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STUDIES ON THE THRIPS (THYSANOPTERA) SPECIES MOST COMMONLY OCCURRING ON CEREALS IN FINLAND

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HELSINKI 1970

PREFACE

The present study was principally carried out at the Department of Pest Investigation of the Agricultural Research Centre at Tikkurila, Finland, in the years 1960—66. During this time the author was employed at the Office for Plant Protectants in both advisory and educational work and as an inspector of plant protectants. Later, in the years 1967—69, the study was continued in the Ahlman Agricultural College, Tampere, in addition to teaching work.

I wish to express my sincere gratitude to Professor Veikko Kanervo, Head of the Department of Pest Investigation, Tikkurila, who made this work possible and whose expert advice has been of immense value to me during all phases of this work. I also wish to thank Professor Esko Kangas, Head of the Department of Agricultural Zoology of the University of Helsinki, for his helpful criticism of the manuscript.

The manuscript was translated by Messrs. Martyn Summerhill and Rolf Erlewein, with linguistic revision by Mrs. Jean Margaret Perttunen; to them all my thanks are due.

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To the Agricultural Research Centre I am greatly indebted for the publication of this work.

Tampere, May 1970

Pekka Köppä

Helsinki 1970. Valtion painatuskeskus

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I. INTRODUCTION

Studies on thrips were begun quite early in Finland. In his publication on the Finnish thrips fauna, O. M. Reuter (1899) mentions as many as 59 different species, more than ten of which occurred on grasses and cereals.

The importance of thrips as pests of cereals and cultivated grasses in Finland has also been recognized for a long time. This emerges most clearly from the reports on the incidence of pests that have been published over the years. For instance, as long ago as 1897—98 attention was drawn to whiteheads on grasses, a phenomenon in which insects were believed to play an important role (E. Reuter 1898, 1899). The pest report of the following year (E. Reuter 1900 b) already gave a clearer explanation of whiteheads and its causes in Finland, and mentioned the grass thrips (*Aptinothrips rufus* Gmelin.), the biology of which was briefly described, as one of the causes.

Whiteheads were later found on cereals also, and various species of thrips were shown to be responsible (E. Reuter 1901 b, 1903, 1906, 1909, 1910, 1912 a, 1912 b, 1914 a, 1914 b, Linnaniemi 1916, 1935, Hukkinen and Vappula 1935, 1936, Hukkinen et al. 1936, Vappula 1935, 1938, 1939, 1956, 1960). The importance of thrips as pests of cultivated grasses and cereals in Finland has been mentioned not only in reports on pests but also in many other publications (E. Reuter 1900 a, 1901 a, 1902, Hukkinen 1917 a, 1917 b, 1925, 1934 a, 1934 b, 1936 c, Brummer 1939, Kanervo 1950, Vappula 1955).

In his monograph on the pest fauna of cultivated plants in Finland, Vappula (1965) bases his survey on data regarding the incidence of pests gathered at the Department of Pest Investigation. He draws particular attention to the destructiveness and economic significance of thrips. Thus in rye the damage to the ear caused by *Limothrips denticornis* Hal. was estimated as 25—30 % in some cases, with a reduction in yield amounting in the worst cases to as much as 5—10 %. *Frankliniella tenuicornis* Uz. may be regarded as one of the most harmful pests of barley. According to studies carried out in 1931 by Kanervo (1950), it caused an average loss of 12 % in barley at 32 localities in Ostrobothnia, 2—30 % of the grains being destroyed. In August 1964, a report was received at the Department of Pest Investigation on a case of damage to Åsa barley at Muhos, where estimates put the yield loss at 50 % or even 70—80 % and in places as high as 100 %, so that it did not pay to harvest the crop. The damage was attributed to *F. tenuicornis*.

Hukkinen (1934 b) mentions *Haplothrips aculeatus* Fabr. as the cause of severe damage to wheat in southwest Finland. Later, Brummer (1939) found that this species was a destructive pest of rye in Finland, for studies in 1937 showed that it was responsible for 2.6—9.1 % of all the empty spikelets observed. Tiittanen (1954) has drawn attention to the damage to grains of wheat caused by *H. aculeatus* in 1950—51.

Apart from direct reduction of grain yield, thrips have also caused a reduction in the quality of the Finnish cereal crop and an increase in its susceptibility to fungal pathogens (Nuorteva 1952, Nuorteva and Kanervo 1952).

Severe damage both to cultivated and to wild grasses has been caused not only by the above species but also by *Chirothrips hamatus* Tryb., *Chirothrips manicatus* Hal. and *Aptinothrips stylifer*

Tryb. and *rufus*. Especially the damage done by *C. hamatus* to meadow foxtail is occasionally very severe (HUKKINEN 1936 c). Reports on pests and other publications do not ascribe much importance to *Anaphothrips obscurus* Müll. as a plant pest in Finland, although it is quite common and abundant on cereals and cultivated grasses (KÖPPÄ 1967).

It is clear from the foregoing that the injuriousness of thrips living on cereals has been convincingly demonstrated in Finland, and that there is good reason to regard these species as pests of economic importance. As the studies of HUKKINEN and KANERVO on these species were never completed, it was decided, in view of the importance of the damage done by thrips to cereal crops, to include this problem in the research programme of the Department of Pest Investigation for the early 1960s. This research consequently got off to a good start, and later, from 1966 onwards, was continued outside the Department.

The present study is the fourth in a series dealing with the thrips species of cereals in Finland. The previous papers in the series dealt with the thrips fauna of cereals (KÖPPÄ 1967), the hibernation of thrips (KÖPPÄ 1969 a) and the sex index of thrips (KÖPPÄ 1969 b).

II. PREVIOUS STUDIES

Along with identification of thrips species and reports of the damage they cause, attention has been devoted to their biological characteristics.

The earliest studies on the subject merely clarified the biology and life cycle of thrips. Thus HALIDAY (1836), who carried out the first extensive study of thrips species, observed that their development was extremely rapid, many generations being produced in a single summer. Yet the author was apparently not completely aware of the developmental stages of thrips, for he neglected to mention any prepupal stage. In his systematic section, he mentions several thrips species, some of which occur in Finland, as inhabiting cereals and grasses, although he placed the main emphasis on *Limothrips cerealium* Hal., which had been recognized as a pest since the beginning of the nineteenth century. JORDAN (1888) provided further details of the development of thrips. His study mentions the prepupal stage. It also describes the mode of reproduction of thrips, the ratios between the sexes, and the dimorphism that occurs in several species.

Towards the end of the nineteenth century, investigators began to pay special attention to the thrips inhabiting cereals and grasses, obviously because these species were widespread and important. One very much studied species was *L. denticornis*, already mentioned by HALIDAY (1836). Much greater knowledge of this species is shown by LINDEMAN (1886, 1887), who referred to it as *Thrips secalina* Lindmn. His studies were carried out in Central Russia, and they provide quite detailed information on the developmental stages of this species and on its life cycle during the course of the summer. The results are evidently based exclusively on observations made in the field. Somewhat later, TRYBOM (1894) published a report on the incidence, biology and injuriousness of the same species in Sweden. Subsequently, information on the biology of this species has been revised and improved. PUSSARD-RADULESCO (1931) studied the biology of the species in France, and especially the migrations of the females from one plant to another. The mating of the species was also described in detail. Von OETTINGEN (1942), in his extensive studies based on observations on samples of thrips taken from grass stands, gives the durations of the developmental stages of this species in field conditions. Some of the most recent studies on the biology of *L. denticornis* have been done by HOLTMANN (1963 a) in West Germany. These studies clarify the development of the species on a number of cereals and the durations of the various development stages on these, and give data on the number of eggs produced by the females, on the sex ratio and on the migrations of the species during the summer. Studies of the biology of *L. denticornis* have also been made by KURDJUMOV (1913 a) in Russia, ROSTRUP et al. (1940) in Denmark, and FRANSSEN and MANTEL (1965 a, 1965 b) in the Netherlands, as well as by others.

The developmental biology of *A. obscurus* has been the subject of relatively little investigation, despite the fact that the species is quite widespread (von OETTINGEN 1955). The most extensive studies were made as much as seventy years ago. Evidently, the economic importance of this species is now rated as rather low. The biology of the species was most accurately described by HINDS (1900, 1902) and FERNALD and HINDS (1900). These latter studies, which were carried out in North America, were based on laboratory rearing tests, and the results supplemented with field observations. The studies provide data on the life cycle, the duration of the different developmental stages, the number of eggs per female, the sex ratio, the number of generations and the occurrence of dimorphism. The sex ratio of the species was also studied in the U.S.A. by CARY (1902) and SHULL (1909, 1914 a). There has been very little research on this species in Europe. Its biology has been studied in Europe chiefly by MORISON (1943, 1957) and WETZEL (1964).

F. tenuicornis is a widespread species of thrips living on cereals (von OETTINGEN 1955). Yet over most of its range it would appear to be of minor importance as a pest, as its biology has been little studied. Some investigations on the subject have been carried out, for instance in Sweden (JOHANSSON 1938), Great Britain (MORISON 1943) and East Germany (WETZEL 1964). It is perhaps in Finland that most attention has been devoted to the species. Passages dealing with the biology of the species occur even in the papers by HUKKINEN (1932, 1936 a), although KANERVO (1950), who began and largely completed his investigations in 1931, gives a more comprehensive picture of the development of the species on cereals, despite the fact that his article is primarily concerned with its destructiveness. It cannot be denied, however, that the developmental biology of this species has been greatly neglected, although more detailed information on the subject is necessary, at least in Finland, in view of its widespread occurrence and great abundance.

H. aculeatus is one of the most extensively investigated species of thrips, mainly because its range is extensive (von OETTINGEN 1955) and the damage it causes is well known (BELING 1872, SZANISZLO 1879, LINDEMAN 1886, 1887, TRYBOM 1895, RIBAGA 1902, KURDJUMOV 1913 b, STRANAK 1920, BLATTNY 1923, KÖRTING 1934, BRUMMER 1939, KRATOCHVIL 1939, BLATTNY et al. 1942, von OETTINGEN 1952 a, TANSKY 1961).

LINDEMAN (1886, 1887) was the first to describe the biology of this species, primarily in the conditions of Central Russia. The conclusions he reports on the development of the species are based on observations made in the field. Later, TRYBOM (1895) mentions some special features in the life of this species, as does KURDJUMOV (1913 a, 1913 b). But only KÖRTING (1930, 1934) seems to have studied the biology of *H. aculeatus* in great detail and to have made accurately controlled laboratory tests by means of which the various developmental stages and their duration could be clarified. The results he obtained in the laboratory were supplemented by field observations. Later studies (BRUMMER 1939, HOLTMANN 1963 a, WETZEL 1964) have revealed certain other features in the life of this species. Attention has been paid to the species not only as a plant pest but also as a natural enemy of various other insects and mites (ZNAMENSKY 1914, BREMER and KAUFMANN 1931, KNECHTEL 1931).

In addition to the above, many other species of thrips live on cereals and grasses. In Finnish conditions, however, the numbers of these other species on cereals are relatively low. Such species include *A. stylifer*, *C. hamatus* and *C. manicatus* (KÖPPÄ 1967). The biology of these species, too, has previously been investigated to some extent. Thus HUKKINEN (1936 c) carried out a thorough study of *C. hamatus* as a pest of the seed of meadow foxtail. The study also includes accurate data on the development of this species. Of the *Aptinothrips* species, the best known in respect of biological characteristics is *A. rufus* (RADULESCO 1930, PUSSARD-RADULESCO 1931, SHARGA 1933), which in Finland mainly inhabits grasses. Some thrips species that occur elsewhere as pests of cereals are not found in Finland at all. Among these, mention may be made of *L. cerealium*, which has long been recognized as a pest (HALIDAY 1836) and the biology of which has consequently been investigated in great detail (JORDAN 1888, KÖRTING 1930, JOHANSSON 1938, LEWIS 1959, 1963, HOLTMANN 1963 a, FRANSSEN and MANTEL 1965 a, 1965 b). Another thrips species of this kind is *Stenothrips graminum* Uz., which is found in various other parts of Europe as a pest of oats (KURDJUMOV 1913 a, KOLOBOVA 1926, KRATOCHVIL 1939, HOLTMANN 1963 a, FRANSSEN and MANTEL 1965 a, 1965 b).

Hibernation is one of the most critical phases in the life cycle of thrips and has also been investigated extensively. Most investigations have been made on the thrips species of cereals and grasses. Studies dealing purely with hibernation have been made by PRIESNER (1924 a), KÖRTING (1928), LEWIS and NAVAS (1962), LEWIS (1962, 1963), WETZEL (1963) and KÖPPÄ (1969 a). In addition, scattered observations on the hibernation of various species of thrips have been published by many research workers (LINDEMAN 1886, 1887, JORDAN 1888, HINDS 1900, 1902, FERNALD and HINDS 1900, HEWITT 1911, KURDJUMOV 1913 a, KÖRTING 1930, HUKKINEN 1932, 1936 a, von OETTINGEN 1936, BAILEY 1938, 1948, ROSTRUP et al. 1940, MORISON 1943, WEITMEIER 1956, HOLTMANN 1963 a, FRANSSEN and MANTEL 1965 a, 1965 b).

The effects of environmental factors on the development and behaviour of thrips have also been studied. Attempts have been made in laboratory and in field cultures to investigate the behaviour of various thrips species — chiefly those infesting cereals — in different conditions of temperature, humidity and light (CEDERHOLM 1963, HOLTMANN 1963 b). Observations have also been made on the effects of various chemical and contact stimuli on thrips (MORGAN and CRUMB 1928, HOLTMANN 1963 b). All factors of this kind have a certain importance in guiding the insects towards suitable places for feeding, reproduction and hibernation.

The environmental factors, weather factors in particular, also have a considerable effect on the sizes of thrips populations on cereals and grasses and their fluctuations in abundance during the course of the growing season (SCHANDER and GÖTZE 1928, JOHANSSON 1938, von OETTINGEN 1942, KLINKOWSKI and EICHLER 1948, SCHOBER 1959, WETZEL 1962, HOLTMANN 1963 a), and it has been found that such factors also have an effect on the abundance of thrips inhabiting other plants (e.g. HORSFALL and FENTON 1922, EVANS 1934, WILKINSON 1939).

The size of thrips populations and their fluctuations in abundance during the summer have been most accurately described by JOHANSSON (1938), von OETTINGEN (1942) and WEITMEIER (1956). Studies of this type are always based on identical samples gathered from the vegetation regularly at short intervals, usually by netting. JOHANSSON (1938) collected his samples from cereal fields, while the other investigators took theirs from stands of grass, from which samples can be taken over a longer period.

III. MATERIAL AND METHODS

The present investigations on the biology and abundance of thrips species infesting cereals were carried out in 1960—69. Cultures were maintained, both indoors in the laboratory and outdoors, in strictly controlled conditions, and these were used to investigate the biological features. The information obtained from these tests was supplemented whenever possible by field observations. Rearing tests were mostly carried out at the Department of Pest Investigation at Tikkurila, but were continued in 1967—69 at the Ahlman Agricultural College in Tampere.

The abundance of thrips was investigated by means of samples netted from various species of cereals. These samples were taken at Tikkurila in 1960—66 and at Somero in 1961—65. Samples of thrips were also collected for the same purpose from leys grown for cutting and seed leys.

The investigations dealt with the biology and abundance of the species *Limothrips denticornis* Hal., *Anaphothrips obscurus* Müll., *Frankliniella tenuicornis* Uz. and *Haplothrips aculeatus* Fabr. These species have been shown to damage cereal crops (Köppä 1967).

A. Experimental studies

1. Biology of development

The present investigations deal with the preoviposition period, host plants, oviposition and development of the individual from egg to adult.

a. The preoviposition period

The females of both the hibernating and the new thrips generation are not immediately able to lay eggs, but the ovaries develop gradually.

To ascertain the duration of the preoviposition period in the hibernation period, samples of rye and of ley grasses were gathered in autumn, winter and spring at intervals of about one month and were dried at room temperature for 24 hours. Then 15 females of the species studied were gathered from the sample and placed individually in glass tubes for oviposition, the tube being 6.5 cm long, with an internal diameter of 0.9 cm (Fig. 1).

The tubes were tightly corked. Each tube contained a shoot of cereal or grass as a substratum for oviposition. The cultures were examined with a microscope every day, and the shoot was replaced when it had become too dry. Except in wintertime, the duration of the preoviposition period was studied from the emergence of the adult onwards, too. The female specimen was transferred to the rearing tube im-

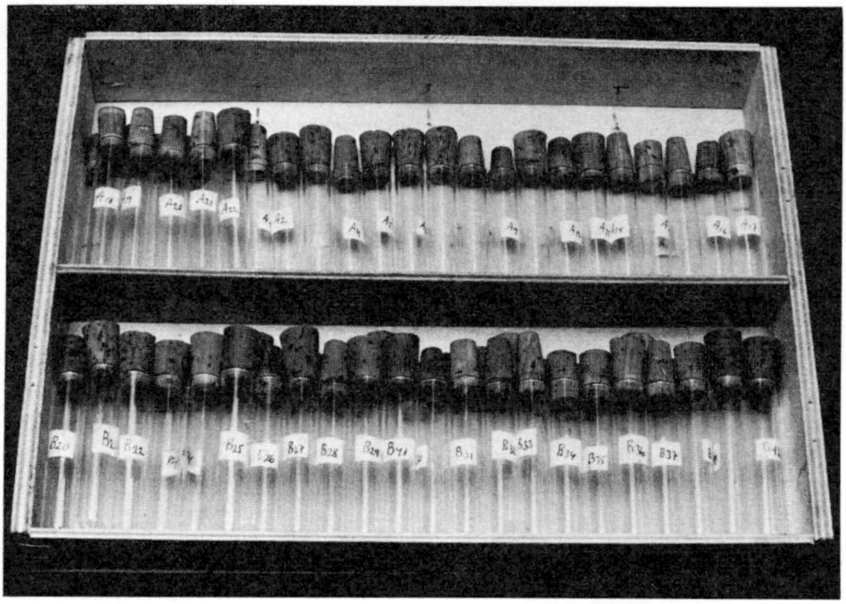

Fig. 1. Glass tubes used for the oviposition cultures of thrips. Photo: Institute of Photography, Helsinki.

mediately after emergence, and a watch was kept for the start of laying.

b. Host plants

As the cultivated cereals and the cultivated and wild grasses in Finland all belong to the same family (*Gramineae*), it can be assumed that the thrips species occurring in great abundance on the cereals are able to reproduce on very many other members of this family. To investigate this question, females of the species studied were placed on shoots of different species of plants and inserted into rearing tubes as above. If the females laid eggs on the shoots and the larvae that hatched were able to survive to adulthood, the plant in question was considered to be a host plant of the species, i.e. a plant, on which it could both feed and reproduce.

c. Oviposition

In the present studies on oviposition, attention was devoted mainly to the number of eggs produced by the females, to the length of the oviposition period and to the distribution of the eggs on the plants.

