*e.g.*, *Xyloterus* spp.) also had an inhibiting influence. Trees killed by *Armillariella mellea* were often attacked, but contrary to Hanson's (1939) view, it was found that siricid larvae will develop in areas containing the mycelium, and in one example, a larva had migrated from one root to another, passing through thick *A. mellea* mycelium during its boring.

The action of primary insect pests such as defoliators and subcortical insects, the effects of which range from weakening or killing individual trees to devastating large areas of forest, produced much of the infested material collected during the surveys. The defoliators, *Lymantria monacha* (L.) and *Choristoneura murinana* (Hübner), seriously weaken trees, which may die and dry out comparatively slowly. This type of material appeared particularly susceptible to attack by *Sirex* and in Gengenbach (Black Forest, Germany) a mass outbreak of *S. noctilio* and *S. juvencus* occurred in 1962 following an attack by *C. murinana* on spruce (*P. abies*). There were approximately 50 siricid exit holes per metre of infested timber, and the numbers of woodwasps during 1962 were compared with swarms of locusts by observers at the time. Another example of defoliation preceding siricid infestation was seen in an avenue of *Pinus radiata* in Sabaudia (Italy). Many trees had been killed after repeated attacks by *Thaumetopoea pityocampa* (Schiffermüller), and several were found infested by *S. noctilio*. A tree defoliated by *C. murinana* in Banska Stiavnica (Czechoslovakia) was infested throughout most of its 29-m length.

Many of the standing trees containing siricids had been previously attacked by bark beetles, notably *Ips* species. Among the Curculionidae, *Pissodes* and *Hylobius* species were responsible for the death of many siricid-infested trees, especially in western coastal France and the Alpes Maritimes. In the Massiv des Maures of southern

France, *Matsucoccus* was responsible for the destruction of large areas of pine, and occasional secondary infestation by siricids occurred. Unsuitable soil conditions may lead to the establishment of the fungus *Heterobasidion annosum*, and in northern Germany several *Pinus sylvestris* that had been killed by *Heterobasidion* were infested by siricids.

Along the western seaboard of France and Portugal, and to a lesser extent along the Mediterranean coastline of Italy, salt spray is responsible for the death or weakening of many trees along the coastal periphery of forests and trees planted in sand dunes to check erosion. The Marinha Grande forest in Portugal, is a notable example, and several dead *P. pinea* and *P. pinaster* killed by salt spray were infested by siricids.

Siricid attack can also occur in trees damaged or killed by lightning. A tree in Rantzau (Germany) that had been struck by lightning in August 1963 was infested with siricid larvae when sampled in April 1964. Several fire-devastated areas were surveyed, including the Massiv des Maures (southern France), Turini (Alpes Maritimes, France), L'Ospedale (Corsica) and La Fou (Tarragon Province, Spain). Large quantities of infested material were obtained from the burnt area at Turini.

Bad forest management resulted in numerous cases of dead, dying and overmature trees, which provided ideal conditions for siricids. For example, in Cintra (Portugal), larvae were found in the branches of an overmature but living *P. radiata* that had been felled, and elsewhere unsuitable soil conditions resulting in waterlogging or exposure of roots by erosion and the consequent weakening of trees led to siricid infestation.

Trees left on the edge of stands after clear-felling of adjacent areas were frequently damaged by solar radiation, which destroyed the cambium and resulted in areas of dead wood down one side of the trunk. These areas were susceptible to woodwasp attack, and examples of such damage were seen in northern Germany.

Fallen trees were major sources of siricid infestations in Europe. The time of falling and rate of deterioration influenced the tree's subsequent attraction to siricids. Felled trees that were left in the forest were frequently attacked, particularly when de-barking was delayed or overlooked, but *Urocerus* spp. were observed ovipositing in trees immediately after felling in Goc (Yugoslavia). Thinnings, brushwood, discarded crowns and stumps remaining after felling operations were a common source of infested material. Logs were often attacked by siricids, although many were from trees that had been infested before felling.

