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STUDIES ON COLEOPHORA CAESPITITIELLA ZELL. (Lep.) ASSOCIATED WITH JUNCUS SQUARROSUS L.

BY

ANTHONY M. JORDAN.

- being a thesis presented in candidature for the Degree of Doctor of Philosophy in the University of Durham, 1955.

Abstract from thesis entitled :-

STUDIES ON *COLEOPHORA CAESPITITIELLA* ZELL. (Lep.) ASSOCIATED WITH *JUNCUS SQUARROSUS* L.

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Investigations on the relationship between the moth, *Coleophora caespititiella* Zell., and the rush, *Juncus squarrosus* L., were carried out on the Moor House Nature Reserve, in the northern Pennines, from 1952 to 1954.

Details of the life-history of *C. caespititiella*, which in the larval stage feeds on the seeds of various rush species, are given. Behaviour studies were carried out on the final instar larvae (marking experiments showed that these visited a mean of 2.28 rush capsules during their feeding period in 1953) and also on the imagines.

J. squarrosus is shown to be broadly distributed over the study area. The capacity of the rush to produce ripe seeds diminished with increasing altitude, and fruiting was less extensive in the cool summer of 1954 than in the two preceeding seasons.

The distribution of *Coleophora* closely corresponded to the degree of ripe seed production by the rush in each season. In all years ripe seed production and *Coleophora* infestation of the rush to any given extent, occurred about 300' higher on the eastern Pennine slopes than on the western. Hymenopterous parasites of the *Coleophora* larvae were recorded only in populations below 1050' on the western and 1525' on the eastern Pennine slopes.

Seasonal surveys of two *Coleophora* populations are described. Heavy mortality was demonstrated in the egg and early larval stages and also in the overwintering larval population in the ground litter. Some evidence for competition between early instar *Coleophora* larvae inside mature rush capsules is presented. It is suggested that competition at this stage would result in a degree of mortality dependent on the density of the initial larval population.

The various mortality factors affecting different *Coleophora* populations are discussed.

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STUDIES ON COLEOPHORA CAESPITITIELLA Zell. (Lep) ASSOCIATED WITH JUNCUS SQUARROSUS L.

I. INTRODUCTION.

This study was originally formulated with a view to obtaining certain information regarding the 'community' of insects either feeding on, or less intimately connected with, the moor rush, *Juncus Squarrosus* L. The Nature Reserve, Moor House Moor (N.R. 80), owned by the Nature Conservancy, was the area of moorland on which most of the field work was carried out. Certain material was also collected from areas of moorland adjoining the Nature Reserve. This investigation began in the summer of 1952 and the field work terminated in the autumn of 1954.

The majority of the insect frequentors of the flowering or fruiting heads of *Juncus squarrosus* are chance visitors. Amongst these are the many Diptera, Jassidae and Cercopidae which are on the rush heads in dry spells in the summer. A somewhat closer association between the rush and nymphs of *Aptinothrips rufus* (Gmelin) (Thysanoptera) (det G.D. Morison), especially in the months of June and July, has been established. These nymphs occur, in considerable numbers, between the developing rush florets, under the bracts of an individual floret, or under the leaves sheathing the flowering stems, throughout the zone of the plants' distribution in the area studied - at heights varying from 650' to 2750' above sea level. J. squarrosus is not the only food source for A. rufus since specimens were also taken during June and July from the new seasons' growth of grasses occurring together with the rush.

A specific relationship is, however, to be found between the rush and the moth Coleophora caespititiella Zell. and it is an analysis of this relationship with which this thesis will be concerned. This moth, in the larval stage, feeds on the developing rush seeds. Information has been obtained regarding the insects' life history and various aspects of larval and adult behaviour. Coleophora populations have been investigated at various heights on both the eastern and western slopes of the Pennines, and for each site sampled information has also been obtained regarding the degree of development of the food-plant on the particular date of sampling. A previous examination of some aspects of this problem has been made by Pearsall (1950), and it was partly in response to some of the queries posed in this work that the present investigation was undertaken. These queries, together with some of the conclusions reached by Pearsall, will be discussed when we come to consider the information obtained on the rush and moth populations in the Moor House area by the present author.

II. LIFE HISTORY OF COLEOPHORA CAESPITITIELLA Zell.

1. Introduction.

Pearsall (1950) has pointed out that the life history of C. caespititiella is very imperfectly known, and indeed, apart from systematic works, literature on this species is very scarce. Descriptions of the various stages, and especially of the imago, are quite adequate, but works concerned with the duration of the various stages, and general biological information about them are very scanty. Of the more general systematic works, dealing largely with imagines, Meyrick (1928) and Pierce and Metcalfe (1935) may be mentioned. Amongst the earlier of the systematic works dealing more particularly with the Coleophoridae is Stainton (1859), which also includes some general notes regarding the mode of life of C. caespititiella in addition to descriptions of the various stages of the species. Barasch (1934) proposes a new system, based exclusively on the structure of the male genitalia, for dividing up the genus Coleophora, to replace the so-called Zeller-Heinemann system where the groups are characterised by the form of the antennae and the colour and markings of the fore-wings. This system has since been modified by Hackman (1948) who takes into account the biology and habitat of the various species, in addition to their genitalia. Particular features regarding the caespititiella-group of this genus are indicated in Hackman (1941). Wood (1892) has general descriptions of the stages, and also notes on the life-history of *C. caespititiella*, and Waters (1928) has some additional notes on the species. Sich (1921/2/3) contains observations on the Coleophoridae as a whole and in the general accounts notes on the ova, larvae and larval cases of *C. caespititiella* are included. These general works will be referred to , when appropriate, later in this account.

This study was, therefore, undertaken with a view to supplementing information concerning the life history of *C. caespititiella*. It was felt that this information would be imperative for the future interpretation of much of the data to be collected in the course of the survey of the rush and insect populations. This has since proved to be the case.

In the following account of the life history of *C. caespititiella* it must be borne in mind that the work was carried out, at heights up to 1500', in the northern Pennines, and care must consequently be taken before applying the results obtained, especially with regard to the time of appearance of each stage, in any area dissimilar to the study area.

2. Ovum.

Adult Coleophora, in both 1953 and 1954, were first observed in the field at the beginning of June, and eggs were found on the rush stems at about the same time. Oviposition, then, apparently begins very soon after the first appearance of the adult moths. It will be shown later that newly emerged females do, in fact, contain eggs which are fully developed and ready for oviposition. (In the warmer conditions of Durham (330') adult Coleophora have been taken from outdoor cages as early as 27th May). In 1953 the first eggs were found on 5th June and in the following year on 9th June.

The eggs are laid when the flower heads of J. squarrosus are fully formed, although not yet in actual blossom. The flowering stems have also not yet attained their full height; for instance at the time of the beginning of oviposition in the summer of 1953 at 1100' the stems varied in height from about four to six inches - that is, not yet half as tall as they will be when fully grown. The act of oviposition has been described by Wood (1891); " the parent moth insinuates her thin, pointed ovipositor within the perianth of a floret, and affixes an egg to the inner surface of a segment." Observations by the present author have shown that eggs may also be laid in the angle between two adjacent florets. Presumably where the eggs are laid will, in part, depend on the state of the flower at the time - if it is not far advanced it would not be thought possible for the ovipositor to pass between two segments of a floret. This is borne out by the fact that eggs laid at the upper limits of the insects' range are, in fact, generally found to occur between two adjacent florets rather than within any one floret. The eggs are thus laid in a site well protected from the elements and it would seem that even in a heavy rain storm few would be washed away. Such sites are also likely to be protected from the activities of predators, and the evidence suggests that predation on the eggs is very limited. A survey of mortality in the egg stage will be referred to in a later section of this thesis.

The length of time spent in the egg stage will presumably be, in part, determined by weather conditions, with temperature playing a particularly important role. Sich (1922), speaking of the Coleophoridae as a whole, refers to a period varying between ten days and three weeks being passed in the egg stage. In the present study area the first eggs, in 1953, were found on 5th June whereas the first larva, and then only one individual amongst about fifty eggs, was not recorded until 30th June. In 1954 the corresponding dates were 9th June and 17th July. The very much longer time taken over hatching in the latter year was probably caused by the cool weather conditions which prevailed over the period. From the two years evidence it would appear that, under the conditions prevailing in the Northern Pennines, a period in excess of three weeks (the time suggested by Sich (1922)) is generally spent in the egg stage. That temperature plays an important part in determining the length of time spent in the egg stage is further shown by a laboratory experiment in which eggs were hatched a week after they were laid, practically a month in advance of eggs in the field.

Viable eggs occur on the rush heads long after the first eggs have hatched; in 1953 they were observed well after mid-July and in 1954 up to the middle of August. Adult moths have been observed ovipositing practically up to the final date before their disappearance for the season. There will obviously be, therefore, quite a long time lag between the hatching times of the first and last eggs in any one area - this fact will be further appreciated whan an examination is carried out of the results obtained during the surveying of various Coleophora populations in 1952, 1953 and 1954.

3. Larva.

The larvae of *C. caespititiella* feed on the seeds of various species of rush and especially on those of *Juncus squarrosus* L. and *J. effusus* L. The following is a list, gathered from various sources in the literature, of the other plants on which larvae of this species have previously been recorded. The nomenclature of the original references has been modified to conform with that in Clapham, Tutin and Warburg (1952):

J. conglomeratus L.	(Stainton (1859), Wood (1892) etc)
J. inflexus L.	(Stainton (1859), Waters (1928) etc.)
J. articulatus L.	(Waters (1928))
J. compressus Jacq.	(Wood (1892))
J. acutiflorus Hoffm.	(Wood (1892))
Luzula pilosa (L) Willd.	(Stainton (1859))

Some of these records are solitary examples and are, very probably, instances of larvae having wandered on to these plants from a more usual food-plant, and are not instances of an initial oviposition there. That such larval wanderings do take place towards the end of the summer will be shown later. In the area surveyed by the present author, the most utilised food plant is *Juncus squarrosus.* In addition larvae have been observed on *J. effusus*, *J. articulatus* and *Luzula campestris* (L.). *J. effusus* is widespread over the region and, within the limits of the moth's distribution, is used quite considerably as a food plant though by no means as extensively as J. squarrosus. J. articulatus only occurs on the lower parts of the Nature Reserve - larvae were observed in 1953 on Sept. 4th feeding on this rush at a point just downstream from the confluence of Crowdundle and Middle Tongue Becks at a height of about 1000' (see Fig. 7 p. 54) Numbers were very low. No previous reference has been found regarding Luzula campestris as a food plant for C. caespititiella larvae, and this is apparently a new record. A number of larvae have been observed feeding on this plant on the eastern slopes of the Pennines near Hill House Farm (fig. 7). This, and probably also the case with J. articulatus, is presumably an instance of the larvae having migrated from neighbouring stems of J. squarrosus on to the Luzula heads to feed. During the oviposition studies referred to in a previous section, which were largely carried out in this area, no oviposition was observed on the Luzula heads and no eggs have ever been found on them.

To return to the eggs of C. caespititiella. After hatching the first instar larvae begin to bore their way into the capsules of the rush. By this time the capsules, especially at the lower levels where the insect occurs, have mostly attained their maximum size, although the contained seeds are, of course, not yet ripe. The seeds are green and soft and presumably easily penetrable by the small first instar larvae. Before entering a rush capsule a larva may move around on its exterior before boring into it. This would appear to be a precarious stage in the life history of the moth and figures will be presented in a future section showing that there is a considerable mortality during this period. Considerable numbers would presumably be washed off or die before being able to enter a capsule. There is also the danger of predation. In stages of the life history immediately preceding this and in those afterwards the insect is in relatively protected surroundings. The eggs, as has already been shown, are laid in well sheltered sites, and once the larvae have bored into the rush capsules they pass the first six weeks or so of larval life within the protecting walls of the capsules.

Entry into the capsule is afforded by eating a hole in the wall, this being usually carried out at the base of the capsule and often at a point on the junction between two segments of the capsule. These two general rules, and especially the latter are, however, by no means invariable. By the time the larvae enter the rush capsules (from about early July in 1953) the capsule wall is quite a sturdy structure and it is a considerable feat for the small first instar larva, which has not fed since it hatched, to effect an entry.

The first six weeks or so of larval life are spent entirely within the confines of one rush capsule. The time actually spent feeding on the original capsule is partly dependent on the state of this capsule, whether it contains ripening seeds, which are a good food source, or seeds which are degenerating, possibly through lack of fertilisation, which are not. In such capsules very small, early instar larvae may be found very late in the season. The time spent feeding within the rush capsules is also somewhat longer at the higher levels of the range of the moth. Here the degree of development of the rush itself is also behind that of the plant at lower altitudes. As will be shown in a later section the life histories of insect and plant are closely correlated throughout their ranges.

Generally speaking only one larva is to be found within any one rush capsule. This is by no means invariably the case and in certain areas where the infestation of the larvae is particularly high two, or occasionally more larvae may be found within a single capsule. It can thus be seen that there are only a limited number of 'food-niches' for the Coleophora larvae to occupy and that when the population reaches a certain size in relation to its food supply, competition is likely to set in. This position will be enlarged on when we come to discuss the population studies which have been carried out, when we will consider whether we have here, in fact, a check on the population size of a density-dependent type.

During the period spent in the rush capsules the larvae moult a number of times. No reference in the literature has been found to the number of larval instars of C. caespititiella, but Sich (1923), referring to the Family in general, states: " I think the Coleophorid has five larval stadia." Accordingly a study has been carried out to elucidate the position with regard to C. caespititiella, and at least this species does not seem to conform with Sich's generalisation.

Following Dyar (1890) a series of measurements were taken of larval head capsule widths; Dyar chose the head as a part not subject to growth during an instar and its width as the most convenient measurement to take. In his work Dyar measured the head capsule of one larva throughout its' growth stages. With C. caespititiella larvae this is impracticable as once a larva has been removed from within a rush capsule it is difficult to replace it in any situation where it can recommence feeding. Accordingly approximately three hundred larvae of various sizes were measured

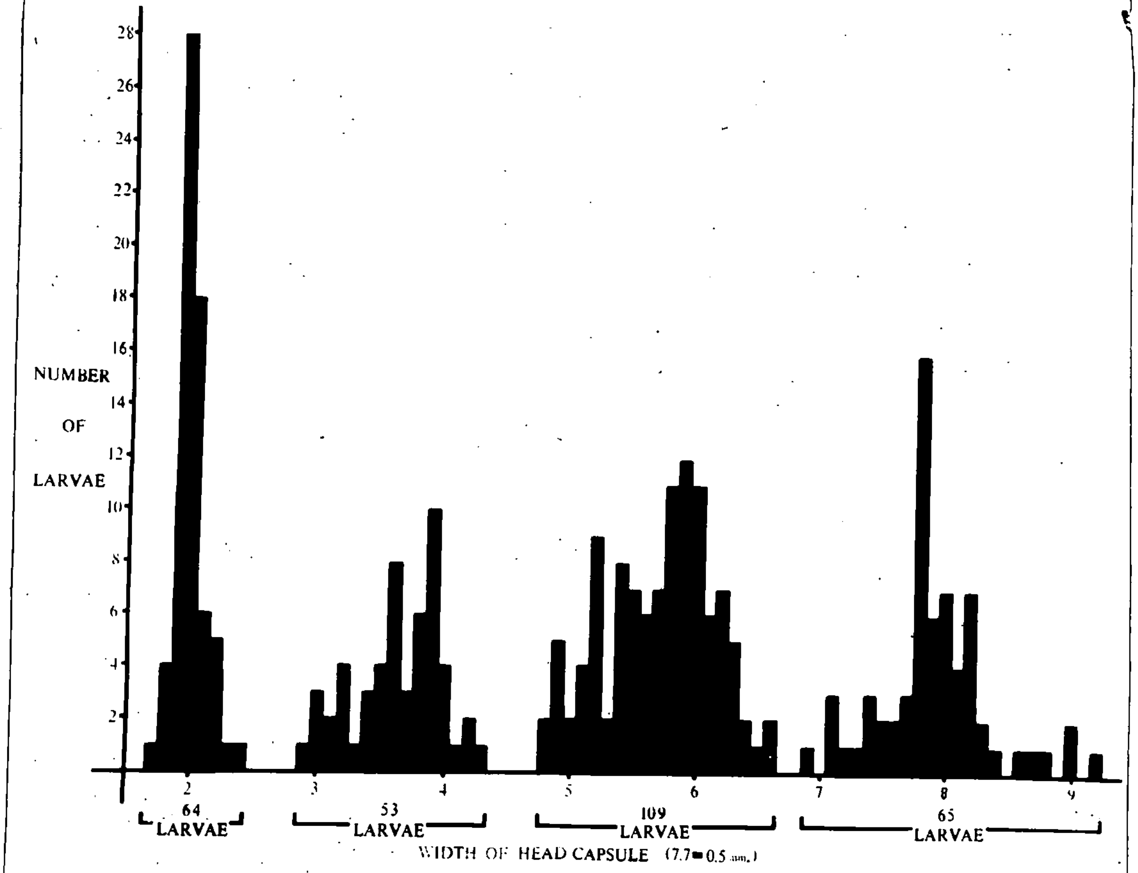

Fig. 1. Width of head capsules of 291 larvae of

C. caespititiella.

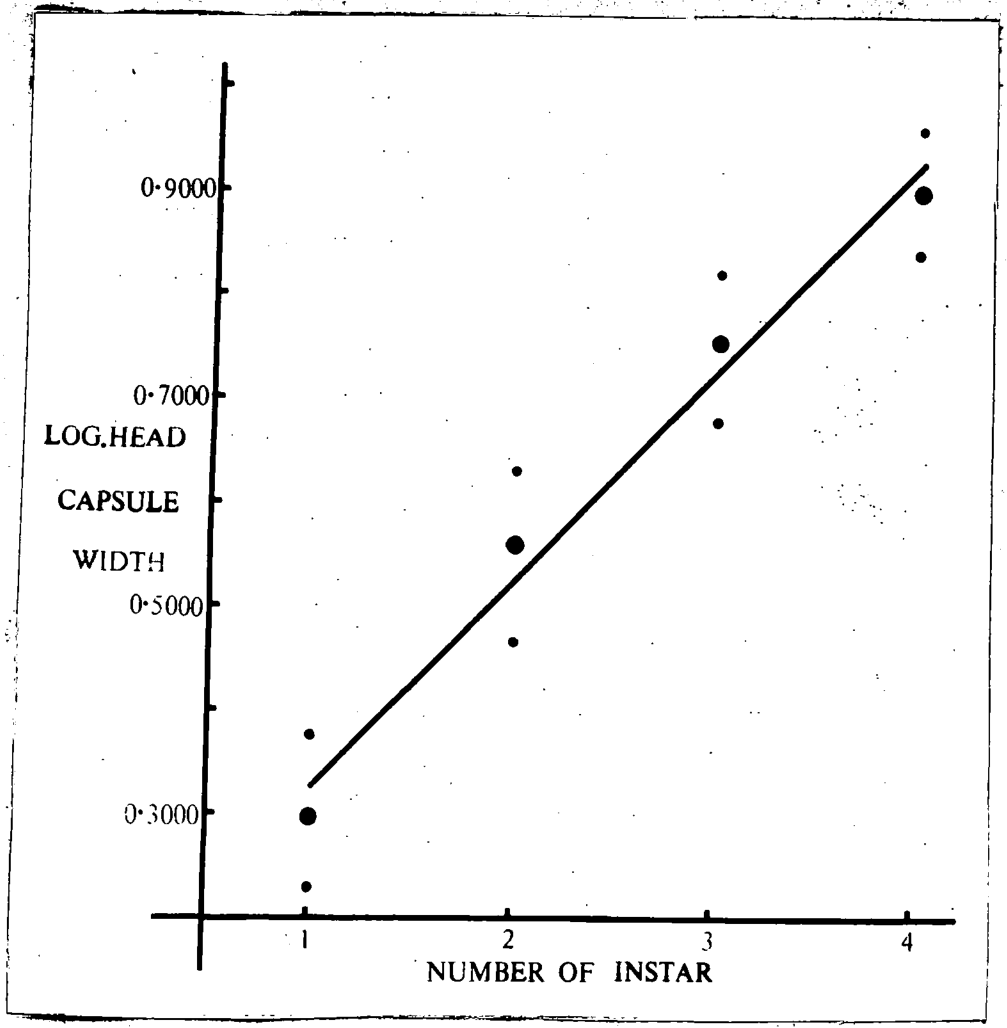

Fig. 2. Mean head capsule widths of the four postulated instars of C. caespititiella plotted on a logarithmic scale. The extreme values for each group of larvae are also given.

and the various figures for head capsule widths are shown in histogram form in fig. 1 (p.14). The measurements were obtained by decapitating the larvae, mounting the heads in lactic acid, and examining them under a microscope.

An examination of fig. 1 shows the existence of four well-defined larval instars. The arithmetic averages (utilising the arbitrary units as in fig. 1) of each of the four sets of figures has been taken and plotted, on a logarithmic scale, against the number of instars. The resultant points are shown on fig. 2 (p.15). Dyar's Law (Dyar (1890)) assumes there to be a constant factor by which each instar increases in size over the instar preceding it. If such were the case here the points on fig. 2 would all be placed on the straight line curve which has been calculated and inserted on fig. 2. In fact, although the fit is close, there is a slight falling off in the factor between succeding instars. Following the more recent practice of expressing the progression factors as the inverse of the original formulation by Dyar, by dividing the head width before moulting into the head width after moulting, the progression factors between the four postulated instars of <u>C. caespititiella</u> have been calculated. They are 1.84, 1.57 and 1.39.

There is considerable evidence from previous workers on Lepidoptera, amongst them Ripley (1923), Forbes (1934), Beck (1950) as well as Calvert (1929) on Odonata, that the "supposed constant factor is not actually constant but tends to decline in succeeding instars" (Beck (1950)). As Beck points out the data used by Dyar himself also show a decreasing ratio in the later stages of many species, and he suggests his 'constants' should be considered 'averages.' Thus the position we have here with regard to C. caespititiella would appear to be typical of the Lepidoptera as a whole. This species also conforms with the situation in many other Lepidoptera, as stated by Forbes (1934), in that it has a 'Dyar's ratio' of more than 1.26, which is the ratio to be expected from the typical condition of insects doubling in volume at each moult. This figure was originally arrived at by Przibram and Megusar (1912), who also suggested that progression factors greater than 1.26 are due to non-manifested cell-divisions. Bodenheimer (1933) refers to them as 'latent divisions' and he has found them to occur in Orthoptera, Odonata, Rhynchota and especially in the Holometabola.

From the above discussion it is apparent that no instar exists between the four demonstrated. There remains the possibility that a larval stadium may have been missed at either or both ends of the curve illustrated in fig. 2. Both these possibilities have been eliminated. In the final days of its development the egg of C. caespititiella can be seen to contain a larva with a well-developed head capsule. Measurement of such head capsules was therefore undertaken to see whether they would correspond to those previously obtained for the postulated first instar. Only seventeen measurements were made, as by this time there was an obvious correlation between the two sets of figures. Using the same units as in fig. 1 the mean of these seventeen figures was 1.888 which differs from the original mean for the deduced first instar by 0.o87. This difference is obviously negligible.

It has also been shown that no fifth instar occurs just before pupation in the spring. This has been proved by measuring head capsules found in larval cases after pupation. Eighteen head capsules have been measured in this way and all the measurements are well within the range of figures given in fig. 1 for the width of the head capsules of fourth instar larvae.

One further point arises from a consideration of fig. 1. It can be seen that there is an increasing variability of the width of the head capsule with each succeeding instar. Thus on the scale used in the figure the various instars span:

Instar 1 - 8/10 units
Instar 2 - 15/10 units
Instar 3 - 19/10 units
Instar 4 - 24/10 units

Such a position is to be expected and can be accounted for on either or both of the following grounds. Larvae hatch at a relatively uniform stage and the sizes of succeeding instars will probably in part depend on the environment, food supply being especially variable, in which they find themselves. Probably rather more important than this is the fact that the same unit of measurement has been used for larvae of different absolute sizes. Thus any small differences in head widths of early instar larvae would be magnified in each succeeding instar, probably to the extent of being placed in a fresh size group.

The duration of each larval instar varies considerably, and there is a considerable overlap of instars; as many as three different instars may be found in any one population at any one time. Such overlap can, in part, be explained by the long oviposition period of the adult moth, probably about a month, as has already been suggested, but it also seems likely that the immediate environment of each larva will be of importance. It has often been noted, for instance, that late, well-fed third instar larvae have been found in rush capsuleswhich, if they had remained uninfected, would have produced copious ripe seeds. Other capsules on the same plant containing shrivelled seeds, which would not have ripened, only had within them small, apparently badly nourished second instar larvae. As would be expected, it seems that the food supply of the larvae can produce marked differences in developmental speeds. In the most favourable circumstances the first three larval instars can be passed through in less than six weeks. Fourth instar larvae, complete with larval cases, were first observed in 1953 at the beginning of August. As will be pointed out in more detail later, they were very much later in the bad summer of 1954. In some instances the fourth instar may not be entered until October. Corresponding with the overlap of larval instars there is also a marked 'succession' of the appearance of larval cases on infected rush capsules.

The larvae of <u>C. caespititiella</u> usually manufacture a gallery of silk within the rush capsules before constructing the larval cases which appear~~s~~ on the exterior of the capsules In many instances the larvae are enclosed within a complete case of silk within a capsule. The composition of these cases, as of the later external ones, is largely silk, together with seed debris adhering to it. Wood (1892) suggests that the larva commences the manufacture of the case either just before or just after the last moult, and following no hard and fast rule. Later in the same year he amends this statement and says that the operation is begun "shortly after the final moult has taken place." From larval head capsule measurements which have been carried out it appears that Woods' earlier statement is the correct one. A number of third instar larvae have been found with perfect larval cases. The galleries within the rush capsules are certainly usually started on in this instar, but the external larval case is usually not begun until the final moult has taken place, but, as has been shown, even this is not invariably so.

A brief description of the appearance of the external larval case is included by Sich (1923) and will not be enlarged upon here. He states: " It is fairly cylindrical, its length about five times its diameter, it is somewhat flattened at the distal end where it is closed by three conical valves which meet at their apices. At the other end is the circular mouth strengthened by a slight lip or flange running outside. Above the mouth the case is slightly restricted."

After the formation of the case the larva may leave its parent capsule and move at will. It generally

Fig.3. Larval cases of C.caespititiella on capsules of J.squarrosus.(x1)

moves to other capsules, complete with its case, which it bores into and feeds on the contained seeds. Details of this larval migration will be considered when dealing with larval behaviour.

The larvae complete their feeding in the autumn and overwinter as final instar larvae within their larval cases. This generally takes place in the plant litter at the base of the stems, although in occasional instances the winter may be spent on the rush heads. Once the larvae have become established in the litter the mouth end of the tube is sealed with a barrier of silk - this is, at least on some occasions, broken before pupation as some larvae have been observed in movement during mild spells in the winter and also in the spring. The larvae of C. caespititiella appear to undergo a true diapause in that they fail to emerge at an early date if brought indoors to warmer conditions.

Normally the larvae of this species do not feed again in the spring, but larvae of C. glaucicolella Wood, a closely related species, which feeds especially on Juncus inflexus, have been observed doing so (Sich (1923)). In the spring of 1953, in the area under study, a number of larvae of C. caespititiella were found feeding on the developing rush capsules of the new years' growth. This was occurring whilst adults of the species were about, and even after the last adult was recorded in the area. Figures, which will be quoted later, for the amount of food available (in the form of rush seeds) to the larvae, at various localities, suggest that one possible reason for this occurrence is a lack of food in the autumn. Waters (1927) suggests another explanation, referring to two larvae of *C. solitariella* Zell., which is normally adult by June, and which he collected in mid-July. One of these remained alive until the following spring and then produced an Ichneumon. Although late feeding larvae in the Moor House area are generally not parasitised, some have, on dissection, proved to contain a larva of Ichneumon type. As we shall see later, this cannot be a common parasite of *Coloephora*, at least in this area, as the apparently most important Ichneumon parasite has an externally feeding larva and, in fact, destroys the moth larva before the onset of winter.

The erratic appearance of larvae of *C. caespititiella* which has been found in the study area is apparently typical of the Coleophoridae as a whole. Waters (1927) states: " A feature in the life-history of many Coleophorids is the great irregularity of their time of appearance." This phenomenon is true with regard to all stages of their life-history.

4. Pupa.

Pupation generally begins about mid-May but living pupae have been found as late as 18th June, and from some late adult emergences in the laboratory, they are known to occur much later than this. Pupal life is of about three weeks duration.

It appears that, just before pupation, the moth larva must turn completely round in its case. This appears to be the only possible explanation of the fact that the adult leaves the case through the apical valves and the pupa is orientated with its head at this end of the case. It seems most likely that the larva reverses its original orientation during the actual process of pupation- certainly larvae found just prior to the time of pupation have their heads still at the mouths of the larval cases.

5. Imago.

As has already been stated the main emergence of C. caespititiella began in early June in both 1953 and 1954. Occasional early specimens have been recorded - in 1954 one specimen was found on 31st May and then no more were recorded until a large number were found on 8th June. Evidence from both these years suggests that a warm dry spell just before the adult is ready to appear is stimulatory to emergence.

Fig.4. Coleophora caespititiella Zell.(x6).

Owing to damage by sheep to emergence traps in the field, no detailed information has been obtained regarding exact emergence dates at various altitudes. From general field observations it appears that there is little, if any, difference between the dates of first emergence at various heights. These observations agree with those of Pearsall (1950).

When this species was at its greatest numbers (early and middle June), in the area under study, it was the only micro-Lepidopteran about in any large numbers.

How many eggs are laid at a time? In some instances only one egg can be found occurring in any one site, but in other cases as many as five have been recorded. Wood (1891) states that two eggs are generally found together and he suggests that they are both laid together by the same parent moth. As a single egg is a common occurrence it seems probable that this is the number generally laid and that any further eggs present are the results of later ovipositions by the same or a different moth parent. Dissection of newly emerged female moths has shown that there are very many eggs present. Normally ten to twenty appear to be of 'maximum' size and apparently ready for immediate oviposition. In addition to these there are large numbers of eggs of decreasing size in the terminal ends of the ovarioles. As many as ninety have been counted in some individuals and the total number may be even greater than this. It seems that the majority of these can be matured and deposited in the course of the insects' life, as individuals towards the end of the season usually contain only a few large eggs. Fertilisation occurs very shortly after emergence, and very early in the season individuals have a swollen bursa copulatrix, with one or more spermatophores present. As many as five were recorded in one individual.

C. caespititiella has also been recorded ovipositing on Juncus effusus. These individuals do not appear to belong to the paler 'effusus' variety referred to in the literature (Wood (1892) and Waters (1928)). There is no obvious colour difference in the series of adults collected in the study area, and the few recorded instances of oviposition on J. effusus are probably chance visits by the darker 'squarrosus' form. This is the typical moorland form, the paler form having been largely recorded in woods and damp places on lower lying ground where J. effusus is the only one of the two rushes in question which occurs.

In 1953 the last live adult to be seen in the field was recorded on 3rd July, and in the following year adults were about for another fortnight after this date. In the laboratory individuals have emerged as late as 24th July and have not died until the beginning of August.