To ascertain the number of eggs laid, 15—20 females were placed singly in rearing tubes for oviposition as above, with a shoot of cereal or timothy as substratum. Every 3 days a fresh shoot was substituted for the one in the tube, and a count was made of the number of eggs on the shoot removed. This was done both with females that had hibernated and with adult females of the new generation that had developed in early summer, the number of eggs being counted separately for each group. On the cessation of egg laying or the death of the females, the length of the oviposition period could be determined. Tests of this type were employed to ascertain the number of eggs laid by *F. tenuicornis* and *A. obscurus*. A different kind of culture tube was used to study the oviposition of *L. denticornis* and *H. aculeatus* (Fig. 2). A glass tube 7 cm long and 1.4 cm in diameter, containing water was sealed with a porous plastic stopper and through a small hole in this a plant shoot was pushed until its cut end dipped into the water. A glass cylinder c. 1.8 cm in diameter and 15 cm long, open at one end and covered at the other with fine-mesh gauze was used to protect the protruding part of the shoot. To keep the parts of apparatus in place, they were sunk into a large hollow cork in such a way that half the thickness of the cork was round the bottom end of the larger tube, and half round the upper end of the smaller tube. The shoots were replaced every 4 days and the eggs on the shoot removed were counted. A shoot on which the ear was emerging from the sheath, and on which the female could therefore lay eggs inside the sheath, was used as the egg-laying substratum for *L. denticornis*. A similar shoot, or one in which the ear had recently emerged from the sheath, was used for *H. aculeatus*. This allowed the females to lay on the ears or spikelets. To facilitate the work of counting the eggs, the upper part of the ear was cut off so that only a few spikelets remained on the rachis.

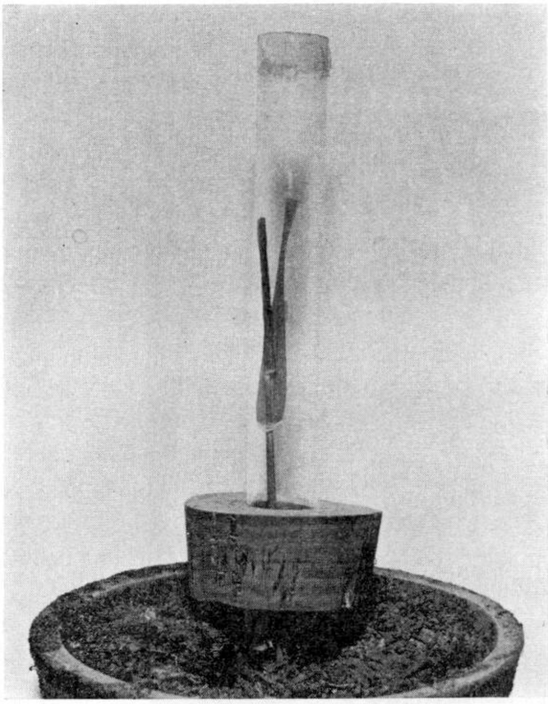

Fig. 2. Rearing tube used for the oviposition cultures of thrips. Fuller description in the text. Photo: J. Rautapää.

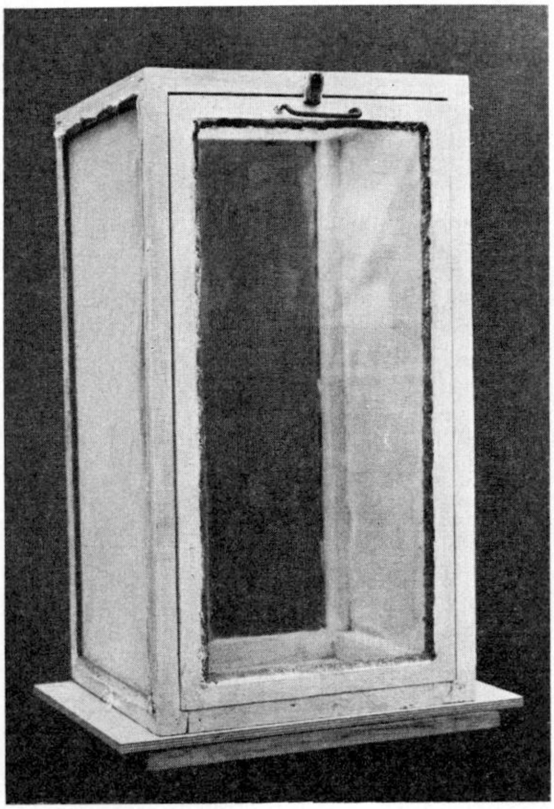

Fig. 3. Cage used for investigating of the distribution of thrips eggs on plants. Photo: Airi Varis.

To ascertain the site where the eggs were laid on the plants, tests were made in cages outdoors. The cages (Fig. 3) used for this purpose were 60 cm high and 30 cm square. The side walls were of gauze; the roof and the back and front walls, the latter of which could be opened, were of glass. Three cereal plants growing in a single pot were placed in each cage, on which 100 females of the thrips species to be studied were allowed to lay for 5 days. The plants were then cut off at soil level, and the distribution of the eggs noted. For this purpose, each leaf was divided into quarters, beginning at the base, and counts were made of the number of eggs on each leaf and each quarter-leaf. On plants that had come or were coming into ear, egg counts were made on the leaves and also inside the sheaths. The uppermost sheath was also divided into quarters for egg counting.

d. Developmental stages

To determine the duration of the egg stage, a fairly large number of females of the thrips species studied were placed in the same kind of culture tubes as were used to ascertain the number of eggs and the oviposition period of *L. denticornis* and *H. aculeatus*. For *F. tenuicornis* and *A. obscurus*, however, shoots with enough leaf area for egg-laying were selected. Some of the cultures were kept indoors in two separate rooms which had fairly constant but slightly different temperatures. Other cultures were kept outdoors, and development in these corresponded more closely to the life cycle in field conditions. The females were allowed to lay eggs in the tubes for 24 hours, and were then removed, the eggs being left to develop in the same conditions. The cultures were checked daily, the temperatures recorded, and hatched larvae transferred singly to shoots or spikelets placed in small glass tubes as described above. The subsequent development of the larvae was checked daily, and moulting recorded whenever possible, in order to ascertain the durations of the various larval instars. When the shoot in the tube began to wilt, it was replaced with a fresh shoot. When the larva had become full-grown, the cultures were examined twice every 24 hours to ascertain as accurately as possible the lengths of the prepupal and pupal stages. Thereafter the shoot did not have to be replaced as food but only to maintain the correct humidity in the rearing tubes. The moulting times of prepupae, pupae and adults were carefully recorded. In the case of species in which both sexes occur, an attempt was also made to compare the rates of development of the two sexes whenever sufficient numbers of females and males were obtained in the cultures.

Endeavours were made to rear the larvae until they reached the adult stage. It was consequently possible to ascertain the whole length of the period of development from the results of the rearing tests in known conditions.

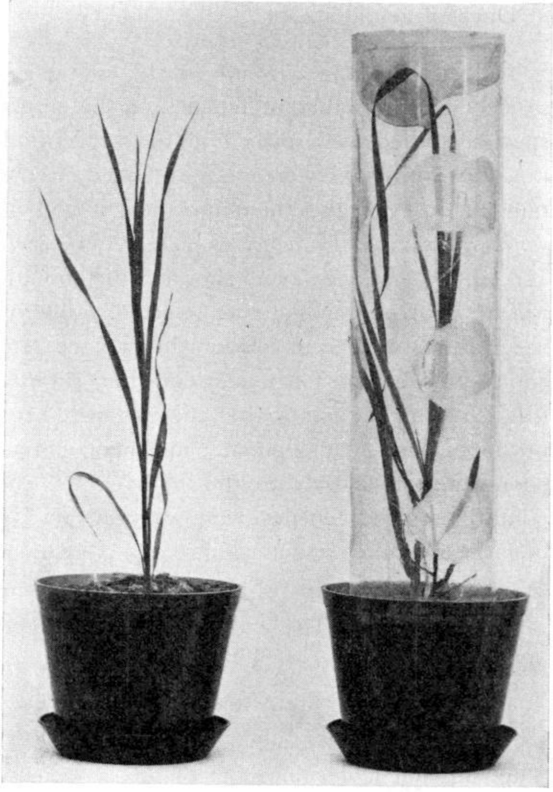

Fig. 4. Plastic box cage used in the investigations on dimorphism. Fuller description in the text. Photo: Institute of Photography, Helsinki.

2. *Dimorphism*

A. obscurus occurs in both a macropterous and a brachypterous form. Individuals of this species were reared in varying conditions in order to discover what factors might be concerned in determining wing length.

The plants serving as food and oviposition substratum were grown individually in flower-pots, and an endeavour was made to select specimens of exactly the same size. The plant and the thrips on it were enclosed within a cylindrical cover of PVC, 37 cm high and 9 cm in diameter (Fig. 4). To the top of the cover was attached a 12 cm extension of gauze which could be pressed together and closed at the top with a plastic clip. Scattered around the plastic cover were nine holes each 3 cm in diameter and also covered with gauze.

To establish the effect of day length, the following tests were set up. Macropterous specimens were inserted for laying in some of the cultures, and brachypterous specimens in others. The food plants were oats and timothy. Some of the cultures were kept in total darkness from 16:00 hrs under light proof covers made of stiff cardboard, under which there was space for 10 flower-pots with test plants. At 08:00 hrs the cover was removed. Photoperiods were established well before the larvae moulted.

Rearing tests were also made by placing varying numbers of this thrips species on plants of the same size, with a view to investigating the effect of population density on wing development. These cultures, like those mentioned above, were kept outdoors. The females were allowed to lay eggs in the cultures as long as they remained alive, and the progeny were allowed to develop into adults. Counts were made of the numbers of brachypterous and macropterous progeny from the different treatments, and the ratios of the two forms were calculated.

Tests were also set up to ascertain the stage at which the species is susceptible to external factors that might affect wing development. For this purpose, the females were allowed to lay eggs for 48 hours on plants growing in flower-pots, and then removed. The plants, with the eggs and subsequent larvae, were taken in a series of cultures at 48-hour intervals and then subjected to short-day treatment, being allowed only 8 hours of light per day. From the wing form of the emerging progeny in these series of cultures, it could be inferred whether these factors have any effect and, if so, at what stage of development the species is susceptible to factors determining wing form.

B. Studies on abundance

Attempts were made to investigate the abundance of thrips species infesting cereal crops, chiefly on the basis of samples netted from various species of cereals. The same data had been employed earlier to ascertain the thrips fauna of cereals (KÖPPÄ 1967). As the samples were netted throughout the growing season, they could be used for comparison of the life cycle of these species of thrips and of the fluctuations in their abundance during the summer. During the growing season samples were netted at intervals of about a week between noon and 14.00 hrs, weather permitting. If it was raining, or the stand was still wet after rain, collection of the sample was postponed to the next fine day. Nor were samples netted when the wind was strong. Every sample comprised 25 double sweeps of the net, equivalent to c. 30 m^2 of field. The sampling method has been described in greater detail in previous studies (KÖPPÄ 1967).

Samples of shoots, ears or panicles were taken from various cereal plants in 1960—61. In 1960, every sample contained 25 shoots, and, in 1961, 50 shoots, ears or panicles, samples being taken throughout the growing season. The results obtained from these samples have been used mainly to supplement the studies on the composition of the thrips fauna made with netted samples and to show on what parts of the plant the various species lived. Mainly because of the small number of specimens obtained from them, however, these samples were not used to clarify the relative abundances of the various species and the fluctuations in these values during the growing season, although such samples are very suitable at the shooting and earing stages, when it is difficult to take samples with a net.

C. Weather conditions during the research period

The weather conditions of the research period are described by two graphs (Figs. 5 and 6), the former showing the average temperatures and the latter the amount of precipitation at Tikkurila in the growing seasons of 1960—66. During these years the cereal crops provided the samples used to investigate the abundances of the thrips and the fluctuations in numbers through the growing season. The average temperatures were obtained from the Department of Meteorology, and are based on measurements made at an altitude of 2 metres by the Department of Plant Husbandry of the Agricultural Research Centre. The average temperatures and the precipitations in the graphs are shown by 5 day-periods for May-August of the different years. The temperature conditions in the growing seasons of the research years show considerable variation (Fig. 5). The summers of 1960, 1961, 1963, 1964 and 1966 were warmer than average, especially in early summer, while the summers of 1962 and 1965 were cool. The relations between the temperature and the rate of development of the thrips, and also the abundance and its fluctuations, are dealt with below in the light of these data.

In Finland, the early part of summer is usually fairly dry. A dry period starts soon after the spring sowing and lasts until the end of June. But there is plenty of rain in late summer, and August is the rainiest month (JUUSELA 1963). This tendency is clearly discernible in the rainfall of the research period (Fig. 6). Rain in late summer in particular is often associated with chilly weather, and these factors in combination may be detrimental to the development of thrips. The light rainfalls that may occur even early in summer may temporarily affect the sampling thrips, for the insects will shelter from the rain and be less easy to catch with a net than in dry weather. Further, rain always interferes with sampling with a net or prevents it entirely.

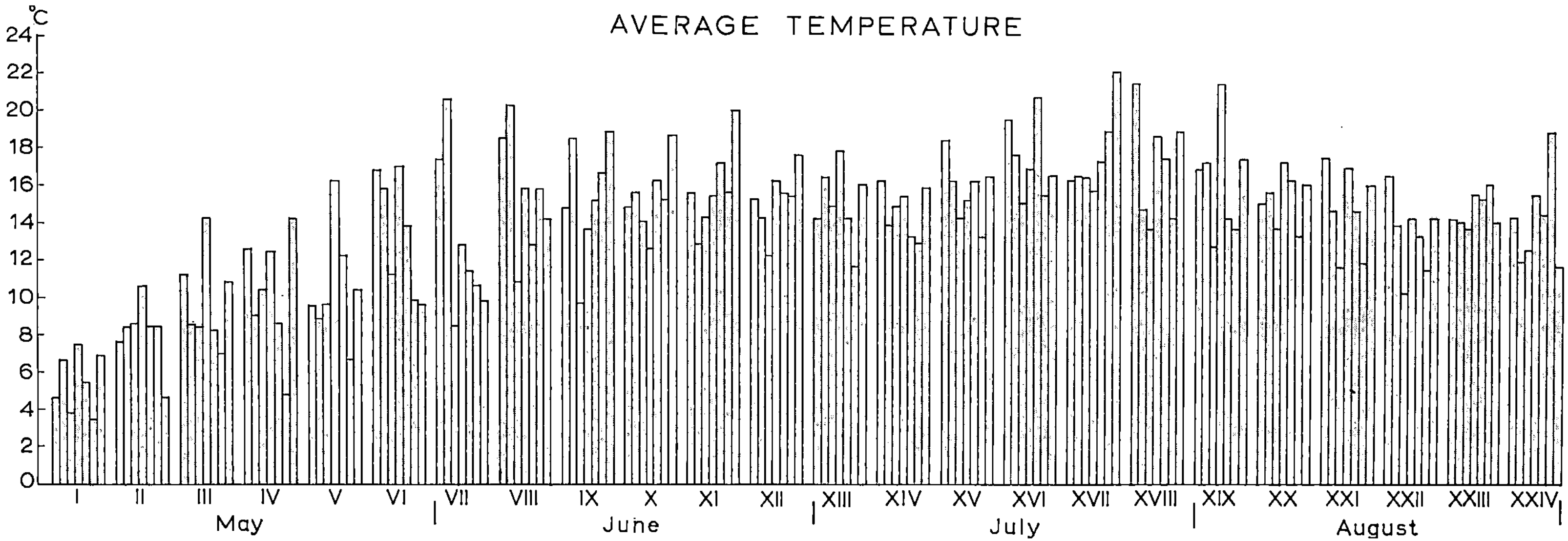

Fig. 5. Average temperatures by 5-day periods at Tikkurila in 1960—66. The periods of the same date are grouped together, the earliest at the left, and the progress of the season likewise runs from left to right.

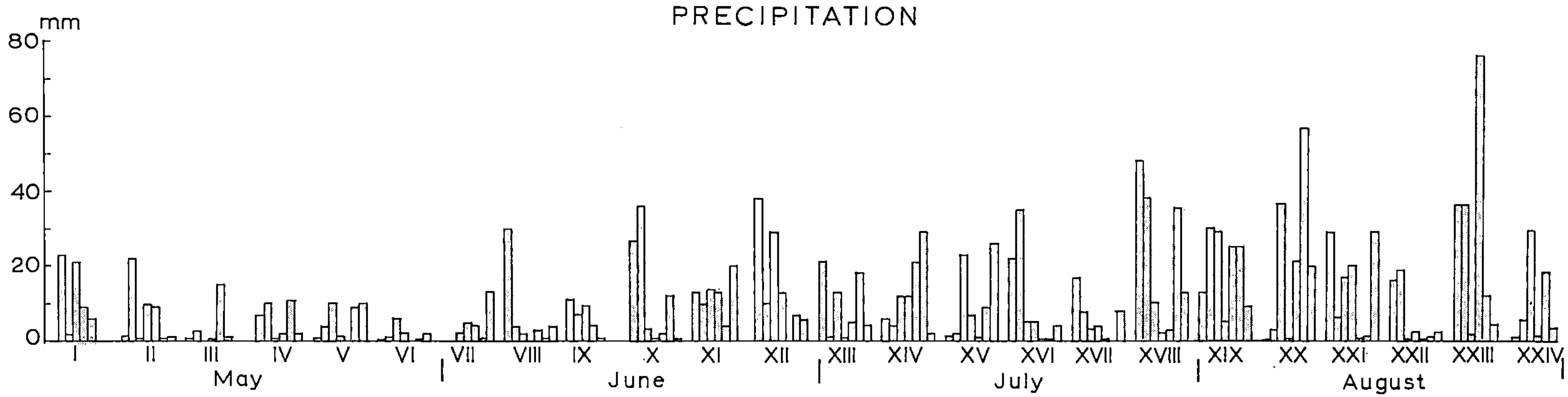

Fig. 6. Precipitation by 5-day periods at Tikkurila in 1960—66. The periods of the same date are grouped together, the earliest at the left, and the progress of the season likewise runs from left to right.