TABLE VII. *Percentage parasitism and host records of parasitoids of siricids*

Species	No. adults emerged	Host species: *S. noctilio*	*S. cyaneus*	*S. juvencus*	*U. gigas*	*U. augur*	*U. sah*	*U. fantoma*	*X. spectrum*	Mean % parasitism
R. persuasoria	8411	+	+	+	+	+	+	+	+	33·7
R. amoena	208	0	+	+	+	+	0	0	+	4·7
M. emarginatoria	77	0	+	+	+	+	0	0	+	5·6
I. l. leucospoides	7639	+	+	+	+	+	+	+	+	21·8
I. r. drewseni	615	+	+	+	+	+	0	0	+	10·0
O. geniculatum	435	+	+	+	+	+	0	0		8·9

Dead standing trees were the most frequent source of siricids (Table IV) and were generally infested for more of their length than fallen trees. Larvae that migrated into the stump and root systems of such trees were always larger than those in the trunk.

Siricid infestation in living trees were of particular interest, but in most cases the infestation sites had been previously damaged, resulting in areas of dead or dying wood. Areas of trunk that were accidentally de-barked during logging operations often acted as foci for siricids. In Germany, trees were frequently infested following de-barking by deer.

Parasitism

The mean percentage parasitism of siricids, based on emergence records from localities where each parasitoid species was recorded, is given in Table VII.

Bioclimatic analysis

The UNESCO-FAO (1963) bioclimatic maps of the mediterranean zone distinguish three major climatic types: mediterranean, where the mean temperature, t, of the coldest month is greater than 10°C; temperate, where t is 0–10°C; and cold, where $t<0$°C Further subdivisions are based on the distribution, nature and intensity of any dry period.

All localities from which siricid and parasitoid material was collected were classified according to the above climatic designations (Appendix). The emergence of insects from the different bioclimatic areas is given in Table VIII.

Discussion

Records of serious woodwasp infestations in Europe are few, and only one or two cases of living trees being attacked and killed have been reported (Ratzeburg, 1844). The secondary role of woodwasps following primary damage by defoliating insects or by scolytid bark beetles is well documented (Bechstein, 1818; Ratzeburg, 1844; Scheidter, 1919; Chrystal, 1928; Schimitschek, 1940) and was confirmed in the present study.

When living trees are attacked by siricids in Europe they are rarely killed. Von Hagen (quoted by Chrystal, 1928) recorded a case in which trees were repeatedly infested for 7 years, but none was killed outright although they suffered a considerable loss of increment. Similarly, Hartig (1860) noted that unhealthy spruce trees being attacked by siricids continued a precarious existence for a long time. In the course of our work, a very few trees were found the death of which could definitely be attributed to siricids. By contrast, the introduced *S. noctilio* in Australia and New Zealand has caused severe damage in the exotic pine forests. Rawlings (1948) recorded 30% losses of *P. radiata* in a 240 300-ha (600 000-acre) forest in New Zealand and in Tasmania 40% of living trees in one plantation were killed (Coutts, 1965). The destructive role played by *S. noctilio* in Australasia is in striking contrast to the woodwasp situation in Europe.

The capacity of *S. noctilio* to kill trees by injecting a conditioning mucus secretion and a phytotoxic fungus during oviposition was established by Coutts (1969*a*, *b*), and Spradbery (1973) demonstrated that *S. noctilio* was the only European species capable of producing phytotoxic symptoms in living trees. The relative volume of the toxic mucus was also considerably greater in females of *S. noctilio* than in those of other siricids (Spradbery, 1977). During the course of our survey, *S. noctilio* was the only species found infesting living trees, although *S. juvencus* has been discovered in a spruce tree exhibiting no obvious phytotoxic symptoms (Spradbery & Kirk, in press). Alhough it is now well established that *S. noctilio* can cause primary damage in forests, other ecological factors have undoubtedly contributed to its pest status in Australasia.

In New Zealand and Australia, the dominant softwood species is *P. radiata*, an introduction from California. Our study (Fig. 6) and those of Rawlings (1948), Wolf (1969) and Spradbery & Kirk (in press) have demonstrated convincingly that *S. noctilio* is virtually confined to *Pinus* species and that other siricids are only rarely associated with pines. Furthermore, the predominantly annual life-cycle of *S. noctilio* (Table II), especially in mediterranean climates, provides a greater potential for population increase than in the other siricid species.