During the emergence period of 1953 adult C. caespititiella were kept alive in honey-jars in the laboratory at Moor House. Certain observations regarding longevity in the laboratory were carried out, and these experiments were repeated in rather more detail during the emergence of 1954. We will first briefly discuss the tentative conclusions arrived at from the 1953 material and then go on to examine the more detailed 1954 experiments.

In 1953 the greatest number of days for a moth to remain alive in captivity was thirty-five. This was a specimen collected from an emergence trap erected in the laboratory grounds in Durham over rush plants transported from the Moor House area. This was taken on the day, or the day after, emergence and this figure must represent more or less the exact length of life of this particular individual. Of the eleven specimens which were kept in 1953, which could be presumed to be newly emerged, the average length of life was 20.8 days (standard error of this mean = 1.84). These were all fed on sugar solution. The last date for a moth to be kept alive in captivity was 5th July, corresponding to 3rd July which was the last date on which living adults were observed in the field. An indication was also obtained, from experiments carried out in 1953, that moths fed on sugar solution lived longer than starved individuals. As will be seen this suggestion was confirmed in 1954.

Table 1 shows the results obtained from keeping adult Coleophora in honey-jars in the laboratory at Moor House during the emergence of 1954. All moths were kept four per jar and were provided with filter paper. In an equal number of instances this was either kept dry, kept damp with tap water or kept damp with a saturated sugar solution. Adults will take up both free water and sugar solution in the laboratory. Three further jars were also set up with three moths in each to act as spares if any other moths either died prematurely by becoming stuck to the filter paper or escaped when the filter paper was being recharged. An inspection of the table shows that certain individuals were used in this manner.

All the moths were collected on the three days 8 - 10th June. The first date was the earliest in 1954 on which any number of adults was observed in the field. Presumably at least the major part of the adults collected on 8th June were only 12 - 24 hours emerged. The age of those collected on the following two days cannot be determined as exactly but it seems certain that few, if any, of the individuals used in the experiment were initially more than three days old.

TABLE 1.

Length of time (in days) spent alive by adult *Coleophora caespititiella* in a series of honey-jars in the laboratory at Moor House in 1954.

	DRY				WATER ONLY				SUGAR SOLUTION			
series 1.	6	7	7	7	11	13	15	17	15	17	21	23
" 2.	7	7	11	11	11	14	17	22	11	23	25	26
" 3.	5	7	7	14	14	16	21	23	14	18	19	28
" 4.	3	6	6	8	10	10	11	16	13	14	14	17
" 5.	4	5	10	13	12	21	21	25	20	20	23	24
" 6.	3	4	6	16	10	20	25	26	12	17	18	26
" 7.	3	5	7	9	9	-	12	14	18	18	20	26
" 8.	3	5	9	9	9	14	20	20	16	28	22	28
" 9.	5	5	6	9	22	26	29	34	17	21	22	29
Replacement series	3	5	10	-	All as replacements				17	19	27	-
Avg. no. days alive	7.00				17.43				19.90			

In calculating longevity the number of days spent in captivity under the given experimental conditions has been used.

From an examination of Table 1 certain conclusions can be reached. The greatest number of days for a moth to be alive in captivity was thirty-four (the corresponding figure for the previous year was thirty-five). This was an individual which was only provided with water. This shows that feeding is not essential for a long life in the laboratory. As we shall see later no feeding by the adult moth has ever been observed in the field, and it seems probable that such does not occur. There is an abundance of free moisture under field conditions which could be, and is, taken up by the moths. The last date for a moth to be alive in captivity was 14th July, which is nine days later than the corresponding date in 1953. As has been mentioned above there was a comparable difference in the time of disappearance of the moths under field conditions.

The thirty-nine moths kept in dry conditions lived for a mean of 7.00 ± 0.49 days. The thirty-five individuals provided with water only lived in captivity for a mean of 17.43 ± 1.06 days, and the thirty-nine provided with sugar solution for 19.90 ± 0.74 days. There is an obvious difference in longevity between those moths kept under dry conditions and the remainder, and the position here has not been examined statistically.

An analysis of variance (Table 2) has, however, been carried out in an attempt to determine whether the difference in longevity, apparent in the above figures between those moths which were given sugar solution and those which were provided with water only, was an effect of the two treatments or due to individual variation between the moths.

TABLE 2

Analysis of variance of the longevity of the moths which were provided with water or with sugar soln.

Source of variation	Sums of squares	Degrees of freedom	Variance estimate
Between treatments	60.89	1	60.89
Within treatments	718.73	72	9.98
Total	779.62	73	

$$\text{From this, } F = \frac{60.89}{9.98} = 6.10.$$

From the table for F we find that the 1% level of F is about 7.0 and the 5% level is just less than 4.0. The value for F in this instance, then, is well above the 5% level and practically at the 1% level, which suggests that feeding the moths in the laboratory is in fact possibly increasing their longevity. Nevertheless it can be seen that the effect of feeding is very slight and that moths can live for a considerable length of time if just supplied with water. Despite careful field observations, feeding by adult Coleophora has never been seen in the open (this subject will be discussed at greater length when dealing with adult behaviour), and these laboratory experiments emphasise the fact that it is not necessary to postulate feeding under natural conditions. A source of free water does, however, appear necessary for existence over about a week, and even in the driest years this is provided by early morning dew. It appears that even a short period of dry weather might quickly reduce a Coleophora population nearing the end of its life-span. Such a period of weather occurred in 1953 just at the time of the sudden disappearance of the adult moths from the field. Over the emergence time of the moths in 1954, the weather was consistently wet, no sudden disappearance was noted, and the date of ultimate disappearance, as we have seen, was considerably later than in the preceding year.

6. Parasites.

So far the normal sequence of events in the life history of Coleophora caespititiella has been described; in many instances this sequence is interrupted due to the action of a parasite. As Sich (1923) suggests the form the larval case takes may be of cryptic value in deceiving casual enemies, but is no protection against special parasites. Few larvae have been found which could have been attacked by carnivorous Coleoptera, Dermaptera, Hemiptera etc. The only instances observed of predation on the imago was of two specimens which had been caught in the web of a Linyphid spider and consumed. Parasitised larvae, however, are quite common in certain areas. As will be shown later parasites only appear to attack Coleophora populations occurring at altitudes below a maximum of 1600 feet.

During the winter months some larval cases can still be found attached to the stems of the rush. As has been described, healthy Coleophora larvae normally overwinter in the litter at the base of the rush plants, and the cases referred to above generally contain larvae attacked by parasitic Hymenoptera. Parasitised larvae are only rarely found in the litter - an internal parasite of Ichneumon type has already been referred to which does not destroy the Coleophora larva until the spring and causes failure to pupate.

The major parasties in this particular area have externally feeding larvae and kill the host before it has time to migrate from the rush capsule to the litter. The parasites then overwinter in the rush capsule.

All the species of parasites present have been induced to emerge at an early date indoors, some by the beginning of December, after only three weeks in the laboratory. Apparently these Hymenoptera do not have a true diapause (this has already been shown not to be the case with *Coleophora*) and the normal developmental period can be considerably reduced by bringing the material into a heated laboratory.

The four species of Hymenoptera which have been bred from *C. caespititiella* larvae have been identified by J.F. Perkins as follows:-

(1) *ICHNEUMONIDAE* - *Ephialtes (Scambus) brevicornis* Grav.

(2) *BRACONIDAE* - *Bracon* sp.

(3) *CHALCIDOIDEA* - Genus nr. *Miotropis*.

(4) *PTEROMALIDAE* - Unidentified males. This is pointed out to be a difficult group to identify at present.

Thompson (1945) does not record any of these Hymenoptera from *C. caespititiella* and these are therefore, apparently new host records for the species. Thompsons's list of *C. caespititiella* parasites is:-

(1) *ICHNEUMONIDAE* - *Gelis instabilis* Först.

(2) *ICHNEUMONIDAE* - *Hemiteles* sp.

(3) *BRACONIDAE* - *Microbracon obscurator* Nees (this record is from Germany).

(4) *BRACONIDAE* - *Microbracon osculator* Nees.

From the Moor House area only *Ephialtes brevicornis* and the species of *Miotropis* have been recorded in any number. Only one individual of the Braconid and a dozen or so Pteromalids have been included in the two hundred or so parasites which have been bred in the laboratory.

None of these parasites has been observed in the field, ~~so their method of~~ attacking *Coleophora* larvae. ~~is unknown~~. Sich (1923) makes some suggestions as to the manner in which this may be carried out with regard to the Coleophoridae as a whole: " they may be able to pierce the case with their ovipositors. If they do this just after the larva has changed its skin, I imagine, they would meet with little resistance. The minute species may gain access to the case by squeezing themselves between the valves at the apex."

Ephialtes brevicornis is the only species which has been observed in the field. The emergence period of this species is lengthy and adults have been taken between early May and the end of August. Does the protracted emergence time of this species suggest that it is not a parasite specific to *C. caespititiella*? When the adult insect leaves the larval case of its host it does so by a characteristic round hole which it bores in the case wall and in 1953 and 1954 these were observed about a month before the moths even emerged. However the early emergence of Ephialtes may only be a result of an increase in the temperature of the environment (as with the material brought into the laboratory) and such individuals may not be able to find a suitable host. The longevity of the species is unknown. There appears to be a most unequal sex ratio in this species, with males in a considerable majority. In the laboratory very many males had emerged before any females appeared. Females appear to be in larger numbers amongst the later emerging individuals. During early August 1953 much activity was observed by female Ephialtes flying amongst the rush heads and it is suggested that it is around this time that oviposition occurs. No oviposition has been observed, this probably being because the females, at least, are very active and fly off even after the slightest disturbance.

Young larvae of Ephialtes may number more than one per host, but no instance of more than one full grown larva in a rush capsule has been observed. The attacked larva is killed before mid-September, when Coleophora feeding is normally completed, and Ephialtes overwinters as larvae in the rush capsules.

The insignificant Miotropis has not been observed in the field and its emergence time is unknown. This species overwinters as pupae and up to three pupae have been observed per host. The attacked larva, as with *Ephialtes*, is destroyed in the autumn and the winter is passed in the rush capsules. Morley and Rait Smith (1933), referring to the genus *Coleophora* as a whole, suggest that some of the Chalcid parasites may be hyperparasites. This is not the case with *Miotropis*, which attacks *C. caespititiella* directly.

No parasites, other than Hymenoptera, have been recorded. Turner (1912) records an individual of *C. artemisiella* Scott which had been attacked by a 'Dipteran' but no more exact references to attack by Diptera on the genus have been found. Dumbleton (1952) records that a nematode parasite (? *Neoaplectana* sp.) is present in New Zealand. He found that three out of twenty overwintering larvae of clover feeding species of *Coleophora* recovered from the soil in one area were parasitised. No evidence of nematode parasitisation has been found in larvae from the present study area.

III BEHAVIOUR OF C. CAESPITITIELLA Zell.

1. Final instar larvae.

a. Introduction.

The reactions of the first instar larva when boring into a rush capsule and those of older larvae within capsules have already been described, (pages 11 - 21).

After a larva has fed for a time on its original rush capsule it can sever the connection of its case to the capsule and move off complete with case. Previously infested capsules contain a mass of seed debris with only an occasional intact seed remaining. Normally this movement began well before the larvae finally passed into the litter for the winter. These wandering larvae may reach other capsules, bore into them, and feed on the contained seeds. In some areas, towards the end of the season, nearly all the rush capsules were at least partially affected in this way. It was during this larval wandering that 'unusual' food-plants were fed on, as in the case of larvae feeding on _Luzula campestris_ which has already been referred to (page 10), as the larvae show a tendency to climb up any upright stem or blade of grass in their vicinity. Silk threads are of importance in assisting larval movement. Larvae in their cases were often seen suspended from the apices of rush stems, and, when blown by the wind, they became entwined in neighbouring stems, and thus became established on a new rush stem. In some instances larvae were observed to move from one capsule into its immediate neighbour by boring through the wall of the first capsule and into that of the second.

In 1953 marking experiments with larvae were carried out to obtain information on the number of capsules consumed per larva. Certain other information was also obtained from these experiments. The larval cases and the rush capsule on which the case originally appeared were marked in a similar way with one or two spots of coloured lacquer. Succeeding capsules on which a marked larva was observed to be feeding were marked in an identical manner. A total of nearly 300 larvae were marked in two experimental areas. One are a was at Station 1 (1525') of transect C (see pages and fig 7. This transect was on the eastern slope of the Pennines near Hill House Farm) where 101 larval cases were marked on the day of their first appearance on the capsules in early August. The other experimental area was at Moor House (1840') where eight sods of J. squarrosus, from the same area as in the above experiment, were planted out at the beginning of August. 194 larvae, which appeared on these rush capsules, were marked during the succeeding weeks.

b. Larvae marked at Station 1 of transect C.

For the first fortnight after marking observations of larval movement were made daily. After this time it became apparent that only rarely did a larva move on consecutive days and the time between observations was increased to three days. Regular observations were discontinued on 8th September, by which time 80 of the original 101 larvae had disappeared. A final observation was made on 26th September, when only five of the original larvae remained. Four of these were dead, and had not moved since they were originally marked, and the fifth was attached to the stem of a rush plant and would presumably have overwintered there. During the period of the marking experiment, four of the original 67 stems on which larvae were marked were eaten off by sheep, with the consequent loss of some larvae. Such larvae are omitted from further discussion.

For the purpose of the calculations which follow it has been assumed that all larvae which disappeared from the rush capsules in the course of the experiment had passed into the litter prior to overwintering. This seems to be a valid assumption, because all stems in the vicinity of the original one were closely examined before any were recorded as having completed their feeding. Further evidence to support this assumption can be gained from the plants in the experimental plot at Moor House. Here larvae started to disappear from the rush capsules at approximately the same date, and in comparable numbers, and here they could not have moved to a new rush stem as all the stems in the plot were artificially transported there, and these were all kept under observation.

Despite the fact that all the living marked larvae had completed their feeding by mid-September there were still considerable numbers of unmarked larvae feeding on the rushes in the area. These larvae were those which 'emerged' later from the capsules. This 'succession' of stages in the life history of the insect has already been referred to (page 19) and reasons for its occurrence suggested.

In determining the number of capsules attacked by individual larvae, only those larvae (80 of the original 101 which were marked) which had completed their feeding by September 8th are considered. Up to this date observations were sufficiently regular to record practically all the larval movement which occurred. It should be noted that there was a variable amount of destruction to the seeds of the capsules which were attacked, but by the end of the summer, in regions of heavy infestation (as in this area in 1953), very few viable seeds remained in capsules which had been attacked by the larvae. Such destruction may, in a few limited instances, have been the effect of more than one larva, but it appears to be a general rule that when a larva was attached to one capsule for at least four or five days (and this was usually the case as will be shown later), it consumed at least the major part of the contents itself. The seeds in the capsule first attacked by the larva are usually all consumed, but the degree of destruction in further capsules which are visited varies.

The 80 larvae in question visited a total of 191 capsules before their feeding was completed. Table 3 illustrates the number of capsules visited by each of these larvae.

TABLE 3

The number of capsules of J. squarrosus attacked by 80 marked larvae at Station 1 of transect C in 1953.

Number of capsules fed on	Number of Larvae.
1	15
2	35
3	20
4	6
5	2
6	2
Totals: Capsules 191 Larvae 80	239

From Table 3 it can be calculated that each larva consumed an average of 2.39 capsules.

c. Larvae marked at Moor House.

In this region 194 larvae were marked over a period from 11th August to 7th September. By 8th September, when regular observations were discontinued, 93 of these had completed feeding, and the following calculations are limited to these larvae. These 93 larvae visited a total of 203 capsules, and Table 4 illustrates the number of capsules visited by each of these larvae.

TABLE 4

The number of capsules of J. squarrosus attacked by 93 marked larvae on plants transported to Moor House in 1953

Number of capsules fed on.	Number of larvae.
1	18
2	48
3	20
4	6
5	1
Totals: Larvae 93 Capsules 203	

From this table it can be calculated that each larvae consumed an average of 2.18 capsules, showing a close similarity to the figure (2.39) obtained at the other experimental area. This suggests that few, if any, of the larvae which were recorded as having completed feeding in this first experimental area, with the rush plants in situ, were incorrectly recorded as such.

d. General conclusions.

The 80 larvae used in the first of the above calculations, together with 37 of the second group of larvae, which were marked at the same time, have been divided up into groups according to the number of rush capsules they attacked during their life. Table 5 shows the average number of days spent on the rush stems by each of these groups of larvae. The table also shows the average number of days spent per capsule by each of these groups of larvae, and the latter relationship is illustrated in fig. 5. (p. 45).

TABLE 5

The number of days spent on rush capsules by various groups of *Coleophora* larvae

Number of capsules fed on	Number of larvae	Mean number of days spent on rush capsules (with the Standard Error of this mean)	Mean number of days spent per capsule
1	20	17.5 ± 1.9	17.5
2	54	18.2 ± 1.0	9.1
3	32	20.8 ± 1.0	6.9
4	7	19.7 ± 1.9	4.9
5	2	26.0	5.2
6	2	19.0 ± 5.0	3.2

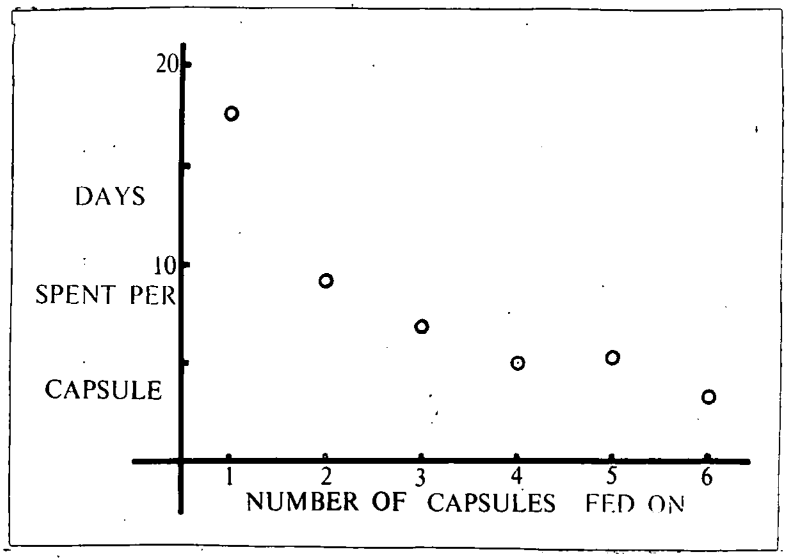

Fig.5. Mean number of days spent per rush capsule by different groups of Coleophora larvae.

From Table 5 it can be seen that the length of time spent on the rush stems did not appear to vary appreciably despite the absolute number of capsules which was attacked. Thus, as is apparent from Fig. 5, the average amount of time spent on each individual capsule tended to decrease as the total number of capsules attacked increased. This suggests that a fairly uniform period was required for feeding, but that some larvae, which remained on their original rush capsule, must have consumed considerably fewer fresh seeds than the other more mobile larvae in the same length of time.

Information was also obtained, from these marking experiments, on the distances which larvae moved during feeding. Whilst feeding they are not limited to capsules on their own stem and, of the 173 larvae on which the calculations were based, 35 had moved to one new stem, 4 to two new stems and 1 to a third new stem before finishing feeding and moving off into the litter. In some of these instances the additional stems were touching the original ones and thus a journey through the basal vegetation would not be involved in order to reach them. In other instances, however, this is not the case and in one case, for example, a larva moved more than two feet through the vegetation mat in the course of four days, from one stem to another. Movement appeared random and larvae have been recorded moving down one stem and then turning round and beginning to feed again on a new capsule on the same stem.

There did not appear to be any diurnal periodicity in larval movement. Larvae have been observed in movement during many daylight hours and larvae, whose positions were recorded just before nightfall, have sometimes been noted feeding on a new capsule on the following morning.

The duration of the feeding period varied considerably, and in some instances larvae moved into the litter ~~after~~ only a few days after the formation of the external case, whereas in others a month or more was spent on the rush capsules. Fig. 6 (page 48) shows the day on which the 117 larvae referred to above, completed feeding and moved off the rush stems. The figure is constructed on a cumulative basis as the later irregularity of observations does not permit the number of larvae which completed feeding on each day to be recorded. As is to be expected this figure shows that the number of larvae leaving the rush stems tended to steadily increase. If the observations had been continued until the last larvae had left the stem, one would expect to find a steady flattening off at the top of the curve. As the figure suggests would be the case, the complete curve would probably be of sigmoid form.

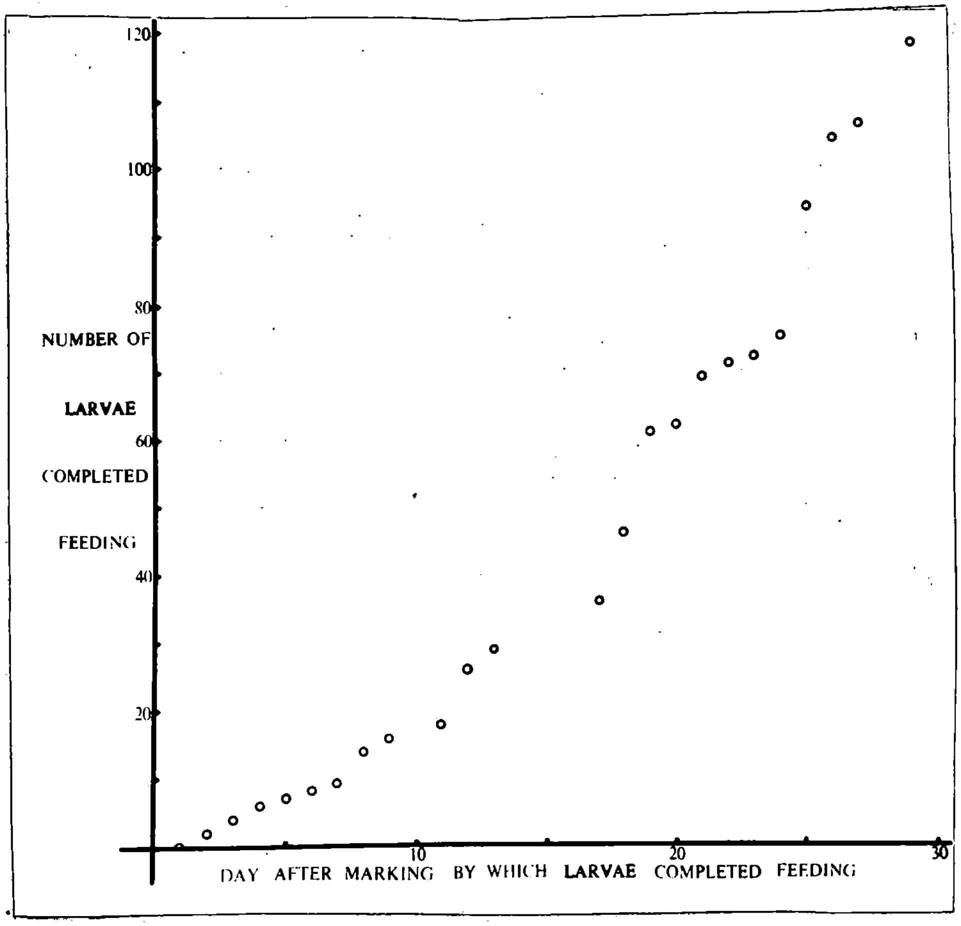

Fig.6. Length of time spent on rush capsules by <u>Coleophora</u> larvae after formation of the larval case.

From general field observations, and also from sorting litter in the laboratory, it was found that Coleophora larvae overwinter in the loose upper layers of the litter. Here they were probably subjected to considerable temperature fluctuations as well as to the danger of becoming waterlogged. It seems unlikely that the larvae will burrow very deeply into the litter, despite the fact that they would be more protected there from extreme temperatures, as conditions in the deeper layers of the litter are acid and practically anaerobic. In a laboratory experiment, to test the position, ten marked Coleophora larvae were placed on a clump of J. squarrosus in a refrigerator and a few hours later crushed ice was placed on the top of the litter. The refrigerator was set so that the temperature of the litter surface was -2°C to -4°C. A fortnight later the litter was hand sorted, and all ten marked larvae were recovered alive from the surface litter. One larva was recovered with its case affixed to a piece of the ice. Larvae can, then, withstand temperatures below freezing point whilst still in the surface litter. Sich (1923) has pointed out that the larval case is lined with a substance impervious to water. He suggests this is "silk applied as a fluid or it may be some special secretion." This may help both to prevent loss of the larva's own moisture and to protect them from becoming waterlogged.

2. Imago.

General observations on this stage have been concentrated on flying activity, oviposition, feeding and pairing.

In the field the adult moths were relatively inactive and they were only rarely found flying more than a foot or two above the vegetation. Much of their time was spent on the developing rush stems and surrounding vegetation, and brief movements from one site to another were not infrequent. They were sufficiently inactive to be caught solely by placing a tube over them, and allowing them to fly to the top of it. Activity was reduced in windy conditions when the moths sheltered quite deep in the vegetation mat when, owing to the extremely cryptic colouration and small size, they were very difficult to see. Flying activity was also observed at night.

Oviposition was observed both in the field and in the laboratory. It occurred throughout the day and night, but both field and laboratory observations suggested that this activity was at a maximum in the evening - especially the hour or two immediately preceding sunset. Oviposition has already been described in a previous section (pages 5 - 7).

No feeding by adult Coleophora was observed in the field, although in captivity they readily took up sucrose solution. The only plants in flower, and likely to contain nectar, in the immediate vicinity of the Coleophora populations were Potentilla erecta (L) Räusch and Galium hercynicum Weigel (= G. saxatile) but no visits to these flowers were observed. These two plants were in flower, at the time of the adult emergence, in both 1953 and 1954, at all heights up to 2000'. P. erecta seemed the more likely food source, and Diptera were noted to be feeding on it. Moths were enclosed in jars in the laboratory with these plants, but no attampt to extract nectar from them was observed. Adult Coleophora in the laboratory were observed feeding on Cercopid 'cuckoo-spit' and this, an extremely abundant substance at the time of the adult emergence, is a possible food source in the field. Despite careful observations, however, no adults were seen feeding on this substance under natural conditions. Adults will readily take up free water in the laboratory and a few instances of moths imbibing early morning dew were observed in the field. From the various foregoing observations it seems that Coleophora does not normally feed in the adult stage. Laboratory experiments (see pages 27 - 32) have shown that moths can live up to a month when provided only with free water, and there seems to be no necessity to postulate that any other substance is taken in the field.

As is the case with oviposition, copulation will occur equally readily both in the field and in the laboratory. Pairs were, in the field, generally found sitting stationary on J. squarrosus stems or leaves, blades of grass, or other upright vegetation. The posture is end to end. In the laboratory pairs were observed to be maintained for periods up to nine hours, but under natural conditions it seems probable that some disturbing factor (wind or other insects, for example), would break up the pair after a much shorter time had elapsed. Both oviposition and copulation were observed up to the end of the period of adult activity.

IV. METHODS OF ANALYSING JUNCUS SQUARROSUS AND COLEOPHORA CAESPITITIELLA POPULATIONS.

1. Sampling methods.

The most convenient time to sample *Coleophora* populations is when either the eggs or the larvae are to be found on the rush heads. From samples of *J. squarrosus* taken over the summer months of 1952, 1953, and 1954 a general picture has been obtained of the size and form of rush and moth populations at various localities in the study area. Fifteen stems were collected from each sample station and the flowering (or fruiting) heads were preserved in 4% formalin. In 1952 all fifteen stems were examined, but in the two following years much more material was collected and the number of stems examined from each locality reduced to ten. It has been shown, from the 1952 material, that this did not appreciably affect the results obtained.

A study of two particular *Coleophora* populations has been carried on continuously over a period of two years and the method of sampling for the insect when overwintering in the litter will be referred to in an appropriate later section of this account (pages 129-30)

2. Areas sampled.

The localities of the various sites sampled are shown in fig. 7.(page 54).

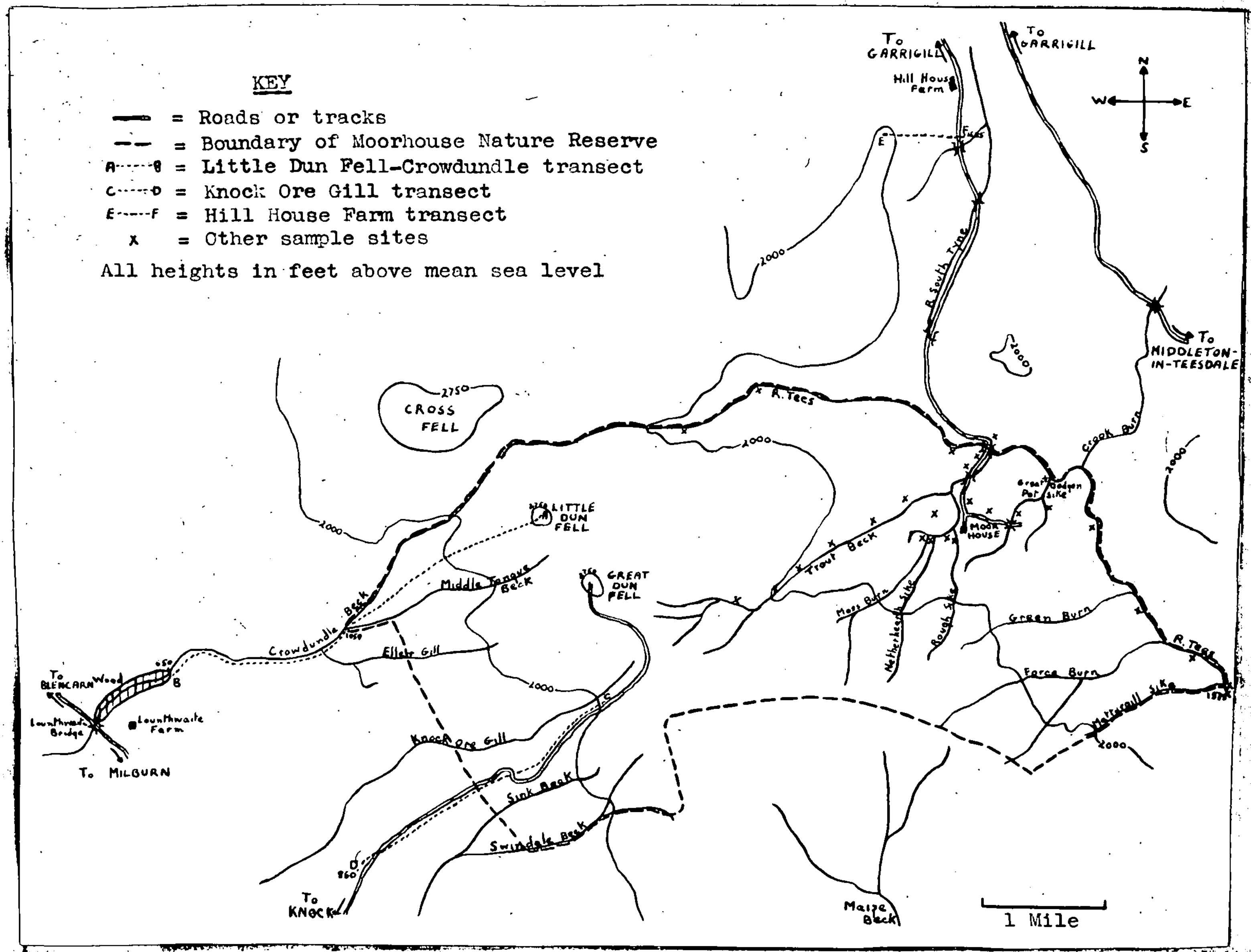

Fig. 7. A sketch-map of the study area in the northern Pennines, showing the positions of the transects and sites from which samples of J. squarrosus were collected.