IV. BIOLOGY OF DEVELOPMENT

A. Limothrips denticornis Hal.

This species is also known under the name *Thrips secalina* Lindmn. (LINDEMAN 1886, 1887).

1. Distribution

L. denticornis occurs everywhere in Europe (PRIESNER 1926). It is also encountered in Asia, e.g. in Siberia (SCALON 1931) and Khazakstan (TANSKY 1961). Von OETTINGEN (1951, 1955) regards this species as largely Eurasian and Palearctic, but it is probably mainly Holarctic, for it also occurs in North America: in the United States (HERRICK 1924, HOOD and HERRICK 1926) and Canada (ANON. 1966).

2. Host plants

L. denticornis lives and reproduces on all species of cereal grown in Finland. It seems, however, to prefer rye and barley, on which its abundance has been shown to be high (KÖPPÄ 1967). Vigorous reproduction of the species on these plants is reflected in the low sex index. *L. denticornis* males are apterous and are thus unable to migrate long distances from one host plant to another. Thus a high proportion of males indicates that a plant is a suitable host for the species. And rye (cf. p. 195, THEOBALD 1922, SOLOVEV 1927, SHCHELKANOVTZEV 1929, STRAWINSKI and SECZKOWSKA 1952) and barley THEOBALD 1922) have been found in particular to suffer the most severe damage. It seems, however, that the species occurs only sparsely on oats in Finland (KÖPPÄ 1967), although elsewhere it has been reported to be one of the most injurious species of thrips on oats (RIBAGA 1902, STRANAK 1920, KRATOCHVIL 1939, BLATTNY et al. 1942).

L. denticornis feeds and reproduces not only on cereals but also on cultivated ley grasses, as can be seen from the results (Table 1) of the host-plant tests carried out in summer 1967. But it cannot reproduce, on ley legumes, although some species of wild grass provide it with suitable sites of reproduction (Table 1). Many of these latter plants are quite common in Finland in fields, by roadsides and on ditchbanks. Together with moss and forest litter, wild grasses also provide attractive hibernation sites for this species. *L. denticornis* is to be found on many plant species in addition to those above, but most of them are only places of temporary shelter providing no facilities for feeding or reproduction.

3. Sex index

Depending on the circumstances, the sex index of *L. denticornis* varies greatly from year to year. It also seems to vary on different species of host plant (KÖPPÄ 1969 b). The results of samples netted at Tikkurila in 1960—65 show that the sex index averaged 72.1 % on rye, this figure showing the proportion of females in the population. It was 82.9 % on barley, 92.3 % on winter wheat, 93.0 % on spring wheat and 90.0 % on oats. Samples netted at Somero gave similar results. The males of this species are thus not as rare as was assumed by SCHILLE (1912), HUKKINEN (1935) and others.

The sex index varies a great deal in the course of the growing season. Only the females of *L. denticornis* hibernate. The first males appear only when the new generation becomes adult, but they are short-lived and die before the coming of winter. This is also suggested by the observations made by BAGNALL (1909), WILLIAMS (1913), MALTBAEK (1932) and MELIS (1960). However at some point during the summer males may be more numerous than females (KÖPPÄ 1969 b). This frequently occurs when the new generation emerges, for the males usually develop more quickly, while some, at least, of the females of the old generation are dead by that time.

4. Hibernation

Forest edges appear to be the most attractive hibernation sites for *L. denticornis* (KÖPPÄ 1969 a),

Table 1. Host plants of *L. denticornis* Hal., *A. obscurus* Müll., *F. tenuicornis* Uz. and *H. aculeatus* Fabr.
(x = occur, o = do not occur, — = not investigated)

Plant species	*L. denticornis*		*A. obscurus*		*F. tenuicornis*		*H. aculeatus*	
	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae
Secale cereale	x	x	x	x	x	x	x	x
Triticum aestivum	x	x	x	x	x	x	x	x
Hordeum vulgare	x	x	x	x	x	x	x	x
Avena sativa	x	x	x	x	x	x	x	x
Zea mays	x	x	x	x	x	x	—	—
Sorghum vulgare v. sudanense	x	x	x	x	x	x	—	—
Phleum pratense	x	x	x	x	x	x	x	x
Alopecurus pratensis	x	x	x	x	x	x	x	x
Festuca pratensis	x	x	x	x	x	x	x	x
F. rubra	x	x	x	o	x	x	x	x
F. ovina	—	—	o	o	x	o	—	—
Dactylis glomerata	x	x	x	x	x	x	x	x
Lolium perenne	x	x	x	x	x	x	x	x
L. multiflorum	x	x	x	x	x	x	x	x
Poa pratensis	x	x	x	x	x	x	x	x
P. annua	x	x	x	x	x	x	x	x
Bromus inermis	—	—	x	x	x	x	—	—
Phalaris arundinacea	—	—	x	x	x	x	—	—
Agvostis vulgaris	—	—	x	x	x	x	x	x
Calamagrostis sp.	x	x	x	x	x	x	—	—
Deschampsia caespitosa	x	x	o	o	x	x	x	x
D. flexuosa	x	x	o	o	o	o	x	x
Triticum repens	x	x	x	x	x	o	x	x
Anthoxanthum odoratum	o	o	x	x	x	x	—	—
Trifolium pratense	o	o	o	o	o	o	o	o
T. hybridum	o	o	x	o	x	o	o	o
T. repens	o	o	o	o	o	o	o	o
T. resupinatum	o	o	o	o	o	o	o	o
Medicago sativa	o	o	o	o	x	o	o	o

where a microclimate suitable for this species is maintained by the grass, moss and litter. Other possible hibernation sites include patches of grass at the roadside, cereal stubble and bark (Köppä 1969 a), under which the species has also been found to hibernate by Priesner (1924 a) and Lewis and Navas (1962).

In this species it is the adult females that overwinter (Köppä 1969 a), although Wetzel (1963) found one male specimen in a collection of thrips gathered during the winter. The possibilities for the wingless male to hibernate seem small, if only for the reason that to reach winter quarters a flight of some distance is usually required and this can only be performed by the females, which have wings.

5. *Developmental stages*

The developmental stages of *L. denticornis*-egg, two larval instars, prepupa, pupa and adult — are shown in Fig. 7, except for the egg stage.

The eggs are pale and translucent. They are elongated and less curved than the eggs of *F. tenuicornis* and *A. obscurus* (Fig. 8).

The length of the eggs varied from 0.288 to 0.360 mm, averaging 0.331 ± 0.002 mm. The breadth of the eggs varied from 0.090 to 0.126 mm, averaging 0.111 ±0.0003 mm. All the eggs, of which there were 616, were measured by the age of 24 hours at latest. The size distribution of the eggs by length and breadth is shown in Fig. 9. The length-breadth ratio, which gives some idea of the shape of the egg, averaged 2.98 in the eggs measured. According to the measurements carried out by Holtmann (1963 a) in West Germany, the length of the eggs of *L. denticornis* was 0.375 mm and the breadth 0.112 mm.

The duration of the egg stage was found to vary greatly with the rearing conditions. In the present studies it varied from 3 to 9 days (Table 2, Fig. 10). Lindeman (1886, 1887), in Central

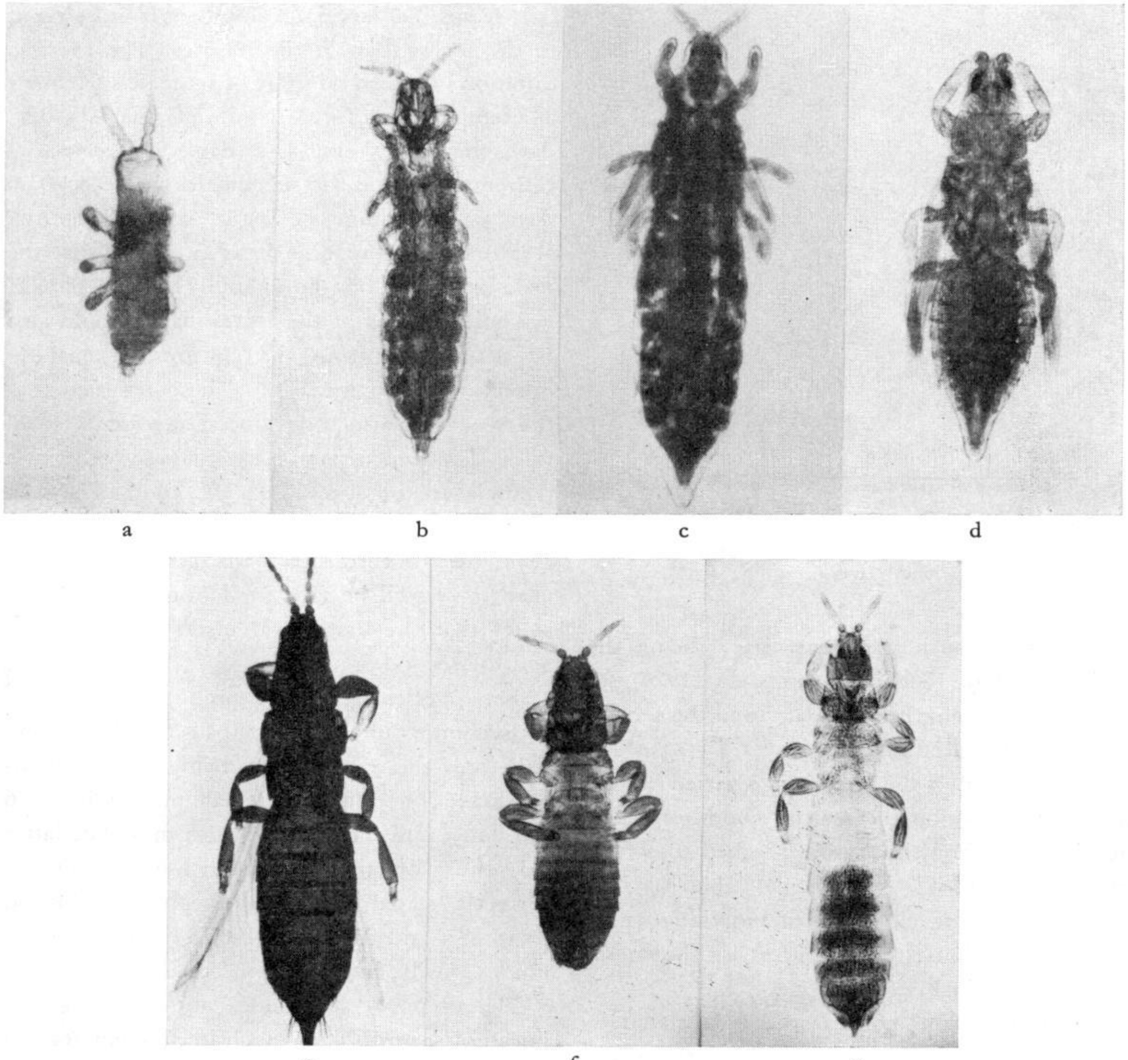

Fig. 7. *L. denticornis* Hal., stages of development: a) 1st instar larva, b) 2nd instar larva, c) prepupa, d) pupa, e) adult ♀ and f) and g) adult ♂. Photos: Institute of Photography, Helsinki.

Russia, found that the duration of the egg stage on rye was 10 days, von OETTINGEN (1942), in Germany, found that it was 11 days on grasses, and HOLTMANN (1963 a), in West Germany, that it was 5—7 days on rye. The average temperatures of the rearing periods were not given in the above studies, but the first two, at least, definitely refer to results obtained in field conditions.

L. denticornis has two larval instars (Fig. 7, a and b). The general colour of the larvae is

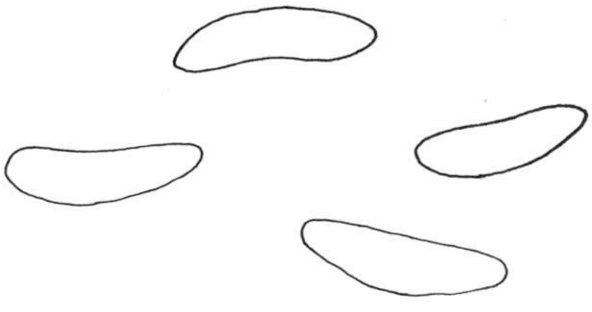

Fig. 8. *L. denticornis* Hal. eggs, about 80 times natural size.

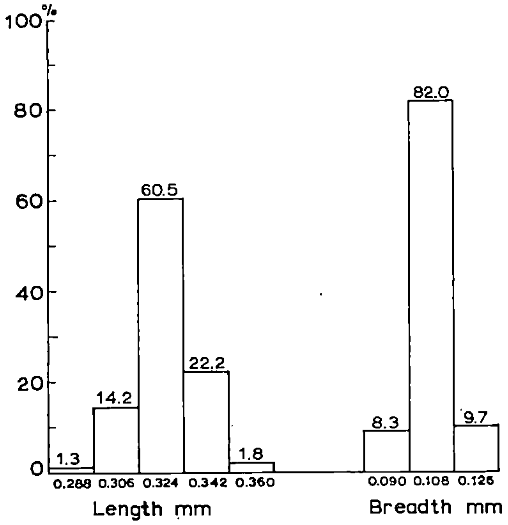

Fig. 9. *L. denticornis* Hal. eggs, size distribution by length and breadth.

rather pale. The head is dark grey, being the darkest part of the body. Priesner (1926) reports that the length of the larvae in the second instar is 1.27—1.56 mm in Austria.

The duration of the larval stage varied a great deal, depending on the rearing conditions; and development from a recently hatched to a full-grown larva took 4—16 days (Table 3). The rate of larval development of individual specimens at various temperatures is shown in greater detail in Fig. 10.

The larval stage of this species is stated to last 17 days in meadow foxtail (von Oettingen 1942) and 28—30 days in rye (Lindeman 1886, 1887). Holtmann (1963 a) found that the larva takes about one week to grow to full size after hatching, and Bournier (1956) that it takes 11 days, but the rearing conditions were not stated in these instances either.

Table 2. *L. denticornis* Hal., duration of egg stage on rye

Rearing place	Average temperature °C	Number of eggs	Duration of egg stage, days	
			Average [1])	Range
Room	+25.0—25.3	13	3.6±0.14	3—4
Laboratory ..	+20.6	7	5.6±0.20	5—6
Outdoor culture	+16.0	13	7.7±0.18	7—9

[1]) In all the results of corresponding average = mean ± standard error.

It seems that larval development is more rapid in the males than in the females. The average duration of the larval stage of six male specimens at a temperature of +25.1—25.7°C was 5.7±0.57 days, the range being 4—8 days, while the corresponding value for six females was 6.8±0.66 days with a range of 6—10 days. Bournier (1956) likewise regards it as probable that the male larva develops more rapidly than the female.

The durations of the larval instars could also be determined from the cultures by making observations on moulting. These revealed that the two larval instars developed at roughly equal rates. The first instar of eight larvae reared at a temperature of +25.1—25.7°C took 3.4±0.21 days on average, and the second instar 3.1±0.12 days. At lower rearing temperatures the differences may well be greater. Holtmann (1963 a) states that the first larval instar takes 10 days and the second 7.

This species enters the prepupal stage after the second moult. The prepupa is translucent and pale, only the red eye-spots being clearly distinguishable (Fig. 7 c). The female pupa is 1.3—1.6 mm long, and the male 1.1—1.5 mm. The latter may thus sometimes be much longer than was formerly stated, e.g. by Priesner (1926) and Franssen and Mantel (1965 a). The prepupa moves slowly, but does not feed.

The prepupal stage does not last long and does not seem to vary much in different rearing

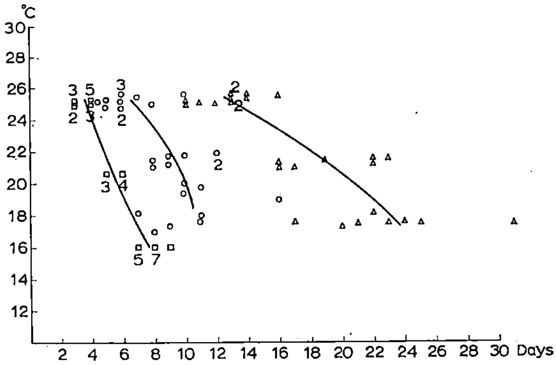

Fig. 10. *L. denticornis* Hal., individual rates of development of eggs (□—□) and larvae (○—○) and development from egg to adult (△—△), at various rearing temperatures. The curves indicate the average durations of the developmental stages.

Table 3. *L. denticornis* Hal., duration of larval stage on rye

Rearing place	Average temperature °C	Number of specimens	Duration of larval stage, days	
			Average	Range
Room	+25.1—25.7	12	6.3±0.45	4—10
Laboratory ..	+21.1—22.0	7	9.7±0.65	8—12
Outdoor culture	+17.0—20.1	9	10.3±0.83	7—16

Table 5. *L. denticornis* Hal., duration of pupal stage on rye

Rearing place	Average temperature °C	Number of specimens	Duration of pupal stage, days	
			Average	Range
Room	+25.0—26.4	12	1.8±0.19	1.0—3.0
Laboratory ..	+20.7—22.6	7	2.8±0.29	2.0—4.0
Outdoor culture	+14.9—21.9	7	3.9±0.60	2.0—6.0

conditions (Table 4). The variation may also have been levelled out by the fact that, even for a developmental period as short as this one, only two observations were made daily. Von OETTINGEN (1942) also reported that the prepupal stage only lasted one day.

On moulting, the prepupa is transformed into a pupa (Fig. 7 d), which likewise takes no food but moves slowly. The pupa differs from the prepupa mainly in its longer wing pads and backwardly directed antennae. The pupa is pale, and only the eyes are distinguishable in color from the rest of the pupa. The length of the female pupa is 1.4—1.8 mm, and that of the male 1.1—1.6 mm. Considerably shorter measurements have been reported previously (PRIESNER 1926, FRANSSEN and MANTEL 1965 a) as the maximum length of the male pupa of this species.

