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THE SIREX WOODWASPS AND THEIR PARASITES.

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ONE of the most important features of modern forestry development in Great Britain and some of our overseas Dominions has been the formation of plantations of exotic coniferous trees. In Great Britain the Douglas fir and Sitka spruce, amongst others, have been very extensively used for this purpose, and in South Africa and New Zealand *Pinus radiata* and other species of pine are being planted on an ever-increasing scale. The introduction of any species into a new environment is always attended with many dangers. On the one hand there is the question of the suitability of soil and climate to the needs of the species, and on the other, the risk that injurious insect or fungus pests may be imported into the country along with the new stock. These introduced pests not only endanger the existence of the exotic trees but may quite possibly extend their attentions to native species. Many examples of this could be quoted, but we shall confine our attention in this article to the situation which has arisen in New Zealand, consequent upon the introduction of an insect enemy of the pine, which has appeared in plantations in many parts of that country. The formation of plantations of exotic conifers has been in progress for over forty years in New Zealand, and the species planted have been mostly pines. These include such well-known forms as *P. radiata*, *P. ponderosa*, *P. muricata*, etc., and in the Province of Canterbury alone the plantations already cover an area of over 32,000 acres, and are being rapidly extended.

So extensive is the area covered by these woods that considerable alarm was felt throughout the country when, some years ago, the rumour spread that an insect borer imported from abroad had begun to attack the trees.

The insect in question, *Sirex juvencus L*, is one of the Family Siricidae (Order Hymenoptera), the members of which are well-known wood borers in coniferous trees, both in Europe and America, where they are popularly termed "woodwasps" or "horntails." The anxiety felt by the general public in

New Zealand was not allayed by the articles which appeared in the press concerning the insect and its work. One of these, written some two years ago, stated that the insect had increased and prospered to such an extent since its introduction into the country that not only was it developing to an unprecedented size in its new home, but that it had also contracted the habit of attacking living trees, to which it was a direct menace.

So great was the alarm occasioned by these statements that the New Zealand Government approached the Imperial Bureau of Entomology requesting that an investigation into the insect parasites of the woodwasps in Europe might be undertaken, with a view to their ultimate collection and exportation to New Zealand, if this were feasible, and some effort at natural control begun.

The work was actually started by the recently established Parasite Laboratory of the Imperial Bureau of Entomology, Farnham Royal, Bucks., in July, 1927, and was carried out in co-operation with the Imperial Forestry Institute at Oxford.

This arrangement was made on account of the fact that one of the writers, as entomologist to the Imperial Forestry Institute, had already begun a study of the woodwasps and their parasites in a small wood of larch and pine at Tubney, Oxon., and the studies which the Bureau wished to undertake were in close alignment with this.

These studies, which have been made for the most part on *S. cyaneus* Fabr., a species closely allied to the New Zealand form, have now been in progress for three years, and in the following pages a condensed account is given of the main results which have been obtained. The subject will be considered under two distinct headings :—

(1) The biology of the Sirex woodwasps and their relation to the forest, and

(2) The parasites of the Sirex woodwasps ; their biology and host-relationships.

The Biology of the Sirex Woodwasps.

In Britain, the woodwasp which is best known to the forester is undoubtedly *S. gigas* L., the large black and yellow species. The insect which was studied in the present case, however, *S. cyaneus* Fabr., is quite as abundant as the former species, and is one of the so-called steel-blue woodwasps, this name arising from the deep blue colour of the females. The biology of this insect was studied at Tubney Wood over a period of two years, and the main features are as follows. The adult wasps fly during the months of August and Septem-

PLATE II.

Oviposition of *Rhyssa persuasoria*, *L.*

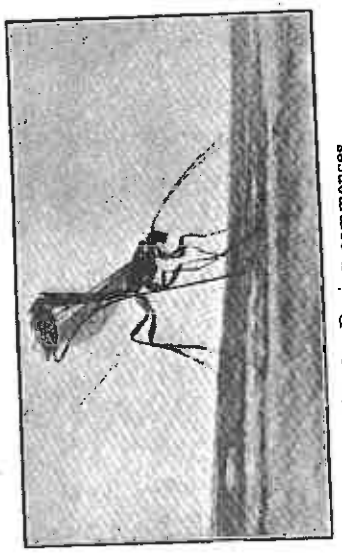

Fig. 2. Boring commences.