In order to obtain a general picture of the insect and food plant on both sides of the Pennines, transects have been sampled on both the eastern and western slopes. In addition to these transects various sites on the eastern side of the Nature Reserve, in the vicinity of Moor House, have been sampled each year.

The three transects which have been sampled are all shown on fig. 7. Of the two on the western Pennine slope the transect from a point at 650' on Crowdundle Beck to the summit of Little Dun Fell (referred to as transect A from henceforth) was the one which was most regularly sampled. The lower limit of this transect was determined by the disappearance of J. squarrosus at that height. Up to a height of approximately 1800' the various sample stations (Nos. 1 - 11) were separated by a vertical distance of approximately 100'. Above this height, to the summit of Little Dun Fell (2750') the remaining sample stations, (Nos. 11 - 15) had a vertical interval of approximately 250' between them. In 1952 only, a second transect, (transect B) was sampled on the western Pennine slopes. This is shown as the Knock Ore Gill transect on fig. 7 and it followed the course of the road on the south bank of the Gill between 860' and 2000', with sample stations at approximately 100' intervals.

The location of transect C (referred to on fig. 7 as the Hill House Farm transect) on the eastern Pennine slope was chosen for a number of reasons. There is, in this area, a relatively steep drop to the east such as does not occur on the typical dip slope on which the eastern part of the Moor House Nature Reserve is located. On these more gentle eastern slopes heather moor is the typical vegetation and in this J. squarrosus is only an irregular component. Such an area is obviously not suited for taking a series of samples across. A further advantage of the area near Hill House Farm is that J. squarrosus occurs in the vegetation down to 1500'. This is not the case in any other area on the eastern slopes near Moor House, except along the River Tees and this area proved to be too inaccessible for regular study. The seven sample stations were each separated by a vertical distance of about 100'

V. STUDIES ON JUNCUS SQUARROSUS L.

I. General distribution over the study area.

J. squarrosus is broadly distributed over the area shown in fig. 7, and occurs even on the highest ground (Cross Fell, 2930'). The lower limit of the rush appears largely to be determined by the upper limit of cultivation. On the western Pennine slopes this height is about 700' (650' along Crowdundle Beck) but on the eastern slopes it is considerably higher. Here meadows are often cut for hay up to 1500' and clumps of the rush are very sporadic below this height.

The western Pennine slope, along transect A , is covered with thin peat, with stunted heather (*Calluna vulgaris* (L) Hull) and *J. squarrosus* abundant down to about 1600'. Below this height bracken, (*Pteris aquilinum* (L) Kuhn.) becomes an increasingly important component of the flora but *J. squarrosus* remains widespread down to about 900'. Below this height it becomes more sporadic until its ultimate disappearance with the beginning of cultivation.

The more gentle eastern slopes are mainly covered with heather moor. In such areas *J. squarrosus* is only a rare component of the flora, except on the terraces of the streams which dissect the moor~~s~~. The plant is x also included in the vegetation which is in the process of recolonising the bottoms of peat hags on the heather moor itself. Some of the eastern slopes are rather more steep and are similar to the upper western slopes in their general appearance - transect C, as has already been mentioned, is located on such a slope. It has already been pointed out that the lower limit of the rush, owing to the effects of cultivation, is very much higher on the eastern slopes than is the case to the west.

The whole of the study area was used as sheep grazing, except in the winter months. Fortunately J. squarrosus did not appear to be particularly desirable to sheep and even the young shoots were, in the main, left uneaten. When the rush stems began to dry off some were nibbled off by sheep but the amount of damage caused in the experimental areas in this manner was negligible. After the end of the summer an increasing number of the rush stems were eaten, but by this time, fruiting, if it was going to occur, had been completed and most of the Coleophora larvae had migrated into the litter surrounding the plants.

Pearsall (1950) pointed out that rush plants growing at various altitudes show considerable differences in form. In the present study area there was a marked gradation from plants at the lower limits of its distribution to those on the fell tops. This gradation involved a progressive retardation of the time of first appearance of the flowering stems and the ultimate length of these, and of the time of flowering and fruiting.

The production of flowers, fruits and seeds diminished as the altitude increased. Pearsall showed that the effects of altitude are differential, affecting the seed production more, flower production less, and vegetative growth least, and, as these effects vary little between districts receiving great differences in rainfall, he concluded that they can be attributed mainly to the diminution of mean temperature with increasing altitude.

In the course of this study it has not been possible to make accurate measurements of all these factors but, as the capacity of rush plants to produce ripe seeds is of importance to Coleophora this particular aspect has been analysed in some detail.

2. Degree of fruiting in 1952, 1953 and 1954.

a. Introduction.

Owing mainly to the retardation of the development of the flowers and fruits a certain altitude is reached above which fertile seeds of J. squarrosus are not usually produced. Pearsall (1950) suggested this is generally about 2,500' to 2,700', but he also quoted an example when, in the exceptionally long and warm summer of 1947, viable seeds were obtained from 3,400' on Ben Wyvis. These general observations have been borne out in the present study, and the effect of temperature further emphasised. In 1952 and 1953 some capsules were found above 2,500' which produced viable seeds, whereas in the cool and wet summer of 1954 fruiting apparently did not occur above 2,100'.

In the following sections the number of capsules producing ripe seeds is expressed as a percentage of the total number of capsules in the sample. No estimate has been made of the number of seeds present in the individual capsules - this probably also decreased with increasing altitude. The data from which figs. 8 - 13 have been constructed are given in Appendix I. A discussion of the method used in estimating the standard errors of the percentage of capsules producing ripe seeds at each sample station is in Appendix III.

b. Western slopes of the northern Pennines.

Since work did not begin until the summer of 1952, it was not possible to take more than one series of samples along the various transects in that year. Transect A was sampled on 21st and 23rd August, and the results are expressed in fig. 8 (p. 61). The differences between the two curves given on this figure represent the number of rush capsules destroyed as a result of <u>Coleophora</u> attack up to the date of sampling. Further capsules would have been destroyed after this time, and in the two succeeding years, samples were taken later in the year in order to obtain estimates of the total destruction. A similar picture of ripe seed production in 1952 was obtained from samples taken along transect B. Discussion of the fruiting of <u>J. squarrosus</u> in 1952 on

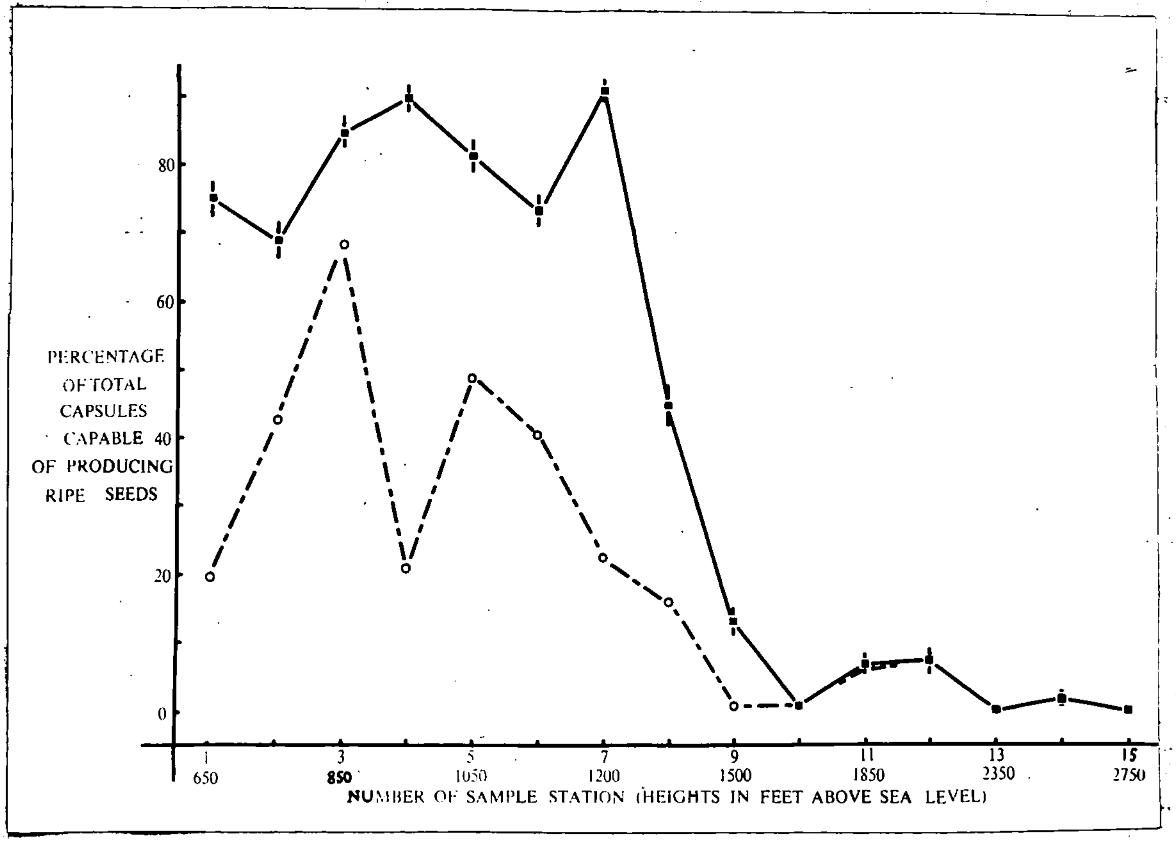

Fig.8. Ripe seed production by J.squarrosus along transect A in 1952.

■———■ = at the beginning of the season (vertical lines indicate standard errors).

○– – –○ =on 21 and 23 Aug.

the western slopes is delayed until the 1953 and 1954 positions have been examined.

In 1953 samples of *J. squarrosus* inflorescences were taken on 8th Aug. and 4th Sept. and from these an estimate of the potential number of capsules capable of producing ripe seeds at the beginning of the season has been calculated for each sample station. The actual number of such capsules present on the respective sample dates has also been calculated and all these values are shown on fig. 9 (p. 63). The fourth curve on fig. 9 has been constructed from a series of points calculated from the August sample data, to show the estimated number of capsules which would have been capable of producing ripe seeds at the end of the season. These capsules would not have been attacked by *Coleophora* larvae. These figures only give a rough estimate of the end of the season position, but the considerable amount of destruction which they indicate was verified by field observations. It has already been pointed out that the extent of the attack in individual capsules varied, and some of these may have had a small number of unharmed seeds at the end of the season. A note is relevant here regarding the methods by which these estimates of end of season fruiting were obtained. When larval behaviour was discussed (see pages 38 - 49), it was shown that in 1953, in two experimental areas, *Coleophora* larvae were found to consume averages of 2.18 and 2.39 rush capsules in their lifetime. In calculating the end of

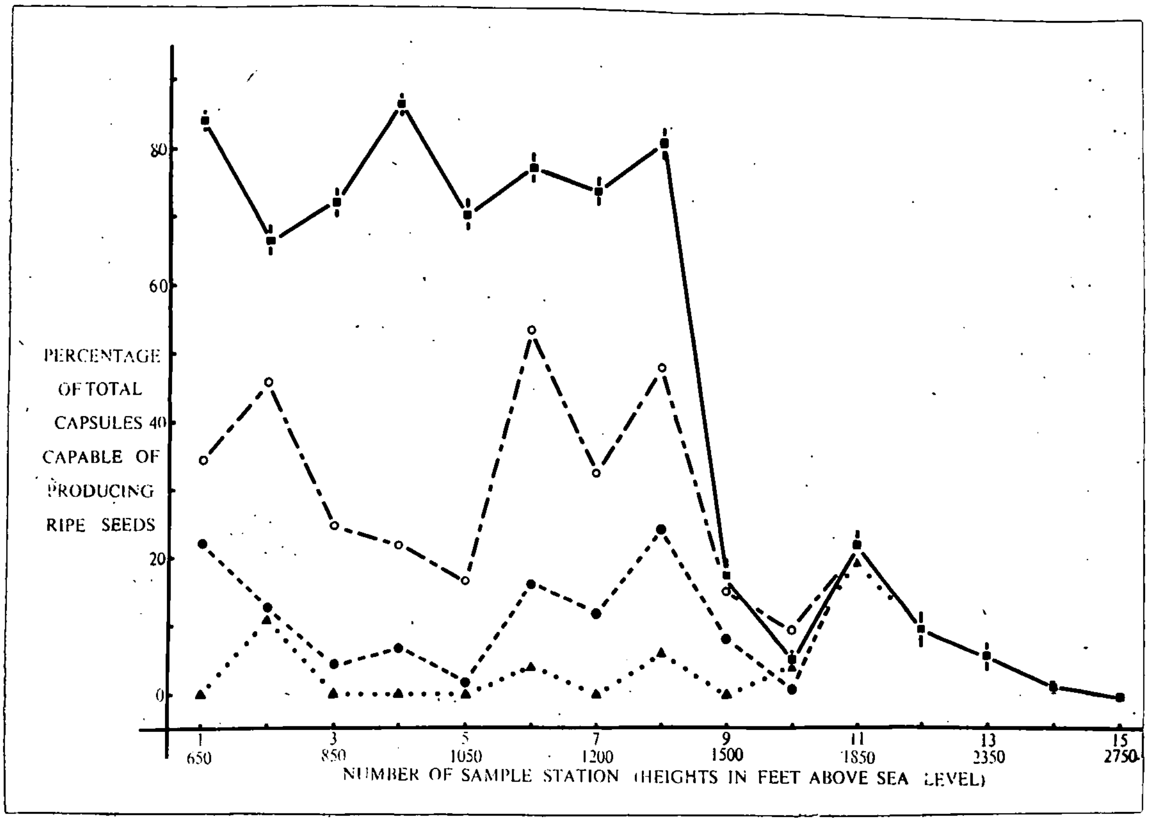

Fig. 9. Ripe seed production by <u>J. squarrosus</u> along transect A in 1953.

■——■ = at the beginning of the season (vertical lines indicate standard errors).

○—-—○ = on 8 Aug.

●-----● = on 4 Sept.

▲..........▲ = at the end of the season (estimated).

season fruiting, it has been assumed that each larva consumed an average of 2.28 (the mean of 2.18 and 2.39) capsules during 1953. The product of this number and the number of living larvae in the August samples is the number of rush capsules expected to be destroyed by the end of the larval feeding period. This number was then subtracted from the number of capsules capable of producing ripe seeds before any Coleophora attack, and the resulting figure expressed as a percentage of the total number of capsules in a particular sample. Thus if x represents the number of living larvae in the August sample, y the number of rush capsules capable of producing ripe seeds at the beginning of the season, and z the total number of capsules in the sample, the percentage of capsules capable of producing ripe seeds at the end of the Coleophora feeding period is given by the expression:-

$$\frac{(y - 2.28x).100}{z}.$$

Providing one realizes that certain initial assumptions are made this is probably a valid method for giving an estimate of the number of rush capsules unharmed and with ripe seeds at the end of the season. From the position of this curve on fig. 9, relative to the other three curves, it is apparent that at least the correct trend is shown by this method. The major assumptions appear to be ; firstly, that larvae moved an equal amount, and consumed a similar quantity of seeds, at all heights from 650' to 1800'. Secondly it is assumed that larvae only attacked capsules which were maturing seeds. This appears to be, in the main, a valid assumption as field observations showed that a larva, on boring into a capsule containing shrivelled seeds, soon moved off and attacked another until a good food source was located. It should be noted, however, that this 'exploring' would have to increase with increasing altitude as the number of maturing fruits per plant decreased. This exploring was also more marked towards the end of the larval feeding period, at the lower sampling stations, when practically all the capsules had been destroyed by other larvae. The third assumption is that the number of larvae alive when the August sample was taken was the same as those present at the end of the season. This also seems to be a valid assumption as very few dead larvae were found within rush capsules. Figures will be presented later (pages135-46) which show that the period of feeding on the rush capsule is not one of marked larval mortality. As larval marking experiments were not carried out in 1952 and 1954, no estimate has been made of the number of rush capsules capable of producing ripe seeds at the end of these seasons.

In 1954 samples of J. squarrosus were taken on 24th Aug. and 1st Oct. Fig. 10 (p. 66) shows ripe seed production in that year.

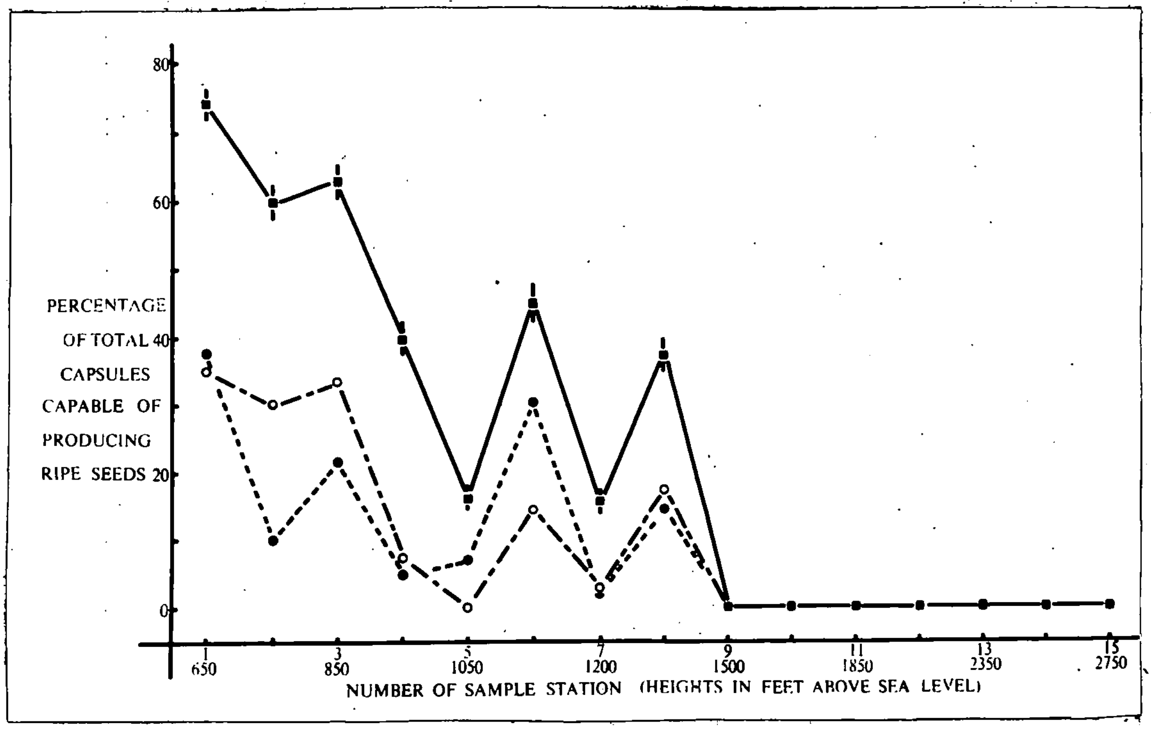

Fig.10. Ripe seed production by *J.squarrosus* along transect A in 1954.

■——■ = at the beginning of the season (vertical lines indicate standard errors).

○——○ = on 24 Aug.

●-----● = on 1 Oct.

On figs. 9 and 10 it will be noticed that some of the curves cross at a few points. This anomaly is, of course, a result of errors of the sampling method. In order to avoid confusion on the figures, the standard errors of the percentage figures arrived at have only been given for the beginning of the season ripe seed production.

From an examination of figs. 8, 9, and 10 it can be seen that seed setting in these years followed a similar pattern. The percentage of capsules capable of producing ripe seeds at the beginning of the various seasons decreased with increasing altitude as expected. The height at which seed setting ceased in the three years was, however, very different. In both 1952 and 1953 seeds were set up to sample station 14 (2,500') whereas, in 1954, none were set above station 8 (1,350'). It can also be seen from these three figs. that seed setting was at a considerably lower level at most sites in 1954 than in the preceding two years. In 1952 and 1953 the position was very similar - with oscillations in the range of approximately 70 - 90% between the lower sample stations (stations 1 - 8) followed by a sharp decline in numbers at about 1,500', above which a few mature capsules were to be found up to 2,500'. In 1954 there was a fairly steady decline in numbers from station 1 (74%) upwards - with none occurring, as we have seen, above station 8. Mean temperatures in 1952 and 1953 were very similar, but the summer of 1954 was much cooler and this is suggested to be the cause of the decrease in seed setting of J. squarrosus. These observations coincide with those of Pearsall (1950), which have already been discussed.

In order to determine whether the fluctuations in the percentages of the total capsules which were capable of producing ripe seeds, that occurred between the lower sample stations in 1952 and 1953 were random and due solely to sampling errors, a heterogeneity χ^2 has been calculated for both years. For stations 1 - 7 (inclusive) in 1952 $\chi^2 = 91.2$ with six degrees of freedom. In 1953, for stations 1 - 8, $\chi^2 = 82.6$ with seven degrees of freedom. Both these figures are extremely significant with $p = < 0.001$. As the observed proportions of ripening capsule to total capsules differ significantly from one another, there was, presumably, some reason other than errors of sampling for this difference in the capacity of neighbouring rush populations to produce ripe seeds. At these heights this is apparently not an effect of altitude. Presumably the reasons for these fluctuations are to be found in the conditions of growth for the rush plants at each sample station. The degree of protection afforded the plants is certainly important and this will be demonstrated in a future section (pages 76-7). Soil conditions (e.g. pH, water content, availability of mineral salts) at each site a re also factors likely to vary the capacity of the plants to mature seeds.

It can also be seen from figs. 8, 9 and 10 that the number of capsules capable of producing ripe seeds after Coleophora had finished, or, in the case of the September samples, nearly finished feeding, was very similar, at the lower sample stations, in 1953 and 1954 (and probably in 1952 also, although no samples were taken) although many more potential ripe capsules were present at the beginning of the former season. It will be shown later (pages 80-105) that this was due to the lower Coleophora populations on the rush plants in 1954. In all three years it can be seen that Coleophora had a considerable effect on the capacity of J. squarrosus to produce ripe seeds at the lower levels.

c. Eastern slopes of the northern Pennines.

Transect C was sampled in 1952, on 20th Aug., the highest station (2,075') being omitted. The percentages of capsules capable of producing ripe seeds on 20th Aug. and before any Coleophora attack are shown on fig. 11 (p 70).

In 1953 samples were taken on 10th Aug. and 5th Sept., and the percentage of ripening capsules on these dates and before Coleophora attack is shown on fig 12 (p. 71). A fourth series of points, estimating the percentage of the total capsules which would have remained after Colephora had finished feeding, have

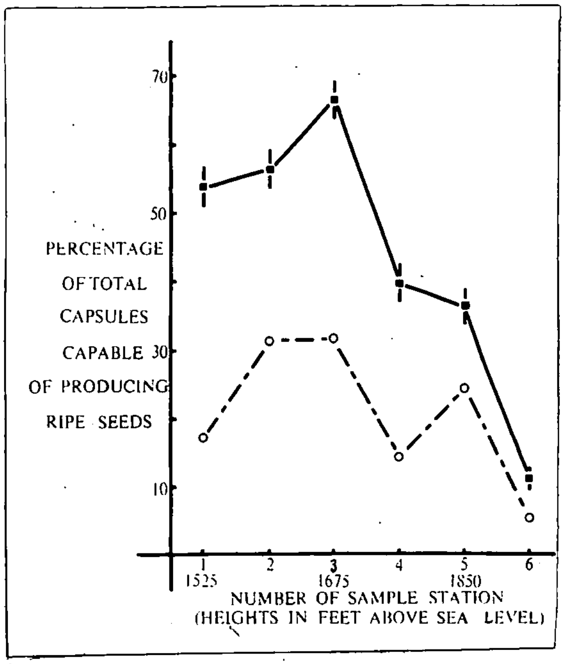

Fig.11. Ripe seed production by <u>J. squarrosus</u> along transect C in 1952.

■———■ = at the beginning of the season (vertical lines indicate standard errors).

○———○ = on 20 Aug.

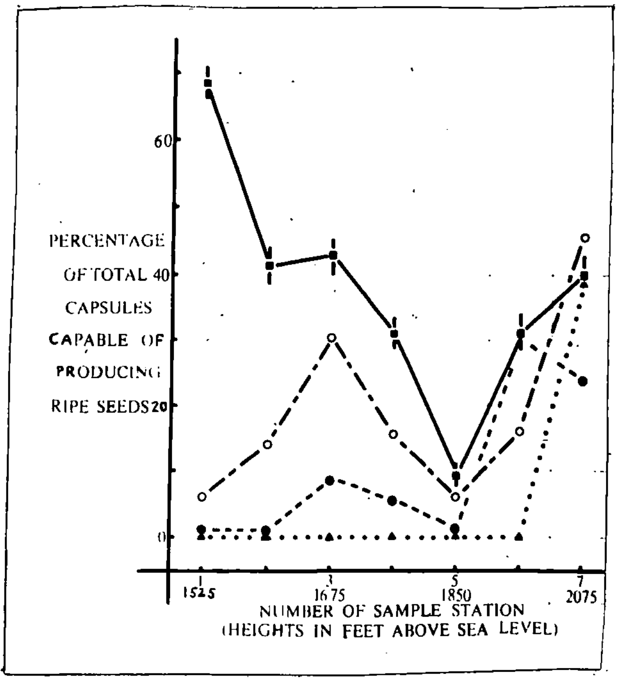

Fig.12. Ripe seed production by *J.squarrosus* along transect C in 1953.

■——■ = at the beginning of the season (vertical lines indicate standard errors).

○———○ = on 10 Aug.

●-----● = on 5 Sept.

▲.........▲ = at the end of the season (estimated).

been calculated from the August samples. These points were calculated by the method already described when referring to transect A. From an inspection of fig. 12 it can be seen that, theoretically, all rush capsules, between stations 1 and 6, containing ripening seeds were attacked to some extent. As described later (pages 98-100) 1953 was a year of particularly heavy Coleophora infestation in this area, and field observations confirmed that very few rush capsules remained intact at the end of the season.

Fig. 13 (p. 73) illustrates the percentages of rush capsules capable of producing ripe seeds along transect C in 1954 - at the beginning of the season and on 18th Aug. and 30th Sept.

From an examination of figs. 11, 12 and 13 it can be seen that seed setting followed the expected course in the three years, in that it generally diminished with increase in altitude. It should be noted that some seeds matured up to the top of the ridge (2,075') in all three years, though the numbers that did so in each year were very different. The effect of the low temperatures during the summer of 1954 was again reflected in the figures for ripe seed production in that year. In the two previous summers this was at a maximum of just under 70% at the lower sample stations and decreased to a minimum of about 10%. In 1954 only one station had a figure for the beginning

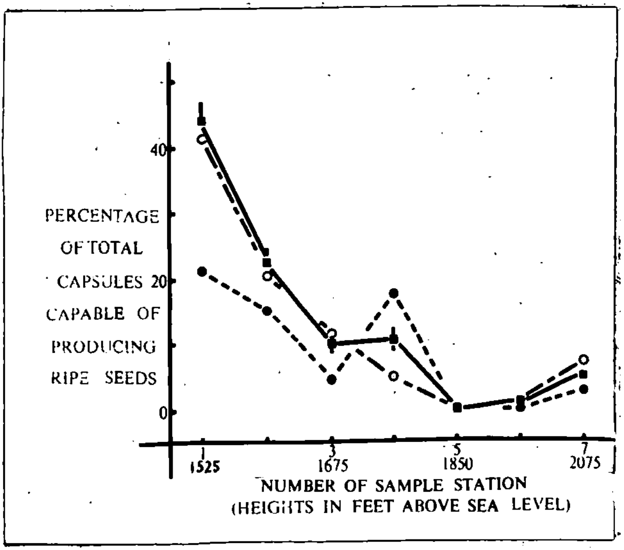

Fig. 13. Ripe seed production by J. squarrosus along transect C in 1954.

■——■ = at the beginning of the season (vertical lines indicate standard errors).

o——o = on 18 Aug.

●-----● = on 30 Sept.

of the season of over 40%; the remainder were all below 25%, with apparently no seeds maturing at station 5. From an inspection of figs 12 and 13 it appears that the position at stations 6 and 7 was rather anomalous. Especially in 1953 the number of capsules with ripe seeds began to increase with increasing altitude after station 5, until at station 7 (2,075') 39.8% of the capsules were maturing seeds at the beginning of the season. Unfortunately this station was not sampled in 1952. This same tendency is apparent in fig 13 for 1954, despite the very much lower absolute figures in that year, when stations 6 and 7 both had a small proportion of ripening seeds, whereas station 5 had none. The most likely explanation for this capacity to produce many ripe seeds at these two stations appears to be that the rush plants at both localities were in extremely sheltered positions. Station 6 was sheltered by a wall on the north side, and station 7 was sheltered in a similar manner from both the north and the west. Further examples of the actual situation of rush plants having an effect on seed production are quoted on pages 76 - 77.

It was noted on the western slopes that the capacity of *Coleophora* larvae to destroy the ripening seeds was considerable. This was especially so in 1952 and 1953 when *Coleophora* numbers were high. In 1954 (see pages 101-2) numbers were very much lower than in the twp preceding years. An inspection of fig. 13

shows that destruction of ripening seeds in that year was considerably less than in 1952 and 1953. In fact, by September, at the lower sample stations, despite the very much lower initial number of capsules capable of producing ripe seeds in 1954, the proportion of these was rather greater than at the same time in the previous year.

In addition to transect C, various scattered sites on the eastern Pennine slopes were sampled in 1952 - 4. Most of these sites were located on the Moor House Nature Reserve, and their positions are marked on fig. 7 (p. 54). Tables showing the percentage of capsules capable of producing ripe seeds at the beginning of each season at these sample sites are to be found in Appendix I. The number of these present on the day of sampling is not given in these tables as <u>Coleophora</u> populations were, in general, very low or non-existent at most of these sample stations. The general decrease in seed setting with increasing altitude is apparent from the figures in these tables. In 1952 and 1953 fruiting occurred to some extent at all the sites sampled - the highest of these being at a point 2,170' along Trout Beck. The effect of the cool summer of 1954 was again emphasised by the very much lower seed-setting in that year compared with 1952 and 1953 In general, seeds were only set at the lowest sample sites (and none were found above 1940') in 1954, and then in smaller numbers than in 1952 and 1953.

The figures for ripe seed production at these various sites frequently showed that rush plants in sheltered sites tended to produce more ripe seeds than exposed plants at the same altitude. Table 6, which is constructed from the figures in Appendix I gives two examples of such pairs of sites. In both these instances the samples from the sheltered sites were collected from plants protected from the west by the banks of a stream, with additional cover afforded by thick clumps of Juncus effusus.

TABLE 6.