The duration of the pupal stage is longer than that of the prepupal stage (Table 5). Depending on the conditions, it varied in the cultures from 1 to 6 days. It also seems to be dependent on the sex of the pupa. The average duration of the pupal stage of six male specimens reared at +25.0—26.4°C was found to be 1.3±0.17 days, with a range of 1—2 days, while that of six females at the same temperature was 2.3±0.17 days on average, with a variation of 2—3 days. Measurements of the duration of the pupal stage of this species have previously been made, e.g. by von OETTINGEN (1942) and LINDEMAN (1886, 1887), the former reporting the value 5 days and the latter 5—6 days. BOURNIER (1956) gives 4 days as the total duration of the prepupal and pupal stages, and HOLTMANN (1963 a) gives it as 5 days. Although the rearing conditions are not stated in detail in these studies, either, it seems that the cultures were kept outdoors.

The wing pads of the pupae begin to darken some 12 hours before the emergence of the adults. The males usually emerge a few days earlier than the females, a fact previously observed, e.g. by von OETTINGEN (1942), BOURNIER (1956) and HOLTMANN (1963 a). This is mainly due to the shorter larval and pupal stages of the males.

The adult female is usually slightly larger than the male (Fig. 7 e, f and g). According to the measurements made, the length of the females is 1.5—1.8 mm and that of the males 1.1—1.7. A fairly large variation seems to occur in the length of the males. They are usually 1.1—1.2 mm in length, as stated, e.g. by PRIESNER (1926) and FRANSSEN and MANTEL (1965 a), but occasionally very large specimens are encountered. This may be due not only to the nutritional conditions during the larval stage but also, as STEELE (1935) found with the species *Thrips imaginis* Bagn., to the temperature during devel-

Table 4. *L. denticornis* Hal., duration of prepupal stage on rye

Rearing place	Average temperature °C	Number of specimens	Duration of prepupal stage, days	
			Average	Range
Room	+24.8—25.9	12	1.0±0.04	0.5—1.0
Laboratory ..	+21.0—23.0	7	1.1±0.07	1.0—1.5
Outdoor culture	+17.2—24.2	8	1.0±0.09	0.5—1.5

Table 6. *L. denticornis* Hal., period of development from egg to adult on rye

Rearing place	Average temperature °C	Number of specimens	Period of development, days	
			Average	Range
Room	+25.0—25.6	12	12.7±0.50	10—16
Laboratory ..	+21.0—21.7	7	19.2±1.20	16—23
Outdoor culture	+17.4—18.1	8	22.9±1.47	17—31

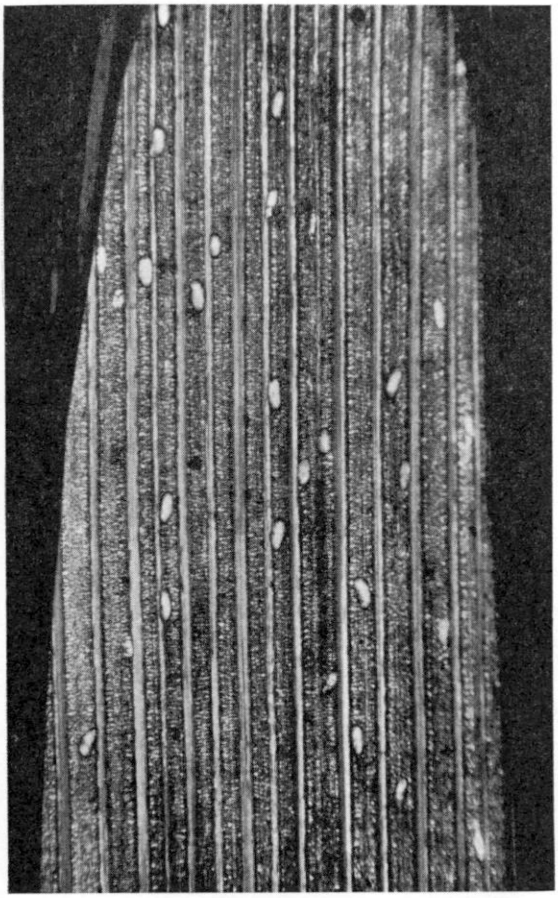

Fig. 11. *L. denticornis* Hal. eggs in sheath of rye. Larvae have already hatched from some of the eggs. Photo: Institute of Photography, Helsinki.

opment. Apart from the variations in size, there are great colour variations in the males of *L. denticornis*. The colour varies from almost entirely pale to completely black.

In the different conditions of rearing, *L. denticornis* developed from egg to adult in 10—31 days (Table 6). The rate of development in the various specimens appears most clearly in Fig. 10. In the indoor cultures, at +25.0—25.6°C, the males developed in 11.6±0.56 days on average and the females in 13.7±0.49. Thus, in a developmental period as short as this one, the average difference in duration of development between the two sexes was about two days, and at lower temperatures the difference may even be considerably greater. According to LINDEMAN (1886, 1887), the development of this species from egg to adult takes 45 days, while according to von OETTINGEN (1942, 1952 a) it takes 34 days, both these periods being considerably longer than those found in the present study. HOLTMANN (1963 a) gives about three weeks as the length of the developmental period.

The adult takes on its normal colouring in 1—2 days, and the females are already able to fly a couple of days after emerging (HOLTMANN 1963 a). The males copulate with the females soon after reaching adulthood. When the first males emerge, the females are still at earlier stages of development. Thus the adult males copulate with females that are still in the pupal stage. This was first reported by PUSSARD-RADULESCO (1931), and has been confirmed later, e.g. by von OETTINGEN (1942), BOURNIER (1956) and HOLTMANN (1963 a).

6. *Life cycle*

Only a small part of the *L. denticornis* population hibernates on winter cereals (KÖPPÄ 1969 a). Most of the females migrate directly from their overwintering sites when spring comes. The spring migration occurs fairly early, when the temperature of the air has risen to +15°C (WETZEL 1962). The species was first netted in the period May 13—22 (Fig. 12). The rye was then 20—40 cm high. The first eggs appeared on the plants 1—2 weeks later. At this latter time the rye is coming into ear.

During the early period of development of the cereal crop, all the thrips are forced to inhabit the leaves. When the ears begin to appear, most of the thrips enter the sheaths, which are then easily accessible. When the ear emerges, most of the females remain within the sheath and their progeny develop there. *L. denticornis* is clearly a species that inhabits the sheath (Tables 7 and 8, JOHANSSON 1946). This fact has also been noted by LINDEMAN (1886, 1887), AHLBERG (1926), MÜHLE (1953, 1958) and HOLTMANN (1963 a).

The adult female of *L. denticornis* has to undergo a period of maturation before becoming

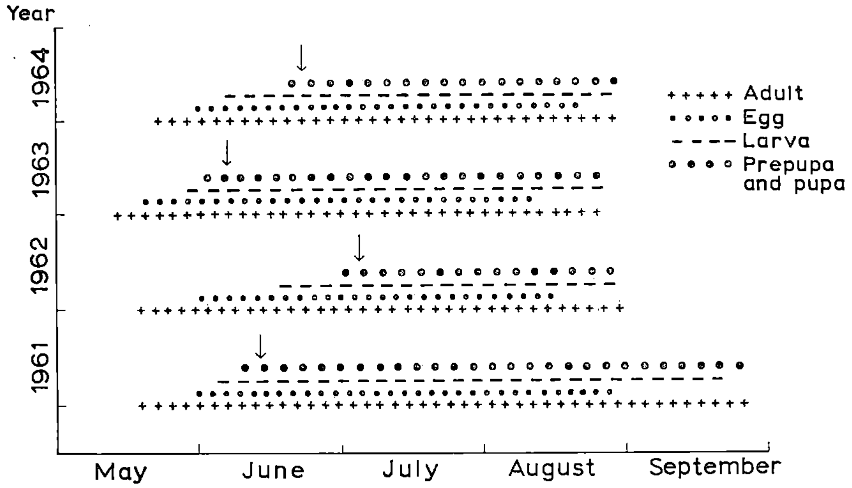

Fig. 12. *L. denticornis* Hal., occurrence of different stages of development on cereal and grass stands, Tikkurila 1961—64. The arrows indicate the emergence of the new generation.

capable of oviposition. Consequently, even the specimens taken from their sites of hibernation in spring did not lay eggs when placed in culture-tubes, and it is clear that it is some sudden endogenous change that causes the onset of oviposition. Bournier (1956) is of the opinion that the egg-laying reflex of this species is inhibited during the early development of the plant, and is only released when the ear emerges from the sheath. The females are, however, able to lay eggs elsewhere than in the sheaths. Large numbers of eggs can also be found on the leaves, especially when the ear is still inside the sheath (Table 9). Thus there is possibly a connexion between egg-laying and changes in responses to light and touch. The females of *L. cerealium*, a close relative of *L. denticornis*, undergo a change when going into hibernation, becoming negatively phototactic and positively thigmotactic, while in the spring these responses are reversed (Lewis 1963). Further, this reversal takes place at a very late phase during the spring, e.g. immediately before the hibernation sites are abandoned. This change of response may well be connected with oviposition, for egg-laying stops when the response changes in the autumn and is resumed after hibernation, when the response is reversed.

The females usually lay their eggs in the sheath (Table 9). Eggs may be found in all the sheaths on the stem, but most by far in the uppermost and most recently opened sheath. Within the sheath the eggs are mostly located on the second and third quarters from the ligule of the leaf, counting downwards, as is shown in the following tabulation.

Table 7. Frequencies of the most important thrips species on shoots and sheaths of cereals, according to samples gathered at Tikkurila, 1960—61

Species of cereal	Number of samples	Sampling period	Number of specimens	% of specimens				Other thrips species
				L. denticornis	*A. obscurus*	*F. tenuicornis*	*H. aculeatus*	
Rye	13	15/4— 9/8	173	60.4	8.9	27.9	—	2.8
Winter wheat	15	16/5—23/8	133	57.1	4.1	32.0	—	6.8
Spring wheat	12	20/6— 8/9	67	26.2	4.8	54.1	—	14.9
Barley	17	20/6— 1/9	144	68.4	0.6	29.2	0.2	1.6
Oats	12	28/6— 5/9	53	1.2	24.5	69.7	—	4.6
Total	69		570	45.4	7.8	40.9	0.1	5.8

Table 8. Frequencies of the most important thrips species on ears and panicles of cereals, according to samples gathered at Tikkurila, 1960—61

Species of cereal	Number of samples	Sampling period	Number of specimens	% of specimens				Other thrips species
				L. denticornis	*A. obscurus*	*F. tenuicornis*	*H. aculeatus*	
Rye	19	9/6—23/8	328	19.0	2.4	50.0	23.9	4.7
Winter wheat	22	20/6—13/9	175	4.4	4.2	68.7	18.0	5.7
Spring wheat	15	20/7— 8/9	59	5.0	8.9	80.5	—	5.6
Barley	13	19/7— 1/9	74	15.0	1.9	70.0	7.3	5.8
Oats	16	18/7— 8/9	139	1.3	20.8	70.9	5.7	1.3
Total	85		775	8.9	7.2	67.1	12.2	4.6

1st quarter	2nd quarter	3rd quarter	4th quarter	Total
74 eggs	112 eggs	595 eggs	13 eggs	794 eggs

The averages of four replicates show that there are significantly more eggs on the third quarter than on the first, second and fourth quarters (the t-values being 4.8**, 4.4** and 5.5** respectively). There were no significant differences in number of eggs between the other quarters.

L. denticornis deposits its eggs singly in the cell tissue of the inner surface of the sheath (Fig. 11). According to the present investigations, the number of eggs laid by a hibernated female was 58—142, the average being 91.0±6.84 eggs. The oviposition period lasted 14—33 days, averaging 23.2±1.30 days. This gives 3.8 eggs as the average daily number of eggs per female. The oviposition cultures were checked every third or fourth day, and the substratum of these cultures was rye. According to Holtmann (1963 a), the number of eggs per hibernated female is 70—120. From studies of ovaries Bournier (1956) concludes that the female may lay about 100 eggs. The related species *L. cerealium* has been found to lay as many as 108 eggs in culture, the maximum duration of oviposition for an individual being 58 days (Lewis 1959).

Table 9. *L. denticornis* Hal., distribution of eggs on rye. 4 replicates

Stage of development of plant	Total	Number of eggs		t-value 1)
		Av. per culture		
		Leaf	Sheath	
Before coming into ear . . .	129	11.0±0.71	21.3± 2.92	3.4*
After coming into ear . . .	810	4.0±2.50	198.5±35.29	5.5**

1) In all the results *** = P < 0.001; ** = P < 0.01; * = P < 0.05.

In Finland *L. denticornis* lays its first eggs on rye between May 23 and June 8, depending on the year. In 1963, when the temperature in May was considerably higher than average (Fig. 5, p. 204), oviposition began early, while in 1962 it was delayed, mainly because of the cool weather. Pussard-Radulesco (1931) claims that the females lay eggs throughout the summer but have to change host plant from time to time to do so, because the same species of plant seldom remains suitable for egg-laying as long as this. Thus females that have already begun oviposition on one species of plant can move to new host plants and establish colonies there. In France, according to Pussard-Radulesco (1931), this species establishes four different colonies of progeny during the summer months. Observations made by Bournier (1956) also suggest that this is possible, at least, the female establishes colonies on several specimens of plant. The migratory character of this species has also been noted by von Oettingen (1930, 1942) and Zawirska (1960).

In spring *L. denticornis* migrates to meadow foxtail at the same time as it migrates to rye (Table 10). Because of the rapid development of meadow foxtail, such migration could occur even earlier. At least, egg-laying starts earlier on meadow foxtail than on rye. The females appear rather early on winter wheat too (Table 10), and soon start to lay eggs. According to Holtmann (1963 a), the number of eggs is smaller on wheat than on rye.

Table 10. *L. denticornis* Hal., occurrence on meadow foxtail, winter wheat and barley, Tikkurila 1961—64

Year	Meadow foxtail		Winter wheat		Barley	
	First specimens	First specimens of new generation	First specimens	First specimens of new generation	First specimens	First specimens of new generation
1961	18.5	13.6	24.5	6.7	11.6	17.7
1962	18.5	4.7	28.5	28.7	—	30.7
1963	21.5	6.6	—	25.6	—	4.7
1964	25.5	22.6	—	—	—	17.7

The larvae hatch from the eggs and live in the sheath in groups of various sizes. They suck at the tissue of the inner surface of the sheath, and destroy large areas of it. The destruction causes the outer surface of the sheath to turn pale.

The first *L. denticornis* larvae were found on winter rye on June 1—21. In 1963, larvae were found on meadow foxtail as early as May 26 (Fig. 12), so about one week earlier. In 1962, a late year, the first larvae of this species were not observed on meadow foxtail until June 17. On winter wheat the first larvae developed 3—4 weeks later than on rye.

On the rye, prepupae began to develop from June 9 to July 3 onwards, and pupae from June 9 to July 7 onwards. On meadow foxtail development was, again, 2—7 days earlier, and on winter wheat about three weeks later.

The first specimens of the new generation were found on meadow foxtail between June 6 and July 4 (Table 10, Fig. 12). On rye the species developed to the same stage between June 14 and July 12. Thus the development of the species was about one week earlier on meadow foxtail than on rye. On winter wheat development was considerably later, and the first specimens of the new generation developed there between June 25 and July 28 (Table 10), i.e. about two weeks later than on rye.

The first specimens of the new generation are males, which develop more rapidly than females. Not all the males develop concurrently and earlier than the females, however, for males do develop from later-laid eggs. Because of the more rapid development of the males it is possible that they may copulate with female pupae which are sexually mature, although the ovaries are only slightly developed at this stage (von OETTINGEN 1952 b, BOURNIER 1956). Although copulation generally occurs, there is no doubt that the female can lay eggs without being fertilized, but all the progeny are then males. Arrhenotokous parthenogenesis occurred in the egg cultures during the research period. BOURNIER (1956) regards reproduction of this kind as characteristic of this species. The females of the newly emerged generation may commence oviposition within a few days. In the present investigations, the duration of the preoviposition period in indoor cultures was 5—18 days. The specimens had developed on rye and meadow foxtail and had laid their eggs on barley. HOLTMANN (1963 a), too, is of the opinion that the specimens of the new generation start to oviposit soon after emergence. BOURNIER (1956), however, on the basis of his investigations on ovaries believes that the females are unable to lay eggs before diapause, which would mean postponement of oviposition to the following summer.

Females from the new generation were selected for two kinds of cultures. In one group of cultures the females were reared with males, while in the other they were reared singly from the larval stage. It became clear from these investigations that the females of both groups were able to lay eggs, although not all of them did so during the autumn. Some lived in the cultures for as long as a couple of months without starting oviposition. The number of eggs per female varied between 20 and 156, averaging 80.0±15.29. Thus the new generation lays almost as many eggs as the generation that has hibernated. A good proportion of the females in the population are already in diapause, and it is only a small proportion that begin oviposition, whereas one hundred per cent of the hibernated females oviposit. The oviposition period varied from 7 to 30 days, averaging 19.9±7.85 days. According to HOLTMANN (1963 a), the females of the new generation lay 70—90 eggs.

These females can lay their eggs on barley, for instance, which has just reached a suitable stage at the time when this species reaches the adult stage on meadow foxtail and rye. It is consequently possible that the new generation establishes its progeny on barley (FRANSSEN and MANTEL 1965 a, 1965 b). It is, of course, just as possible that the eggs on barley are laid by females that have hibernated and migrated to the barley from other plant species. Specimens of the new generation were first observed on barley on July 4—30 (Table 10). At that same time, the species may reproduce not only on barley but also on spring wheat and, to some extent, on oats. Generally, the development of the second generation, on spring cereals, takes place in more favourable conditions than those of the first generation, on meadow foxtail and rye, because the temperature conditions, in particular, are then most favourable for the development of the species.

L. denticornis seeks a hibernation site fairly early in the autumn. In Germany, entrance into hibernation may begin early in August and end about mid-September (von OETTINGEN 1936, 1942). In the different years of the research period, the last specimens of the species were found on crops between August 23 and September 24. The males are usually dead by then. In the laboratory, the females in cultures ceased ovipositing in the last third of August.