TABLE VIII. *Percentage of siricids and their parasitoids emerging from different bioclimatic areas*

	COLD AXERIC	Temperate medium	Temperate sub-dry	Transitional	TOTAL TEMPERATE	Meso-mediterranean *a*	Meso-mediterranean *b*	Thermo-mediterranean *a*	Thermo-mediterranean *b*	Xerothermo-mediterranean	TOTAL MEDITERRANEAN
Siricids											
S. noctilio	2·2	21·7	0·4	0	22·1	40·9	13·3	19·9	1·6	0	75·7
S. cyaneus	90·2	7·0	0	2·9	9·8	0	0	0	0	0	0
S. juvencus	88·2	0·7	0·8	10·3	11·8	0	0	0	0	0	0
U. gigas	53·2	37·3	0·7	8·8	46·8	0	0	0	0	0	0
U. augur	100·0	0	0	0	0	0	0	0	0	0	0
U. sah	0	0	100·0	0	100·0	0	0	0	0	0	0
U. fantoma	100·0	0	0	0	0	0	0	0	0	0	0
X. spectrum	95·0	4·4	0	0·6	5·0	0	0	0	0	0	0
Mean	57·0				20·8						22·2
Parasitoids											
R. persuasoria	61·0	25·0	2·4	4·9	32·2	2·9	0·9	1·6	0·3	0	5·7
R. amoena	100·0	0	0	0	0	0	0	0	0	0	0
M. emarginatoria	100·0	0	0	0	0	0	0	0	0	0	0
I. l. leucospoides	34·7	12·1	4·8	0·9	17·8	41·2	0·9	5·1	0·2	0	47·4
I. r. drewseni	89·3	10·7	0	0	10·7	0	0	0	0	0	0
O. geniculatum	87·0	13·0	0	0	13·0	0	0	0	0	0	0
Mean	52·1				24·6						23·3

a = attenuated; *b* = accentuated.

Although living trees are attacked by *S. noctilio* in Europe, extensive damage in pine forests has never been recorded (Hall, 1968). Moreover, during experiments in England to compare the effects of *S. noctilio* mucus and fungus injected artificially or by oviposition, only one *P. radiata* was killed (Spradbery, 1973), whereas all treated trees died in a similar study in Australia (Coutts, 1969*b*). The physiological activity of the mucus from European and Australian *S. noctilio* females is identical, yet a relatively slower and less pronounced response by *P. radiata* under European conditions has been

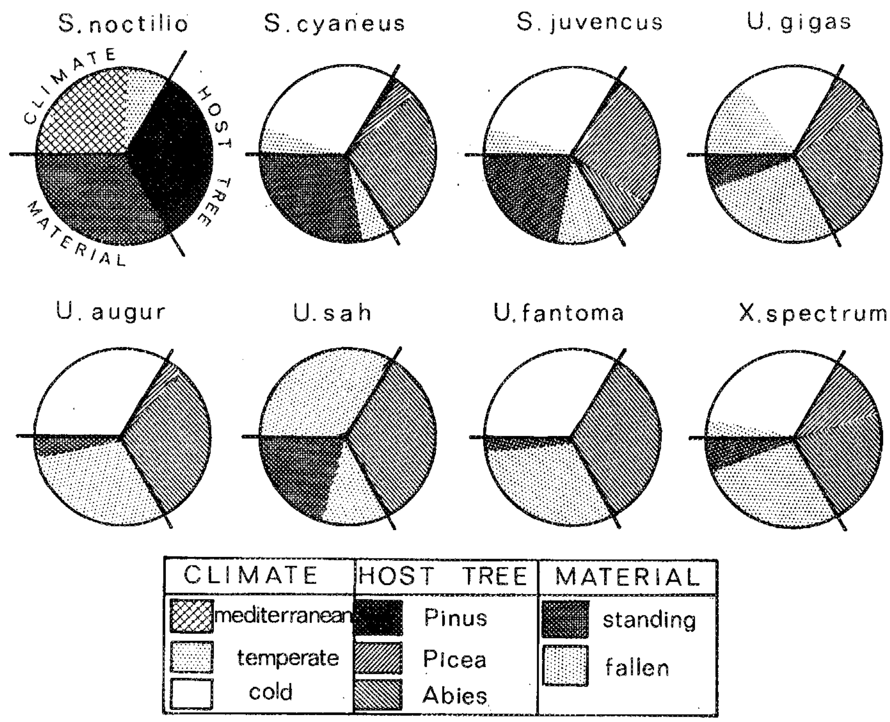

Fig. 6.—Distribution of siricid woodwasps in relation to climate, host tree genera and type of infested timber (based on CSIRO survey).