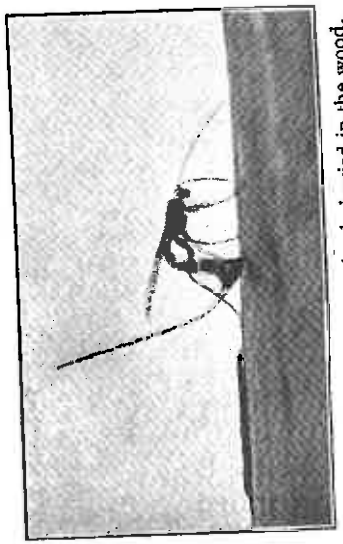

Fig. 4. Ovipositor completely buried in the wood.

Fig. 1. Exploring the wood surface.

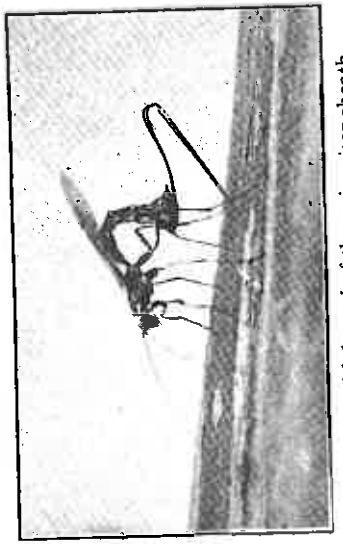

Fig. 3. Withdrawal of the ovipositor sheath.

PLATE III.

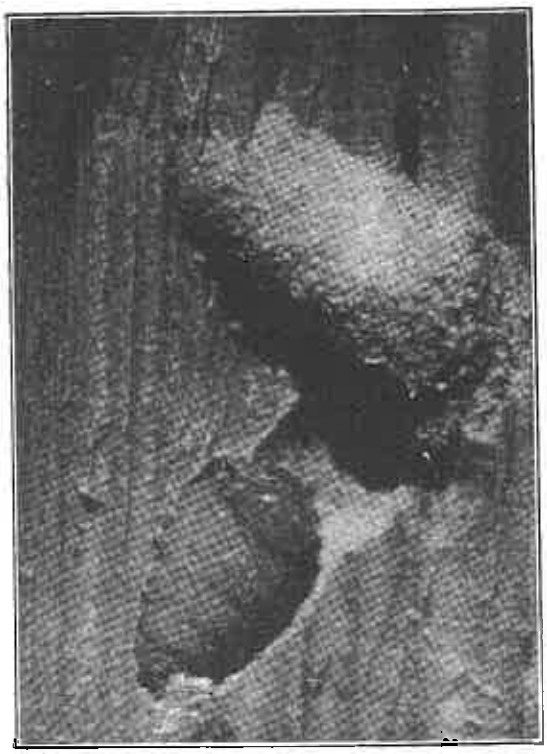

Fig. 1. Sirex larva lying in the tunnel bearing on its head the egg of Rhyssa.

Fig. 2. Head of the same larva enlarged showing (left) young Rhyssa larva just hatched, and (right) another larva just emerging. Note the tail of the egg on the right.