Percentage of total capsules of J. squarrosus capable of producing ripe seeds at nearby pairs of sample sites, illustrating the effect of exposure.

Altitude (feet)	Date of sample	Exposed site	Sheltered site
1870	1952	15.7 ± 2.3	52.9 ± 3.0
	1953	8.2 ± 2.1	14.9 ± 3.0
	1954	1.0 ± 0.7	16.2 ± 3.0
1710	1952	10.3 ± 2.3	64.5 ± 3.3
	1953	13.9 ± 2.7	48.1 ± 4.9
	1954	2.9 ± 1.3	2.9 ± 1.4

Table 7 gives a similar set of figures to those in Table 6 for two sites along Trout Beck, where the higher sample station was in a marked depression, and the lower one was exposed on the bank of the stream.

TABLE 7.

Percentage of total capsules of J. squarrosus capable of producing ripe seeds at two sites along Trout Beck, illustrating the effects of exposure.

Date of sample	Exposed site at 1875'	Sheltered site at 1940'
1952	3.6 ± 1.2	45.5 ± 3.5
1953	4.4 ± 1.3	36.5 ± 3.7
1954	0	3.2 ± 1.6

d. Differences apparent between the western and Eastern Pennine slopes.

It has been pointed out that 1952 and 1953 were very similar years, with regard to seed setting, on both slopes of the Pennines. In both years, as figs. 11 and 12 show, proportions of up to 70% of capsules producing ripe seeds were found at station 1 (1525') of transect C. At the equivalent height on the western slopes only 15% of such were found, and above this height the capacity for seed setting rapidly diminished to a very low level. In these years, on the eastern slopes, none of the transect sample stations had values for seed setting below 10%. The same degree of difference between comparable heights on the two slopes was also apparent from the transect samples taken in the cool summer of 1954. On both slopes the fruiting capacity of J. squarrosus was much lower than in the preceding two years. On the western slopes no seeds were set above 1,350', whereas, at the lowest sample station of the eastern transect (1,525'), 44.2% of the capsules present were capable of producing ripe seeds. At 1,850' the first sample was taken which contained no ripening seeds, but above this a few capsules were found to be capable of producing ripe seeds up to 2,075', at the rather exceptional sample stations 6 and 7.. It has already been explained that it was not possible to obtain samples of J. squarrosus from below 1525' on the eastern Pennine slopes in the study area, but above this height, it is apparent that, in all three years during which this investigation was carried out, the capacity of the rush to seed, to any given extent, was possessed about 300' higher on the eastern slopes than on the western.

It can also be seen from figs 8 - 13 that the effect of Coleophora larvae on the production of rush seeds extended to a greater altitude on the eastern slopes. This situation is further discussed on pages 106-8.

as by the time the later larvae manufacture their cases, the earlier ones have already passed into the surrounding vegetation prior to overwintering. Pearsall's figures will therefore tend to be underestimates of infestation. In the central Lake District, in 1942, he found that the frequency of the larvae decreased rapidly from a maximum of about 40% of the capsules at 700', with no signs of the moth above 1,800', although J. squarrosus occurs in that district up to 3,000'. Only in the long warm summer of 1947 did he find larvae above this height, when some were found at 2,000' on the south-facing slopes of Saddleback. In the same year Pearsall recorded no signs of infestation above 1,400' in the Eastern Highlands.

In the investigations carried out in the northern Pennines, which are now to be discussed, a similar general picture has been obtained of the altitudinal distribution of the moth. As Pearsall pointed out, this is much more restricted than that of the rush on which it lives

2. Western slopes of the northern Pennines.

a. Coleophora distribution.

It has already been pointed out that it was only possible to sample all the transects once during the summer of 1952. As these samples were not taken until August, the initial size of the Coleophora populations could not be determined in 1952.

In 1953 and 1954 egg counts were carried out in July. Transect A was sampled on 21st and 23rd August 1952. It is probable that by this date, no larvae had completed their feeding, although some had moved on to fresh rush capsules from their original capsule, and any empty capsules were noted. A specimen sheet on which the original observations for each sample station were recorded, is included in Appendix II. Percentage Coleophora infestation along this transect, on the one sampling date in 1952, is included on fig. 21 (page 111). Between the lowest sample station (650') and about 1,200' the degree of Coleophora infestation varied between limits of about 15% and 50%, A heterogeneity χ^2 has been applied to the proportions of infected to total capsules found at stations 1 - 7 inclusive. From this, $\chi^2 = 112.0$ with six degrees of freedom. This is extremely significant with $p = < 0.001$. It is thus apparent that the observed proportions infected differed significantly from each other. Possible reasons for these differences are discussed on pages 164-7 . Above 1,200' Coleophora began to decline in numbers until, by about 1,850', no larvae were present in the rush capsules. This corresponds to the situation described by Pearsall (1950) which has already been referred to.

In order to confirm the results obtained along this transect, a further transect was sampled in 1952 on the western Pennine slopes. Transect B was sampled on 16th September. By this date some larvae had completed their feeding and were thus not included in the population figures obtained. Despite the fact that the figures obtained for the population at each sample station were not total, a close correlation in the general picture of the altitudinal distribution of *Coleophora* was found between this transect and transect A. (see Appendix II). Up to about 1,200' *Coleophora* populations were shown to fluctuate from one sample station to another. Above this height *Coleophora* numbers rapidly dropped and none were recorded above 1,800'. This situation corresponded closely to that found along transect A in 1952, and, in the two succeeding years transect B was not sampled in order to allow a more detailed survey of the other transect to be carried out.

Transect A was first sampled on 17th June in 1953, in order to obtain an egg count. It has already been pointed out that the oviposition period of *C. caespititiella* is very prolonged, and owing to this it was found that the number of eggs present in these samples was much lower than those present in later samples. Accordingly a further series of samples was collected on 5th July, by which time it was known that the adult appearance was over. By this date a number of the eggs had hatched, so the initial egg population would, presumably, have been somewhat higher than these figures obtained for early July would suggest.

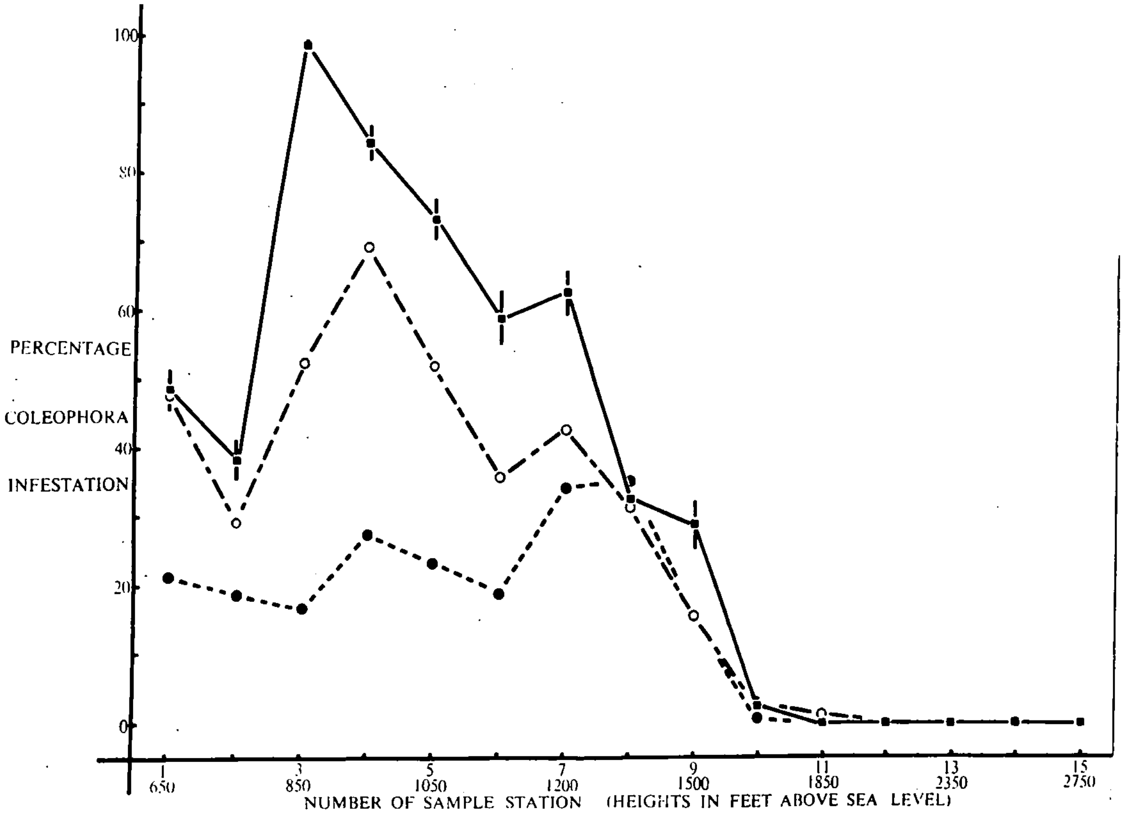

Fig.14. Coleophora infestation of J.squarrosus along transect A in 1953.

■——■ = on 5 July (vertical lines indicate standard errors).

○– – –○ = on 8 Aug.

●- - - -● = on 4 Sept.

It will be shown later that the egg-hatching period of C. caespititiella is indeed one of considerable mortality (see pages 135-45). Samples of rush stems, in 1953, were also collected on 8th Aug. and 4th Sept. Percentage Coleophora infestation along transect A in 1953 is illustrated in fig. 14 (p. 83). This shows that the degree of infestation, by eggs and larvae, in July steadily decreased from station 3 (850') where there was an infestation of 98.8 ± 0.7%, to 1,850'. At station 3 practically all the ripening rush capsules had larvae already inside them, or eggs on them. Stations 1 and 2, below 850', had infestations of only 48.7 ± 3.1% and 38.5 ± 3.1%, but the reason for this sharp drop in the size of the initial population at these two lowest sites is not known. It should be noted that the upper limit for Coleophora in 1953 was practically identical to that found to be the case in 1952.

As the August samples were collected just as the larval cases were beginning to appear on the rush capsules, the figures obtained from these are comparable with those from the 1952 samples. The August 1953 samples showed a similar picture to those taken at the same time in the previous year, in that the size of neighbouring Coleophora populations between 650' and 1,200' varied considerably. In 1953 the populations tended to be somewhat higher and the limits of variation were 29.3 ± 3.0% and 69.3 ± 3.1%.

A heterogeneity χ^2 has been applied to the proportions of infected to total capsules found at stations 1 - 8 inclusive. From this $\chi^2 = 104.4$ with seven degrees of freedom. This is extremely significant with $p = < 0.001$. Possible reasons for the differences between these adjacent populations will be discussed later, but it is of interest to note here that the three peak populations in 1952 and 1953 occurred at the same three sample stations - numbers 1 (650'), 4 (950') and 7 (1,200').

The differences between the July and August populations shown on fig. 14 represent the mortality during that period, but this is not so between the populations shown in August and September. By the beginning of September a number of the larvae had finished feeding and had moved off the rush stems. The September figures, then, represent the number of larvae still feeding at the time the transect was sampled. This set of samples was mainly taken with a view to obtaining estimates of the parasite populations along the transect. From the close conformity of this curve with that for the August populations between stations 8 and 11 it can be seen that feeding was more prolonged at the upper limits of the range of Coleophora. This subject will be enlarged upon after the position in 1954 has been examined.

Coleophora populations were sampled along transect A in 1954, at corresponding stages in their development to the times when they were sampled in the previous year. The moth was considerably slower in its development in 1954, and the three sets of samples were taken on 22nd July, 24th Aug. and 1st Oct. Coleophora infestation on these three dates is shown in fig. 15 (page 87). The populations of eggs and larvae at the end of July showed a rather different form to those of the previous year. In 1954 the largest population was found at station 8 (1,350'), where 78.8 ± 3.0% infestation was recorded. From 650' up to this height Coleophora populations varied between infesting 26.4 ± 3.6% and 71.2 ± 3.0% of the rush capsules. These lower level populations were somewhat smaller than in the previous year. Above 1,350' population size rapidly declined and the last eggs were recorded at 1,700', that is, the same height that they were recorded to in 1953, although, in that year a small number must have been laid above 1,700' as two larvae were present in the August sample taken from station 11 (1,850').

The samples taken during August 1954 can be compared to those taken at the same stage in the insect's life history in the preceding two years. By the time the August samples were taken in 1954, it can be seen from fig. 15 that a considerable mortality had occurred, and that this had resulted in very much smaller populations

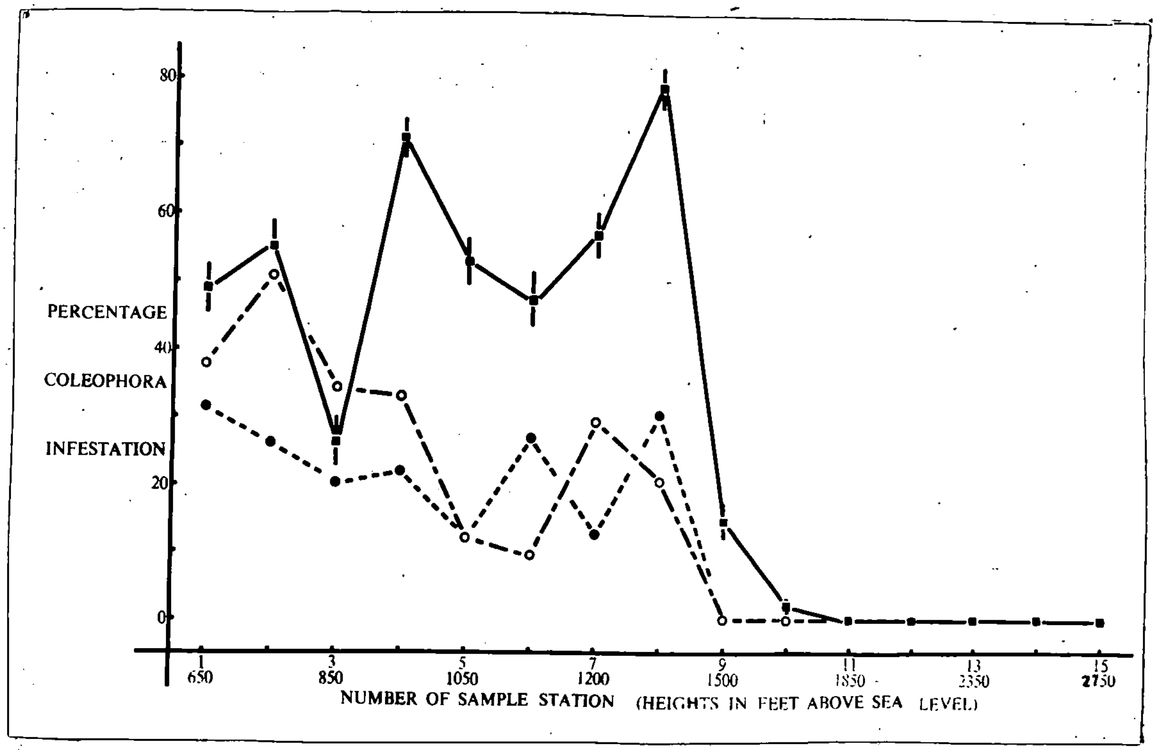

Fig. 15. *Coleophora* infestation of *J. squarrosus* along transect A in 1954.

■——■ = on 22 July (vertical lines indicate standard errors).

o———o = on 24 Aug.

●-----● = on 1 Oct.

than in the preceding two years along much of this transect. Up to 950' populations were of comparable size to populations at these sample stations in 1952 and 1953, but above this height populations were very much lower than those in the previous two years, except for a partial recovery at stations 7 (1,200') and 8 (1,350'). As in 1952 and 1953, relatively high populations were recorded at stations 1, 4, and 7, although only at the latter was there an actual peak in 1954. These lower sample stations obviously differed even more significantly from each other than in 1952 and 1953 and no heterogeneity χ^2 has been calculated for 1954. The last larvae were recorded at station 8 (1350'). This was about 500' lower than in either 1952 or 1953. In 1954, despite the fact that eggs were laid up to 1700', no larvae managed to establish themselves above 1,350'. The reasons for this very different distribution of Coleophora in 1954 will become apparent later (see pages 110-15).

From the curve on fig. 15 for Coleophora infestation on 1st Oct., it can be seen that feeding was much more prolonged in 1954 than in the previous year. Only at stations 1 - 4 (we have already seen that these were the only stations with comparable larval numbers to the previous two years) had many larvae moved off the rush plants and above this height the numbers of larvae present at each sample station were very similar to those present in the samples taken in August. No larvae were recorded above 1,350' - thus confirming the position observed on 24th August.

Some of the stations sampled during the late summer months of 1953 and 1954 apparently had a higher infestation of Coleophora than was the case from earlier samples. This anomalous situation was, of course, a result of errors of the sampling method. In order to avoid confusion on figs. 14 and 15 standard errors have only been inserted on the values arrived at for percentage Coleophora infestation in July.

Fig. 16 (page 90) illustrates the differences, in the size of Coleophora populations in August, that were apparent along transect A during the three years during which samples were taken. From the same samples the percentage of the total rush capsules capable of producing ripe seeds before Coleophora attack has been calculated and these values are included on fig. 16. It appears, from this figure, that there may have been a correlation between the number of ripe seeds produced and the degree of Coleophora infestation at any particular site. This possibility is examined at some length in pages 109-19 . Fig. 16 shows that at stations 1 - 3 the proportions of ripe seeds and the infestation of Coleophora larvae were approximately the same in all three years. Above these stations the number of both declined in 1954 until, at station 9 (1,500') neither

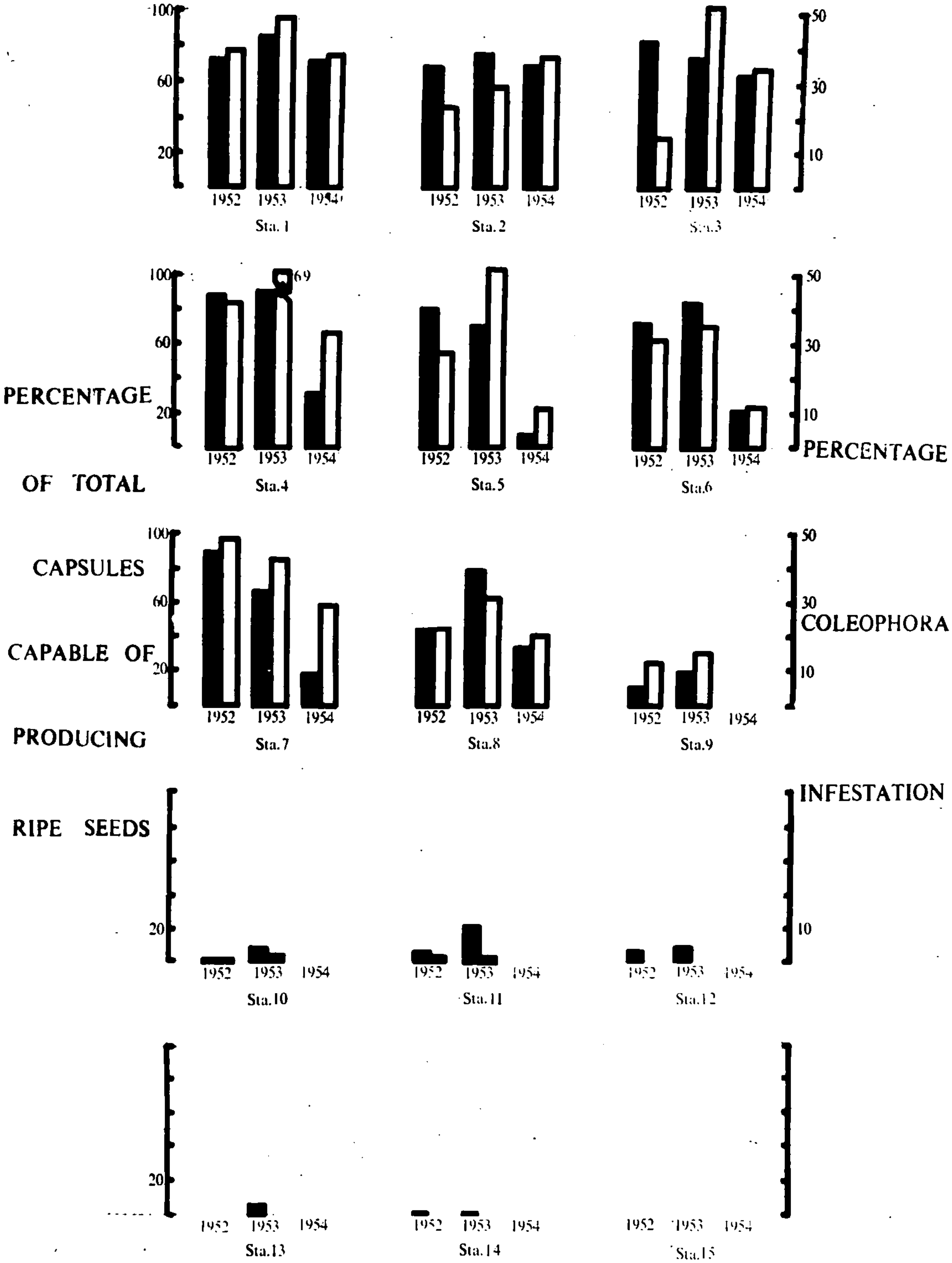

Fig.16. Ripe seed production by J.squarrosus at the beginning of the season (calculated from the August samples) and Coleophora infestation of the rush during August along transect A in 1952-4.

was present in the sample which was examined. In 1952 and 1953 a few ripe seeds were produced up to station 14 (2,500'), and a few Coleophora larvae were present in these years up to station 11 (1,850'). Fig. 16, then, emphasises the conclusions we have already arrived at in previous sections of this account; these were that, whereas 1952 and 1953 were very similar years, regarding both the fruiting capacity of J. squarrosus and the degree of Coleophora infestation, 1954 was very different in both these respects.

It was shown, when describing the life-history of C. caespititiella, that oviposition occurs at approximately the same time at all heights from 650' to the upper limits of the species' range. In the samples taken in July the numbers of eggs and larvae making up the total population were recorded separately, and larvae without or with larval cases in the August and September samples were similarly noted. From this information it has been demonstrated that the time taken over development increased with altitude. Eggs took longer to hatch at the higher sample stations and a larger proportion of eggs to larvae was found, in the July samples, at the upper sample stations than in samples from lower altitudes. Table 8 gives the absolute numbers of eggs and larvae found at station 1 (650') and station 9 (1,500') in the samples taken in July 1953 and 1954

The proportion of each to the total population is shown as a percentage.

TABLE 8.

Numbers of Coleophora eggs and larvae found at two sample stations of transect A in July and the proportions of each to the total population.

	Station 1 (650')				Station 9 (1,500')			
	Eggs		Larvae		Eggs		Larvae	
	No.	% of total	No.	% of total	No.	% of Total	No.	% of total
1953	43	33.1	87	66.9	21	42.9	28	57.1
1954	45	44.1	57	55.9	24	92.3	2	7.7

The formation of larval cases at the upper stations of the transect also took place correspondingly later than at the lower stations. Table 9 gives the absolute numbers of larvae without or with cases at stations 1 and 9 in the samples taken in August 1952, 1953 and 1954. The proportion of each to the total Coleophora population is shown as a percentage.

It should be noted that, as the transect was sampled at slightly different times in each year, the figures in Tables 8 and 9 are only comparable between sample stations and not between each year.

TABLE 9

Numbers of Coleophora with or without cases found at two sample stations of transect A in August, and the proportions of each to the total population.

	Station 1 (650')				Station 9 (1,500')			
	Without cases		With cases		Without cases		With cases	
	No.	% of total	No.	% of total	No.	% of total	No.	% of total
1952	15	13.5	96	86.5	27	77.1	8	22.9
1953	68	56.2	53	43.8	26	100	0	0
1954	61	79.2	16	20.8	0	0	0	0

The feeding period was also noticeably longer for larvae in the higher level populations, and this has already been shown to have been the case in 1953 and 1954 when the September samples from the higher stations of the transect contained practically the same number of larvae as the samples taken a month previously.

b. The distribution of Coleophora parasites.

The major parasites of Coleophora in the study area have been shown to be Ephialtes brevicornis (Ichneumonidae), and Miotropis sp (Chalcidoidea) (pages 33 - 37), and only populations of these species will be referred to here. Populations of parasitised

Coleophora larvae at each sample station have been expressed as a percentage of the total number of larvae in the sample. It has already been pointed out that in the case of *Miotropis*, more than one individual can be supported by one *Coleophora* larva. Full records of parasitism at each sample station are in Appendix II.

In 1952 parasites were only recorded from stations 1 - 3 of transect A. Percentage parasitism is included on fig. 21 (page 111). *Miotropis* was the only species recorded from station 1, and *Ephialtes* was the only species present in the samples collected from the other two stations. The situation along transect B in the same year was similar to this. Parasites were included in samples taken from the only two sample stations below 950'. At 950' only *Ephialtes* was present as a parasite of the *Coleophora* larvae, but at 850' both *Ephialtes* and *Miotropis* were represented in the parasite population. Along both these western transects, larvae from the higher areas were free from parasites in 1952.

In 1953 and 1954 parasitised larvae were counted in the samples taken in September or October. By the time these samples were collected some healthy *Coleophora* larvae had already left the rush heads, and thus, in order to obtain an estimate of the percentage of the total population parasitised at each sample station, the parasitised larvae in the September or October samples have been expressed as a percentage of the estimated population in August. These Coleophora population figures have been calculated by utilising the proportion of Coleophora larvae to J. squarrosus capsules observed in the August samples, which were taken when all the larvae were still feeding on the rush heads.

The percentage of the Coleophora population parasitised at each sample station along transect A in 1953 is shown in fig. 17 (page 96). From this it can be seen that the standard error of each of these population figures is large, and these figures must, therefore, only be considered as estimates. In order to obtain an accurate picture of these parasite populations very much larger samples would be required. Populations of the two species of parasite which were present were recorded separately and these, together with the total population size, are shown on fig. 17. In 1953 parasites extended 200' higher up the transect than in the previous year, and they were recorded up to 1,050'. Ephialtes parasitised a small proportion (generally between 5 - 10%) of the Coleophora larvae at all stations from 1 to 5, but Miotropis was recorded only from stations 1 and 2, where, however, it was present in quite large proportions (23.7% and 17.6% of the larvae respectively) of the Coleophora populations. The spatial distribution of the parasites in 1953 was

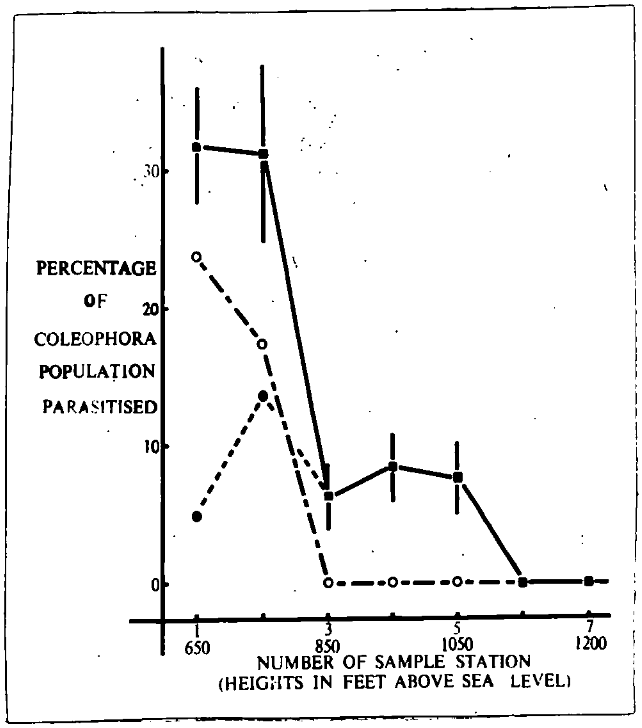

Fig.17. Percentages of the *Coleophora* populations parasitised along transect A in 1953.

■——■ = total parasitism (vertical lines indicate standard errors).

●- - - - -● = parasitised by *Ephialtes brevicornis*.

○——○ = parasitised by *Miotropis* sp.

broadly similar to that in the previous year, when *Ephialtes* extended considerably further up the transect than *Miotropis*. The total parasitisation (*Ephialtes* and *Miotropis*) at stations 1 and 2 in 1953 was 31.8 ± 4.2% and 31.25 ± 6.5% respectively, the highest percentage parasitism of *Coleophora* observed during this work.

In 1954 *Ephialtes* was the only species recorded along transect A. It was present, in low numbers, at stations 1 to 5, with the exception of station 2. (see fig. 23, page 113). The delayed development of *Coleophora* in 1954, compared with 1952 and 1953, has already been referred to. It could be suggested that the absence of *Miotropis* from even the lowest sample stations in 1954 might have been due to this. The Chalcid may have emerged at a time when no *Coleophora* larvae had appeared from inside the rush capsules (this has been shown to have occurred about three weeks later in 1954 than in 1953 and 1952), and thus were not available as a host. The life-histories of *Coleophora* and *Ephialtes*, however, appear to have been sufficiently correlated to have allowed successful parasitisation in all three seasons. *Ephialtes brevicornis* has been recorded from a number of different host species elsewhere, but it is not known whether it is a specific parasite of *Coleophora* in the study area.

3. Eastern slopes of the northern Pennines.

a. *Coleophora* distribution.

Transect C was first sampled on 20th Aug. 1952 and the percentage *Coleophora* infestation on that date is included on fig. 24 (page 116). Station 7 (2,075') was not sampled in 1952. Between the three lowest sample stations (1525' - 1675') infestation fluctuated between 23.1 ± 2.5% and 33.2 ± 2.9%, but above this height the degree of infestation declined. Even at 1,970', however, 5.3 ± 1.3% of the rush capsules were found to be attacked by *Coleophora*.