B. Anaphothrips obscurus Müll.

HALIDAY (1836) assigned this species to the genus *Thrips* (*T. obscura* Müll.), and TULLGREN (1917) to the genus *Euthrips* (*E. obscurus* Müll.), UZEL (1895) assigned it to the genus *Anaphothrips* (*A. virgo* Uz.), and HINDS (1900, 1902), FERNALD and HINDS (1900) and SHULL (1909, 1914 a) to the same genus (*A. striata* Osb.). O. M. REUTER (1899) was the first to refer to the species as *A. obscura* Hal., practically its present name.

1. *Distribution*

A. obscurus occurs everywhere in Europe (PRIESNER 1964), Asia (SCALON 1931, TANSKY 1961, KUROSAWA 1968), North America (HINDS 1900, 1902, FERNALD and HINDS 1900, HEWITT 1911, 1914, MOULTON 1911, MORGAN 1913, STRICKLAND 1956), Australia (McCARTHY 1933) and New Zealand (DOULL 1956).

According to HUKKINEN (1942), this species occurs in Finland right up into Lapland.

2. *Host plants*

Among cereals, oats and barley are especially attractive to *A. obscurus* (KÖPPÄ 1967). HEWITT (1911, 1914) refers to the species as an economically important pest of oats. Yet it is quite commonly found on rye and wheat too. This species has been found to reproduce on all these cereals and also on maize (Table 1, p. 206). On this last-mentioned plant it has also been found by KNOWLTON and THOMAS (1933), and on sugar cane by BIANCHI (1945).

In addition to cereals, many cultivated and wild grasses may be attacked by *A. obscurus* (Table 1, p. 206). In respect of its host plants it shows a close resemblance to *F. tenuicornis*. The larvae of *A. obscurus* cannot live for very long on cultivated legumes, although oviposition may occur very exceptionally on these plants. The macropterous and brachypterous forms of this species apparently reproduce on the same species of plants.

3. *Sex index*

The male of *A. obscurus* has apparently not been found in Europe (PRIESNER 1964). KUROSAWA (1968) states that it is absent from Japan too. But males of this species have been found in North America, e.g. on *Ammophila arenaria* L.

Table 11. Length of *A. obscurus* Müll. *f. macroptera* and *f. brachyptera* specimens

Wing form	Vegetation	Number of specimens	Length, mm	
			Average	Range
Macropterous	Rye	319	1.407±0.007	1.110—1.850
	Ley	161	1.438±0.010	1.147—1.739
Brachypterous	1st year ley	94	1.345±0.015	1.110—1.665
	3rd year ley	104	1.325±0.014	0.962—1.665

plants (Shull 1909, 1914 a, 1914 b). Cary (1902) had already described the male of this species, but his determination of the species seems to have been erroneous (Shull 1909). Twice during the research period copulating thrips were found in which the female of the pair was *A. obscurus* and the male *F. tenuicornis* (Köppä 1969 b, Fig. 2, p. 68). It is possible that it was on account of a similar event that Cary (1902) described a male as belonging to the species *A. obscurus.*

A. obscurus is usually regarded as reproducing parthenogenetically, and it has been possible without difficulty to rear it for several generations without males. Its parthenogenetic reproduction is thelytokous, i.e. the eggs develop into females only. The significance of the locally and sporadically occurring males to the development of this species remains unknown. A similar kind of reproduction is also found in other species of thrips. Among such species are *Thrips tabaci* Lind. (Hooker 1907, Priesner 1933, Speyer 1934, Ghabn 1948, Morison 1957) and *A. rufus* (Williams 1913, Morison 1924, Radulesco 1930, Speyer 1935), the males of which are found only in certain regions and in certain seasons.

4. *Dimorphic forms*

A. obscurus occurs in both the macropterous (*f. macroptera*) and the brachypterous (*f. brachyptera*) form. Specimens of the macropterous form have a ground colouring of pale yellow with darker patches here and there. The wings, which are greyish, are long and cover the entire abdomen. The mean lengths and range of lengths of the macropterous specimens taken from various biotopes are shown in Table 11.

The brachypterous specimens are more uniformly and brightly yellow than the macropterous ones, for the dark patches on the thorax and abdomen are less distinct or absent. The wings are scale-like and extend over the thorax. There are two pairs of these scales, the front pair covering the hind pair. The front pair of wing scales, which are beset with short stiff spines in longitudinal rows, extend almost to the hind margin of the thorax. The hind pair of scales have no such spines, but are covered with fine setae as are the front pair. Measurements established that the brachypterous specimens are shorter than the macropterous ones (Table 11), as had previously been noted by Cary (1902). But no great differences were found in the lengths of specimens of either of the forms gathered from various biotypes (Table 11). Hinds (1900) has previously described in detail the characteristics and differences of *A. obscurus* specimens with differing wing forms, and has reached the conclusion that brachypterous specimens were longer than macropterous ones.

5. *Hibernation*

A. obscurus winters in highly varied biotopes. Some of the population migrate to winter cereals during the autumn and overwinter in the sheaths of the shoots. This species is also found hibernating in patches of grass growing by the roadside and in grass leys, and to a smaller extent in cereal stubble. The brachypterous form seems to be commoner than the macropterous form in populations hibernating in cultivated and wild grasses (Köppä 1969 a).

6. *Developmental stages*

The developmental stages in *A. obscurus* are the same as in *L. denticornis.* They are shown in Figs. 13 and 14, with the exception of the egg

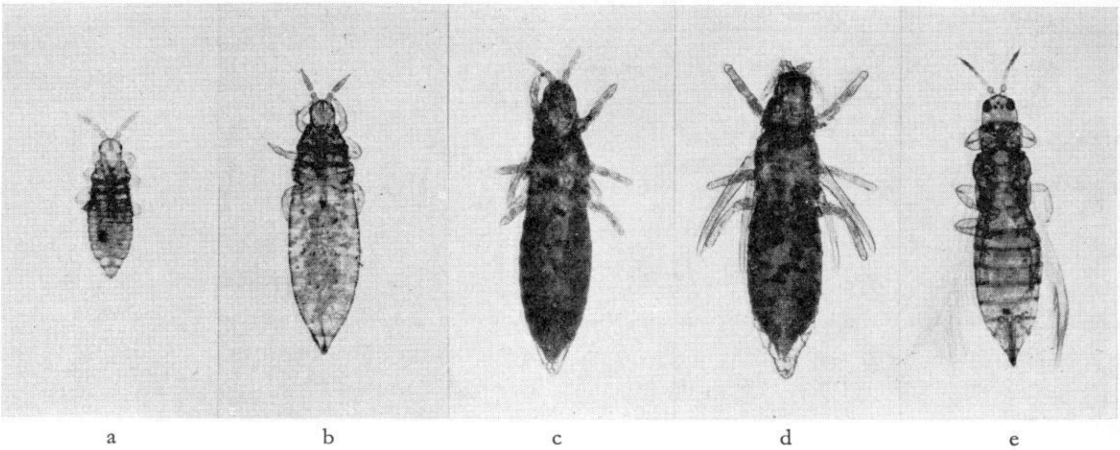

Fig. 13. Developmental stages of *A. obscurus* Müll. *f. macroptera:* a) 1st instar larva, b) 2nd instar larva, c) prepupa, d) pupa, and e) adult. Photos: Institute of Photography, Helsinki.

stage. Only the adult, pupal and prepupal stages (Fig. 14 a, b, c) of the brachypterous form are shown, these being distinguishable from the respective stages of the macropterous form.

The eggs of *A. obscurus* are pale and translucent. They are usually narrower, more regular, smaller and less curved than the eggs of *F. tenuicornis* (Fig. 15, cf. Fig. 22, p. 230).

The eggs of the macropterous and the brachypterous form are of the same size and shape (Table 12). The eggs of the two forms also resemble each other in respect of their size distribution (Fig. 16).

Hinds (1900) reported that the eggs of this species are slightly larger than they were found to be in the present study; he gave the length as 0.265—0.330 mm with an average value of 0.288 mm, and the breadth as 0.085—0.145 mm, average 0.110 mm.

The egg stage of *A. obscurus* lasted 4—10 days, i.e. slightly longer than that of *F. tenuicornis* (Table 13, cf. Table 30, p. 230). A similar difference

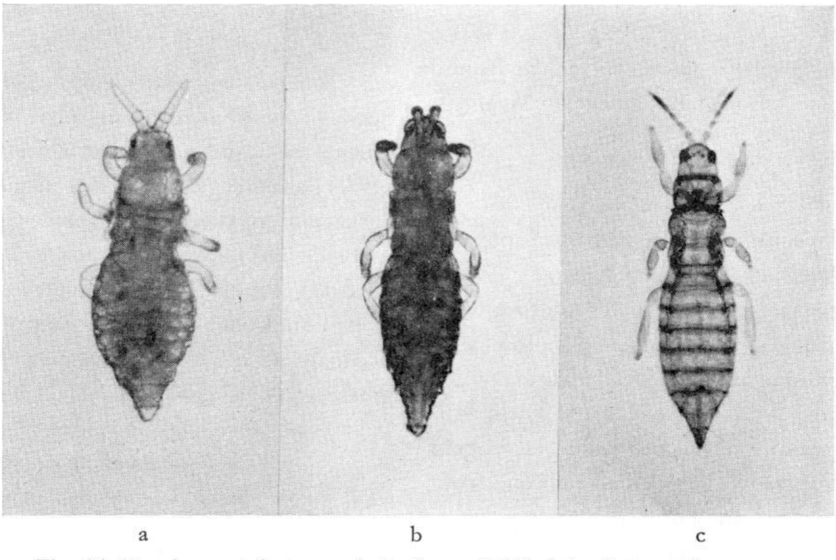

Fig. 14. Developmental stages of *A. obscurus* Müll. *f. brachyptera:* a) prepupa, b) pupa, and c) adult. Photos: Institute of Photography, Helsinki.

Table 12. *A. obscurus* Müll., size of eggs.

Wing form	Number of eggs	Length of eggs		Breadth of eggs		Length—breadth ratio
		Average	Range	Average	Range	
Macropterous	618	0.259±0.0005	0.224—0.296	0.095±0.0004	0.072—0.108	2.73
Brachypterous	609	0.258±0.0005	0.224—0.296	0.095±0.0004	0.072—0.108	2.72

was found in all the cultures. The egg cultures of these two species were started at the same time, and the *F. tenuicornis* larvae hatched distinctly earlier in all cases. There was no noteworthy difference, however, between the durations of the egg stages of the macropterous and brachypterous forms (Table 13). The difference seems to be greatest in outdoor cultures but is probably due to the fact that the number of hatching larvae of the macropterous form was very small. The egg stage lasted roughly as long on rye and timothy as on oats, and no differences could be observed between the different wing forms in these cases either. The egg stage becomes distinctly longer with decreasing temperature (Fig. 17), this being confirmed by the result of another outdoor culture reared at a temperature of +15.0—16.0°C, in which the egg stage averaged 15.5 days for the brachypterous form and 15.0 days for the macropterous form. Hinds (1900) gives similar data for the duration of the egg stage, finding that the larvae hatched 10—15 days after oviposition, and in the case of summer generations after as little as 4—7 days.

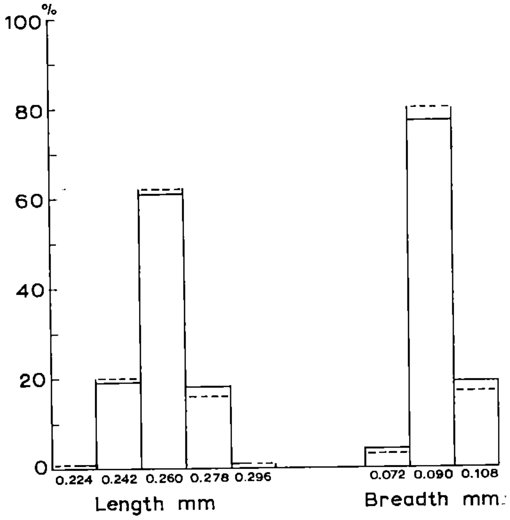

Fig. 16. *A. obscurus* Müll. *f. macroptera* (———) and *f. brachyptera* (- - - -), eggs size distribution by length and breadth.

On hatching from the egg the larva is about 0.3 mm long, very soft and almost white (Fig. 13 a). Hinds (1900) gives a detailed description of the larval stages of this species and of the hatching of the larva from the egg. The full-grown larva (Fig. 13 b) is about 1.2 mm long (Hinds 1900). The green contents of the intestine are clearly visible through the pale skin.

The larval stage of this species lasted 6—16 days, i.e. slightly longer than that of *F. tenuicornis*

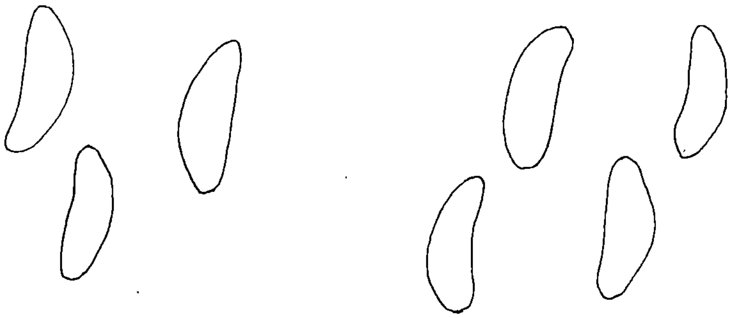

Fig. 15. Eggs of *A. obscurus* Müll. *f. macroptera* (left) and *f. brachyptera* (right), about 80 times natural size.

Table 13. *A. obscurus* Müll., duration of egg stage on oats

Parental wing form	Rearing place	Average temperature °C	Number of eggs	Duration of egg stage, days	
				Average	Range
Macropterous	Room	+26.0—26.2	16	5.1±0.09	5— 6
Brachypterous		+26.0—26.2	23	5.4±0.15	4— 7
Macropterous	Laboratory	+21.6—21.7	15	7.8±0.10	7— 8
Brachypterous		+21.6—21.7	12	7.8±0.75	6— 9
Macropterous	Outdoor culture	+19.6—19.7	6	9.5±0.23	9—10
Brachypterous		+19.6—19.7	24	9.1±0.64	8—10

(Table 14, cf. Table 31, p. 230). The difference, however, can not be detected in the laboratory cultures, and the reason is obviously the very great variation in the duration of the larval stage of *F. tenuicornis*. There are no noteworthy difference, either, in the duration of the larval stage between the macropterous and brachypterous forms.

Hinds (1900), apparently, did not consider it possible that *A. obscurus* had a prepupal stage separated from the pupal stage by a moult. But Priesner (1926) was convinced of the existence of a prepupa, although he did not give a detailed description of it. In the present investigations the existence of a prepupal stage was established and it was also possible to determine its duration in several specimens. The antennae, legs and wing pads (Figs. 13 c and 14 a,) are colourless and translucent, the remainder being pale yellow except for the eye spots, which are bright red. The length of the prepupa of the macropterous form varies from 0.9 to 1.2 mm, and that of the brachypterous form from 0.9 to 1.1 mm.

This species has a very short prepupal stage (Table 15). When it was reared indoors, clear differences could not be found between the durations of the prepupal stages of the two wing forms. In the outdoor cultures, however, the brachypterous form seems to pass through its prepupal stage more rapidly than the macropterous form, although a difference in rearing temperature of a few degrees did occur, owing to the fact that the cultures of the different wing forms could not be started simultaneously.

The pupal stage (Figs. 13 d and 14 b) resembles the prepupal stage in all respects save that its antennae are directed backwards over the head and its wing pads are longer. The length of the pupa varies from 0.9 to 1.2 mm in the macropterous form, and from 0.9 to 1.1 mm in the brachypterous form.

The pupal stage lasted about twice as long as

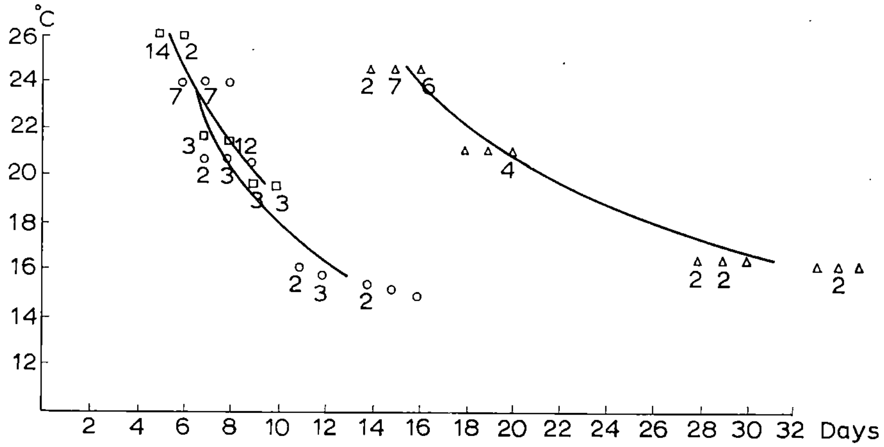

Fig. 17. *A. obscurus* Müll. *f. macroptera*, individual rates of development of eggs (□—□) and larvae (○—○) and development from egg to adult (△—△), at various rearing temperatures. The curves indicate the average durations of the developmental stages.

Table 14. *A. obscurus* Müll., duration of larval stage on oats

Wing form	Rearing place	Average temperature °C	Number of specimens	Duration of larval stage, days	
				Average	Range
Macropterous	Room	+23.9	15	6.6±0.16	6— 8
	Laboratory	+20.5—20.8	6	7.8±0.31	7— 9
Brachypterous		+20.5—20.9	9	8.3±0.37	7—10
Macropterous	Outdoor culture	+15.0—16.1	9	13.0±0.60	11—16
Brachypterous		+13.9—14.9	11	13.1±0.29	12—15

Table 15. *A. obscurus* Müll., duration of prepupal stage on oats

Wing form	Rearing place	Average temperature °C	Number of specimens	Duration of prepupal stage, days	
				Average	Range
Macropterous	Room	+24.0	15	1.2±0.05	1.0—1.5
	Laboratory	+21.5—22.0	6	1.2±0.24	1.0—1.5
Brachypterous		+21.5—22.0	9	1.5±0.17	1.0—2.0
Macropterous	Outdoor culture	+14.2—16.4	9	2.6±0.16	2.0—3.5
Brachypterous		+18.5—19.3	11	1.5±0.08	1.0—2.0

the prepupal stage (Table 16). The effect of temperature on the duration of this stage becomes clearly evident from the results of the indoor and outdoor cultures. There seems, again, to be a difference between the two wing forms in the outdoor cultures, the brachypterous form developing more rapidly, although the difference in rearing temperature may have been to some extent responsible for this difference. Hinds (1900) maintains that the development of this species from larva to brachypterous adult occurs in 2—3 days, and to macropterous adult in 4—5 days, thus implying that the later development of the brachypterous form is more rapid.