ber, and the females are as a rule much more frequently seen than the males, which fly higher up in the tree tops, where pairing is believed to occur. The female is a large, handsome insect, deep blue in colour, and may attain a length of one and a half inches. Apart from her colour she is easily recognised by the powerful ovipositor which projects well beyond the tip of the abdomen. (Plate 1, Fig. 1). Any coniferous species may be chosen for egg laying, but in the present instance larch was the favourite; indeed the only host tree which was attacked at Tubney. The egg tunnel which the wasp excavates in the wood with her ovipositor may measure up to ½in. in depth, and in it a number of eggs, varying from two up to six or seven, are deposited. The young larvae on hatching bore their way at right angles to the egg tunnel for some distance before they descend into the deeper layers of the wood. The minimum duration of the larval life is two years, but it is known that this is exceeded in many cases, although it is not possible to say with certainty what the maximum duration of the larval life may be. Probably, under normal forest conditions, a three-year larval life is the maximum period. During the greater part of its life the larva tunnels the wood in all directions, leaving the tunnel behind it, thickly packed with wood refuse, the peculiar nature of which is a certain indicator of its presence. (Plate 1, Fig. 2). When mature the larva may be lying at a distance varying from half an inch to two inches from the wood surface, and here pupation takes place, without any cocoon being constructed. As a rule, however, the larva when about to pupate places itself at a convenient angle to the wood surface, so as to allow the future adult insect to emerge, by boring its own way out through the wood, which it does after a pupal period of five to six weeks.

The emergence hole made by the adult insect is circular and can thus be distinguished at a glance from similar holes made by longicorn beetles (Coleoptera, Cerambycidae), which are, as a rule, markedly oval-shaped. Such, in brief, are the salient features of the life cycle, which does not differ greatly among the various species. To some features of this life cycle we shall return when we come to consider the biology of the parasites, but before doing so we must turn our attention to a consideration of the forest relations of the woodwasps in general. This question, which must be regarded as fundamental to the proper understanding of the Sirex problem in New Zealand, will be discussed here only with reference to standing trees; all reference to Sirex as an enemy of timber in yards, warehouses, etc., being omitted. Sirex, in company

with other insects of like habit, occupies a definite place in the vast complex of living organisms which make up the forest environment. The studies made in Tubney Wood, which were supplemented by further observations in other parts of England, showed that in no case was the insect able to attack trees which had even half of their normal crowns remaining. In other words, Sirex is never to be regarded as a primary enemy of green trees; other factors must supervene before the tree is in a fit condition for the insect's work. These factors may be either unfavourable soil conditions, as at Tubney, where waterlogged soil was the initial cause of ill-health; or fungus disease, as one so often finds in silver fir or larch attacked by *Fomes annosus* or *Armillaria mellea*.

The important point to note here is that, so far as one can see, the tree must be very sickly, that is, must have lost nearly all its crown, before the insect will select it for attack. This phenomenon is not peculiar to Sirex. Many insect borers show the same predilection for sickly trees, and the well-known larch longicorn beetle, *Tetropium gabrieli* Weise is a case in point. This beetle is well known to be a sure indicator of disease in larch, and at Tubney it is commonly found both preceding and also coinciding with woodwasp attack. As to the exact nature of the factors, physical or chemical, which determine the insect's choice of a tree, we are in almost complete ignorance. It is remarkable, however, to find that in many cases the insect itself makes serious mistakes in its calculations, for which it pays with its life. One finds, for example, that quite often in trees the bark of which is still fresh and resinous the females are caught while ovipositing, the fibres of the wood closing in upon the ovipositor and holding the creature a prisoner. Standing trees which have been dead some time are not usually selected for oviposition, but as long as their wood is sound the chances are that adults may emerge from them. No larvae are left in the wood as a rule once it reaches an advanced stage of decay. In the case of felled stems the insect's choice lies as a rule along similar lines, but cases are on record of adults ovipositing in wood which would seem to have been too dry for the purpose, and for successful oviposition there is no doubt that fresh logs are always preferred. These brief considerations bring us to the heart of the Sirex problem in New Zealand, and quite recently an investigation into the forest relations of *Sirex juvencus* in New Zealand was undertaken by Mr. A. C. Clark, formerly a forestry student of the Canterbury School of Forestry. Mr. Clark's results were

published in a paper entitled, "The Infestation of *Sirex juvencus* in Canterbury," and they confirm our main results in every way.