Transect C was first sampled in 1953, on 7th July. It has already been pointed out, with reference to the transects on the western slopes (page 82), that this was the earliest time at which samples could be taken in order to obtain an estimate of *Coleophora* populations after oviposition. Some eggs had already hatched by this date, so the initial number of eggs laid along the transect was probably higher than the July sample figures would suggest. Samples of rush inflorescences were also collected on 10th Aug. and 5th Sept. Percentage *Coleophora* infestation along transect C in 1953 is given in fig. 18 (page 99). This shows that the infestation, by eggs and larvae, in July steadily diminished from station 1 (1,525') and station 2 (1,575') up to the top of the ridge, (station 7, 2,075'). At the bottom two sample stations *Coleophora* eggs and larvae were extremely abundant and

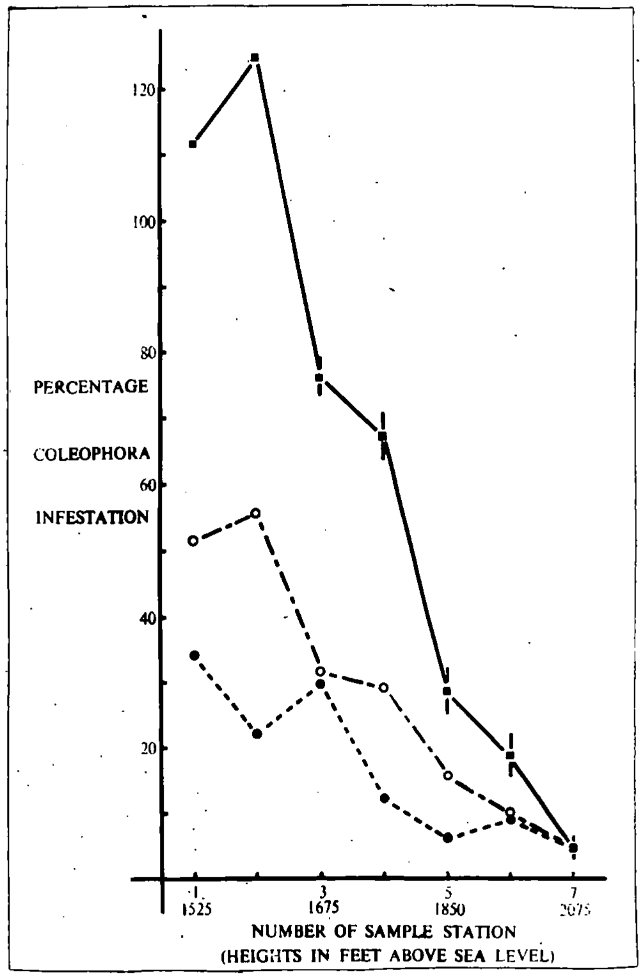

Fig. 18. *Coleophora* infestation of *J. squarrosus* along transect C in 1953.

■ ——— ■ = on 7 July (vertical lines indicate standard errors).

○ — - — ○ = on 10 Aug.

● - - - - - ● = on 5 Sept.

totalled more than the number of rush capsules present. Infestation was 111.5% and 124.3% respectively at these two stations. At 2,075' a small population (4.5 ± 1.7% infestation) was present.

The samples taken in August 1953 were taken at an approximately equivalent time in the moth's development as the samples of August 1952. The two sets of figures are therefore comparable. From station 3 (1,675') to station 7 (2,075') the Coleophora populations were of similar size in 1952 and 1953. At stations 1 and 2, however, percentage Coleophora infestation was very much greater in 1953 than in 1952. Here Coleophora infestation was 51.5 ± 3.8% and 55.6 ± 4.1% respectively (27.3 ± 2.7% and 23.1 ± 2.5% in 1952). These high August population figures emphasised the very large numbers of eggs and larvae which were found in the July samples from these stations.

It has already been explained, whilst referring to transect A (page 85), that the differences between the July and August populations represented the mortality which occurred between the two sampling dates, but that this was not the case with the August and September samples. The populations still feeding on 5th Sept. along transect C, shown on fig 18, indicate that feeding was more prolonged at the upper limits of the range of Coleophora. This is shown by the close conformity of the August and September population curves at the top sample stations of the transect. A similar situation was noted on the western Pennine slopes (page 85).

In 1954, *Coleophora* populations were sampled at stages corresponding to those sampled in 1953. As on the western slopes the moth was considerably slower in its development in 1954 and the three sets of samples were taken on 2ist July, 18th Aug. and 30th Sept. (see fig. 19, page 102). From this it can be seen that the populations of eggs and larvae in July were very much lower than at the same time in 1953. Maximum infestation (37.6 ± 3.5%) was at station 3 and, in general, infestation diminished with increasing altitude to station 7 (2,075') where it was 1.7 ± 1.0%.

The populations of *Coleophora* larvae along transect C in August 1954 were very much smaller than in the preceding two years. Infestation decreased from 17.3 ± 3.0% at station 1 to 2.4 ± 1.4% at station 6 No larvae were induded in the sample from the highest sample station, and there was only 0.5 ± 0.5% infestation at station 5.

It was shown (page 88) that feeding on the western Pennine slopes was more prolonged in 1954 than in the preceding two years. This was also the case along transect C in that year. The number of larvae present on the rush stems in September 1954 can be seen from fig. 19 to have been very similar to those present in

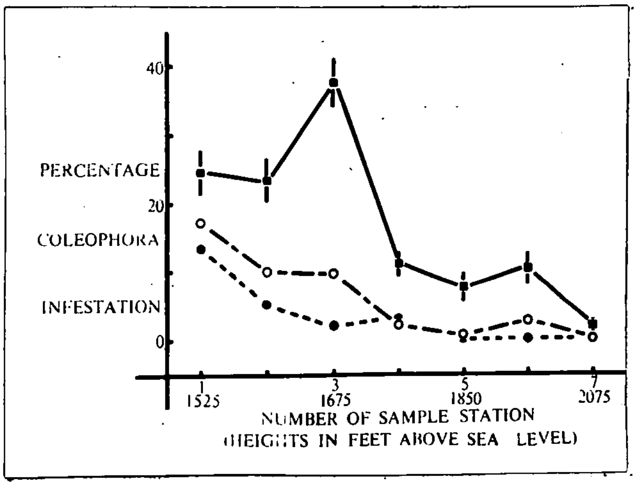

Fig.19. Coleophora infestation of J.squarrosus along transect C in 1954.

■——■ = on 21 July (vertical lines indicate standard errors).

○——○ = on 18 Aug.

●-----● =on 30 Sept.

the August samples. This was especially so at the upper stations of the transect, where, it has been shown that feeding was more prolonged than at lower altitudes.

Fig. 20, (page 104) shows the differences, which have already been remarked, between Coleophora population sizes along transect C in August in the three years during which samples were taken. From the same samples the percentage of the total rush capsules capable of producing ripe seeds before Coleophora attack has been calculated, and these values are included on fig. 20. The possibility of a correlation between the two sets of figures is examined on pages 109-119 Apart from station 1 (1,525'), where the proportion of rush capsules capable of producing ripe seeds was about the same in all three years, both the number of ripe seeds and the Coleophora populations at each sample station were considerably lower in 1954 than in the two previous years. This was shown(pages 89-91) also to be the case on the western slopes and the reason for the decline in seed setting was suggested to have been the lower mean temperatures during the summer of 1954. Factors which possibly limited the Coleophora populations are discussed on pages 119-28 The large Coleophora populations at stations 1 and 2 in 1953, referred to above, are also apparent from fig. 20.

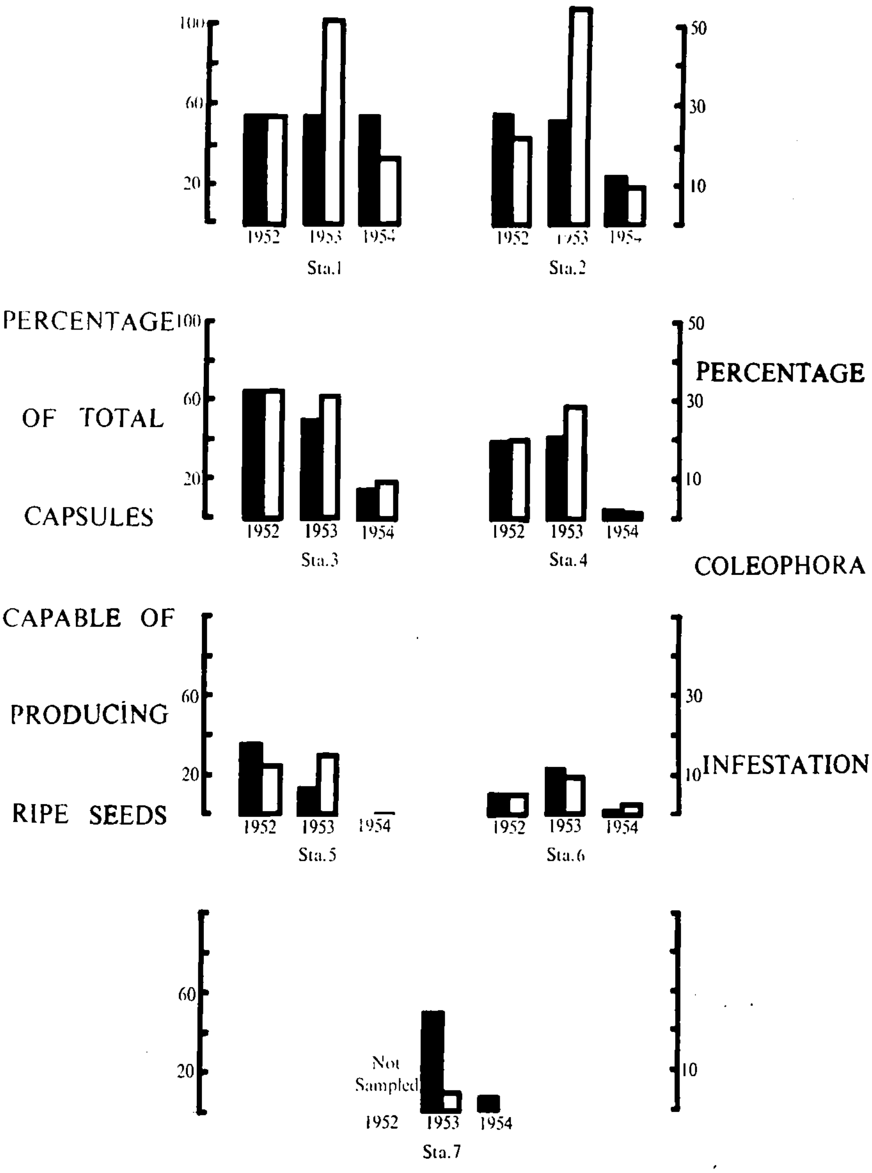

Fig.20. Ripe seed production by J.squarrosus at the beginning of the season (calculated from the August samples) and Coleophora infestation of the rush during August along transect C in 1952-4.

Evidence from transect C shows that *Coleophora* eggs and larvae at the upper limits of the insect's altitudinal range required a longer period for development on the rush inflorescences than individuals at a lower level. This was shown to be the case with transect A on the western Pennine slope and the position there was discussed in detail on pages 91-93.

Percentage *Coleophora* infestation in 1952 - 4 has also been obtained for the scattered sites (see fig. 7, page 54) on the eastern Pennine slopes. Tables giving the results obtained are in Appendix II. In the years during which this investigation was carried out *Coleophora* numbers were low at all these sites, and in many areas there was no *Coleophora* population at all. The distribution appeared to be random with small populations separated by considerable areas with no *Coleophora*. The populations were greater in number and size in 1952 and 1953 than in the cool summer of 1954, and thus confirmed the position observed along the transects in the latter year. The highest (altitudinal) *Coleophora* population was recorded at 2,170' along Trout Beck in 1953. In 1954 no *Coleophora* were found above 1,780'.

b. The distribution of *Coleophora* parasites.

Coleophora parasites were only recorded from station 1 (1,525') of transect C on the eastern Pennine slopes. *Ephialtes brevicornis* was present in very small numbers in each of the three years during which this investigation was carried out. Only in 1953 were the numbers sufficient for any larvae to be present in the samples of ten rush stems which were taken. Adult Ephialtes were observed in this area in 1953, and the species has been bred off in the laboratory from rush stems collected in the locality. Specimens of the unidentified Pteromalid were also obtained from material from station 1.

4. Differences apparent between the western and eastern Pennine slopes.

a. Coleophora distribution.

It has already been shown (pages 77 - 78) that the capacity of J. squarrosus to produce ripe seeds was possessed up to about 300' higher on the eastern Pennine slopes than on the western slopes, in all three years during which observations were carried out. There was also a difference in the ripe seed setting at lower, equivalent, altitudes on the two slopes. From the two foregoing sections it is apparent that a similar situation existed regarding the degree of Coleophora infestation of the rush on the eastern and western slopes in the three years.

Coleophora infestation at 1,525' on the eastern slopes (transect C) in August was 27.3 ± 2.7% in 1952 and 51.5 ± 3.8% in 1953, whereas at 1,500' along transect A infestation was 12.3 ± 1.9% in 1952 and

15.5 ± 2.8% in 1953. In July 1953 the differences were even more marked; 111.5% on the eastern slopes and 29.2 ± 3.5% on the western. Similar differences were apparent at other equivalent heights on the two slopes. It was unfortunate that transect C could not be continued below 1.525', because it was thus not possible to determine the form the Coleophora populations would have taken at lower altitudes on the eastern slopes. On the western slopes a height was reached (this was shown on page 84 to have been about 1,200') below which no steady increase in population size occurred. There was shown to be considerable fluctuation in the degree of infestation in these lower level populations. From fig. 24 and fig. 18 it appears that these fluctuations may have begun at about 1,600' on the eastern slopes, and populations below this level would probably not have been much greater than that recorded at 1, 525'. In 1952 and 1953 Coleophora eggs or larvae were not recorded above station 11 (1,850') of transect A, whereas along transect C they occurred up to station 7 (2,075') and, in 1953, some were found at 2,170' on the east side of the Nature Reserve.

In 1954 the number of Coleophora eggs found on the rush heads was lower on both slopes, especially at the lower sample stations of each transect, than in the preceding two years. Eggs were laid up to 1,700' on the western slopes and up to 2,075' on the east. Except at the lowest three sample stations of transect A, the number of *Coleophora* larvae which established themselves in the rush capsules was also much lower on both slopes. In addition, larvae were only found up to 1,350' on the western slopes and 1,970' on the eastern slopes in 1954.

b. The distribution of *Coleophora* parasites.

The distribution of *Coleophora* parasites was markedly limited by altitude and all species were recorded only from the lower stations of each transect. On the western slopes none were recorded above 1,050', whereas both *Ephialtes brevicornis* and the Pteromalid were present at 1,525' on the eastern slopes. As with *Coleophora*, it appears that the parasites also extended higher up the eastern slopes than they did on the western slopes. *Miotropis* was not recorded from the eastern slopes, but this species was extremely abundant, in 1952 and 1953, at the lowest sample stations of the western transects. It is probable that *Coleophora* populations at 1,500' on the eastern slopes were too high for this species to attack. The reason why *Miotropis* only attacked the lowland larval populations is not known.

5. The relationship between seed-setting in *J. squarrosus* and the distribution of *C. caespititiella.*

a. Introduction.

When discussing *Coleophora* populations on the western and eastern Pennine slopes, it was suggested that there was a possible relationship between the proportion of rush capsules capable of producing ripe seeds and the percentage *Coleophora* infestation at the various sample stations. This suggestion has been examined by comparing the numbers of *Coleophora* larvae which managed to establish themselves in the rush capsules, with the proportions of ripening capsules in each particular area. The samples taken in August 1952 - 4 have been examined in this way as these contained the complete number of feeding larvae and, as little mortality occurred during this period of larval life (see pages 135-46), these samples therefore gave an estimate of the total feeding *Coleophora* population at each sample station. Figs. 21 to 26 illustrate percentage *Coleophora* infestation and the percentage of the total capsules capable of producing ripe seeds at the beginning of the season, which have been calculated from the August samples, at the various stations along transects A and C in 1952 - 4. These topics have been independently discussed in preceding sections.

b. Western slopes of the northern Pennines.

Fig. 21 (page 111) shows Coleophora infestation and ripe seed production by J. squarrosus along transect A in 1952. In this and the following five figures the vertical scale for the latter is half that for percentage Coleophora infestation. There can be seen to be a very close correlation between the two curves in fig. 21 and this is particularly noticeable above about 1,200'. Above this height ripe seed production rapidly decreased and the populations of Coleophora larvae showed a correspondingly sharp decline. Above 1,500' values for both were very small. A few ripe seeds were present up to 2,500' but no moth larvae were recorded above 1,850'.

Fig. 22 (page 112) shows that a similar position existed in 1953. The closest correlation again existed above about 1,200' whilst below this height the two factors showed considerable fluctuations between adjacent sample stations.

In preceding sections (pages 67 - 68 and 86 - 88) it was pointed out that both ripe seed production and Coleophora infestation were considerably depressed along this transect in 1954, compared to 1952 and 1953. The lower larval populations in that year became understandable when these population figures were compared with those for ripe seed setting in J. squarrosus. The two sets of values are shown in fig. 23 (page 113).

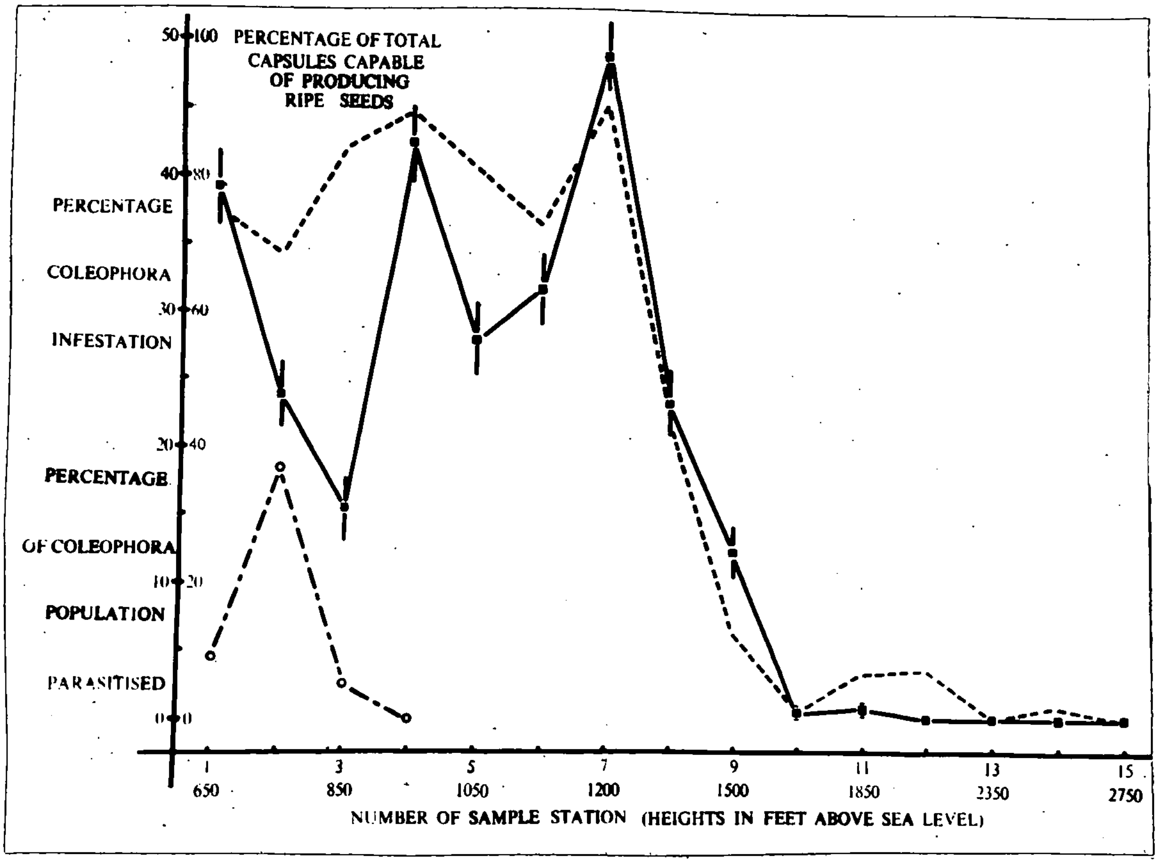

Fig.21. Ripe seed production by *J. squarrosus* at the beginning of the season (calculated from the August samples) and *Coleophora* infestation of the rush during August along transect A in 1952. The percentages of the *Coleophora* populations parasitised are also shown.

■——■ = *Coleophora* infestation (vertical lines indicate standard errors).

------- = Ripe seed production.

o----o = Percentage of *Coleophora* parasitised.

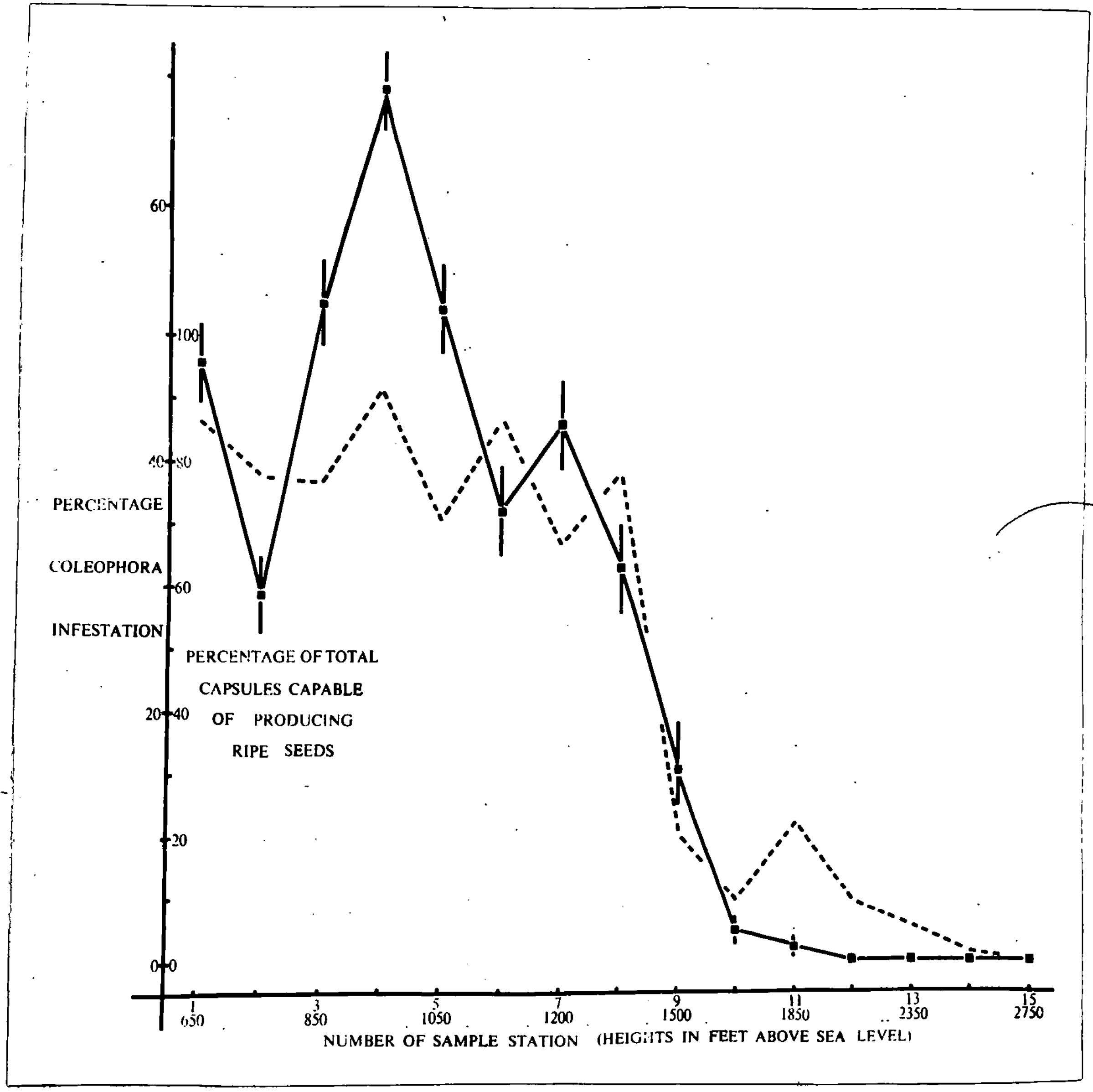

Fig.22. Ripe seed production by J.squarrosus at the beginning of the season (calculated from the August samples) and Coleophora infestation of the rush during August along transect A in 1953.

■——■ = Coleophora infestation (vertical lines indicate standard errors).

------- = Ripe seed production.

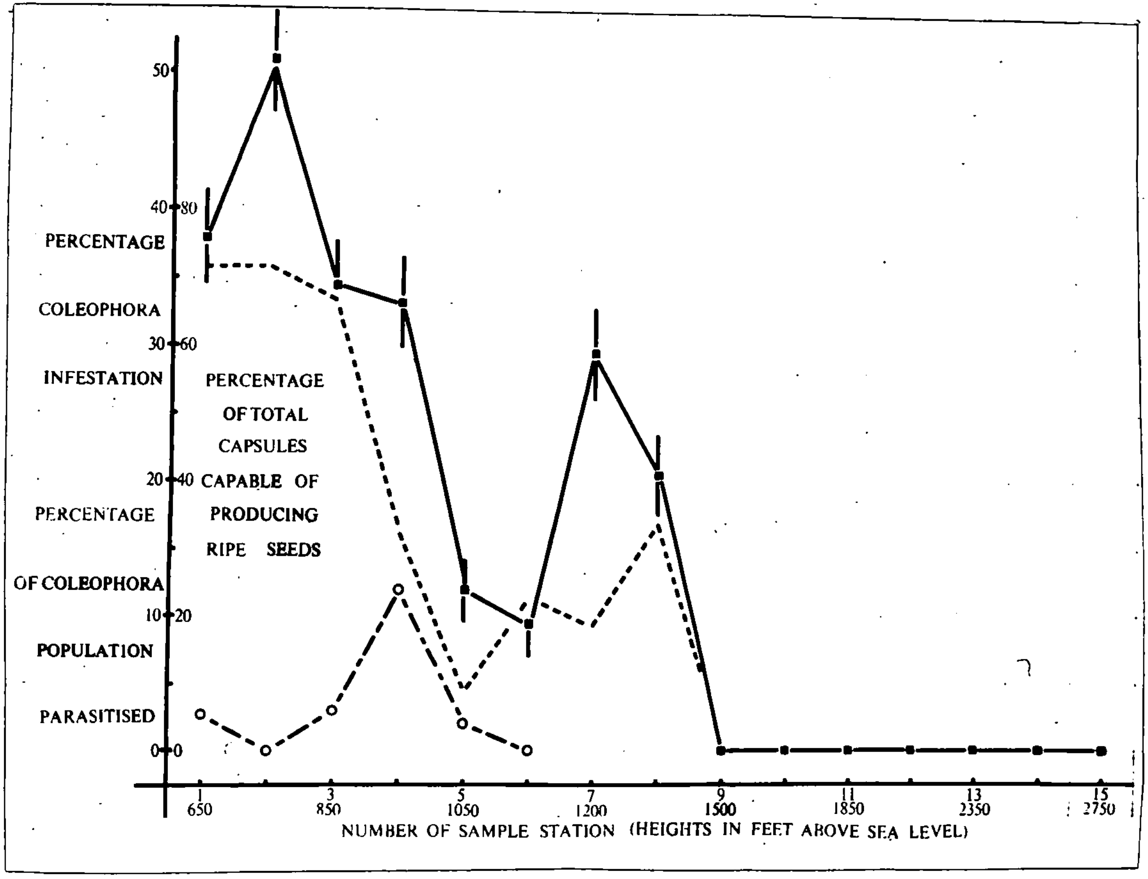

Fig.23. Ripe seed production by *J.squarrosus* at the beginning of the season (calculated from the August samples) and *Coleophora* infestation of the rush during August along transect A in 1954. The percentages of the *Coleophora* populations parasitised are also shown.

■——■ = *Coleophora* infestation (vertical lines indicate standard errors).

------ = Ripe seed production.

o——-—o = Percentage of *Coleophora* parasitised.

It has been pointed out that at the lowest four sample stations percentage Coleophora infestation was comparable to the previous two years. From fig. 23 it can be seen that in these areas the number of ripening seeds was also high. Above these sample stations ripe seed production rapidly declined with a partial recovery at stations 6 - 8. The Coleophora populations conformed very closely to the above situation, and the degree of infestation by the larvae rapidly declined above station 4, with a temporary increase at stations 7 and 8. Ripe seeds were not produced above station 8 (1,350') and no larvae were recorded above this height in 1954. It has been pointed out, following Pearsall (1950), that the fruiting capacity of J, squarrosus is probably largely determined by temperature, and that 1954 was a very much cooler summer than the summers of 1952 and 1953. This would appear to explain the much reduced amount of seed set along this transect in 1954. At the lower levels, with the increased mean temperatures due to decreased altitude, conditions were apparently suitable for seed to be set in much the same proportions as in previous more typical summers. 1954 emphasised the dependence of Coleophora on its food-plant which had already been deduced from the position in 1952 and 1953. On pages 86 - 87 it was shown that the number of eggs laid by Coleophora along this transect was only slightly below the numbers laid in 1953. Eggs were laid up to 1,700' (which was the upper limit of the populations sampled in July 1953). The distribution of Coleophora larvae in August (see fig. 23) seems to be explicable on the basis that only at the lowest sample stations were there sufficient ripe seeds to support larval populations of comparable sizes to those present in 1952 and 1953. It has already been shown (pages 86-8) that egg and early larval mortality was less than elsewhere along the transects at these sites in 1954. Above about 900', as the number of ripe seeds produced by the rush decreased, a much smaller number of larvae were able to establish themselves in the rush capsules. No ripe seeds were produced above 1,350' and no larvae were recorded from above this height in 1954.

c. Eastern slopes of the northern Pennines.

Fig. 24 (page 116) shows Coleophora infestation and ripe seed production by J. squarrosus along transect C in 1952. It is apparent that there was a very close correlation between the values for these factors at the stations sampled, and both tended to diminish with increasing altitude.

In 1953 (fig. 25, page 117) the correlation between seed setting in J. squarrosus and the Coleophora infestation was not so close as it was in 1952.

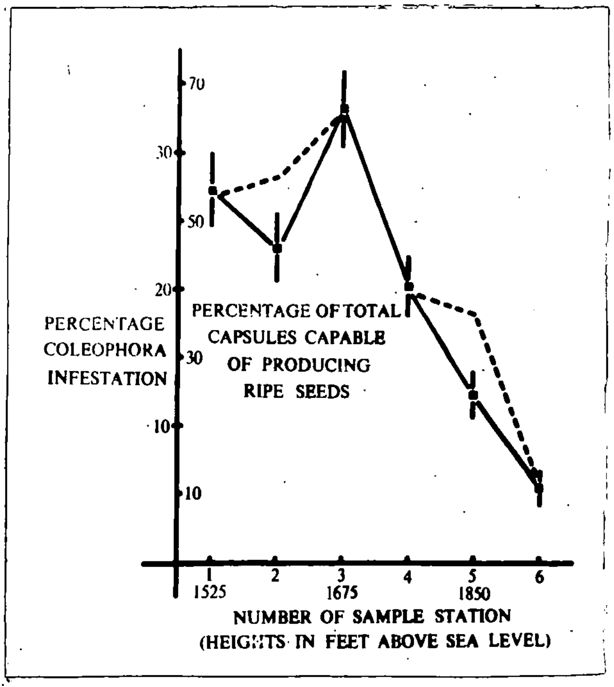

Fig.24. Ripe seed production by <u>J. squarrosus</u> at the beginning of the season (calculated from the August samples) and <u>Coleophora</u> infestation of the rush during August along transect C in 1952.

■——■ = <u>Coleophora</u> infestation (vertical lines indicate standard errors).

------ = Ripe seed production.