With the approach of adult emergence, the wing pads of the macropterous form of *A. obscurus* acquire a dark shade. Moulting itself is rapid. Müller (1928) made detailed observations on some species of thrips and found, for instance, that at +17°C the process takes 40 minutes.

The development of *A. obscurus* from egg to adult took 14—35 days, depending on the rearing conditions (Table 17). The time taken by various specimens of the macropterous form to develop are given in Fig. 17. In laboratory conditions, with parallel rearing of the brachypterous and the macropterous forms, no distinct difference was found between their rates of development. In the outdoor cultures, however, there seems to be a slight difference to the advantage of the brachypterous form.

7. *Life cycle*

A. obscurus overwinters on winter cereals and on leys, and begins to oviposit there in spring as soon as the weather permits.

There is a preoviposition period, the ovaries of *A. obscurus* maturing gradually during the winter (Fig. 18). Specimens of this species collected outdoors in October did not begin to lay

Table 16. *A. obscurus* Müll., duration of pupal stage on oats

Wing form	Rearing place	Average temperature °C	Number of specimens	Duration of pupal stage, days	
				Average	Range
Macropterous	Room	+24.0	15	2.4±0.05	2.0—2.5
	Laboratory	+22.0—22.2	6	2.7±0.24	2.5—3.0
Brachypterous		+22.0—22.3	9	2.5±0.13	2.0—3.0
Macropterous	Outdoor culture	+13.8—15.0	9	6.0±0.18	5.0—7.0
Brachypterous		+15.8—18.0	11	4.5±0.23	4.0—6.5

Table 17. *A. obscurus* Müll., duration of development from egg to adult on oats

Wing form	Rearing place	Average temperature °C	Number of specimens	Duration of development, days	
				Average	Range
Macropterous	Room	+24.6—24.8	15	15.3±0.18	14—16
	Laboratory	+21.3—21.4	6	19.5±0.34	18—21
Brachypterous		+21.3—21.4	8	20.1±0.60	17—22
Macropterous	Outdoor culture	+16.3—16.6	9	31.1±0.91	28—35
Brachypterous		+16.6—18.2	11	28.5±0.56	26—33

until about six weeks later. But females collected in December oviposited a week after being placed in cultures. From February onwards there was no noteworthy change in the time between exposure to warmth and oviposition in this species. The greatest differences between the preovipositions of the two wing forms apparently occur early in the winter, and the differences level out later on.

If *A. obscurus* females are reared from early in the winter in circumstances favourable for oviposition, not all of them begin to lay. During the winter the proportion of ovipositing females gradually increases, and by March is almost 100 %. But the increase is slower than in *F. tenuicornis*. Throughout the winter the proportion of ovipositing specimens is slightly higher in the brachypterous population than in the macropterous population (Fig. 19). The maturation of the ovaries and the proportion of ovipositing females followed the same trend on rye as on timothy.

Moreover, specimens of this species were gathered from their hibernation sites at the end of April and placed in cultures for oviposition. It was then found that hibernated macropterous females began to lay in 2.9±0.18 days on average on rye, and 3.3±0.49 days on timothy (Table 18). The figures for brachypterous females were 3.3±0.28 days and 2.7±0.13 days respectively, and there was thus no noteworthy difference between the wing forms in this respect either.

In spring, *A. obscurus* begins to lay at about the same time as *F. tenuicornis*. Thus the development of the new generation on rye coincides with that of the latter species (cf. p. 233).

A. obscurus inserts its eggs into the leaf tissue (Table 19). Only a few of the eggs are deposited in the sheaths; in the lowest sheaths of the youngest plants but, in plants that have come into ear, almost exclusively in the uppermost sheath.

The eggs of *A. obscurus* are much more evenly distributed over the leaf blade than are those of *F. tenuicornis* (Fig. 20), but the eggs are most

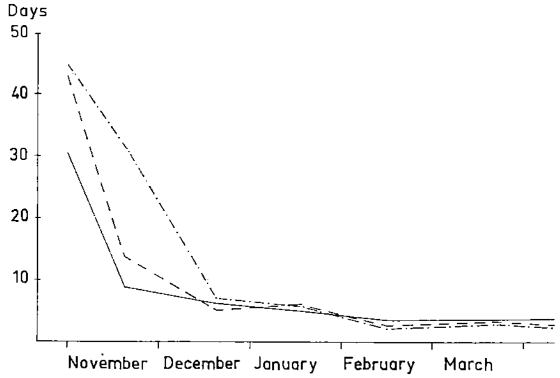

Fig. 18. *A. obscurus* Müll. *f. macroptera* (- - - - -), *A. obscurus* Müll. *f. brachyptera* (—·—·—) and *F. tenuicornis* Uz. (———), number of days elapsing before start of oviposition after being brought indoors, winter 1968—69.

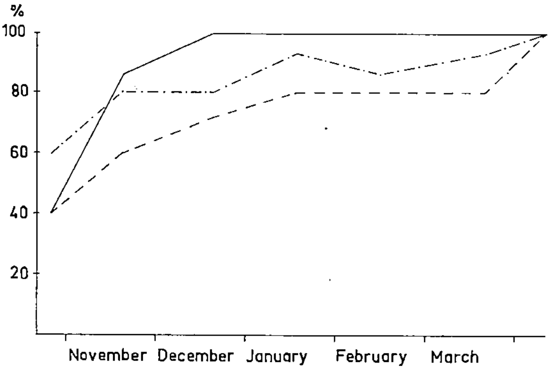

Fig. 19. *A. obscurus* Müll. *f. macroptera* (- - - - -), *A. obscurus* Müll. *f. brachyptera* (—·—·—) and *F. tenuicornis* Uz. (———), proportion of egg-laying females in the population, winter 1968—69.

Table 18. *A. obscurus* Müll., duration of preoviposition period

Wing form	Generation	Food plant	Average temperature °C	Number of specimens	Preoviposition period, days	
					Average	Range
Macropterous	Hibernated	Rye	+20.0—21.0	15	2.9±0.18	2— 4
		Timothy	+20.0—21.0	15	3.3±0.49	2—10
	New generation	Oats	+24.0—25.0	20	1.8±0.38	1— 3
Brachypterous	Hibernated	Rye	+20.0—21.0	15	3.3±0.28	2— 6
		Timothy	+20.0—21.0	14	2.7±0.13	2— 3
	New generation	Oats	+23.0—24.0	16	4.5±0.66	2— 9

numerous on the leaf quarter nearest the ligule and become definitely fewer towards the leaf tip (Table 20). The eggs in the sheaths are chiefly located in the quarter nearest the ligule. The females of this species are rather delicately built, which may be the reason why they are not so prone to enter the lower, restricted parts of the sheath as are, for example the females of *L. denticornis* and *F. tenuicornis.*

About the middle of May oviposition also begins on timothy, on which the reproduction of *A. obscurus* is very vigorous.

The number of eggs of macropterous females was about the same on both rye and timothy (Table 21). In terms of laying, timothy is a somewhat poorer plant than are cereals, for its leaf tissue hardens very rapidly in summer and thus provides a suitable laying substratum for a very brief period only. Also, the eggs laid on timothy leaf tissue very often lie crosswise to the leaf veins. This, again, suggests that oviposition may not be as easy on timothy as on cereals. In the present investigations the average number of eggs per brachypterous hibernated female seems to be smaller than in the macropterous form (Table 21). The plant for oviposition was timothy in both cases. The numbers of eggs found in these investigations were far higher than the figures given in previous reports. Hinds (1900) states that the females of this species lay 50—60 eggs on average, 72 being the maximum.

On rye and timothy the oviposition of this species goes on for about one month on average, but individual females may lay for more than six weeks (Table 21). In cultures kept by Hinds (1900) the egg-laying period was 4—6 weeks.

In 1963, when the weather was extremely favourable for the development of thrips (Figs. 5 and 6, p. 204), the larvae in leys began to hatch on May 25—26, the first prepupae were found on May 31, and the first adults of the new generation on June 3. Thus the development of this species was about one week behind that of *F. tenuicornis* on rye (cf. p. 233).

Most of the new generation of *A. obscurus* migrate from winter cereals, and particularly from leys, to spring cereals, a phenomenon previously observed (Strickland 1956, Schober 1959). A very large-scale migration from leys to spring cereals was seen in 1963. In that same year a distinct migration of this species from ley to adjacent winter wheat also occurred at Tikkurila. The migration of this species from leys to spring cereals in chiefly due to the fact

Table 19. *A. obscurus* Müll., distribution of eggs on plant. 4 replicates

Plant and its stage of development	Number of eggs			t-value
	Total	Average per culture		
		Leaf	Sheath	
Rye				
Before coming into ear	2 757	684.5± 93.75	4.8± 1.34	7.2***
After coming into ear	1 979	474.3± 49.03	20.5± 5.38	9.3***
Oats				
Before coming into panicle	4 460	980.8±120.65	134.3±48.32	6.4***
After coming into panicle	5 476	1 265.5±205.45	103.6± 6.83	5.7**

Table 20. *A. obscurus* Müll., distribution of eggs on rye by leaf-blade quarters (Quarter I = quarter nearest to ligule). 4 replicates

Leaf-blade quarters	Number of eggs		t- value			Number of eggs	t- value		
	Total	Average per culture before earing	I	II	III	Average per culture after earing	I	II	III
I	3 356	507.0±65.16				332.0±32.45			
II	933	133.8± 8.03	5.7**			99.5±11.54	6.7***		
III	314	42.0± 2.38	7.1***	10.9***		36.5± 7.53	8.9***	4.6**	
IV	32	1.8± 0.47	7.7***	16.3***	16.9***	6.3± 4.12	10.0***	7.6***	3.4*

that the leaf tissues of grasses, especially of timothy, begin to be less suitable for purposes of feeding and reproduction. Silage and haymaking on leys and pastures also force the species to seek new quarters.

In the research years the first specimens of *A. obscurus* to be found on oats were observed between June 15—26. The first eggs appeared on the plants at roughly the same time.

In one series of cultures on oats the number of eggs per macropterous female averaged 145.5± 12.08 (Table 21), with a maximum of 216. In another series 13 macropterous females of the species laid an average of 170.0±10.86 eggs, the maximum being 226. The number of eggs per brachypterous female on oats was considerably smaller (Table 21), although one specimen laid total of 232 eggs, which is more than the total for any of the macropterous specimens. The distribution of the eggs on the leaves was the same in oats as in rye (Table 20). The numbers of eggs on the leaf quarters, beginning from the ligule, were 1898, 1216, 711 and 98 prior to panicle formation and 3083, 1418, 499 and 62 subsequent to panicle formation. The calculated t-values for the average numbers of eggs in the former case were 2.0 between the first and second leaf quarters, 3.0* between the second and third, and 8.1*** between the third and fourth. In the latter case the respective t-values were 3.1*, 3.4* and 3.9**. Most of the eggs had been inserted in the tissue of the upper side of the leaf.

A. obscurus thrives on the leaf surface and is not prone to force its way into the opening sheaths. Individuals of the species, however, can be found in numbers in the ears and panicles of various cereals (Tables 7 and 8, pp. 211 and 212, Johansson 1946, Mühle 1958, Wetzel 1962).

A. obscurus larvae were first netted from oats in samples taken between June 28 and July 2 in the various years and were subsequently found throughout the growing season. The number of larvae reached a peak in the latter half of July. The larvae initially lived mainly on the leaves, but were later also found on the panicles when these had come out and also to some extent in the sheaths. The larvae seem to prefer the inner surfaces of the glumes surrounding the spikelets, where they obtain sufficient protection and sufficient nutrition from the developing grain.

The pupae of this species are found in protected parts of the plant, such as the sheaths and spikelets. This species may also pupate in the soil (Morison 1943). The first prepupae and pupae

Table 21. *A. obscurus* Müll., oviposition period and number of eggs

Wing form	Generation	Food plant	Number of specimens	Oviposition period, days		Number of eggs	
				Average	Range	Average	Range
Macropterous	Hibernated	Rye	20	28.1±2.19	14—48	119.2± 7.27	84—175
		Timothy	20	27.9±1.90	13—41	116.4±11.45	51—207
	New generation	Oats	17	25.6±2.33	12—41	145.5±12.08	64—216
		Timothy	13	21.0±1.23	14—28	105.7± 5.61	80—143
Brachypterous	Hibernated	Timothy	20	22.4±1.25	13—30	95.2± 4.18	66—139
	New generation		15	25.5±1.58	15—36	95.6± 4.73	78—142
		Oats	15	25.4±1.86	14—39	113.0±10.64	54—232

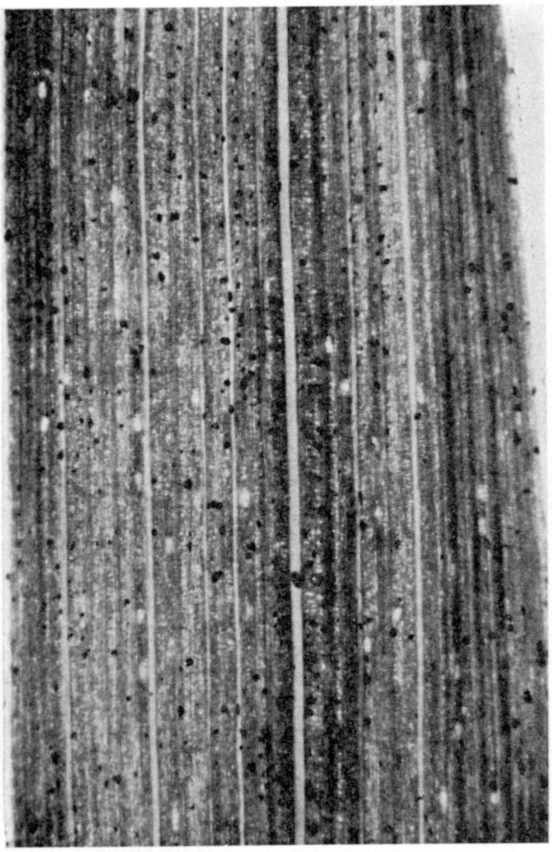

Fig. 20. *A. obscurus* Müll. eggs on leaf-blade of oats. Black flecks are excreta. Photo: Institute of Photography, Helsinki.

occurred on oats between July 12 and 17, and the first adults soon afterwards. Although the adults of the second generation of this species began to emerge soon after mid-July, the peak abundance of adults did not occur until some time later, e.g. in 1964 between August 3 and 10 (Fig. 36, p. 252).

The second generation begins to lay a few days after emerging. The laying substratum is then usually the tillers of oats and the grasses forming the undergrowth in the nurse crop.

The *A. obscurus* population develops on the other spring cereals — spring wheat and barley — concurrently with its development on oats. During the harvesting of spring cereals in the autumn some of the macropterous form migrate to sprouting winter cereals fields and overwinter there. This migration has previously been noted by STRANAK (1912). Some of these thrips may move to the grass developing under the nurse crop and overwinter there. Part of the population remains in the leys for hibernation. In unfavourable autumns some *A. obscurus* may have to remain on the stubble of the spring cereals, and may easily be destroyed there by the autumn ploughing.

8. Dimorphism

There are two main forms of *A. obscurus*, the macropterous form and the brachypterous. PRIESNER (1926) also mentions a hemimacropterous form, with a wing length between those of the main forms.

The existence of macropterous and brachypterous forms of this species was noted by HALIDAY as long ago as 1836. Both wing forms have subsequently been reported by HINDS (1900, 1902), FERNALD and HINDS (1900), MALTBAEK (1932), CAPPELLETTO (1934), JOHN (1934), HUKKINEN (1935), von OETTINGEN (1942, 1952 b), MORISON (1943), BAILEY (1948), FRANSSEN and MANTEL (1962) and WETZEL (1964). Some researchers regard the macropterous form as commoner than the brachypterous (JOHN 1934, HUKKINEN 1935), while others (HINDS 1900, 1902, FERNALD and HINDS 1900, von OETTINGEN 1942, BAILEY 1948) regard the brachypterous form as the commoner in autumn and in early

Table 22. The wing forms of the progeny of *A. obscurus* Müll., females of different wing forms in outdoor rearing tests

Parental wing form	Generation	Number of cultures	Number of progeny	% of progeny	
				Macropterous	Brachypterous
Macropterous	Hibernated	19	163	60.5	39.5
	New generation	10	123	51.8	48.2
Brachypterous	Hibernated	20	197	51.0	49.0
	New generation	10	137	48.4	51.6

Table 23. Effect of photoperiodicity on wing form of *A. obscurus* Müll.

Parental wing form	Food plant	Length of photoperiod	Number of cultures	Number of progeny	% of progeny	
					Macropterous	Brachypterous
Macropterous	Oats	Normal day	10	69	66.9	33.1
Brachypterous	Timothy		10	94	20.8	79.2
Macropterous	Oats	Short day	9	101	—	100.0
Brachypterous	Timothy		10	77	—	100.0

summer. According to Hinds (1900), c. 98 % of the *A. obscurus* adults that hibernate are of the brachypterous form, while 90—95 % of the progeny of the overwintered specimens develop long wings. It thus seems evident that females of either wing form may have macropterous and brachypterous progeny.

Hereditary and external factors may affect the wing form of insects. Among the possible external factors are light, nutrition, population density and temperature; and the effects of all these except the last-mentioned were investigated. The effects of the various factors on the wing form in thrips have probably not been investigated before.

Hereditary factors. — *A. obscurus* is a thrips species that reproduces parthenogenetically, and males of the species have never been encountered in Europe. There is consequently no possibility for the wing form to be passed down to progeny by a male, as is the case with certain other groups of insects (Picard 1931, Sellier 1953).

Macropterous and brachypterous females of *A. obscurus* produce progeny with both wing forms (Table 22). The ratio between the wing forms in the progeny is entirely dependent on the prevailing conditions. Table 22 shows the total numbers of progeny of females of each wing form on timothy and oats, two plants on which this species reproduces.