Mr. Clark made a comprehensive survey of the pine plantations in the district of Canterbury, and studied the conditions in plantations of *P. radiata, ponderosa* and *muricata*. He found that in many of the plantations where Sirex attack occurred no proper thinnings had been carried out, with the result that they contained many suppressed and unhealthy trees. These were selected by Sirex for attack in every case. Further, on certain areas where the root systems of the trees were shallow and defective, due to unfavourable soil conditions, there was a marked tendency to Sirex attack, whereas on deep well-drained soils the amount of attack was negligible. Finally, Mr. Clark points out that in many cases there is a decided possibility that the Sirex attack is following upon fungus disease, in this case a leaf-cast fungus (*Botryodiplodia pinea*), which is apparently widespread, and which in its turn is probably induced by unfavourable soil conditions or faulty silviculture. These facts, Mr. Clark submits, should be given every consideration in dealing with Sirex in New Zealand, and with that verdict we heartily agree. The importation of insect parasites to assist in the natural control of the insect can only be relied upon to provide an additional safeguard after the more radical measures of control by silvicultural means have been put into operation.

This brings us to the second portion of this article, the biology and host relationships of the Sirex parasites, which we may now consider. There are two important parasites of the Sirex woodwasps, both of which have been studied in detail during the past three years. The first of these, *Rhyssa persuasoria L.*, belongs to the Family Ichneumonidae of the Order Hymenoptera, and is a large, handsome species, the females of which may attain a length of 2½ to 3 inches measured from the front of the head to the tip of the long ovipositor which projects for some distance beyond the tip of the abdomen. This parasite and its near relative in America, *Thalessa lunator*, also a Siricid parasite, has been known to entomologists for over a century, but in spite of this fact no complete account of its habits has ever appeared in print. Space will not permit of our giving more than a brief account of this interesting insect here, and the full significance of the creature's habits can only be satisfactorily grasped by watching it at work.

The adults fly from the end of May onwards until the middle of September, and are at the height of their activity in June

and July. It is a bright sunny day in the month of July and we are standing beside a log infested with Sirex on which three or four large female Rhyssa are busily engaged on their task of oviposition. Close observation of their movements is quite simple, as the insect is so absorbed in her task that she takes not the slightest notice of our inquisitive gaze. She is surveying the surface of the wood with her antennae, the tips of which are evidently the seat of sensation and recognition of the presence of her quarry (Plate II., Fig 1). She is locating the Sirex larvae which are burrowing in the log unseen to her. Having located a promising spot, she raises her wings slightly and then proceeds to elevate the abdomen preparatory to manoeuvring the long ovipositor into a vertical position, which feat is accomplished by using one of the hind legs as a guide.

The ovipositor once in position lying in a narrow space between the basal joints of the hind legs, the operation of boring begins (Plate II., Fig. 2). At first the two outward protecting sheaths of the ovipositor, as well as the egg tube proper, take part in the work, but as the operation proceeds the two sheaths are withdrawn and the egg tube continues its work alone (Plate II., Fig. 3). It may be noted at this point that although the insect can, and frequently does, bore its way directly into solid wood, quite as often advantage is taken of any cracks or crevices there may be which will give it a start and so lessen the labour involved. The ovipositor proper is inserted into the wood up to the fullest extent as a rule, and this operation may be completed in as short a time as ten minutes or may take considerably longer (Plate II., Fig 4). If the insect has been successful in finding a Sirex larva where she has burrowed, which is by no means always the case, the egg now passes down the ovipositor tube and is laid on the larva's body, at any point which may be convenient (Plate III., Fig. 1). The egg is elongate and sausage-shaped and has a long tail.

It is of interest to note at this point that Rhyssa does not only parasitise the larvae of Sirex, but will also lay her eggs on the pupae. Cases of this have been found several times during our work this year. The young larva hatches from the egg in two to two and a-half days and at once buries its jaws in the body of its victim (Plate III., Fig. 2). Subsequent development proceeds with extreme rapidity. In little more than three weeks the destruction of the host is complete, and in its place there lies in the wood cell an elongate, cylindrical, legless grub, with a narrow pale-coloured head, rudimentary

PLATE IV.

Fig. 1. Ibalia adult ovipositing in larch.