demonstrated (Spradbery, 1973). The major difference between the two studies was the timing of the treatments. In Europe, *S. noctilio* is the last siricid species to emerge, the flight period in temperate areas occurring in August–September and in mediterranean areas in September–December (Fig. 4). In Tasmania, *S. noctilio* emergence takes place in January–May, with peaks in January–February and March (Taylor, 1969). It was established by Kile *et al.* (1974) that there are seasonal changes in the susceptibility of *P. radiata*, susceptibility being greatest in summer and least in autumn and winter. The differences in the cycles of *S. noctilio* emergence and tree susceptibility in Australia as compared with Europe may be an important factor contributing to the pest status of *S. noctilio* in Australia.

S. noctilio was the only siricid found in the mediterranean bioclimatic area, although *S. cyaneus* F., *S. juvencus* and *U. gigas* were found in small numbers in the transitional zone (Table VIII). All areas in Australia where *P. radiata* is grown have bioclimatic

Parasitoids											
R. persuasoria	61·0	25·0	2·4	4·9	32·2	2·9	0·9	1·6	0·3	0	5·7
R. amoena	100·0	0	0	0	0	0	0	0	0	0	0
M. emarginatoria	100·0	0	0	0	0	0	0	0	0	0	0
I. l. leucospoides	34·7	12·1	4·8	0·9	17·8	41·2	0·9	5·1	0·2	0	47·4
I. r. drewseni	89·3	10·7	0	0	10·7	0	0	0	0	0	0
O. geniculatum	87·0	13·0	0	0	13·0	0	0	0	0	0	0
Mean	52·1				24·6						23·3

a = attenuated; *b* = accentuated.

homologies with European, north African and Turkish localities where *S. noctilio* is endemic (Kirk, 1974). Thus, all Australian stands of *P. radiata* are vulnerable to *S. noctilio*. However, it appears unlikely that any other European siricid will become established in Australia, although several species have been intercepted by quarantine authorities (Morgan, 1968).

S. noctilio became established in Australia without its complement of natural enemies and, since 1957, attempts have been made to introduce parasites from many different countries to provide a measure of biological control (Taylor, 1967, 1976). Absence of the restraint that parasites impose on *S. noctilio* populations must be a significant factor in the epidemiology of *S. noctilio* in Australia. Overall parasitism by insect parasitoids of siricids in Europe was 35–40%, although infested timber was not exposed to parasites after collection and this figure would be a gross under-estimate under field conditions. In Tasmania, parasitism of *S. noctilio* by insects has reached 70% (Taylor, 1976), and the nematodes, *Deladenus* spp., that sterilise female siricids (Bedding, 1972) have parasitised more than 70% of hosts in some areas (Bedding & Akhurst, 1974).

Some of the parasitoid species have failed in culture in Tasmania, notably *Megarhyssa emarginatoria* (Thunberg) and *Rhyssa amoena* Gravenhorst (Taylor, 1976). The reasons for these failures would appear to be climatic incompatibility, because both these species were restricted to axeric native zones. For similar reasons, it seems improbable that the innocuous siricid, *Xeris spectrum* (L.), could be successfully established in Australia as an alternative host for parasitoids and nematodes as suggested by Bedding & Akhurst (1974).

To summarise, it appears that the acute pest status of *S. noctilio* in Australia has been brought about by a combination of ecological circumstances that have maximised the opportunities for its establishment, multiplication and subsequent dispersal. *S. noctilio* has become one of the greatest threats to the Australian softwood industry because the climate is highly compatible in a region with an abundance of suitable host trees, the woodwasp has the capacity to condition living hosts more effectively than was thought possible by northern hemisphere entomologists, and because it lacked the constraints imposed by natural enemies.