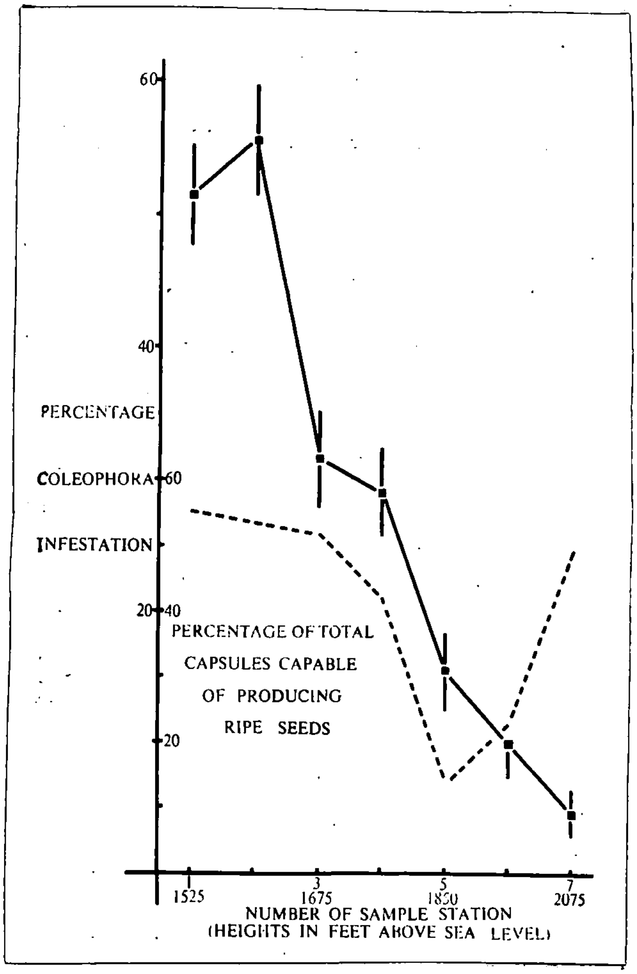

Fig.25. Ripe seed production by *J.squarrosus* at the beginning of the season (calculated from the August samples) and *Coleophora* infestation of the rush during August along transect C in 1953.

■——■ = *Coleophora* infestation (vertical lines indicate standard errors).

------- = Ripe seed production.

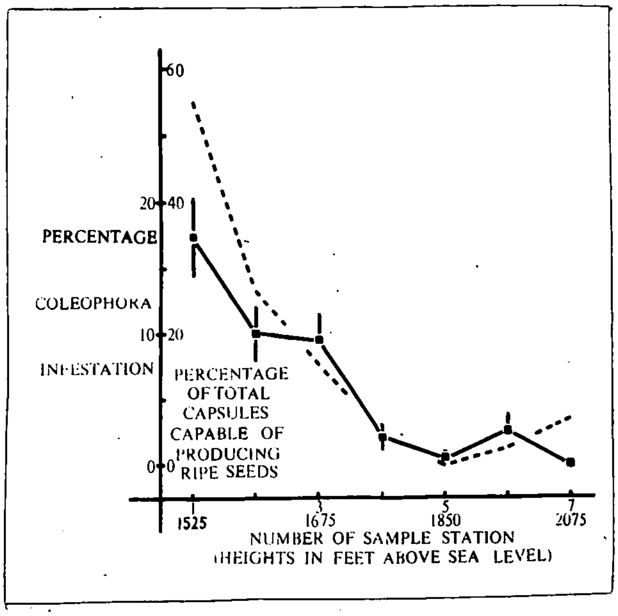

Fig.26. Ripe seed production by *J.squarrosus* at the beginning of the season (calculated from the August samples) and *Coleophora* infestation of the rush during August along transect C in 1954.

■———■ = *Coleophora* infestation (vertical lines indicate standard errors).

------- = Ripe seed production.

At stations 1 and 2 there were very large larval populations, whereas the proportions of capsules capable of producing ripe seeds were only 55.0% and 53.5% of the total capsules in these samples. Practically all these capsules contained at least one Coleophora larva. Above station 2 (1,575') both ripe seeds and larvae declined in number, and the latter continued to do so up to station 7 (2,075') despite the fact that ripe seeds began to increase in numbers again above station 5 (1,850'). Possible reasons for this situation are discussed on pages 126-7.

As on the western slopes both ripe seed setting and Coleophora infestation were very much lower along transect C in August 1954 than in the preceding two years. From fig. 26 (page 118) it can be seen that Coleophora numbers in that year were closely dependent on the fruiting capacity of J. squarrosus at each sample station. Both showed a general tendency to decline with increasing altitude.

6. Possible factors limiting the size of Coleophora populations.

In a future section of this account (pages 129 - 147) seasonal surveys of certain Coleophora populations are discussed, but, from the preceding sections some of the factors which appeared to be controlling the Coleophora populations in the study area during 1952 - 4 can be seen. So far only egg and larval populations have been discussed but it is generally the case with insect populations that the major factors affecting the species density affect the larval stages. Lack (1954), summarising the position suggested that this is because larvae live longer, eat much more food, and are subject to heavy mortality. This appears to be so with C. caespititiella.

There is no evidence from the years during which this investigation was carried out that oviposition was limited in any way other than by the number of female moths and their fecundity. Both these factors probably varied from year to year, as shown for many insect species (eg. Weber, 1931 and Titschack, 1928), according to weather conditions and feeding conditions in the previous summer. During oviposition future mature capsules of J. squarrosus are indistinguishable from the remainder of the capsules and eggs are laid under the perianth segments of a single rush flower or in the angle between two adjacent rush flowers. The number of sites suitable for oviposition is thus considerable. Up to five eggs have been found in one such site. The highest infestation of Coleophora eggs, (together with some early instar larvae) was found in July 1953 at station 2 of transect C. The observed infestation of 124.3% represented a mean of less than one egg per potential oviposition site. It is suggested, therefore, that, under normal field conditions, the number of sites suitable for oviposition was never a limiting factor to the *Coleophora* populations. Extremely high egg numbers would be required before this factor could become operative.

It has been shown that along the transects sampled during 1952 - 4 there was a close correlation between the number of maturing rush capsules and *Coleophora* infestation at each sample station. This was shown to be a particularly close association at the upper limits of the insect's range on the two Pennine slopes. Possible reasons for the existence of an upper limit tp *Coleophora* populations, well below the upper limits of its food-plant, will now be discussed. The major factor is obviously closely connected with altitude; but does this factor directly affect the moth populations or does it act indirectly on them through some effect on *J. squarrosus*? Owing to the close correlation between the capacity of the rush to produce ripe seeds and the size of the *Coleophora* population in each area, it seems that the latter is the case. On the eastern Pennine slopes the rush was shown to have seeded to a considerably greater altitude than on the western slopes, and *Coleophora* also occurred correspondingly higher on the eastern slopes. It has already been mentioned that Pearsall (1950) suggested that the diminution of mean temperature with increasing altitude is the probable reason for the reduction of fruiting in J. squarrosus. It is suggested here that this failure to produce ripe seeds above a certain height is the cause of the upper limit for Coleophora. Whether this temperature difference is sufficient to explain the very marked difference in the capacity of the rush to seed on the two slopes of the Pennines observed in 1952 - 4 is not known. From evidence which has already been presented (pages 76 - 77) it is suggested that the effect of greater exposure on the rushes on the western slopes may well be an important contributory factor affecting the plants' capacity to produce ripe seeds.

Coleophora larvae, therefore, appear to be severely restricted by the availability of a suitable food supply at their upper limit. It has also been shown that, in 1952 and 1953, no eggs were laid above this limit of ripe seed production. This is suggested to be due to the relative inactivity of the adult moth (page 50) and that owing to this, eggs were not laid very far from the area in which the female moths emerged. Thus if, in an exceptional year, seeds were set up to a greater height than in 1952 and 1953, it suggested that these rushes would not be colonised by Coleophora, except as a result of (probably relatively rare) transportation of a fertilised female moth by wind. The position in 1954, which provided the converse of this situation, is discussed below.

Pearsall (1950) suggested a rather different reason for the non-occurrence of *Coleophora* larvae on the higher rush populations. He found that only the early maturing fruits were infected by *Coleophora*, and he postulated an incapacity for the moths to oviposit on unopen flowers of *J. squarrosus*. It was suggested by Pearsall, and since confirmed in the present investigation, that the main population of mature *Coleophora* individuals emerge at approximately the same time at all altitudes. Pearsall suggested that the moths may infect any rush flowers that are then open, and, as the number of such flowers in July diminishes with increasing altitude, the altitudinal range of the insect is severely limited. He explained the absence of the mature moths from higher levels by assuming a temperature bar to their development above a certain height, such as has been shown to occur in *Planaria alpina* (Beauchamp, 1937). Pearsall did, however, suggest that this may not be the only factor affecting the distribution of *C. caespititiella* as he points out that in the high rainfall area of the Western Highlands and Islands the insect is much less common and that this situation is not easily explained if temperature alone is considered. Unfortunately the extent of rush fruiting in the area is not recorded.

The two factors in Pearsall's theory will be discussed separately. Firstly he states that oviposition can only take place on open rush flowers. When eggs are laid within the perianth segments of a single flower this is so, but it has already been shown that eggs are also laid between two adjacent flowers. At the upper limits of the Moth's range eggs are generally to be found in these latter sites. This was especially so in 1954. The cool summer of that year adversely affected J. squarrosus, flowering being much later and the amount of ripe seed set much less than in the preceding two years. Along transect A Coleophora emerged only a few days later than in 1953 and eggs were laid up to 1,700' (2,075' along transect C). At this height no flowers were open and all the eggs were laid in the angle between adjacent flowers. Larvae from such eggs could only become established if there were ripening rush seeds present when the eggs hatched. This would account for the fact that Pearsall, in August, only observed the early maturing fruits at greater altitudes to be infected by Coleophora. Only such fruits would contain seeds to feed developing larvae, and any larvae which might have bored into other fruits would have died, or migrated to a new capsule, through lack of a suitable food supply. In 1954 no ripe seeds were set at the upper sample stations of transect A and despite the fact that eggs were laid up to 1,700' larvae were not able to establish themselves above 1,350'.

Secondly, Pearsall suggested a temperature bar to the development of the moth at the upper limits of its range. The more likely reason for the occurrence of the upper limit to the populations appears to be that temperature is acting indirectly on *Coleophora* through an effect on the capacity of *J. squarrosus* to produce ripe seeds. Evidence for this can again be obtained from the samples taken in 1954. Despite the fact that low temperatures during that season resulted in later flowering and much decreased fruiting at the upper levels of transects A and C, *Coleophora* populations emerged and oviposited up to the same heights to which larvae were present in the preceding autumn. Owing to the lack of a suitable food supply at these upper sample stations, as we have seen, no larvae became established in 1954. This was especially noticeable on the western Pennine slopes. It is therefore suggested that in 1952 and 1953 no eggs were found above 1,850' (on the western slopes) because there was no larval population established above this height in the preceding year. The adults which eventually resulted from these eggs remained in a very limited area and oviposited there. This relative inactivity has been shown in a number of insects (eg. *Urophora jaceana* Varley, 1947), and surmised for *C. caespititiella* from field observations. If the temperatures in 1955 allow fruiting of *J. squarrosus* to occur up to the altitudes observed in 1952 and 1953 this hypothesis could be tested by observing whether Coleophora could re-establish itself very much above the height (1,350') to which it was suppressed in 1954.

Relative inactivity of adult Coleophora would also explain the small number of larvae, relative to the number of mature rush capsules, present in the samples from station 6 (1,970') and 7 (2,075') of transect C in 1953 (see fig. 25, page 117). In that year many more ripe seeds were produced than was to be expected at these two high sample stations. These were 'pockets' of high fruiting (see page 74) and many fewer ripe seeds were produced at station 5 (1,850'). As these two areas had only produced a few ripe capsules in 1952 only a small Coleophora population was raised. Assuming no immigration from lower level populations, the few adult moths present would not have been able to provide sufficient eggs to colonise all the available larval food" niches." A similar position probably existed with some of the scattered sites sampled on the east side of the Moor House Nature Reserve where ripe seeds were sometimes produced in relative abundance. Many factors are of importance if a Coleophora population is to be present in such an area - whether adults are present at all, and, if so, whether they are present in sufficient numbers to ensure fertilisation. In an area of spasmodic rush fruiting, or in a 'pocket' of fruiting surrounded by an area of relatively barren plants, the difficulties to the establishment of a *Coleophora* population would obviously be increased. Chance transportation of fertilised female moths by wind may be of importance in the establishment of occasional populations, as were observed in 1952 - 4 in such areas, if the imagines are indeed as inactive as the evidence suggests.

We will now examine some of the factors which may have been operative in controlling the size of *Coleophora* populations at lower levels. The rapid change in population size between about 1,200' and 1,850' on the western slopes and 1,600' and 2,075' on the eastern slopes has been shown to have closely followed the proportion of rush capsules producing ripe seeds at the various sample stations between these altitudes. Below these heights, however (and this was especially noticeable along the longer western transects), oscillations occurred between neighbouring *Coleophora* populations. The correlation between ripe seed production and the *Coleophora* populations was not so close at these altitudes but even here there is some evidence (see pages 62 - 69) that in some cases the established larvae had probably eaten all their available food supply by the end of the season. Fluctuations in the capacity of neighbouring rush populations to produce ripe seeds could have been caused by many factors. These have not been investigated but soil conditions (such as soil type, drainage, pH, availability of mineral salts) and the degree of exposure of the particular plants would all obviously have to be taken into account. Some observations regarding the importance of the latter as a factor governing ripe seed production were given on pages 76-7. Nevertheless the differences in size between neighbouring Coleophora populations observed in 1952 - 4 were not solely to be explained on the basis of the available food supply. It seems significant that it was just from these lower areas that the parasites of Coleophora were recorded. The possible effect of the parasites on Coleophora numbers is referred to in the general discussion on pages 163 - 76 , where the implications of the probability of food supply having directly governed the sizes of at least some of the populations is also discussed.

VII. SEASONAL SURVEYS OF CERTAIN C. CAESPITITIELLA POPULATIONS.

1. Introduction.

All references to Coleophora populations so far have been based on the results obtained from sampling the stages of the insect (eggs and larvae during their feeding period) which occur on the inflorescences of J. squarrosus. Two Coleophora populations were, however, quantitatively sampled at intervals throughout the period July 1953 - November 1954. From these surveys certain information has been obtained regarding mortality at various stages in the life history. Owing to the fact that only just over one year's (though two complete Coleophora feeding seasons were included) results were obtained, any conclusions which are reached must necessarily be tentative.

The two populations chosen for these surveys were at approximately the same height on opposite slopes of the Pennines. Station 1 (1,525') of transect C was chosen as the lowest site available on the eastern slopes and station 9 (1,500') of transect A was chosen at a comparable height on the western slopes.

2. Sampling methods.

When sampling for eggs and for larvae still feeding on rush seeds, the sampling technique which has already been described was used. During November 1953 and 1954 the pre-winter populations of larvae in the plant litter at the base of the rush stems were estimated by collecting a known quantity of litter and hand sorting this in the laboratory. After an initial thorough sorting, the litter from each turf was subjected to a second examination. No living larvae were recovered in these second examinations, although empty larval cases of previous years were occasionally found. It has already been mentioned (page 49) that larvae probably overwinter in the upper layers of the litter and that careful hand sorting results in practically all of them being extracted. The total number of old larval cases in each sample was considerable (see later tables) and it seems that old larval cases can remain in the litter, in a recognizable condition, for some years. Some of these contained cast pupal skins. Eight turfs, representing a total area of $\frac{1}{2}$ sq.m., were examined on each occasion in this manner. Owing to this lengthy process it was not possible to carry out similar studies on any area other than the two mentioned above. It was impracticable to sample the emerging adult moths in situ owing to damage by sheep to the emergence traps. Accordingly in May 1954 $\frac{1}{2}$ sq. m. of turves were collected from both experimental areas and these were planted out at Moor House within an enclosure. Emergence traps were erected over these and the traps were inspected at regular intervals for adult moths. Fig. 27 (page 131) shows the experimental plot at Moor House.

Fig.27. Emergence traps at Moor House, spring 1954.

From these sampling techniques figures were obtained for the percentage in fection by *Coleophora* of the total rush capsules (eggs and feeding larvae) and for the numbers of larvae or adults per sq. m. These two sets of figures have been made capable of interpretation in terms of one another with the aid of figures obtained for the mean number of flowering stems of *J. squarrosus* which occurred per sq. m., each year, in the two areas. These were obtained by throwing a quadrat frame (¼ m. sq.) thirty times in each area. The mean number of rush capsule per sq. m. can then be found. This method is obviously only applicable to areas, such as the two which were examined, where the rush is plentiful and uniformly spread over the area.

In the results which follow, *Coleophora* populations have been expressed as numbers per sq. m. together with the infestation of *J. squarrosus* which this represents.

3. Results.

a. Station 9, transect A.

During 1953 there was found to be a mean of 53.3 ± 6.72 flowering stems per sq. m. at this sample station. In 1954 the corresponding figure was 46.4 ± 6.75. These figures have been used to obtain the figures for the *Coleophora* populations per sq. m. which are given in Table 11.

Samples of rush inflorescences were collected on 5th July, 8th Aug, and 4th Sept. 1953. At this sample station the total population was still feeding on the rush capsules in early September. This site was next sampled on 9th Nov. 1953 when ½ sq. m. of litter was collected and later examined in the laboratory. Table 10 shows the total number of Coleophora larval cases which were extracted.

TABLE 10.

Coleophora larval cases recovered from ½ sq. m. of litter collected from station 9, transect A on 9 Nov. 1953.

No. of turf.	Living larvae	Dead larvae	Empty cases	Cases of previous year(s) population
1	3	0	3	1
2	0	0	1	1
3	1	1	1	3
4	1	0	1	0
5	3	0	0	2
6	2	0	0	1
7	0	0	0	1
8	1	0	1	0
Totals	11	1	7	9

The larval cases included in column 5 of Table 10 all contained recognisable remains of a *Coleophora* pupal case. These cases had, therefore, been in the litter for at least a year, and this was probably also so with most of the empty cases included in column 4, from their general appearance. The possible significance of the fact that few, if any, of the empty larval cases were manufactured in 1953 is discussed on page 147.

In May 1954 ½ sq. m. of litter was transported to Moor House and emergence traps were erected over it. No adult *Coleophora* were recorded. This fact's significance is also discussed after the results obtained from the sample station on the eastern slopes have been discussed.

During the summer of 1954 this station was sampled on 22nd July, 24th Aug. and 1st Oct. On 22nd July *Coleophora* eggs were present on the rush inflorescences, but, owing to the failure of *J. squarrosus* to produce ripe seeds at this height in 1954, no larvae were able to establish themselves, and none were recorded in the August and October samples. No litter sample was taken from this site in 1954.

Table 11 summarises the data obtained for this sample station, between July 1953 and October 1954. For comparison *Coleophora* infestation in August 1952 is also given.

TABLE 11.

Coleophora populations at station 9, transect A
1952-4

Date of sample.	Number of Coleophora individuals per sq. m.	Percentage Coleophora infestation.
21st. Aug 1952	-	12.3
5th July 1953	261.2	29.2
8th Aug. 1953	53.3 138.6	15.5
4th Sept. 1953	154.6	15.7
9th Nov. 1953	22.0	2.4
Spring 1954	?	?
22nd July. 1954	120.6	14.4
24th Aug. 1954	0	0
1st Oct. 1954	0	0

Percentage Coleophora infestation during the period covered by Table 11 is shown in fig 28 (page 136).

b. Station 1, transect C.

During 1953 there was a mean of 47.5 ± 7.97 flowering stems of J. squarrosus per sq. m. at this sample station. In 1954 the corresponding figure was 75.7 ± 6.64.

Samples of rush inflorescences were collected on 7th July, 10th August and 5th Sept. 1953. The sample taken on the last of these dates did not give an estimate

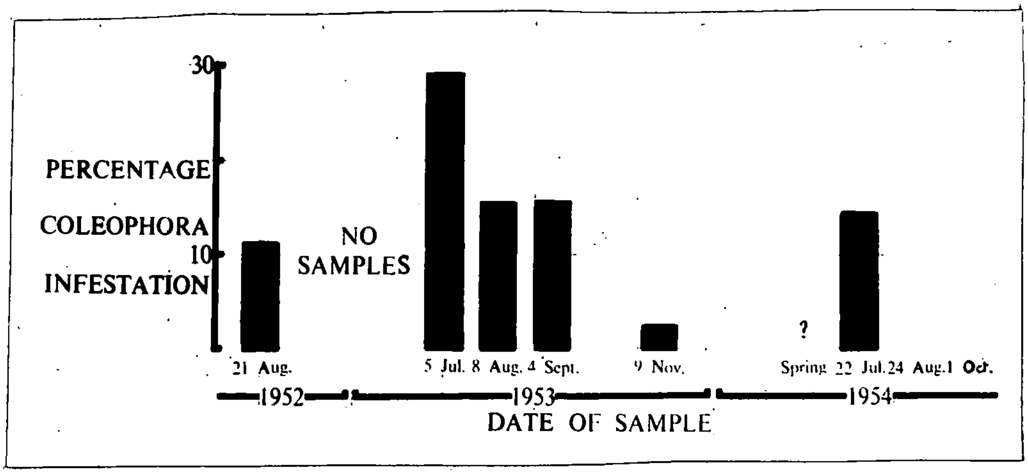

Fig. 28. Coleophora infestation of J. squarrosus at station 9, transect A, 1952-4.

of the total Coleophora in early September. By this time a number of larvae had completed feeding, left the rush capsules and migrated into the plant litter where the winter was to be spent. The 5th. Sept. sample thus only gave an estimate of the number of larvae still feeding on that date. This site was next sampled on 18th Nov. 1953 when ½ sq. m. of litter was collected and later examined in the laboratory. Table 12, (page 138) shows the total number of Coleophora larval cases which were extracted.

The larval cases in Table 12 are divided into the same categories as described above for Table 10. In addition larval cases containing evidence of parasitisation in 1953 (1) or in previous years (14) are also included. The latter group of larval cases all contained Ichneumon pupal remains with the exception of one case which contained a dead Ephialtes brevicornis adult. It was suggested, referring to station 9, transect A, that few if any of the empty larval cases were manufactured in 1953. From the general appearance of these cases it is also suggested that the empty cases collected from this sample station were, in the main, manufactured prior to 1953.

In May, 1954, ½ sq. m. of litter was transported to Moor House from this area and emergence traps were erected over this. Five adult Coleophora were later collected from this material. The original sample was

TABLE 12.

Coleophora larval cases recovered from 1/2 sq. m. of litter collected from station 1 transect C on 18 November, 1953.

No of turf.	Living larvae.	Dead larvae.	Parasitised larvae.	Empty cases.	Cases of previous year(s) population.	Cases of previous year(s) population (parasitised).
1	4	1	0	14	7	1
2	2	2	0	6	7	1
3	2	2	1	22	19	2
4	5	0	0	9	10	0
5	0	1	0	19	10	2
6	1	1	0	13	15	2
7	1	0	0	17	2	1
8	5	0	0	12	11	5
Totals	20	7	1	112	81	14

composed of eight turves, and the five adults emerged from four of these.

During the summer of 1954 this station was sampled on 21st July, 18th Aug. and 30th Sept. By the latter date a few larvae had left the rush stems and migrated to the litter, and these larvae are not included in the estimate of population size for that date. A litter sample was collected from this station on 22nd Nov. 1954. Only one living larva had been found by the time that half the litter had been sorted. The remainder of the sample was not examined, as it was thought that the pre-winter population was too low to estimate for by the method employed. Empty larval cases and larval cases containing recognisable _Coleophora_ pupal remains were found, in the amount of litter which was sorted, in comparable numbers to those recovered in Nov. 1953.

Table 13 (overleaf) summarises the data obtained for this sample station between July 1953 and November 1954. For comparison, _Coleophora_ infestation in August 1952 is also given.

Percentage _Coleophora_ infestation during the period covered by Table 13 is shown in fig. 29, (page 141).

TABLE 13.

Coleophora populations at station 1, transect C
1952 - 4

Date of Sample.	Number of Coleophora individuals per sq.m.	Percentage Coleophora infestation.
20th Aug. 1952	-	27.3
7th July 1953	826.5	111.5
10th Aug. 1953	413.25	51.5
5th Sept. 1953	275.5	34.1
18th Nov. 1953	40.0	5.1
Spring 1954	10.0	1.3
21st July 1954	317.9	24.4
18th Aug. 1954	204.4	17.3
30th Sept 1954	159.0	13.5
22nd Nov. 1954	?	?

4. Conclusions.

Before considering the possible significance of the results obtained from the series of samples taken from these two experimental areas, one obvious difference between the two areas is apparent. It was pointed out on page 106 that egg and larval populations were much larger, in all three years during which the investigation was carried out, on the eastern Pennine slopes than at

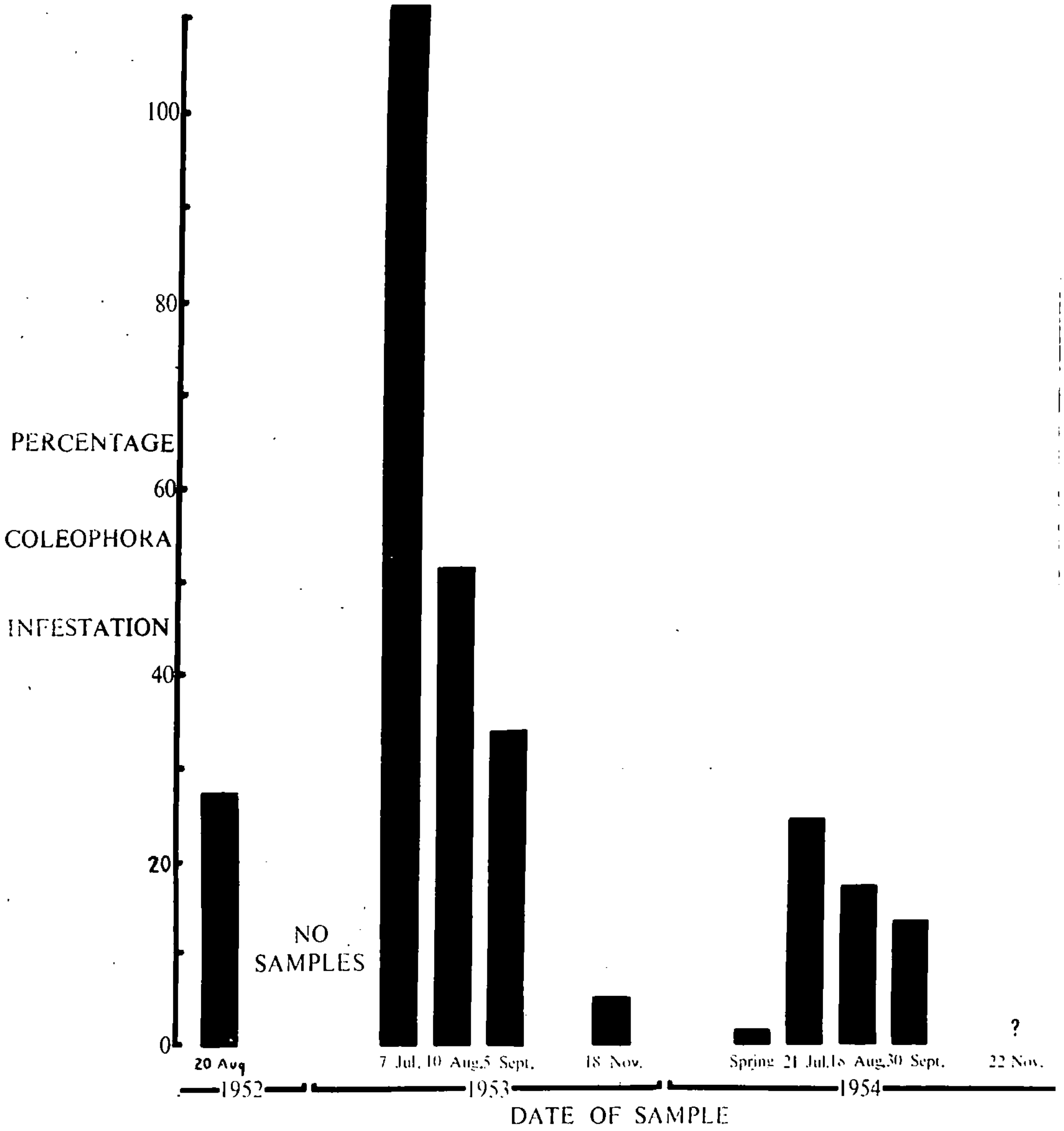

Fig.29. *Coleophora* infestation of *J.squarrosus* at station 1, transect C, 1952-4.

comparable altitudes on the western slopes.

Tables 11 and 13 and figs. 28 and 29 (which are on the same scale) show that the differences in Coleophora population size were apparent throughout the season in these two areas, each at a height of approximately 1,500'.

The method employed for sampling egg and feeding larval populations has already been discussed (page 53) and shown to give a reasonably accurate measure of population size. Standard errors have been estimated for the July, August and September sample figures and these are given in Appendix II.

The figures obtained for pre-winter larval populations and for the adult emergence will be discussed here. From Tables 10 and 12 (especially the latter) it can be seen that considerable numbers of Coleophora larval cases were extracted by hand-sorting ½ sq. m. of litter. Thorough sorting was, therefore, capable of extracting the larval cases. The number of living larvae, however, was quite small (11 and 20) in both instances. It has already been pointed out that few, if any, of the empty cases which were found were manufactured by the 1953 larvae, and the number of cases containing dead larvae (presumably 1953) was low in both areas (1 and 8). Thus a large number of 1953 larvae and their cases (also in 1954 at station 1, transect C) probably disappeared between the time when they left the rush stems and the time when the samples were taken in November. It is not suggested that the actual numbers of larvae obtained are themselves of significance. The amount of litter examined was small, and before any statistical analysis could be applied to the results obtained, much more material would have had to be examined. It is, however, suggested that most, and probably all the living larvae which were in these samples were extracted and that the figures for population size which were obtained illustrate a considerable mortality since the larvae had been in the litter. The only reference to post-feeding Coleophora larval numbers is, apparently, Dumbleton (1952). His results are not comparable to the above as he was working on a number of species which feed on clovers in New Zealand. The results are of interest in that some of the populations he found in the spring were much larger than were present in the litter in the preceding autumn in the present investigation. A paddock where white clover was damaged during one season was found in the following spring to have a living larval population of the order of 20 per sq. ft. A younger paddock nearby had a population of 5 per sq. ft.

The figures for the numbers of adults which emerged in the spring of 1954 from these two areas must also be treated with extreme caution. Only ½ sq. m. from each sample station was netted at Moor House, and the number of adults which was obtained was, therefore, unavoidably low. With emergence traps sufficiently strong to prevent damage by sheep, this disadvantage could be overcome in any future continuation of this study by extensive trapping in situ. Bearing in mind these disadvantages, the figures obtained do show an anticipated tendency. The numbers of adults which were obtained indicated a drop in population size from the pre-winter population, and also confirmed the position, shown throughout the study, for populations on the western to be smaller than corresponding ones on the eastern slopes. To the extent that they are in keeping with the picture of general population decline, which was shown, by other sampling methods, to have occurred over the preceding months, it is felt that the figures for adult emergence in 1954 are of value.

Certain general conclusions can be arrived at, bearing in mind the deficiencies of the figures obtained for the pre-winter and spring populations, regarding the form of Coleophora populations throughout the season, as illustrated in these areas between July 1953 and November 1954. Two periods of heavy mortality are apparent from Tables 11 and 13 and figs. 28 and 29.