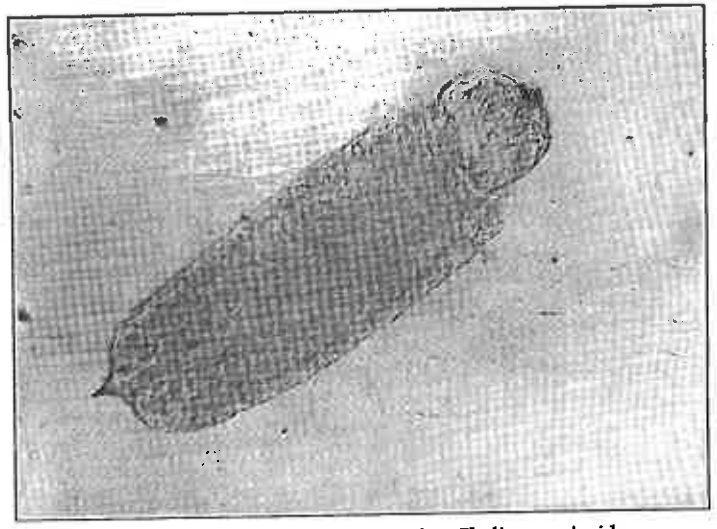

Fig. 2. Young Sirex larva showing Ibalia egg inside.

PLATE V.

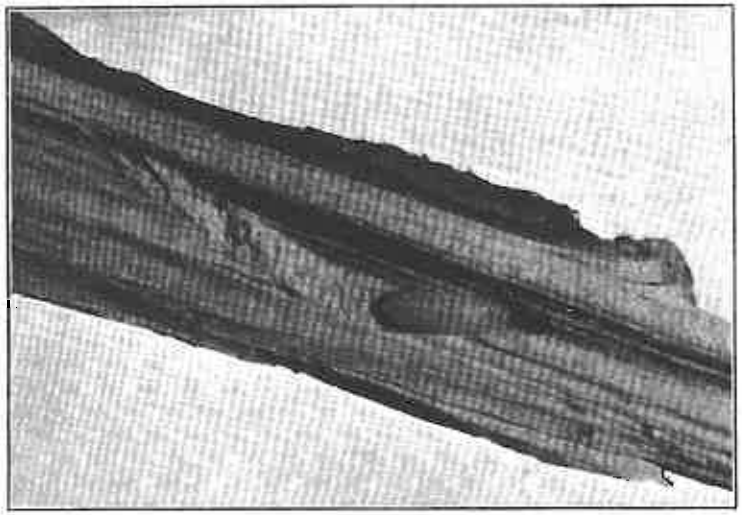

Fig. 1. Mature larva of Ibalia lying in Sirex tunnel.

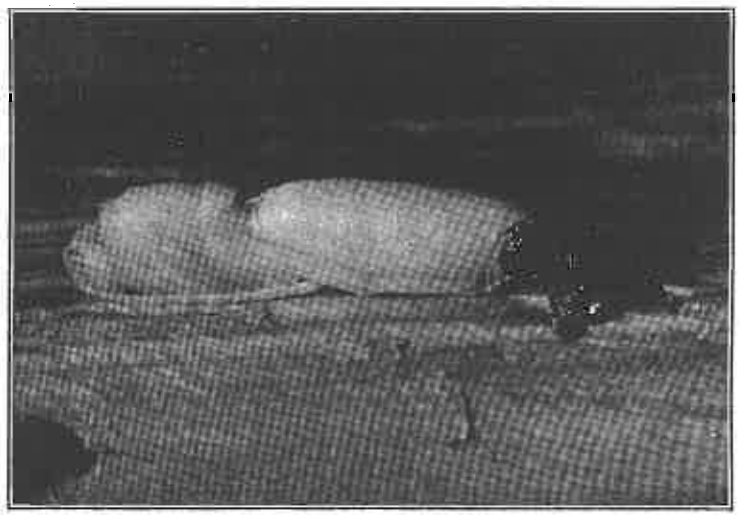

Fig. 2. Ibalia pupa.

mouth parts, and a somewhat blunt tail. This larva is fully-fed and will remain in its wood cell all through the winter and spring of the following year, a period of some nine or ten months. The early summer sees a change to the pupal stage, which lasts only a few weeks, after which the adult insect cuts its own way out of the wood by a circular hole similar to that of the wood wasp, but of smaller diameter. The above account gives the main features of the life cycle of this parasite, but some further observations on the species will be given later when we consider the question of its transmission to New Zealand.