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Appendix

Collections of siricid-infested material during 1963–70 in the various bioclimatic zones

Map ref. no.	Locality	Altitude (m)	Tree species	No. 1-m logs
Axeric (cold)				
	NORWAY			
1	Nordmarker	380	*Pinus sylvestris*	6
			Picea abies	14
2	Rakkestad	200	*P. abies*	29
	SWEDEN			
3	Skokloster	100	*P. abies*	11
4	Sandvreten	100	*P. abies*	22
	GERMANY			
5	Fallingbostel	50	*P. sylvestris*	12
			P. abies	5
6	Forst. Rantzeau	20	*P. sylvestris*	5
			P. abies	48
7	Gahrenburg	170	*P. abies*	14
8	Ebesberger	442	*P. abies*	38
9	Gegenbach	740	*P. abies*	70
	NETHERLANDS			
10	Loneker	20	*P. abies* } *P. sylvestris* }	7
	BELGIUM			
11	Eupen	150–400	*P. abies*	30
12	Beauraing	150–400	*P. sylvestris*	137
	SWITZERLAND			
13	Chatillon	800–900	*Abies alba*	301
14	Bulle area	700–1600	*P. abies*	100
			A. alba	37
	FRANCE			
15	Vosges	400	*A. alba*	15
16	Turini area	1600	*Larix decidua*	19
			P. abies	47
			A. alba	112
			P. sylvestris	4
	ITALY			
17	Camaldoli area	1000	*A. alba*	96
18	Bolzano	250	*A. alba*	5
19	Carnia	100	*A. alba*	6
	CZECHOSLOVAKIA			
20	Kralovka	500	*P. abies*	5
21	Hodrusa	700	*A. alba*	26
	HUNGARY			
22	Jarvokuti	300	*P. abies*	14
23	Sopron	400	*P. abies*	13

Map ref. no.	Locality	Altitude (m)	Tree species	No. 1-m logs
	YUGOSLAVIA			
24	Zalesina	600–800	*A. alba*	70
25	Toliscina	900	*A. alba*	27
26	Knezina	750	*A. alba*	4
27	Belasica	800	*A. alba*	4
	BULGARIA			
28	Borovetz	1400	*A. alba*	13
	GREECE			
29	Pertouli area	1000	*Abies borisii-regis*	22
	TURKEY			
30	Uludag	2000	*Abies bornmuelleriana*	12
31	Ugurlu	1200	*Abies cilicica*	28
32	Gedigi	1500	*A. cilicica*	6
33	Namrun	1400	*A. cilicica*	11
34	Sogut area	1400–1600	*A. cilicica*	27
	ITALY			
35	Gambari	1600	*A. alba*	4
	FRANCE (Corsica)			
36	D'Aitone	1500	*A. alba*	49
	ALGERIA			
37	Chrea	1500	*Cedrus atlantica*	17
	MOROCCO			
38	Ifrane	1800	*C. atlantica*	1
			Pinus pinaster	14
	SPAIN			
39	Sierraguadarama	100	*P. abies*	5
			P. sylvestris	10
Temperate medium				
	UNITED KINGDOM			
40	Fort Augustus	100–200	*L. decidua*	22
			Pseudotsuga macrocarpa	9
41	Yorkshire	100–150	*L. decidua*	11
			P. abies	16
			Picea sitchensis	2
42	Thetford	30	*L. decidua*	16
			P. sylvestris	10
43	Windsor	50	*P. sitchensis*	>200
44	Wareham	70	*P. sylvestris*	3
45	Exeter	30	*P. abies*	39
			P. sitchensis	11
46	Mortimer	100	*P. sitchensis*	3
47	Cynwyd	150	*L. decidua*	9
			Abies grandis	2
48	Baronscourt	100–400	*P. sitchensis*	5
			Pseudotsuga spp.	14
			L. decidua	16
			P. abies	10