Coleophora eggs and first instar larvae, before they became established inside the rush capsules, were subjected to considerable mortality. This mortality probably resulted from the action of a number of factors;

the extent of the destruction caused by each particular agent has not been determined. Some eggs failed to hatch; possibly some were unfertilized. Washing off of the eggs by rain, owing to the extremely sheltered sites in which they were deposited, was probably not important. Physical destruction in this manner was, however, probably responsible for a considerable mortality of the newly hatched larvae. These larvae have been seen wandering over the outside of the rush capsules during this period and they are then extremely vulnerable to predation as well as to washing off. No predation was observed during this period of the life history, however. Owing to the staggered oviposition of this insect hatching is also staggered and the whole larval population is not, therefore, on the outside of the capsules (and thus not subjected to any one particularly heavy rainstorm) at any one time. The possibility of competition between early instar larvae in the rush capsules is discussed in the next section.

Once the larvae were established in the rush heads mortality was low for the rest of the feeding period. This can be seen from the close conformity of the August and September populations in the two areas which were surveyed (it must be borne in mind that, at the eastern site, some larvae had completed feeding when the September samples were taken). During this period the larvae are probably protected from extremes of climate, as well as from predators, by the walls of the rush capsules. There already appears to have existed at this stage an approximate balance between larval numbers and their ultimate food requirements. A possible mechanism for bringing this situation about is discussed on pages 148-62.

Coleophora larvae are subjected to parasite attack during the feeding period. In the two areas where these surveys were carried out only very few larvae were found dead in the rush capsules. No parasites were present in any of the samples taken from station 9, transect A and no dead larvae were found among the 55 larvae present in the August and September samples. At the eastern sample station in 1953, 3 of the 146 larvae counted in August and September were dead. Only one of these had been killed as a result of parasitisation, a larva of Ephialtes brevicornis being present. In 1954 no parasites were present in the samples and 2 of the 50 larvae present in the August and September samples were dead. Although parasites were shown to be in greater number at the lower sample stations (and killed off over 30% of the Coleophora larvae present in 1953 at two sites (see page 97)), at the two sites at which this seasonal survey was carried out parasites were not, in the years in which this investigation was carried out, playing any important part in controlling population size.

A second period of considerable mortality in these two populations was during the time spent by the larvae in the litter. The reduction was considerable by as early as mid-November. This reduction in the populations was not only a disappearance of larvae, but generally of the larval cases as well. Tables 10 and 12 show that only very few dead larvae were recorded in their cases in the litter. No cause of this larval mortality has definitely been established. Owing to the fact that by far the greater part of this mortality was accompanied by the loss of larval cases as well, it seems probable that insect predators (eg. staphylinid beetles and spiders) and physical factors were not important destructive agents. Sheep grazing of the surface litter (where the larvae are situated) presumably destroyed a certain number, but it seems probable that mice and voles were responsible for the greater part of this mortality. Mice and vole runs were present in both areas. The figures for the spring emergence in 1954 suggest that mortality of this nature continued, as would be expected, throughout the winter.

VIII. SOME EVIDENCE FOR COMPETITION BETWEEN EARLY INSTAR COLEOPHORA LARVAE.

It was suggested on page 146 that Hymenopterous parasites were not the major factors controlling the majority of the Coleophora populations which were sampled. It was shown that mortality from this cause was limited during the period of this investigation and that no parasites were present in the upper populations on the two slopes. At the sites sampled during 1953 and 1954 there was generally an excess of eggs laid to the eventual number of sites suitable for colonization by larvae (rush capsules containing ripe seeds). These populations were considerably reduced, probably by failure of some eggs to hatch and by the other causes suggested on page 145, but none of these factors would be capable of governing population density. Smith (1935) pointed out that, in order to control population density, the controlling factor must be governed by the density of the population controlled. He defined a factor acting in such a manner as density-dependent. Nicholson (1954), emphasizing that population density can be governed only by factors which react to density change, pointed out that the term 'density-dependent factor' has often been used in a loose sense as the effect of population density on a significant environmental element or quality.

Accordingly he introduced the term 'density-governing factor' which is identical to 'density-dependent factor' according to definition (Smith, 1935). In the present investigation intra-specific competition between the larvae at some stage would result in mortality of this nature. Competition, if it occurred, beteen early instar larvae in the rush capsules would result in a degree of mortality dependent on the density of the original population and, thus, overcrowding at this stage would be potentially able to limit the population density.

Discussing early larval mortality in Urophora jaceana, which forms galls in the flower heads of Centaurea nemoralis, Varley (1947) stated that, "the population density of the gall fly would begin to increase the larval competition within the flower heads only when the percentage of flower heads attacked rose to well over 50%." In no instances did gall fly larval populations reach these proportions in the field However, many instances were recorded where Coleophora larvae were initially established in well over 50% of the mature rush capsules at all heights on the Pennine slopes. It was shown on pages 42-43 that Coleophora larvae in 1953 required a mean of just over two rush capsules during their feeding period. From figs. 21 - 26 it can be seen that the percentage of ripening rush capsules was, on the average, just about double the percentage Coleophora infestation at each site.

In other words the number of established larvae in August approximately equalled that number which could be supported by the available food supply. Owing to this correlation between larval numbers and their ultimate food requirements in all three years there appeared to be some factors controlling numbers at the stage when the first instar larvae were colonizing the rush capsules. It seems probable that this regulation was brought about by competition between the early larvae, but that this competition was not directly for food, as at this time there was plenty of food for their small requirements.

It was shown in an earlier section of this account (pages 135-45) that a considerable mortality occurred between July and August in many of the Coleophora populations which were sampled in 1953 and 1954. Was any of this mortality due to competition between the early larvae? The position along transect A in 1953 provides some data to test this hypothesis. Fig. 9 (page 63) shows that ripe seed production by J. squarrosus along this transect in 1953 was relatively constant between stations 1 - 8. Fig 14 shows that the initial numbers of Coleophora eggs and larvae at these stations varied considerably. In the following calculations it has been assumed that an arbitrary figure of 50% of the eggs present in the July samples hatched and that the resulting larvae became established in the rush capsules, together with the larvae which were already present. A theoretical initial larval infestation can thus be arrived at (column 2, Table 14). This infestation has been expressed as a percentage of the percentage of the total capsules capable of producing ripe seeds at the beginning of the season (col. 3). The percentage mortality which occurred between July and August is given in column 4.

TABLE 14.

The density of *Coleophora* larvae and July - August mortality along transect A, 1953.

Sample station	Theoretical initial larval % infestation of total rush capsules	Density (%) of larvae relative to ripening rush capsules.	% mortality July - Aug.
1 (650')	40.8	48.6	0
2	31.4	47.1	6.7
3	83.5	115.8	37.0
4	77.1	89.2	10.1
5	68.6	97.7	23.9
6	54.8	71.1	34.1
7	52.9	72.0	18.7
8 (1350')	28.0	34.7	0

It seems probable, as there was no mortality at two sample stations, that the initial assumption of 50% mortality outside the rush capsules was in fact too high. All the figures for percentage mortality in the rush capsules, given in table 14 are probably, therefore, underestimates. From this table it can be seen that the degree of mortality bore no apparent relationship to the altitude of the sample station. There was no apparent decreased mortality at the lower sample stations because of faster development of eggs and larvae in such situations. Fig. 30 (page 153) graphs the figures given in columns 3 and 4 of table 14. A regression curve can be fitted to the points on fig. 30 and an analysis of variance has been carried out (table 15).

TABLE 15.

Analysis of variance of the mortality in *Coleophora* larval populations along transect A, 1953.

Source of variation	sums of squares	degrees of freedom	Variance estimate.
Due to regression.	896.94	1	896.94
Residual.	573.89	6	95.65
Total.	1470.83	7	

$$F = \frac{896.94}{95.65} = 9.4$$

From the table for F the 1% level is about 13.74 and the 5% level about 5.99. The value for F in this

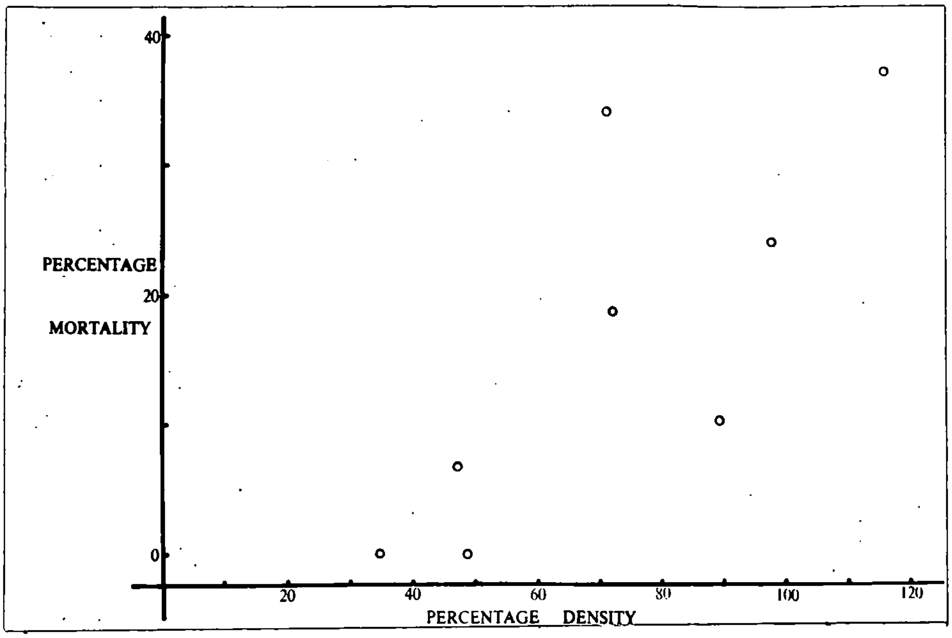

Fig.30. The relationship between the initial density of Coleophora larvae, relative to ripening rush capsules, and July-August mortality at stations 1-8, transect A, 1953.

instance then, is between the 1% and 5% levels which suggests that there was probably a relationship between the density of the initial larval populations and the mortality which occurred between July and August, 1953. It seems probable, therefore, that competition was occurring between the early larvae in the rush capsules.

In view of the possible importance of larval competition in *Coleophora* populations, indicated above, the frequency distribution of larval number per rush capsule in July has been analysed and compared with that in August. Sufficient data for this comparison to be made are available for two sets of two neighbouring sample stations in 1953 and the results are given in tables 16 and 17 (pages 155 and 156). The purpose of this analysis is to attempt to see whether larval mortality was possibly greater when there was more than one larva per capsule than when there was one per capsule. In the July sample in each table the number of unhatched eggs is given (at the foot of the column) and in columns 4 - 7 of tables 16 and 17 the theoretical figures are given calculated as being expected after the eggs had hatched (in columns 4 and 5, approximately 100% and in columns 6 and 7, approximately 50% establishment of the larvae from these eggs has been assumed) and assuming that the larvae from these eggs invaded capsules regardless of whether or not they already contained larvae, and in the same proportions

TABLE 16.

Number of *Coleophora* larvae per rush capsule at sample stations 3 and 4, transect A, 1953

No of larvae per capsule.	JULY SAMPLES		ALL EGGS HATCHED				AUGUST SAMPLES	
			0% mortality		50% mortality			
	No. of capsules	% of total capsules	No. of capsules	% of total capsules	No of capsules	% of total capsules	No. of capsules	% of total capsules
0	206	45.1	160.9	35.2	183.4	40.1	193	44.3
1	194	42.5	196.6	43.0	195.4	42.8	219	50.2
2	52	11.4	83.1	18.2	67.5	14.8	24	5.5
3	4	0.9	14.5	3.2	9.3	2.0	0	0
4	1	0.2	1.7	0.4	1.3	0.3	0	0
5	0	0	0.2	0	0.1	0	0	0
Total capsules	457		457		457		436	
Total larvae	314 (+107 eggs)		414		364		267	

TABLE 17.

Number of *Coleophora* larvae per rush capsule at sample stations 1 and 2, transect C, 1953.

No of larvae per capsule.	JULY SAMPLES		ALL EGGS HATCHED				AUGUST SAMPLES	
			0 % mortality		50% mortality			
	No. of capsules	% of total capsules	No of capsules	% of total capsules	No of capsules	% of total capsules	No. of capsules	% of total capsules
0	182	54.0	74.0	22.0	128.0	38.0	167	53.4
1	113	33.5	154.0	45.7	133.5	39.6	127	40.6
2	35	10.5	81.2	24.1	58.1	17.2	17	5.4
3	5	1.5	22.8	6.8	13.9	4.1	2	0.6
4	2	0.6	3.8	1.1	2.9	0.9	0	0
5	0	0	1.2	0.4	0.6	0.1	0	0
Total capsules	337		337		337		313	
Total larvae	206 (+193 eggs)		406		306		167	

as the larvae present in the July samples. It must be emphasized that these figures are purely theoretical as the exact extent of egg and larval mortality outside the capsules was not determined. These figures do, however, indicate the expected trend of infestation before any mortality had occurred.

Both tables 16 and 17 indicate that mortality had occurred within the rush capsules before the August samples were taken and that this had resulted in a different frequency distribution of larvae within rush capsules, from that in July or from the two theoretical positions which were calculated. Would random larval mortality within the rush capsules account for the distributions which were observed in August? Tables 18 and 19 (pages 158 and 159) give the expected situation in August if mortality within the rush capsules had been unrelated to the density of larvae per capsule. In each table egg and early larval mortality (of the unhatched eggs present in the July samples) outside the rush capsules has been assumed as both 0% and 50% to correspond with the positions in tables 16 and 17 above. The theoretical August frequency distributions of larvae per capsule have been calculated by assuming a degree of random mortality required to reduce the early larval populations within the capsules to the actual numbers observed in August.

TABLE 18.

Percentage distribution of *Coleophora* larvae per rush capsule at sample stations 3 and 4, transect A, 1953.

No. of larvae per capsule	0 % mortality outside capsules.		50% mortality outside capsules		observed August distribution
	Theoretical initial distrib.	Theoretical Aug. distr. (30% mortality)	Theoretical initial distrib.	Theoretical Aug. distr. (20% mortality)	
0	35.2	49.8	40.1	49.3	44.3
1	43.0	38.3	42.8	39.1	50.2
2	18.2	10.5	14.8	10.3	5.5
3	3.2	1.5	2.0	1.1	0
4	0.4	0.1	0.3	0.1	0

TABLE 19.

Percentage distribution of <u>Coleophora</u> larvae per rush capsule at sample stations 1 and 2, transect C, 1953.

No. of larvae per capsule	0% mortality outside capsules.		50% mortality outside capsules		observed August distribution
	Theoretical initial distrib.	Theoretical Aug. distr. (50% mortality)	Theoretical initial distrib.	Theoretical Aug. distr. (40% mortality)	
0	22.0	51.8	38.0	56.8	53.4
1	45.7	37.8	39.6	33.3	40.6
2	24.1	8.9	17.2	8.4	5.4
3	6.8	1.3	4.1	1.1	0.6
4	1.1	0.2	0.9	0.2	0
5	0.4	0	0.1	0	0

In all cases, with one exception, it can be seen from tables 18 and 19 that the proportions of capsules containing one larva were considerably greater in the observed August figures than would be expected if the mortality which had occurred was entirely random. Capsules containing more than one larva were correspondingly fewer than expected if the mortality was random. The one reasonable fit beween a predicted August condition and that which was actually observed is given in table 19 (column 3). In this calculation it was assumed that all the eggs present in the July samples resulted in larvae which all became established in the rush capsules. This seems an extremely unlikely occurrence.

It seems, then, that the mortality of the larvae in the rush capsules was possibly not random, and that competition had occurred between the early larvae and that this tended to reduce the number of larvae per capsule to one. Indeed, it is difficult to visualize a cause of mortality, other than competition between the larvae, likely to result in the killing off of any numbers of larvae once they were in the comparative security of the rush capsules. A negligible number of dead larvae of any instar were found within the many rush capsules which were dissected.

It is not suggested that all the mortality which occurred at this time was related to the initial population density. Some mortality would probably be due to larvae first entering a capsule which would not ultimately produce ripe seeds. The proportion of uninfected capsules would therefore tend to be greater than expected in August (and would, in fact, produce a still greater discrepancy between the theoretical conditions in tables 18 and 19 and the conditions which were actually observed in August). In the areas covered by tables 16 and 18, 15.6% of the rush capsules failed to produce ripe seeds and the corresponding figure for the other area was 45.7%. Any larvae which had initially colonised rush capsules (and in July these capsules were not distinguishable by eye) would have died or migrated owing to lack of a suitable food supply, thus increasing the number of uninhabited capsules and, incidentally, if they reached new capsules, increasing the degree of competition. At greater heights on the two slopes, where capsules which would not have produced ripe seeds were in very much larger numbers, this would be a means of controlling the number of larvae which established themselves independent of the initial density of the population. There is also a possibility that the later hatched larvae may be able to select capsules containing ripening seeds as, by this time, these are larger than the remainder.

These topics will require further investigation with regular sampling throughout this period and with the consequent implication of very much larger numbers.

It does appear, however, that competition was occurring between the early larvae within the rush capsules. As the degree of mortality which resulted depended on the initial numbers of larvae present such mortality would be potentially able to control the ultimate population size.

It seems that early larval mortality within the rush capsules could arise in one of two ways. Owing to the staggered oviposition of this species hatching is also staggered and the larval populations are of varying age composition. Larger, earlier hatched larvae may be cannibalistic on smaller larvae in the capsule which they are inhabiting. Such a situation is known in the Lepidoptera and occurs, for instance, in many Lycaenidae (see Ford 1945). Chapman (1915) described the case with Maculinea arion, which is phytophagous up to the last instar, but where the larger larvae devour the smaller or those which are moulting. An alternative would be that the larger larvae in the rush capsules force smaller ones to migrate from the capsule. Such larvae would, therefore, be once more exposed on the outside of the rush capsules and might be unable to re-establish themselves in new capsules.

IX DISCUSSION.

C. caespititiella has proved an insect particularly suited to the investigation of certain population problems. Owing to the close association of the early stages of its life history with the rush, J. squarrosus, it has been possible to obtain information on populations of the insect at various heights on an area of Pennine moorland. The association between the insect and rush, and the consequent ease with which populations can be sampled is probably the major factor in making this a suitable species to study. Although the remainder of the life history, apart from the brief adult life, is spent in the dense litter at the base of the same plants, the whole of this time is spent within the larval case, manufactured when the larva was still feeding. With careful hand-sorting these cases can be extracted from the litter. A further advantage of this species is that there is only one generation per annum, and thus, although successive stages do overlap, equivalent stages of successive generations do not and, therefore, factors affecting the various stages of each generation can be examined.

The present investigation could be considered as a preliminary to a more detailed investigation on these lines. Some knowledge of the life-history and general biology, together with information regarding the species' distribution in the northern Pennines, has now been accumulated. It seems likely that the seasonal surveys, which were carried out on two *Coleophora* populations from July 1953 to November 1954, indicate the line which would most repay investigation in the future. A closer analysis of the effects of the different mortality factors operative at different stages in the life-history is required. Despite the lack of this detailed information some conclusions can be drawn regarding the importance of various mortality factors affecting the species density at various localities. It was suggested (pages 148-62) that competition between the early larvae for food niches was probably the major reaction governing population density in some of the *Coleophora* populations which were investigated during 1952-4. It was thus, in these instances, the space-property of food supply which appeared to be competed for and the mortality which occurred at this stage seemed generally to reduce the populatinns to a density corresponding to the ultimate larval food requirements.

In some of the lower sites which were investigated the correlation between *Coleophora* numbers and/ripening capsules of *J. squarrosus* was not so close and the differences in size of neighbouring *Coleophora* populations were not solely to be explained on the basis of the available food supply. In some areas, for instance, *Coleophora* egg and larval numbers in July were well below those which could be accomodated by the available ripening capsules. In such areas it was shown (pages 150-4) that mortality due to larval competition was reduced (this is to be expected if this early larval mortality is indeed density-dependent, as defined by Smith 1935). It was just from these areas that Coleophora parasites were recorded. Oscillations in parasite and host numbers were first predicted, independently by Lotka (1925) and Volterra (1926, 1931), and Nicholson and Bailey (1935), amongst others have made more recent theoretical analyses. Such oscillations have been observed by de Bach and Smith (1941) and others under laboratory conditions.

Under field conditions the number of factors affecting animal populations is considerably more than was operative in the relatively simple laboratory experiments mentioned above. Schwerdtfeger (1942) came to the conclusion that there is a complex of interacting factors affecting insect populations and that different factors are operative at different stages, and with varying intensity, in an insect's life-history. Working on four species of leaf-eating Lepidoptera from German coniferous forests he found that high parasite numbers accompanied the catastrophic falls which occurred from peak moth populations. He gave no data on the percentage parasitised when the populations were rising from low values. The oscillations in population size were not regular and did not, in the main, accord with the theoretical situation, as predicted by Nicholson and Bailey (1935). Varley (1947) pointed out that, in a fluctuating environment, oscillations cannot be regular. The results he obtained from a two-year survey of factors affecting populations of the Knapweed Gallfly, *Urophora jaceana*, and its Chalcid parasite, *Eurytoma curta*, lead him to the conclusion that they were a glimpse of irregular oscillations occurring about a steady density.

The evidence from the present investigation does not suggest any regular oscillation in parasite and host numbers at the sample stations where parasites were present. However, a more detailed investigation of one of these lowland populations might have revealed that oscillations of this type were, in fact, occurring, despite the considerable fluctuations in the physical environment which, if it is widely agreed, ultimately, either directly or indirectly, governs the distribution and densities of all animals in the field (Uvarov 1931, Nicholson 1933, Solomon 1949 and others). It has already been pointed out (page 95) that the sampling method employed was quite adequate for obtaining estimates of the *Coleophora* populations, but, as the parasite numbers were generally low, there was a considerable error to the mean figures obtained for the parasite populations.

At the lower levels of transect A, *J. squarrosus* occurred in relatively isolated areas. Owing to the inactivity of the adult moths it was probable that only very little interchange occurred between adjacent Coleophora populations, and that therefore the samples taken in 1952-4 were from quite distinct populations. In such an area Nicholson (1933)(see his c.40) predicted that the oscillations in each of the populations would be out of phase with each other. Varley (1947) in the study already referred to, found that the rate of dispersal of the host and parasite species he was dealing with was not sufficiently rapid either to equalise the populations (which were only a few hundred yards apart) or to synchronize the oscillations over these distances. It is suggested that a similar position existed with the Coleophora populations at the lower sample stations of transect A in 1952-4.

There appeared to be, therefore, many mortality factors which operated on the Colepphora populations which were investigated (some of these were enumerated on pages 144-7). These appeared to operate with varying intensity on the different populations. In some instances populations appeared to be checked from unlimited expansion by non-reactive factors which, as defined by Nicholson (1954) bore no relationship to the density of the population at any stage. At the upper levels of the Pennine slopes this is probably true each year as in these areas ripening capsules are comparatively few and larvae which enter non-mature capsules would of necessity die or be forced to migrate through lack of a suitable food supply. In such a manner only comparatively few larvae would reach ripening capsules and the larval population would be maintained in the following year at a low level as few adults are present in such areas. The possibilities of immigration, owing to the relative inactivity of the adult moths, are probably slight. Some of the lower populations were probably also kept below a critical larval density by mortality factors bearing no relationship to population density in the same or preceding seasons. Parasites, although in some areas causing considerable larval mortality in some years, were apparently unable to maintain the population consistently at a density below that corresponding to the ultimate larval food requirements. The fecundity of the adult moths, in areas heavily parasitised in the preceding summer, was generally sufficient to provide an excess of larvae to available rush capsules in the following year. As soon as larval numbers reached a critical density relative to ripe rush capsules in any area, it is suggested that competition between the larvae within these capsules occurred and the population was reduced to a level consistent with the available food supply. As pointed out by Nicholson (1954) an additional source of mortality (within the limits of the population tolerance) would not increase mortality, as mortality due to reactive factors would be reduced. The governing reaction with the Coleophora populations investigated in 1952-4 appeared to be competition between the early larvae within the ripening rush capsules.

This competition was thus for the space-quality of the available food supply, rather than for food supply itself. Occasional instances were, however, recorded when practically all the ripening rush capsules were initially colonised by Coleophora larvae and, in such instances, competition probably occurred between the larvae for food towards the end of the season. In August 1953, for instance, at station 1 (where 53 of 63 mature capsules were infected) and station 2 (54 of 74) of transect C this was probably the case. Although some Coleophora larvae were shown to feed on only one capsule during their lifetime, the mean number required was more than double this. There seemed to be, therefore, a considerable excess of larvae established in the rush capsules in these areas, to that which the available food could support, despite more than 50% mortality in the egg and early larval stages at these two sites. In the following July there were many fewer eggs at these two sites than in the preceding year. Solomon (1949) pointed out that density-dependent action, in a case where food supply is the limiting factor, arises "both from the automatically reduced share per individual when there are more individuals and from the action of the population in reducing the total." In other words, there is a limited capacity of the environment to maintain large numbers of the species concerned. The same author also stated the "there is a tendency for some individuals to get an adequate share while others do poorly, and perhaps fail to get enough for survival." It appears possible that there was a heavy winter mortality or a lowering of fecundity in the resulting adults, or a combination of both these factors as a result of an insufficient food-supply in the preceding summer, which caused the much lower number of eggs observed at these two sites in 1954. This suggestion by Solomon (1949) can be compared to the 'carrying capacity' of the environment ideas of Kalabukhov (1935), Errington (1946) and others. In the present study it is suggested that the capacity of the environment (relative to food supply in this particular instance) is not normally over-reached as the density-dependent (in the sense of Smith, 1935) early larval mortality normally ensures an approximate correlation between larval numbers and their ultimate food requirements in a given area. Although, therefore, in most areas the majority, if not all, of the ripening rush capsules are attacked by the end of the season, some viable uneaten seeds still remain in some capsules and despite the considerable destruction of seeds which occurs there are still sufficient seeds, owing to the large initial numbers which are produced, to ensure the continuance of the rush populations.

Nicholson (1954) divided competition into two categories. He defined these as, firstly, 'scramble' in which all members of a population obtain some of the element which is competed for, and, secondly, 'contest' in which an all or none rule operates. Scramble is thus essentially inefficient as some, or sometimes all, the requisite is dissipated by individuals which obtain insufficient for survival (compare Solomon, 1949, referred to above). Contest, however, is efficient as all the requisite is used in maintaining the population. Except in the few instances when direct competition for food supply occurred towards the end of the larval feeding period, competition between Coleophora larvae appears to be essentially of the 'contest' type. Although the small larvae succeed in entering the rush capsules before they are consumed or driven out by larger larvae already present, they are at this stage very small and the amount of food dissipated in this way would be extremely limited. The bulk of the available food supply is thus utilised in maintaining the population.

Although, as has already been pointed out, it is the space quality of the available food supply which appears to be competed for, rather than nutriment itself, it seems that *Coleophora* populations are generally limited by the amount of food (in the form of mature rush capsules) available in each area. The fact that food supply often appeared to be the limiting factor to population size has a number of implications. Darwin (1859) pointed out that "the amount of food for each species.......gives the extreme limit to which each can increase," and goes on to indicate that this limit is seldom reached in nature. This situation has been confirmed by many authorities and in the majority of cases some factor or factors operate to reduce the numbers of the species before this ultimate controlling factor comes into operation. Nicholson (1954), for instance, emphasised that insect enemies of plants are generally reduced by their own enemies before they are limited by food shortage. A few instances have been described when insect species under natural conditions have their potential increase offset by limitations of food supply. Salt (1932) showed that the potential increase of *Lucilia sericata* was especially offset by a restricted supply of suitable food for the larvae, and Ullyett (1950), showed that in *Lucilia* and *Chrysomia* the larvae were limited by food shortage.

Limitation of food supply, however, does not appear to be an important factor controlling the numbers of insects in natural populations, except when they are in extreme abundance. Howard and Fiske (1911), analysing the unfavourable factors affecting populations of various species of leaf-eating Lepidoptera came to the conclusion that parasites were predominant at moderate densities, disease when the insects had reached a density far beyond the average level, and famine at the very highest level. There are a number of examples where such overpopulation functions as a check on numbers when abundance outstrips resources. Barber (1926) found that in years of excessive corn-borer (Pyrausta nubilalis)abundance in New England, larval overpopulation resulted in the corn being reduced to a mere shell and many borers died of starvation. Voûte (1946) gave examples of certain forest insects which, under outbreak conditions, overate their food supply.

Under less natural conditions food supply often acts as a limiting factor to population growth. For instance, the mealybug, Icerya purchasi, which was accidentally introduced from Australia into California, and which became a pest in the citrus groves was limited in numbers only by the available food supply. Its natural predator, the ladybird, Vedalia cardinalis, was introduced and now both species are relatively uncommon (Nicholson, 1947).

Those Coleophora populations which were apparently limited by the available food supply throughout the period of the present investigation are, therefore, apparently rather unusual. Whether or not this species actually occurs in a given area is thus dependent on climate as "any temporary deviations of the climatic factors, however slight they may be, affect the percentage of survival, either directly or indirectly (through natural enemies and food plants) and thus influence abundance " (Uvarov, 1931). Climate, and, as postulated by Pearsall (1950), especially temperature affects the capacity of J. squarrosus to produce capsules containing ripe seeds, which in turn affects the size of the Coleophora population which these capsules can support. This effect of temperature on seeding of the rush, and so on Coleophora larval numbers conforms to the expected situation where "the distribution and densities of all animals are ultimately dependent upon the physical environment" (Nicholson, 1933, and also see Uvarov, 1931, Solomon, 1949, and many others). A summer of low mean temperatures, and 1954 was such a summer in the area in which these investigations were carried out, thus considerably depresses the numbers of larvae capable of being supported by J. squarrosus. As is to be expected this effect was especially strong in 1954 on the upper larval populations. It was shown on pages 107 - 8 that the only rush populations which seeded to approximately the same extent in 1954 as in the two preceding seasons were those at and below 850' on the western Pennine slopes. Only at these levels were the *Coleophora* populations of feeding larvae of comparable size to those present in 1952 and 1953. Above this height ripe seed production by *J. squarrosus*, and *Coleophora* larval numbers were both shown to have been much less, and both ceased at a much lower altitude, than in the preceding two summers.

It seems probable, as already pointed out, that there is a complex of interacting factors affecting *Coleophora* populations and that each factor acts with varying intensity at different altitudinal levels and in different seasons. The suggestion that competition for the space quality of food supply, which generally ensures an approximate balance between larval numbers and their ultimate food requirements, is the ultimate 'density-governing factor' (Nicholson 1954) determining the size of at least some *Coleophora* populations needs to be further examined in the future by detailed analyses of the different mortality factors operative throughout the life-history at various localities. Early larval mortality requires especially close examination and the suggestions which have been made regarding competition at this stage should be further tested. Seasonal surveys designed to obtain information of this nature need to be carried out on *Coleophora* populations throughout the species range in the Moor House area. The populations examined should include one of the low level populations, on the western Pennine slopes, where *Coleophora* parasites were present in considerable numbers in 1952-4, as well as the two populations which were preliminarily examined during the present investigation.