The second parasite, *Ibalia leucospoides* Hochenw., belongs to the Hymenopterous family Cynipidae, in which the majority of the species are gall makers on plants. As in the case of Rhyssa, this insect has been long known to be a parasite of the Sirex wood wasps, but it has always been considered a very rare species, and its biology has therefore remained obscure up to the present time. The insect is a much smaller creature than Rhyssa, varying in length from one-half to three-quarters of an inch. The general appearance of the adult, especially the female, is sufficiently remarkable to ensure that once it has been observed it cannot easily be forgotten. The head and thorax are black and shining, while the abdomen is of a rich mahogany colour, and remarkably compressed laterally, so that when the insect is viewed from above the dorsal surface of the abdomen appears like a knife edge. The insect is found upon the wing from the end of August up to the early part of October and, as with Sirex and Rhyssa, the females are much more commonly observed in the open, busily ovipositing in the Sirex-infested trees.

Close observation of the oviposition habits is comparatively simple. The insect moves rapidly over the bark using her antennae to explore all its cracks and crevices and keeping the abdomen in constant motion. The first sign which the observer gets that she has run her quarry to earth, is the vertical position which the antennae assume. If one follows her movements at this point with a pocket lens, it will be seen that the antennae are exploring the oviposition tunnel of a woodwasp. Once satisfied that all is well, the insect then applies the tip of her abdomen to the tunnel mouth and releases the ovipositor sheath which up to now has lain concealed in a groove along the lower side of the abdomen. The ovipositor proper, which runs down this sheath, is a tiny tube which when not in use is curled up inside the abdomen like a watch spring. The end of the sheath is now inserted into the tunnel mouth and the ovipositor is gradually lowered into

the tunnel. (Plate IV. Fig. 1.). The length of the ovipositor and the depth of the Sirex egg tunnel correspond very closely so that the insect is able to reach the bottom of the tunnel if she wishes.

She is looking for the eggs, or young larvae of the woodwasp, which are this time lying in the egg tunnel (Plate IV., Fig. 2). Inside these she deposits one, or more rarely two, elongate sausage-shaped eggs, and as the average tunnel of the woodwasp contains, a number of eggs varying from 2 up to 6 or 7, the parasite can, and usually does, lay her eggs in several individuals in the same tunnel.

This oviposition habit is of the greatest interest as it affords us one more example of the remarkable way in which the insect host and its parasite are often linked together. For Ibalia, the finding of a Sirex egg tunnel is a vital matter, as in no other way could she reach the host, her tiny ovipositor being much too weak and slender to pierce the solid wood, as the more powerful weapon employed by Rhyssa is able to do. The larva of Ibalia, on hatching, spends the greater part of its life within the body of the Sirex larva in which it lives for over a year before growth is complete. When this time arrives the parasite makes its way out of the host larva, which is now only an empty shell and soon shrivels up. The parasite is now left in full possession of the wood cell, and is a white cylindrical grub, somewhat resembling that of Rhyssa, from which it differs however in the structure of its mouth parts, among other things (Plate V., Fig. 1). These larvae are always found lying in the superficial layers of the wood, and it is now known that the parasitised larvae of Sirex never bore downwards into the deeper layers of the wood, but, on the contrary, rather tend to bore outwards towards the bark. This is almost certainly a preparation for the emergence of the adult parasite, as its larva once the host has been destroyed, cannot bore further on its own, and must remain in the wood cell for a period of over six months when pupation takes place (Plate V., Fig. 2). The pupal period lasts for 5 to 6 weeks and the adult insect bores its own way out, making a similar exit hole to those of Sirex and Rhyssa.