Photoperiodism. — Some investigators have observed that the proportion of brachypterous specimens in the *A. obscurus* population increases towards the autumn. This could be due either to the shortening of the photoperiod or to a decrease in temperature, or perhaps to both together. The effect of photoperiodism on the wing form of *A. obscurus* was investigated in outdoor cultures, some of which were kept in darkness from 16:00 hrs to 08:00 hrs, while the others were allowed to develop at the prevailing normal length of day at Tampere in June. Photoperiods were begun three days after these cultures had been established.

None of the *A. obscurus* that developed under a short photoperiod grew long wings, while with normal daylight a large number of brachypterous and macropterous adults developed (Table 23). Under these circumstances day-length seems to have a very great influence on the development of the wing form.

A short photoperiod has likewise been found to cause shortness of wings in cicada (Kisimoto 1956 d, Johno 1963). Rivnay (1937) also reported that light has an indirect effect on the development of wings in aphids.

Table 24. Effect of food plant on wing form of *A. obscurus* Müll.

Parental wing form	Generation	Food plant	Number of cultures	Number of progeny	% of progeny	
					Macropterous	Brachypterous
Macropterous	Hibernated	Oats	10	69	66.9	33.1
	New generation		5	69	80.2	19.8
Brachypterous	Hibernated		10	103	81.3	18.7
	New generation		5	65	78.8	21.2
Macropterous	Hibernated	Timothy	10	94	54.2	45.8
	New generation		5	54	17.7	82.3
Brachypterous	Hibernated		10	94	20.8	79.2
	New generation		5	72	11.9	88.1

Nutrition. — That nutrition affects wing form has earlier been shown in the development of insect species living as parasites (LICHTENSTEIN and PICARD 1917, PICARD 1923, SCHMIEDER 1933). It seems, however, that in phytophagous species the quality of the food, i.e. the host plant, is also of great significance in determining whether the species develops long or short wings. In tests with *A. obscurus* oats were selected to represent the cereals and timothy to represent the cultivated grasses. The species occurs in great numbers on both these plants. The cultures were reared outdoors. They revealed that on oats the females of either wing form mainly produce macropterous progeny, while on timothy most of the progeny are usually of the brachypterous form (Table 24). The tendency was the same both in cultures reared from hibernated specimens and those reared from the new spring generation.

The abundances of the different wing forms of *A. obscurus* on various plant species could be clarified in some degree from material netted for systematic studies. The thrips material collected from cereal plants in 1963—66 was studied for this purpose. However, only the 1963 material was available from winter wheat. The abundance of the different wing forms of *A. obscurus* on various species of cereals is shown in Table 25. The table shows that on cereals most of the population was of the macropterous form. The proportion of brachypterous specimens on the various cereals varied from 0.1 to 4.6 per cent. Brachypterous specimens have occasionally been found on cereals in the summer, and no marked increase in the abundance of this form was noted towards the autumn. WETZEL (1964) came to the same conclusion in his investigations. This may be largely due to the fact the *A. obscurus* females reproducing on cereals in late summer lay their eggs mostly on the tillers growing out from the base of the cereal plant, where the developing adults remain after emerging. Because of the shortness of the tillers, such specimens are not likely to be netted in the normal way. But obviously, a considerable proportion of the *A. obscurus* developing on cerals in the autumn are of the brachypterous form. This is mainly indicated by samples taken for studies on overwintering or of samples otherwise taken in winter from the nurse crop stubble, in which the proportion of brachypterous specimens in the population was very high.

Table 25. Frequencies of the different wing forms of *A. obscurus* Müll. on various cereal plants, according to to samples netted in 1963—66

Species of cereal	Number of samples	Number of specimens	% of specimens	
			Macropterous	Brachypterous
Rye	82	951	97.1	2.9
Winter wheat	6	783	99.9	0.1
Spring wheat	47	3 269	97.3	2.7
Barley	59	2 063	96.4	3.6
Oats	113	11 080	95.4	4.6
Total	307	18 146		

In 1963—64, samples were netted from oats grown on different soils. The proportion of brachypterous specimens in these samples varied from 1.9 to 2.9 % (Table 26), values which do not differ greatly from the average obtained from oats during the different years (Table 25).

Table 26. Frequencies of the different wing forms of *A. obscurus* Müll. on oats growing on various soils, Tikkurila 1963—64

Soil	Number of samples	Number of specimens	% of specimens	
			Macropterous	Brachypterous
Finesand	16	3 582	97.1	2.9
Sandy clay	17	2 246	98.1	1.9
Sandy clay with organic matter	17	3 141	97.4	2.6
Total	50	8 969		

Samples were also netted from ordinary oat fields and from oats grown as nurse crop. In this case, too, the variation was very slight, the proportion of the brachypterous form in the population varying between 1.8 and 3.1 % (Table 27).

Table 27. Frequencies of the different wing forms of *A. obscurus* Müll. on oats and on oats as nurse crop, Tikkurila 1963—64

Vegetation	Number of samples	Number of specimens	% of specimens	
			Macropterous	Brachypterous
Oats	25	3 856	96.9	3.1
Oats as nurse crop	25	5 113	98.2	1.8
Total	50	8 969		

Table 28. Frequencies of the different wing forms of *A. obscurus* Müll. on cutting leys 1963—66 and some seed leys at Tikkurila 1966

Vegetation	Number of samples	Number of specimens	% of specimens	
			Macropterous	Brachypterous
Cutting ley	56	6 249	61.7	38.3
Timothy ley	10	1 676	50.4	49.6
Cocksfoot ley	8	181	66.2	33.8
English ryegrass ley	11	1 902	67.5	32.5
Total	85	10 008		

In leys grown for cutting or for seed, the proportion of the brachypterous form in the *A. obscurus* population was considerably greater than it was on cereals (Table 28). The 4-year average for grass leys at Tikkurila was 38.3 %, i.e. a good third of the specimens were brachypterous. Samples could usually only be netted from the former type of leys early in the summer, before cutting. The migration of this species from grass leys to other types of vegetation may have had some effect on the results, for only the macropterous specimens migrate.

From seed leys, samples were netted in 1966 only. In cocksfoot and English ryegrass about one-third of the population were brachypterous, but on timothy almost one half were brachypterous. Samples could be taken up to mid-August from English ryegrass only, while on the other leys grown for seed sampling had to discontinued at the end of July because of harvesting. The absolute and relative numbers of brachypterous specimens were at their peak at the end of June and in the first days of July, after which their proportion in the netted samples declined.

The amount of food may also affect the wing form of an insect. This effect becomes particularly evident in cases where the number of specimens on a plant is so great that there is not enough food for all the developing individuals. Drying and wilting of the plants from other causes may also lead to a food shortage. The effect of density on insect wing form has been studied a great deal. BADONNEL (1948, 1949) found that an increase in density in *Psocoptera* causes an increase in the proportion of macropterous specimens in the population. Similar results have also been obtained by KISIMOTO (1956 a, 1956 b, 1956 c, 1956 d, 1959), JOHNO (1963) and RAATIKAINEN (1967) on plant-hoppers and by KENNEDY (1956) on grasshoppers.

The investigations on dimorphism in *A. obscurus* did not clearly reveal any effect of density on wing form (Table 29). No actual food shortage occurred during the investigation of this factor, but it was assumed that the effect is caused by some stimulus between larvae as well as food deficiency during the larval stage (BADONNEL 1949, LONG 1955, JOHNO 1963).

Temperature. — The significance of temperature as a factor affecting wing form has also been a subject of study for a long time. MARCHAL (1927 a, 1927 b, 1930, 1931, 1936) observed seasonal dimorphism in a species of *Trichogramma* in which the brachypterous specimens occur in the spring generation immediately following the winter. In this case, brachyptery is related to low temperature. CHOPARD and BELLECROIX (1928), RIVNAY (1937) and BADONNEL (1949) refer to similar effects of temperature, although the observations made by BADONNEL show that temperatures above +23°C had the opposite effect on his *Psocoptera* to the effect of increased density, i.e. it decreased macroptery.

Table 29. Effect of density on wing form of *A. obscurus* Müll.

Parental wing form	Generation	Food plant	Density specimens per plant	Number of progeny	% of progeny	
					Macropterous	Brachypterous
Brachypterous	Hibernated	Timothy	2	68	47.0	53.0
			5	98	32.5	67.5
			10	116	51.1	48.9
Macropterous	New generation		1	52	35.8	64.2
			10	80	47.4	52.6
			20	124	55.2	44.8

The effect of temperature on *A. obscurus* could not be investigated by means of actual tests, because no rearing sites with identical light conditions but differing temperatures were available. Yet there are indications that in *A. obscurus*, too, an increase in rearing temperature may cause an increase in the proportion of macropterous specimens. This conclusion was reached by testing recently hatched larvae taken from rearing sites identical as regards temperature to other rearing sites and observing that they developed the two wing forms in different proportions according to the subsequent rearing temperature. At room temperature (+23—+25°C) only one specimen out of ten developed short wings, in the laboratory (+20—+22°C) 5 out of 11 did so, and in outdoor cultures (+16—+18°C) all 9 larvae did so. There were also differences in the amounts of light at the sites of rearing, and this too may have had some effect, although if so, this should have been the opposite. Be this as it may, the effect of temperature on the wing form of *A. obscurus* requires more investigation.

A development stage susceptible to external factors. — Long (1955) found that the larval stage of grasshoppers is extremely susceptible to external influence, and that the mere propinquity of, say, 2—3 larvae causes changes in colour and a shortening of the larval stage. According to Kisimoto (1959), in the plant-hopper *Nilaparvata lugens* Ståhl., the third nymphal instar is the stage that is most sensitive to the effects of density, and the wing form of the specimen is determined by the time of the final nymphal instar.

Investigations were made to ascertain the developmental stage of *A. obscurus* affected by day-length. Use was made of a series of cultures in which *A. obscurus* females had been allowed to lay for 48 hours. At two-day intervals these cultures were shaded one by one and subsequently allowed a short day only (eight hours of daylight per day). The wing form of the specimens was observed, and it was found that the first two cultures, which were allowed only a short photoperiod after two and four days respectively had elapsed since oviposition, produced brachypterous specimens only, 18 and 8 specimens respectively. The third culture in the series, which was shaded from the sixth day after oviposition, produced two macropterous as well as six brachypterous specimens. The fourth, fifth and sixth cultures, in which shading was started 8, 10 and 12 days after the onset of oviposition, produced 13, 5 and 2 macropterous specimens and 3, 3 and 2 brachypterous specimens respectively. Thus the borderline case in the development of wing form occurred six days after the onset of oviposition. As, in indoor cultures such as the above, the egg stage lasted 5.1 to 5.4 days on average (cf. Table 13, p. 218), the first specimens must have been in the larval stage when first shaded, although still very small. True, the cultures that were later shaded also produced brachypterous specimens, but this can be explained, at least in part, by the variations occurring in the duration of the egg stage. It can thus be concluded from the rearing tests performed that day-length, at least, has an effect on the wing form of *A. obscurus*, either very early in the larval stage or immediately before the larvae hatch.

C. Frankliniella tenuicornis Uz.

This species was at one time referred to the genus *Physopus* and known as *P. tenuicornis* Uz. (e.g. Uzel 1895, O. M. Reuter 1899, E. Reuter 1901 a, Schille 1912, Hukkinen 1917 a, Blattny 1923). Since the 1920s, it has been placed in the genus *Frankliniella.*

1. Distribution

F. tenuicornis is found in various parts of Europe (Uzel 1895, Ribaga 1902, Schille 1912, Bagnall 1912, 1913, Williams 1913, Tullgren 1917, Theobald 1922, Blattny 1923,

KNECHTEL 1923, JOHN 1925, 1934, MALTBAEK 1932, BAGNALL and JOHN 1935, KELER 1936, MORISON 1943, von OETTINGEN 1951, PELIKAN 1952, STRAWINSKI and SECZKOWSKA 1952, MÜHLE 1953, 1958, FRANSSEN and MANTEL 1962, MANTEL 1969). Outside Europe, this species is also found in Asia (JOHN 1924, BLUNCK 1958, TANSKY 1961, KUROSAWA 1968) and North America (WATSON 1922, 1923, HOOD and HERRICK 1926). Von OETTINGEN (1955) describes this species as circumpolar.

In Finland, the species is distributed throughout the country, including northernmost Lapland (HUKKINEN 1942).

2. *Host plants*

During the research period *F. tenuicornis* was the most numerous of the thrips species occurring on cereals (KÖPPÄ 1967). On both winter and spring cereals it was found in far greater abundance than any other species of thrips. It reproduces vigorously on all the species of cereals (Table 1, p. 206), and may be an important pest of these (cf. p. 195). It also feeds and reproduces on maize, as has been ascertained by other researchers (HOOD and HERRICK 1926, HÅRDH 1955, BLUNCK 1958, FRANSSEN and MANTEL 1962).

Apart from the cereals, *F. tenuicornis* reproduces on many cultivated and wild grasses (Table 1, p. 206). It should be mentioned in particular that the females also lay on *Deschampsia caespitosa* L., but the larvae cannot feed on this grass, apparently because of the strange surface conformation of its leaves. It is also probable that reproduction cannot occur on *Deschampsia flexuosa* L. or *Festuca ovina* L. either, for the stringy leaves of these species are not suitable sites of laying and nutrition. Some eggs were also found on the stipules of a number of ley legumes, but the larvae were unable to survive for very long on these plants.

3. *Sex index*

The results of the samples netted at Tikkurila in 1960—65 show that the sex index of this species varies greatly from year to year even on one and the same species of cereal. It also varies a great deal between the different species of cereal even with a single year. Yet the average sex index of this species is roughly the same on different species of cereal. Thus at Tikkurila it was 77.2 % on rye, 77,3 % on oats, 79.4 % on winter wheat, 82.2 % on spring wheat and 76.1 % on barley (KÖPPÄ 1969 b). At Somero the sex index of this species averaged 73.9 % on rye, 73,6 % on barley, 76.2 % on oats and 90.9 % on spring wheat. Thus males of this species were obviously far commoner than has been stated by HUKKINEN (1936 a) and WETZEL (1964).

The sex index of *F. tenuicornis* varies during the growing season. As it is only the females that hibernate, the sex index is 100 % at the beginning of the growing season. It falls to half of this, and even lower, when the new generation becomes adult (KÖPPÄ 1969 b). Later on, as the males begin to die off at the approach of winter, the sex index rises again to 100 %.

4. *Hibernation*

F. tenuicornis overwinters, i.e. its adult females overwinter, mainly on shoots of winter cereals and on cereal stubble (KÖPPÄ 1969 a). Overwintering on any other biotopes, such as leys and wild grasses, is probably only incidental.

5. *Developmental stages*

The developmental stages of *F. tenuicornis* are the same as those of *L. denticornis* and *A. obscurus*. Excluding the egg stage, they are shown in Fig. 21.

The egg is pale and translucent. It is elongated and frequently broader at one end and more curved than that of the previous species (Fig. 22).

Measurements were made of 616 eggs of this species, and the length was found to vary between 0.224 and 0.314 mm, the average length being 0.276±0.003 mm. The respective figures for egg breadth were 0.090—0.126 mm and 0.112±0.002 mm. Thus the eggs are shorter and

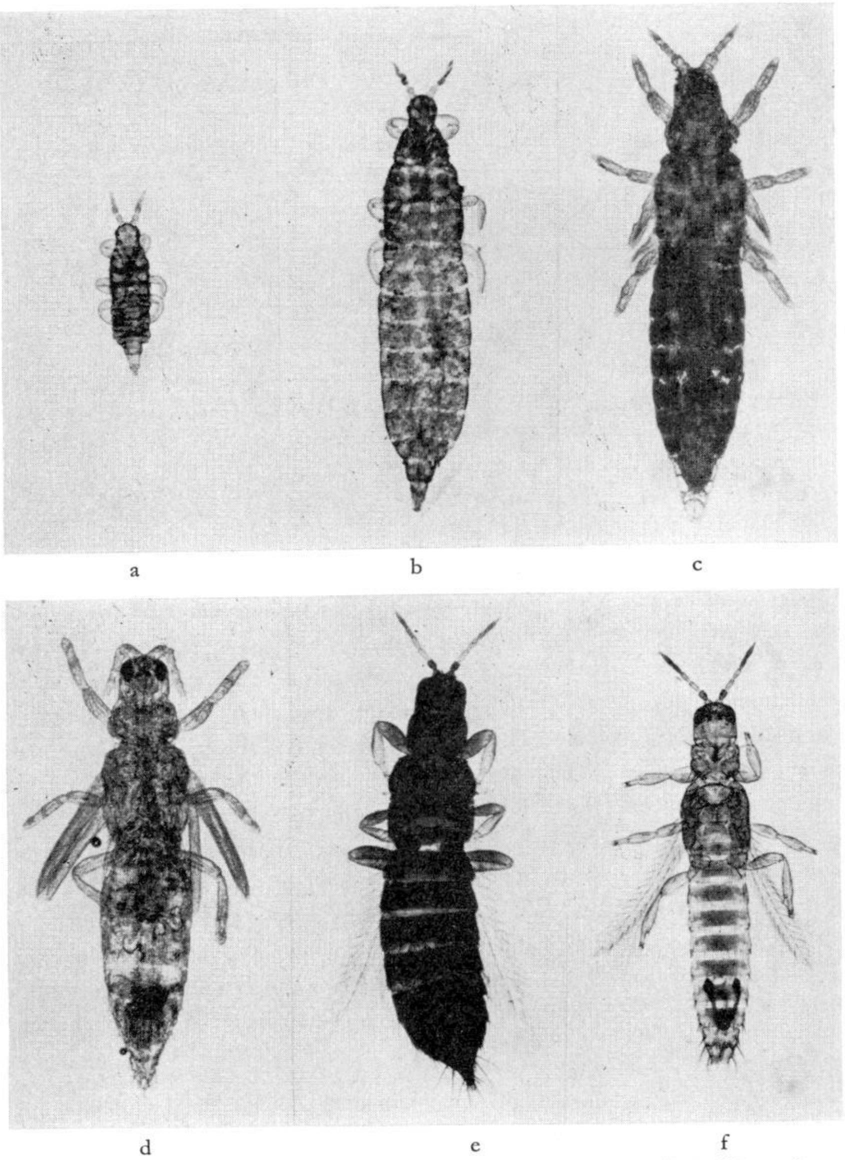

Fig. 21. *F. tenuicornis* Uz. developmental stages: a) 1st instar larva, b) 2nd instar larva, c) prepupa, d) pupa, e) adult ♀ and f) adult ♂. Photos: Institute of Photography, Helsinki.

relatively broader than those of *L. denticornis* and *A. obscurus*, as shown by their small length-to-breadth ratio, 2.46. Fig. 23 shows in greater detail the distribution into size classes of the lengths and breadths of the measured eggs.