X. SUMMARY.

1. Investigations on the relationship between the rush, Juncus squarrosus L. and the moth Coleophora caespititiella Zell. were carried out on the Moor House Nature Reserve between July 1952 and the autumn of 1954.

2. The systematic and general biological literature concerned with C. caespititiella is reviewed and the life history pointed out to be imperfectly known.

3. Emergence of adult moths began at the beginning of June and oviposition commenced soon after this. Eggs are laid under the perianth segments of the individual rush florets and also in the angles between adjacent florets. Eggs, in the field, remained at least three weeks before hatching.

4. Larvae of C. caespititiella were recorded feeding on J. effusus L., J. articulatus L., and Luzula campestris L., in addition to J. squarrosus.

5. The first instar larvae bore into rush capsules and feed on the contained seeds.

6. The existence of four larval instars is demonstrated. The third or fourth instar larvae manufacture a silken case, and after this move, with case, from one capsule to another and continue feeding. Feeding is completed in the autumn and the larvae overwinter, within their larval cases, in the plant litter at the base of the rush stems.

7. Some larvae were found feeding again, in the following spring, on the new years' growth of rushes, and it is suggested that this may have been due to an insufficiency of food in the previous autumn.

8. Pupation occurs in the spring and this stage is of about three weeks duration.

9. Dissection of female moths showed that there are at least 90 eggs present on emergence. 10 - 20 of these appear ready for immediate oviposition.

10. Laboratory experiments in 1954 showed that moths kept in dry conditions had a mean life in captivity of 7.00 - 0.49 days. Others provided with free water lived for 17.43 - 1.06 days and others with sucrose solution for 19.90 - 0.75 days.

11. Four species of Hymenopterous parasites were recorded from *Coleophora* larvae from the study area. The two commonest parasites were *Ephialtes brevicornis* (Grav.)(Ichneumonidae) and a species of a genus near *Miotropis* (Chalcidoidea).

12. Marking experiments showed that *Coleophora* final instar larvae visited a mean of 2.28 rush capsules during their feeding period in 1953.

13. The length of time spent on the rush capsules after the formation of the larval case varied between a few days and more than a month.

14. Adult moths were found to be relatively inactive. Pairing and oviposition took place in the field and in

the laboratory at all times of the day and night and continued throughout the period of adult activity. No feeding by adult moths was observed in the field and it is suggested that a supply of free water is sufficient for survival under natural conditions.

15. Samples of *J. squarrosus* inflorescences were collected from three transects and other sampling sites in the study area. The rush is shown to be broadly distributed over the area.

16. The degree of fruiting by *J. squarrosus* in 1952-4 is discussed. A larger proportion of the total capsules produced ripe seeds in 1952 and 1953 than in 1954. The upper altitudinal limit of fruiting in 1954 was much lower than in the two preceding years. This is suggested, following Pearsall (1950), to have been due to the lower mean temperatures during 1954.

17. In all three years the capacity of the rush to produce ripe seeds, to any given extent, was possessed about 300' higher on the eastern Pennine slopes than on the western.

18. The general distribution of *C. caespititiella* in the study area is described from samples of eggs and feeding larvae collected in 1952-4.

19. On the western slopes in 1952 and 1953 the upper limit for *Coleophora* was about 1850'. Percentage infestation of rush capsules increased to about 1200' below which it varied within wide limits. In 1954

larval infestation was generally lower and no larvae were recorded above 1350', although eggs were laid up to 1700'.

20. *Coleophora* parasites were not recorded above 1050' on the western slopes.

21. *Coleophora* larvae were present up to the top of the eastern transect (2075') and on the Nature Reserve they were recorded up to 2170'. Infestation decreased with increasing altitude. The degree of larval infestation of *J. squarrosus* capsules was much lower in 1954 than in 1952 and 1953.

22. *Coleophora* parasites were present only at the lowest site (1525') sampled on the eastern slopes.

23. There was a difference in percentage *Coleophora* infestation on the two slopes comparable to that shown for ripe seed production by *J. squarrosus*.

24. A close correlation, especially at the upper sample stations, between the number of larvae established in rush capsules and the percentage of the total rush capsules capable of producing ripe seeds in each area in 1952-4 is demonstrated.

25. The upper limit of *Coleophora* populations is suggested to be due to the failure of the rush to normally produce ripe seeds above a certain altitude, and also to the relative inactivity of the adult moths.

26. Even at the lower sample stations there is some evidence that *Coleophora* larvae had eaten all the

available food supply by the end of the season. This was not invariably so, and at these stations Hymenopterous parasites were present.

27. Seasonal surveys of two Coleophora populations are described. Overwintering populations in the litter and the adult emergence were estimated, in addition to egg and larval populations on the rush inflorescences. Despite deficiencies in some of the sampling techniques heavy mortality was demonstrated in the egg and early larval stages and also in the overwintering population in the litter. Possible causes are suggested.

28. It is suggested that at least the majority of the Coleophora populations examined in 1952-4 were not limited in size by Hymenopterous parasites.

29. Some evidence for competition between early instar Coleophora larvae inside mature rush capsules is presented, and it is pointed out that competition at this stage would result in a degree of mortality dependent on the density of the initial larval population.

30. The factors making C. caespititiella particularly suitable for the investigation of certain population problems are enumerated.

31. It is pointed out that there were many mortality factors which operated with varying intensities on the different Coleophora populations which were investigated.

32. In some years, some populations, it is suggested, were checked from unlimited expansion by non-reactive

factors (Nicholson, 1954) which bore no relationship to the density of the population at any stage.

33. It is suggested that as soon as larval numbers reached a critical density, relative to ripe rush capsules in any area, competition between the larvae within these capsules occurred and reduced the population to a level consistent with the available food supply.

34. Such competition was then for the space quality of the available food supply.

35. As temperature determines the capacity of *J. squarrosus* to produce ripe seeds the distribution and density of *C. caespititiella* is ultimately dependent on climate.

36. Some of the implications of the fact that food supply often appeared to be the limiting factor to population size are discussed.

37. Suggestions are made regarding possible future work in this field.

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APPENDIX I.

RIPE SEED PRODUCTION BY J. SQUARROSUS.

1952 - 4.

Table 1. - Little Dun Fell - Crowdundle transect (transect A).

Table 2. - Knock Ore Gill transect (transect B) 1952 only.

Table 3. - Hill House Farm transect (transect C).

Table 4. - Sites on the eastern Pennine slopes.

In order to avoid undue complication of the tables, individual estimated standard errors are not given for the percentage of capsules producing ripe seeds along the transects on all dates on which they were sampled. The range of the estimated standard errors, is however given in each instance.

TABLE I.

Sample station	Height (feet)	1952					1953						1954		
		Total capsules	% producing ripe seeds at beginning of season	% on 21 + 23 Aug.	Total capsules Aug sample	Total capsules Sept sample	% producing ripe seeds at beginning of season	% on 8 Aug	% on 4 Sept	% at end of season	Total Capsules Aug sample	Total Capsules Sept sample	% producing ripe seeds at beginning of season	% on 24 Aug.	% on 1 Oct.
1	650	283	74.9 ± 2.6	19.4	253	269	83.9 ± 1.6	34.4	21.9	0	203	175	74.3 ± 2.2	35.0	37.7
2	750	319	68.7 ± 2.6	42.6	232	229	66.6 ± 2.2	45.7	12.7	10.8	179	168	59.9 ± 2.6	30.2	10.1
3	850	247	84.6 ± 2.3	68.0	211	234	72.1 ± 2.1	24.6	4.3	0	206	182	62.9 ± 2.5	33.5	21.4
4	950	304	89.5 ± 1.8	20.7	225	195	86.4 ± 1.7	21.8	6.7	0	190	199	39.8 ± 2.5	7.4	5.0
5	1050	280	81.1 ± 2.3	48.6	203	180	70.2 ± 2.3	16.7	1.7	0	201	211	16.3 ± 1.9	0	7.1
6	1130	331	72.8 ± 2.4	39.9	180	191	77.1 ± 2.2	53.3	16.2	3.9	139	177	45.3 ± 2.8	14.4	30.5
7	1200	397	90.7 ± 1.5	21.9	200	237	73.5 ± 2.1	32.5	11.8	0	180	184	15.7 ± 1.9	2.8	2.2
8	1350	292	44.5 ± 2.9	15.4	165	183	80.7 ± 2.1	47.9	24.0	6.1	171	178	37.5 ± 2.6	17.5	14.6
9	1500	284	12.7 ± 2.0	0.4	168	185	17.6 ± 2.0	14.9	8.1	0	159	156	0	0	0
10	1700	243	0.4 ± 0.4	0.4	172	138	5.2 ± 1.2	9.3	0.7	4.1	168	138	0	0	0
11	1850	290	6.6 ± 1.5	5.9	185	188	21.7 ± 2.1	21.1	21.3	19.5	168	-	0	0	0
12	2000	204	6.9 ± 1.8	6.9	-	126	9.5 ± 2.6	-	9.5	9.5	146	-	0	0	0
13	2350	207	0	0	-	140	5.7 ± 2.0	-	5.7	5.7	105	-	0	0	0
14	2470	185	1.6 ± 0.9	1.6	-	153	1.3 ± 0.9	-	1.3	1.3	141	-	0	0	0
15	2750	156	0	0	-	143	0	-	0	0	105	-	0	0	0
Range of estimated standard errors:-			0.4 - 2.9	0.4 - 3.0			0.9 - 2.6	2.2 - 3.9	0.7-3.2	0.9 - 2.9			1.9 - 2.8	1.2 - 3.4	1.1 - 3.7

TABLE 2

Sample station	Height (feet)	1952		
		Total capsules	% producing ripe seeds at beginning of season	% on 16 Sept.
1	860	239	80.7 ± 2.6	50.2
2	950	234	86.3 ± 2.2	47.4
3	1200	237	54.0 ± 3.2	5.1
4	1350	177	70.6 ± 3.4	29.9
5	1500	237	34.2 ± 3.1	10.5
6	1600	231	1.3 ± 0.9	0
7	1750	181	43.1 ± 3.7	38.7
8	1850	198	9.6 ± 2.1	9.6
9	1900	228	0.4 ± 0.4	0.4
10	2000	189	5.3 ± 1.6	5.3
Range of estimated standard errors:-			0.4 - 3.7	0.4 - 3.6

TABLE 3.

Sample station.	Height (feet)	1952			1953						1954				
		Total capsules	% producing ripe seeds at beginning of season	% on 20 Aug.	Total capsules		% producing ripe seeds at beginning of season	% on 10 Aug.	% on 5 Sept.	% at end of season	Total capsules		% producing ripe seeds at beginning of season	% on 18 Aug	% on 30 Sept
					Aug sample	Sept sample					Aug sample	Sept sample			
1	1525	271	53.9 ± 3.0	17.3	169	170	68.4 ± 2.5	5.9	1.2	0	156	156	44.2 ± 2.8	41.7	21.2
2	1575	294	56.5 ± 2.9	31.3	144	178	41.3 ± 2.7	13.9	1.1	0	191	174	22.5 ± 2.2	20.4	14.9
3	1675	268	66.4 ± 2.9	31.7	165	191	42.7 ± 2.6	30.3	8.4	0	211	208	10.0 ± 1.5	11.4	4.3
4	1740	305	39.7 ± 2.8	14.4	187	209	31.1 ± 2.3	15.5	5.3	0	187	136	10.5 ± 1.7	4.8	17.6
5	1850	324	36.4 ± 2.7	24.4	149	151	9.3 ± 1.7	6.0	1.3	0	207	166	0	0	0
6	1970	319	11.3 ± 1.8	5.6	132	147	31.2 ± 2.8	15.9	29.9	0	127	173	1.0 ± 0.6	1.6	0
7	2075	Not sampled			134	122	39.8 ± 3.1	45.5	23.8	38.8	154	157	4.8 ± 1.2	7.1	2.5
Range of estimated standard errors:-			1.8 - 3.0	1.3-2.8			1.7 - 3.1	1.8-4.3	0.8-3.9	-			0.6 - 2.8	1.1-3.9	1.2-3.3

TABLE 4.

Sample Station.	Height (feet)	1952 Total Capsules.	1952 % producing ripe seeds	1953 Total capsules	1953 % producing ripe seeds	1954 Total capsules	1954 % producing ripe seeds.
Gt. Dodgen Pot sike.	1770	200	12.5 ± 2.3	163	24.5 ± 3.7	146	1.4 ± 1.0
Netherhearth	1780	235	29.4 ± 3.0	159	15.7 ± 2.9	159	2.5 ± 1.2
Valley Bog	1830	244	9.0 ± 1.8	195	2.1 ± 1.0	149	5.4 ± 1.9
Bog Hill Mine	1830	248	5.6 ± 1.5	119	21.8 ± 3.8	148	18.2 ± 3.2
Rough Sike	1870	280	52.9 ± 3.0	141	14.9 ± 3.0	154	16.2 ± 3.0
Moss Burn A	1870	237	31.6 ± 3.0	179	26.8 ± 3.3	162	0
Moss Burn B	1870	249	15.7 ± 2.3	171	8.2 ± 2.1	200	1.0 ± 0.7
Netherhearth Sike	1870	195	39.0 ± 3.5	182	14.3 ± 2.6	203	3.4 ± 1.3
Burnt Hill	1870	Not sampled		205	14.1 ± 2.4	151	6.0 ± 1.9
R. Tees	1520	184	25.0 ± 3.2	166	4.8 ± 1.7	158	14.6 ± 2.8
R. Tees	1575	287	34.8 ± 2.8	198	16.2 ± 2.6	148	25.0 ± 3.6
R. Tees	1610	250	40.8 ± 3.1	157	26.1 ± 3.5	147	8.2 ± 2.3
R. Tees	1670	254	24.0 ± 2.7	177	5.6 ± 1.7	149	8.7 ± 2.3
R. Tees	1710	257	20.2 ± 2.5	181	17.1 ± 2.8	151	9.3 ± 2.4
Tees Bridge	1740	224	12.1 ± 2.2	172	18.6 ± 3.0	188	1.1 ± 0.8
R. Tees	1750	194	4.1 ± 1.4	144	7.6 ± 2.2	141	9.2 ± 2.4
R. Tees	1815	205	27.8 ± 3.1	172	32.6 ± 3.6	198	2.5 ± 1.1
R. Tees	1850	246	41.1 ± 3.1	153	8.5 ± 2.3	166	4.8 ± 1.7
Trout Beck	1710	174	10.3 ± 2.3	166	13.9 ± 2.7	171	2.9 ± 1.3
Trout Beck Bridge	1710	211	64.5 ± 3.3	104	48.1 ± 4.9	139	2.9 ± 1.4
Trout Beck	1780	229	28.8 ± 2.9	153	6.5 ± 2.0	148	2.0 ± 1.2
Trout Beck	1840	239	20.5 ± 2.6	189	16.4 ± 2.7	132	12.1 ± 2.8
Trout Beck	1875	224	3.6 ± 1.2	251	4.4 ± 1.3	132	0
Trout Beck	1940	200	45.5 ± 3.5	167	36.5 ± 3.7	126	3.2 ± 1.6
Trout Beck	1975	269	4.5 ± 1.3	127	47.2 ± 4.4	129	0
Trout Beck	2170	Not sampled		156	20.5 ± 3.2	125	0

APPENDIX II.

COLEOPHORA INFESTATION OF J. SQUARROSUS.

1952 - 4.

Table 1. - Specimen sheet on which the original data were recorded.

Table 2. - Little Dun Fell - Crowdundle transect (transect A).

Table 3. - Knock One Gill transect (transect B) 1952 only.

Table 4. - Hill House Farm transect (transect C).

Table 5. - Sites on the eastern Pennine slopes.

In order to avoid undue complication of the tables, individual estimated standard errors are not given for the percentage Coleophora infestation along the transects on all dates for which they were sampled. The range of the estimated standard errors is, however, given in each instance.

TABLE 1.

~~Site or~~ Transect: Little Dun Fell-Crowdundle.

Sta No. 3 Height: 850' Date: 8-8-53

	No of stems	"Mature" fruits	Coleophoras with cases	Coleophoras without cases	Capsules with exit holes (contents eaten)	Cases without larvae	"Non-mature" fruits	No. still flowering	Other animals	General Remarks
A	1	15 (5)	3 a.b.	5+2dead a.b.	2	-	3	-	-	a.b.d.e.g.n.-- 2
	1	11 (6)	4d.e.	3 d.e.	1 c	-	7	-	-	in/on one capsule
	1	23 (8)	5 f.	7+1 dead	2 f.	-	2	-	-	c.o.s.v.--capsule
	1	13 (5)	4	4	-	-	4	-	-	would not have
	1	15 (2)	5 g.k.	11 g.h.	-	-	10	-	-	produced ripe seeds
B	1	7 (3)	2	2 l.	1	-	4	-	-	f.--2capsules
	1	18 (9)	7 m.n.	2 n.	2	-	3	-	-	joined together by
	1	22 (3)	9 q.	8 p.r. +1 dead o.	5	-	4	-	-	silk tube.
	1	11 (6)	1	4	-	-	8	-	1 thrip nymph.	t.--as f. and one
	1	27 (5)	7	18 s.t.u.v.	1 t.	-	4	-	-	capsule as c.
C	1									h.l.p.r.u.--2 in
	1									one capsule.
	1									k.m.q.--2 on one
	1									capsule.
	1									
Totals	10	162 (52)	47	64+4 dead	14	0	49	0	-	

Degree of Coleophora infestation:- 52.6%-Living larvae; 54.5%-total larvae

Capsules capable of producing ripe seeds:- 76.8%-at beginning of season. 24.6%-on sample date

TABLE 3.

Sample station	Height (feet)	16 September 1952		
		Larvae still on rush stems	% infestation	% of larvae in Col. 3 parasitised
1	860	44	18.4 ± 2.5	4.5 ± 3.1
2	950	60	25.6 ± 2.9	33.3 ± 6.1
3	1200	59	24.9 ± 2.8	0
4	1350	35	19.8 ± 3.0	0
5	1500	31	13.1 ± 2.2	0
6	1600	2	0.9 ± 0.6	0
7	1750	4	2.2 ± 1.1	0
8	1850	0	0	0
9	1900	0	0	0
10	2000	0	0	0
Range of estimated standard errors:-			0.6 - 3.0	3.1 -6.1

TABLE 2.

Sample station	Height (feet)	1952 21 + 23 August larvae	 % infestation	 % larvae parasitised	1953 5 July eggs + larvae	 % infestation	 8 August larvae	 % inf.	 4 September larvae	 % inf.	 % larv parasit	1954 22 July eggs + larvae	 % infestation	 24 Aug Larvae	 % in	 1 October larvae	 % inf.	 % larvae parasitised.
1	650	111	39.2 ± 2.9	4.5 ± 2.0	130	48.7 ± 3.0	121	47.8	57	21.2	31.8 ±	102	49.0 ± 3.5	77	37.9	55	31.4	2.7 ± 1.9
2	750	76	23.8 ± 2.4	18.4 ± 4.6	92	38.5 ± 3.1	68	29.3	43	18.8	31.25 ±	101	55.2 ± 3.7	91	50.8	44	26.2	0
3	850	38	15.4 ± 2.3	2.6 ± 2.6	240	98.8 ± 0.7	111	52.6	39	16.7	6.2 ±	39	26.4 ± 3.6	71	34.5	37	20.3	2.9 ± 2.0
4	950	129	42.4 ± 2.8	0	181	84.6 ± 2.5	156	69.3	54	27.7	8.3 ±	163	71.2 ± 3.0	63	33.2	44	22.1	12.0 ± 3.5
5	1050	78	27.9 ± 2.7	0	154	73.3 ± 3.0	106	52.2	42	23.3	7.6 ±	108	52.9 ± 3.5	24	11.9	26	12.3	2.1 ± 2.0
6	1130	105	31.7 ± 2.6	0	93	59.2 ± 3.9	65	36.1	36	18.8	0	72	47.4 ± 4.0	13	9.4	48	27.1	0
7	1200	195	49.1 ± 2.5	0	141	62.7 ± 3.2	86	43.0	82	34.6	0	131	56.9 ± 3.3	53	29.4	23	12.5	0
8	1350	68	23.3 ± 2.4	0	62	32.8 ± 3.4	52	31.5	65	35.5	0	149	78.8 ± 3.0	35	20.5	54	30.3	0
9	1500	35	12.3 ± 1.9	0	49	29.2 ± 3.5	26	15.5	29	15.7	0	26	14.4 ± 2.6	0	0	0	0	0
10	1700	1	0.4 ± 0.4	0	5	2.6 ± 1.1	4	2.3	1	0.5	0	3	1.9 ± 1.1	0	0	0	0	0
11	1850	2	0.7 ± 0.5	0	0	0	2	1.1	0	0	0	0	0	0	0	0	0	0
12	2000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	2350	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	2470	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	2750	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Range of estimated Standard Errors.			0.4 - 2.9	2.0 - 4.6		0.7 - 3.9		0.8-3.6		0.6-3.5	2.3 - 6		1.1 - 4.0		2.3-3.7		2.3 - 3.5	1.9 - 3.5

TABLE 4.

Sample station	Height (feet)	1952		1953									1954			
		20 August		7 July		10 August		5 September			21 July.		18 August		30 September	
		larvae	% infestation.	eggs & larvae	% infestation	larvae	% inf.	larvae	% inf.	% larvae parasitised	eggs & larvae	% infestation	larvae	% infestation	larvae	% inf.
1	1525	74	27.3 ± 2.7	174	111.5 -	37	51.5	58	34.1	1.0 ± 0.9	42	24.4 ± 3.3	27	17.3	21	13.5
2	1575	68	23.1 ± 2.5	225	124.3 -	30	55.6	39	21.9	0	42	23.2± 3.1	19	9.9	9	5.2
3	1675	89	33.2 ± 2.9	168	76.0 ± 2.9	52	31.5	57	29.8	0	73	37.6 ± 3.5	20	9.5	4	1.9
4	1740	62	20.3 ± 2.3	132	67.0 ± 3.4	54	28.9	25	12.0	0	29	10.9 ± 1.9	4	2.1	4	2.9
5	1850	40	12.3 ± 1.8	45	28.5 ± 3.6	23	15.4	9	6.0	0	13	7.4 ± 2.0	1	0.5	0	0
6	1970	17	5.3 ± 1.3	25	18.7 ± 3.4	13	9.8	13	8.8	0	16	10.3 ± 2.4	3	2.4	0	0
7	2075	Not sampled		7	4.5 ± 1.7	5	4.5	6	4.9	0	3	1.7 ± 1.0	0	0	0	0
Range of estimated standard errors:-			1.3 - 2.9		1.7 - 3.6		1.8 - 4.1		1.9 - 3.6	-		1.0 - 3.5		0.5 - 3.0		0.9 - 2.7

APPENDIX III.

METHOD EMPLOYED IN THE ESTIMATION OF STANDARD ERRORS.

The variance of the percentage values obtained for rush capsules producing ripe seeds and for Coleophora infestation at each sample station can be represented by the following formula:-

$$V = \frac{pq}{\Sigma N} \% .$$

where p = the proportion of the capsules producing ripe seeds (or with Coleophora).

q = 1 - p = the proportion of the capsules not producing ripe seeds (or without Coleophora).

N = The number of capsules on each stem.

The standard error (= standard deviation) of this is

$$\sqrt{\frac{pq}{\Sigma N}} \% .$$

The above value for the variance of the percentage figures obtained is correct, subject to one assumption. This is that the number of ripe seeds (or Coleophora) were in the same proportion to the total capsules on each stem included in the particular sample. If this is so, $E(X) = Np$ and $\text{var}(X) = Npq$.

where E(X) = the estimated number of ripening capsules (or Coleophora) per stem.

The above formula for the variance of the percentage values can then be derived.

The above assumption appears to be the expected biological position. In a stem with a larger number of capsules than a neighbouring stem, it would be expected that a proportionately larger number of these would be capable of producing ripe seeds than on the neighbouring stem. Similarly, as oviposition appears to be random, and the number of available oviposition sites on a stem is relative to the total capsules, one would expect more Coleophora eggs or larvae to be present on a stem with a large number of capsules than on a neighbouring stem with fewer capsules. In neither instance, of course, are exact proportions to be expected.

In order to test this assumption, a number of samples have been examined, and fig. 31 gives the position, at two stations along transect A in 1952, for both ripe seed production at the beginning of the season and for Coleophora infestation on 21st Aug. The 1952 samples were chosen as fifteen stems were examined from each station in that year, compared with ten in the two following years. The values given are those for sample stations 4 and 7 where the largest figures for percentage ripe seed production and for Coleophora infestation were obtained in that

TABLE 5.

Sample Station.	Height (feet)	1952		1953		1954	
		Larvae	% infestation	Larvae	% infestation	Larvae	% infestation
Gt. Dodgen Pot Sike	1770	11	5.5 ± 1.6	9	5.5 ± 1.8	1	0.7 ± 0.7
Netherhearth	1780	6	2.6 ± 1.0	2	1.3 ± 0.9	0	0
Valley Bog	1830	5	2.0 ± 0.9	0	0	0	0
Bog Hill Mine	1830	2	0.8 ± 0.6	0	0	0	0
Rough Sike	1870	0	0	0	0	0	0
Moss Burn A	1870	2	0.8 ± 0.6	0	0	0	0
Moss Burn B	1870	6	2.4 ± 1.0	0	0	0	0
Netherhearth Sike	1870	1	0.5 ± 0.5	0	0	0	0
Burnt Hill	1870	Not sampled		1	0.5 ± 0.5	0	0
R. Tees	1520	11	6.0 ± 1.8	2	1.2 ± 0.8	2	1.3 ± 0.9
R. Tees	1575	31	10.8 ± 1.8	23	11.6 ± 2.2	9	6.1 ± 2.0
R. Tees	1610	8	3.2 ± 1.1	3	1.9 ± 1.1	0	0
R. Tees	1670	9	3.5 ± 1.2	2	1.1 ± 0.8	1	0.7 ± 0.7
R. Tees	1710	0	0	0	0	0	0
Tees Bridge	1740	12	5.4 ± 1.5	1	0.6 ± 0.6	0	0
R. Tees	1750	0	0	0	0	0	0
R. Tees	1815	16	7.8 ± 1.9	0	0	0	0
R. Tees	1850	0	0	0	0	0	0
Trout Beck	1710	2	1.1 ± 0.8	1	0.6 ± 0.6	0	0
Trout Beck Bridge	1710	10	4.7 ± 1.5	1	1.0 ± 1.0	0	0
Trout Beck	1780	4	1.7 ± 0.8	0	0	1	0.7 ± 0.7
Trout Beck	1840	4	1.7 ± 0.8	0	0	0	0
Trout Beck	1875	0	0	0	0	0	0
Trout Beck	1940	0	0	1	0.6 ± 0.6	0	0
Trout Beck	1975	0	0	4	3.1 ± 1.5	0	0
Trout Beck	2170	Not sampled		1	0.6 ± 0.6	0	0

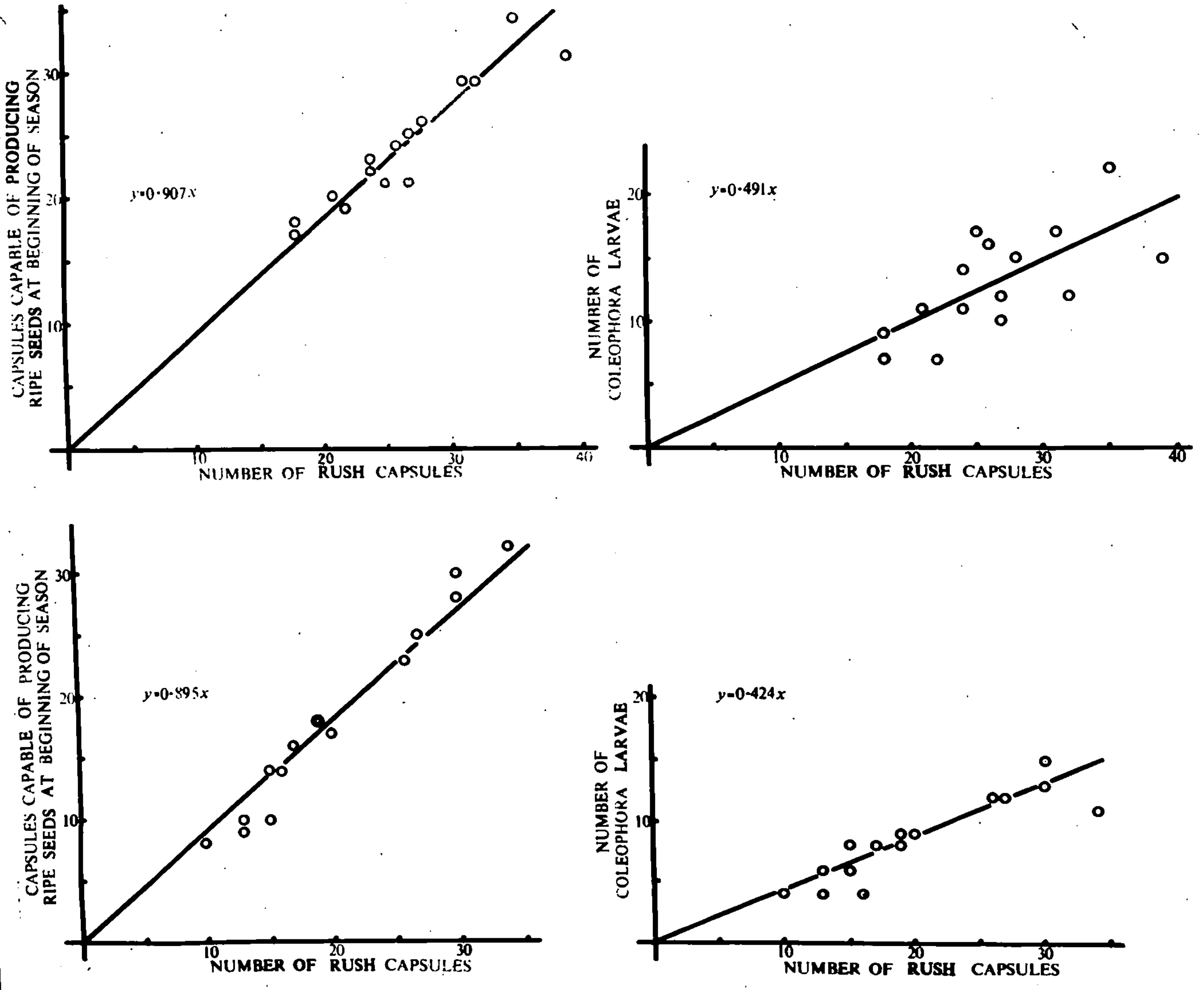

Fig.31. Numbers of J.squarrosus capsules capable of producing ripe seeds at the beginning of the season, and of Coleophora larvae, on each of fifteen rush stems, at two sample stations of transect A in 1952.

year. For smaller percentage values there is not such a close similarity in the proportions between each stem, but with lower values greater variation is to be expected.

Fig. 31 does, however, suggest that the statistical method employed is valid, in that there appeared to be a very definite relationship between the proportions of ripening capsules (and Coleophora) to the total capsules between the various stems included in each sample.