Having thus dealt in outline with the biology of these two parasites we may now briefly discuss their respective values as enemies of the woodwasp. Firstly, as to the relative abundance of the two species in Britain. Unfortunately, the work has not been in progress long enough to enable us to obtain any reliable figures, but we know at any rate that wherever the woodwasps are found both parasites are present. In the case of Rhyssa, recent experiments under

taken on behalf of the Imperial Bureau of Entomology in North Devon, have shown that it is quite abundant in these parts, and probably the same conclusions will be reached in the case of Ibalia when further investigations have been made. Of the two parasites Ibalia would appear to be the more efficient, as her restriction to the Sirex egg tunnel renders her almost certain of a victim every time. Rhyssa, on the other hand, very often spends a lot of time boring oviposition holes in places where no Sirex larvae is present, guided to such places, no doubt, by the odour which the larva has left behind, and which is conveyed in some way we do not understand, to the terminal joints of her antennae. In this connection it has been suggested that the parasite might possibly hear the larva working in the wood below, and certainly in the case of some larvae of longhorn beetles the noise of their working in the wood is often audible to the human ear, even at the distance of a few feet. It seems much more likely, however, in the present case that the olfactory sense is concerned, when one finds eggs laid upon the inert pupae of the woodwasp as well as on its larvae.

At present there seems to be no reason why these two parasites should not be sent to New Zealand, and the Imperial Bureau of Entomology is now arranging for collections of the larvae to be made in as large numbers as possible. This is by no means an easy matter, owing to the large amount of wood which has to be cut up in order to secure the larvae. The difficulty has, however, we hope, been met by establishing dumps of Sirex-infested logs in various parts of North Devon, which serve as traps for both Sirex and the parasites. This method has been in progress for some months, and from these logs we hope to collect a large number of the parasite larvae. These will be removed from the wood and shipped to New Zealand in gelatine capsules, packed in sawdust, which form quite suitable receptacles for them, and in which, they will without any difficulty go through their stages.

The length of time which is spent by both parasites as fully developed larvae, solves the difficulty which transport to a distant country like New Zealand, would otherwise present. On arrival there it will be necessary to have suitable Sirex material ready for the use of the emerging adults, and in the case of Ibalia, its arrival must be timed to coincide with the egg laying period of Sirex in New Zealand.

At present, of course, the scheme is still untried, and it would be premature to attempt any forecast of its results. There seems to be no reason, however, why both these species should not be established in New Zealand, provided proper

care is taken in the initial stages of their propagation there. The difficulties attending such work are, however, many, and over-confidence in the final results is inadvisable. To rely solely on the parasites as a means of control of Sirex in New Zealand is out of the question, but this is not to say that no attempt should be made to introduce them. This will be well worth while, if by so doing we may hope to establish them as useful allies of the forester in his war against the insect; and if the scheme succeeds even partially, the efforts which have been made will be amply repaid.

* SOME ASPECTS OF FOREST ECOLOGY
WITH SPECIAL REFERENCE TO SOIL CONDITIONS.

By E. J. SALISBURY, D.Sc.,

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IN approaching the problems that are presented by the ecology of forests and woodland it is desirable that our concept of what is implied by these terms should be, so far as is possible, defined. To the student of plant ecology the terms woodland and forest denote plant communities, in which not only is the tree layer a prominent feature but the other living constituents bear a definite relation to one another and to the physical and biological environment by which they are surrounded and which, moreover, these living constituents have themselves in part determined.

To the student of forestry the concepts do not necessarily connote more than the presence of the trees themselves. To the forester the artificial plantation may be of more importance as a timber-producing unit than the natural woodland, whilst if all the timber trees be felled the status of the woodland from the forester's point of view has entirely altered, whereas to the ecologist it is still the same community modified by the removal of the tree layer. The artifact so produced still retains many, if not most, of its characteristics as a plant community.

The ecologist is concerned with the interrelations between all the constituent organisms and their physical environment, with their relation to the historic factors of the past and with the inevitable successional changes of the future. This ecological viewpoint can, however, only be of importance to the forester in so far as the development of the tree layer and the maintenance of its welfare is dependent upon the other members of the community directly, or indirectly to the conditions they induce. By this it is not insinuated that foresters are not cognisant of the advantages that accrue from the presence of natural forest conditions, but the two viewpoints clearly raise the question as to what differences,

* Paper read before the Forestry Sub-section of the British Association, Glasgow, September, 1928.