Map ref. no.	Locality	Altitude (m)	Tree species	No. 1-m logs
49	Ballykelly	10	*Abies nobilis*	17
50	Newcastle	50	*P. sitchensis*	2
			L. decidua	2
51	Glenarm	150	*P. abies*	1
			L. decidua	5
	EIRE			
52	Glenmalure	300	*P. sitchensis*	3
			L. decidua	1
53	Parknasilla	3–15	*A. nobilis*	31
			P. sitchensis	11
			A. alba	6
			A. grandis	9
	FRANCE			
54	Cisai	200–300	*A. alba*	27
55	St. Jean de Montes	10	*Pinus pinaster*	13
56	St. Isidore	10	*P. pinaster*	12
	SPAIN			
57	Sort	800	*Pinus nigra*	5
58	Las Munacas area	200–400	*Pinus radiata*	114
Temperate sub-dry				
	SPAIN			
59	Cordal peone	400	*P. radiata*	11
60	Castanedo	400	*P. pinaster*	4
61	Yunqera	1200	*Abies pinsapo*	6
	MOROCCO			
62	Bab Taza	1300	*A. pinsapo*	30
Transitional				
	PORTUGAL			
63	Covilha	400	*P. pinaster*	15
	FRANCE (Corsica)			
64	Vivario	100–1000	*P. pinaster*	3
	ITALY			
65	Arezzo	1100	*A. alba*	3
	GREECE			
66	Granitis	600	*A. borisii-regis*	4
	TURKEY			
67	Cangal	1300	*A. bornmuelleriana*	30
68	Meryamana	900–1200	*Picea orientalis*	36
Meso-mediterranean (attenuated)				
	TURKEY			
69	Orhaneli	450	*Pinus brutia*	6
70	Kazdag	800	*P. nigra*	13
			Abies equi-trojani	7

Map ref. no.	Locality
	ITALY
71	Umbra
72	Sabaudia
	FRANCE (Cor
73	L'Ospedale are
	SPAIN
74	La Fou
75	Navehonde
	PORTUGAL
76	Marinha Grand
77	Sr. Monte Junt
	ALGERIA
78	Bainemh
Meso-mediterranean (ac	
	MOROCCO
79	O Nefifikh
80	El Harhoura
	SPAIN
81	Guadalmedina
82	Carresquetas
83	El Saler
	GREECE
84	Panagia area
85	Evia area
86	Parnis
Thermo-mediterranean (a	
	TURKEY
87	Yenice
	TUNISIA
88	Remel
	MOROCCO
89	Tangier area
Thermo-mediterranean (a	
	SPAIN
90	Aznalcazar
91	Huelva

Map ref. no.	Locality	Altitude (m)	Tree species	No. 1-m logs
	ITALY			
71	Umbra	700	*A. alba*	5
72	Sabaudia	10	*P. radiata*	64
	FRANCE (Corsica)			
73	L'Ospedale area	800	*P. pinaster*	72
	SPAIN			
74	La Fou	800	*P. nigra*	4
75	Navehonde	800	*P. nigra*	6
	PORTUGAL			
76	Marinha Grande	100	*P. pinaster*	33
77	Sr. Monte Junto	300	*P. radiata*	23
			Pinus halepensis	3
			P. pinaster	284
	ALGERIA			
78	Bainemh	10	*P. halepensis*	8
Meso-mediterranean (accentuated)				
	MOROCCO			
79	O Nefifikh	10	*P. halepensis*	77
80	El Harhoura	5	*Pinus pinea*	21
			P. halepensis	14
	SPAIN			
81	Guadalmedina	500	*P. halepensis*	23
82	Carresquetas	1000	*P. halepensis*	4
83	El Saler	2	*P. halepensis*	15
	GREECE			
84	Panagia area	15–500	*P. brutia*	6
85	Evia area	600–1000	*A. borisii-regis*	5
			A. cilicica	6
86	Parnis	1200	*A. borisii-regis*	3
Thermo-mediterranean (attenuated)				
	TURKEY			
87	Yenice	500	*P. brutia*	6
	TUNISIA			
88	Remel	5	*P. halepensis*	70
	MOROCCO			
89	Tangier area	30	*P. brutia*	31
			P. pinea	12
Thermo-mediterranean (accentuated)				
	SPAIN			
90	Aznalcazar	30	*P. pinea*	22
91	Huelva	5	*P. pinea*	16