The duration of the egg stage of *F. tenuicornis* varied between 4 and 8 days, depending on the rearing conditions (Table 30, Fig. 24). It thus seems to be longer than the egg stage of *L. denticornis* but shorter than that of *A. obscurus* (cf. Table 2, p. 208 and Table 13, p. 218).

The larva of *F. tenuicornis* (Fig. 21 a and b) is pure yellow in colour. It moves much faster than the larvae of the other two species previously discussed. PRIESNER (1926) gives 1.47 mm as the length of a second-instar larva.

The duration of the larval stage of the *F. tenuicornis* reared varied between 5 and 15 days (Table

Fig. 22. *F. tenuicornis* Uz. eggs, about 80 times natural size.

Table 30. *F. tenuicornis* Uz., duration of egg stage on oats

Rearing place	Average temperature °C	Number of eggs	Duration of egg stage, days	
			Average	Range
Room	+25.8—26.0	14	4.2±0.10	4—5
Laboratory ..	+21.5—21.7	12	6.4±0.19	6—8
Outdoor culture	+18.2—20.4	9	7.2±0.15	7—8

Table 31. *F. tenuicornis* Uz., duration of larval stage on oats

Rearing place	Average temperature °C	Number of specimens	Duration of larval stage, days	
			Average	Range
Room	+23.4—23.7	13	6.4±0.23	5— 8
Laboratory ..	+19.8—20.8	12	8.5±0.38	6—11
Outdoor culture	+13.6—15.1	10	12.3±0.55	10—15

31). This great variation in the development of the individual larvae is most clearly demonstrated in Fig. 24. The investigations did not reveal any clear difference between the sexes in rate of larval development, for the larval stage of the 5 male specimens lasted on average 6.3±0.22 days, while that of the 7 females was 6.4±0.38 days.

On moulting the larva enters the prepupal stage (Fig. 21 c), in which stage its eye spots are red. The head, antennae, legs, wing buds and the tip of the abdomen are translucent. The rest of the prepupa is distinctly yellow. The length of the male prepupa varies between 0.9 and 1.1 mm, and that of the female prepupa between 1.1 and 1.3 mm. This species has a very short prepupal stage, which varied between 0.5 and 3.0 days, depending on the rearing conditions (Table 32).

The prepupal stage is followed by a pupal stage (Fig. 21 d) that resembles the prepupal stage in respect of colouring. Priesner (1926) did not find or describe the female pupa of this species. He gave 1.17 mm. as the length of the male pupa. This must have applied to a rather large specimen, for the present measurements showed that the length of the male pupa varies between 0.9 and 1.1 mm. The respective figures for the female pupa are 1.1 and 1.4 mm. The duration of the pupal stage varied between 1.5 and 5.0 days under the different rearing conditions, i.e. roughly within the same limits as that of *L. denticornis* (Table 33, cf. Table 5, p. 209), although the average temperature in the former cultures was slightly lower. No clear-cut

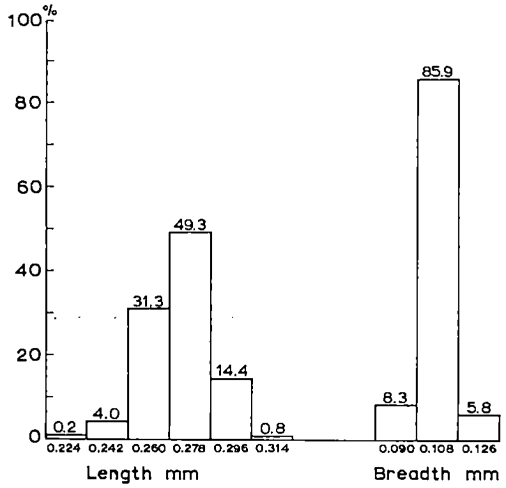

Fig. 23. *F. tenuicornis* Uz. eggs, size distribution by length and breadth.

Table 32. *F. tenuicornis* Uz., duration of prepupal stage on oats

Rearing place	Average temperature °C	Number of specimens	Duration of prepupal stage, days	
			Average	Range
Room	+23.0—24.0	13	1.1±0.08	0.5—1.5
Laboratory ..	+20.7—21.5	12	1.6±0.20	1.0—2.5
Outdoor culture	+15.1—16.0	10	2.2±0.13	1.5—3.0

Table 33. *F. tenuicornis* Uz., duration of pupal stage on oats

Rearing place	Average temperature °C	Number of specimens	Duration of pupal stage, days	
			Average	Range
Room	+23.5—24.0	12	2.0±0.09	1.5—2.5
Laboratory ..	+20.3—21.3	11	2.8±0.15	2.0—3.5
Outdoor culture	+14.8—16.3	10	4.3±0.06	4.0—5.0

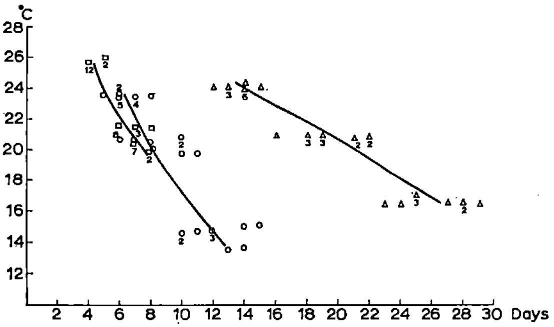

Fig. 24. *F. tenuicornis* Uz., individual rates of development of eggs (□—□) and larvae (○—○) and development from egg to adult (△—△), at various rearing temperatures. The curves indicate the average durations of the developmental stages.

differences could be found between the two sexes in the duration of the pupal stage.

The wing buds of the pupa begin to darken about 12 hours before the adult emerges. The adult male is 0.9—1.2 mm long and the female 1.2—1.5 mm (Fig. 21 f and e).

It seems that the development of *F. tenuicornis* from egg to adult takes roughly the same time as that of *L. denticornis*, allowing for the fact that the cultures of these two species differed somewhat in temperature (Table 34). The variation in the rate of development of individual specimens in quite wide, as is demonstrated most clearly in Fig. 24.

The adult male copulates with the adult female. Copulation usually takes only a few second, but individual specimens may copulate for a longer time. The copulation of adult thrips has been described in greater detail by Franssen and Mantel (1964). Apart from females of its own species, *F. tenuicornis* males were once or twice found copulating with females of *A. obscurus f. macroptera.*

Table 34. *F. tenuicornis* Uz., duration of development from egg to adult on oats

Rearing place	Average temperature °C	Number of specimens	Development from egg to adult, days	
			Average	Range
Room	+24.0—24.4	12	13.7±0.23	12—15
Laboratory ..	+20.7—21.2	11	19.3±0.57	16—22
Outdoor culture	+16.5—17.2	9	26.0±0.70	23—29

6. Life cycle

F. tenuicornis overwinters to a considerable extent on winter cereals (Köppä 1969 a), where it begins to oviposit in spring when the weather gets warmer.

There is a preoviposition period and maturation of the ovaries proceeds gradually during the winter (Fig. 18, p. 220). Towards the end of October oviposition did not begin until roughly one month after the specimens had been put into the cultures, but from the end of November onwards laying began sooner, within less than 10 days. After January, and until the spring, there was no longer any noteworthy change in the situation. Towards the end of April the specimens introduced into indoor cultures started to lay in 4.1±0.84 days on average, the variation between individual specimens being 3—6 days.

It also seems that the proportion of ovipositing females in the population has increased by the spring (Fig. 19, p. 220). Of the specimens placed cultures at the end of October, only 40 % oviposited, but the proportion then increased rapidly and from the end of December onwards was 100 per cent. It is possible, of course, that if the females from the earlier cultures had survived long enough, they might have begun to lay; but the females in the cultures usually lived for quite a long time. For instance, one specimen placed in a tube on October 24, 1968, did not die until February 7, 1969, but although its lifespan was 106 days it did not begin to oviposit.

The preoviposition period of this same species had been investigated earlier, in the winters of 1967 and 1968. Late in the winter of 1967, the females began to oviposit on average 3.0±0.20 days after being placed in cultures. The range was then 2—4 days and the rearing temperature +22°C. The females of the species taken for rearing towards the end of March 1968 began to lay on average 2.0±0.13 days afterwards, the range being 1—3 days. This culture was kept at an average temperature of +23.0°C. In the series of cultures in winter 1968—69 the rear-

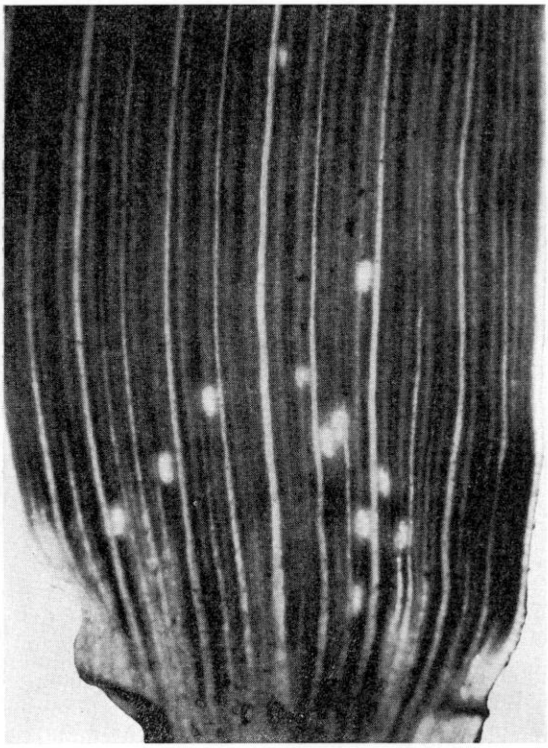

Fig. 25. *F. tenuicornis* Uz. eggs at base of barley leaf-blade. Larvae have already hatched from some of the eggs. Photo: Institute of Photography, Helsinki.

ing temperature was +20.0°C, and the differences in results may have been largely due to differences in the temperature conditions. The relative severity of the winter may naturally cause changes in the duration of the preoviposition period from one year to another.

As *F. tenuicornis* hibernates in winter cereals, it is possible to net samples of it from them as soon as the species begins to move and netting is technically feasible. In spring 1968 the first eggs were found on rye leaves on May 2, and in 1969 on May 6, but oviposition does not usually occur before mid-May (Fig. 26).

While rye is in an early stage of development and the shoots rather short, the females usually lay their eggs within the leaf tissue. Most of these eggs are deposited in the uppermost leaves, the young cell tissue of which seems to be the most suitable for oviposition. The lower leaves, which are about to dry up, do not carry many eggs but there may be large numbers of eggs in the sheaths of these leaves, which are wide enough for the females to gain entry (Table 35). When the rye ears appear, the females enter the uppermost leaf sheaths and lay their eggs in the cell tissues of the inner surface. Most of the eggs, however, are still laid in the leaves. Thus the species does not seem to prefer the sheaths as much as does *L. denticornis* (Tables 7 and 8, pp. 211 and 212) but can be regarded as being equally an inhabitant of the leaves, ears and sheaths. According to observations made by Johansson

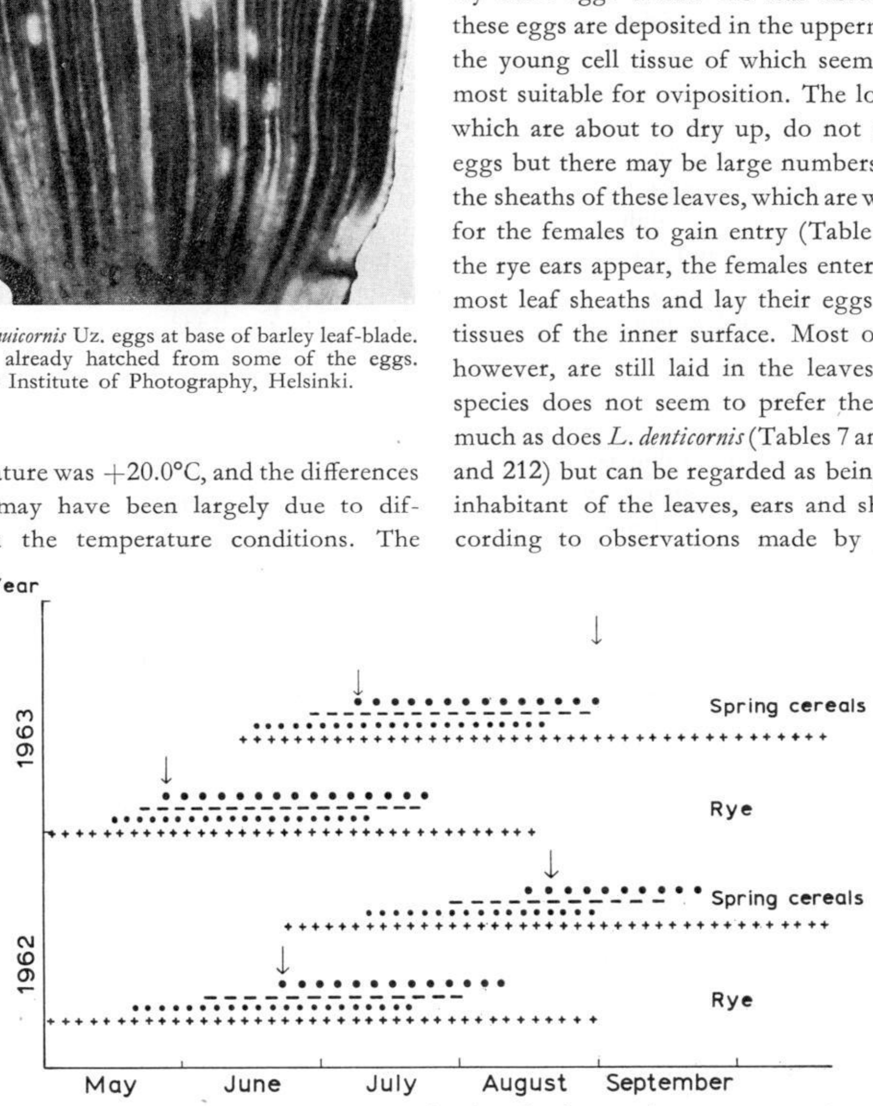

Fig. 26. *F. tenuicornis* Uz., occurrence of various developmental stages on rye and spring cereals 1962—63 (adult + + +, egg • • •, larva ———, prepupa and pupa ● ● ●). The arrows indicate the emergence of the new generation.

Table 35. *F. tenuicornis* Uz., distribution of eggs on plant. 4 replicates

Plant and its stage of development	Number of eggs			t- value
	Total	Average per culture		
		Leaf	Sheath	
Rye				
Before coming into ear	2 621	447.0±50.39	208.3±66.03	2.9*
After coming into ear	964	196.7±51.29	44.3±21.24	2.7*
Oats				
Before coming into panicle	2 177	269.2±49.68	275.0±33.10	0.1
After coming into panicle	1 439	179.3±18.23	180.5±26.42	0.1

(1946), specimens of this species are found mainly on the surface of the ears.

On the leaves the eggs are distributed mainly in the first quarter, counting from the liqule (Table 36, Fig. 25, cf. KANERVO 1950). On the sheaths, they usually occur in the uppermost quarter, closest to the ligule. Thus the females of this species do not apparently push down into the sheaths as far as do the females of *L. denticornis*, which lay their eggs mainly in the second and third quarters of the sheath counting downwards (cf. tabulation on p. 212). *F. tenuicornis* eggs were found to be distributed in the sheaths as shown below (lst quarter = quarter closest to the ligule).

Plant	1st quarter	2nd quarter	3rd quarter	4th quarter	Total
Rye	117	31	29	—	177 eggs
Oats	495	162	65	—	722 eggs

The difference between the numbers of eggs located on the first and second sheath quarters of oats was very significant (t-value = 7.4***).

F. tenuicornis lays a far greater number of eggs than does *L. denticornis*, and its oviposition period is also much longer (Table 37, cf. p. 212). The differences in respect of *A. obscurus* are nowhere near so great.

The larvae hatched from the eggs remain or move rapidly on the base of the leaf blades and on the spacious upper parts of the topmost sheath. They are also found in abundance on the lower sheaths, and a good number move to the ears when these emerge from the sheath.

In the different years the first *F. tenuicornis* larvae netted were found from May 25 to June 5 (Fig. 26). In 1963, when the early summer was warm (Fig. 5, p. 204), they hatched far earlier than they did in the unfavourable weather conditions of 1962. At Ylistaro, Southern Ostrobothnia, in 1931, KANERVO (1950) found the first larvae early in June. In that year the average May temperature at Ylistaro was +9.7°C, while at Tikkurila it was only +8.5°C in 1962, and +13.0°C in 1963. *F. tenuicornis* larvae of the second instar have been found in Russia as early as mid-May (ION 1930).

Subsequent to the larval stage the prepupae and pupae prefer the most protected parts of the plant, such as the sheaths and between the spikelets of the ear. Because of their protected mode of life, prepupae and pupae are seldom found in netted samples.

The first adults of the new generation emerged between May 27 and June 22 during the various

Table 36. *F. tenuicornis* Uz., distribution of eggs on rye by leaf-blade quarters (Quarter I = quarter nearest to ligule). 4 replicates

Leaf — blade quarters	Number of eggs		t- value			Number of eggs	t- value		
	Total	Average per culture before earing	I	II	III	Average per culture after earing	I	II	III
I	2 304	401.5±51.95				174.5±43.65			
II	199	32.5± 1.75	7.1***			17.3± 6.86	3.6*		
III	65	11.3± 0.72	7.5***	11.1***		5.0± 1.78	3.9**	1.8	
IV	8	1.8± 1.18	7.7***	14.6***	6.8***	0.3± 0.25	4.0**	2.5*	2.6*

Table 37. *F. tenuicornis* Uz., number of eggs and duration of oviposition period on rye and on oats

Food plant	Generation	Number of specimens	Oviposition period, days		Number of eggs	
			Average	Range	Average	Range
Rye	Hibernated	20	32.7±1.82	13—50	140.5±11.81	53—252
	New generation	20	31.9±2.04	18—45	156.6±13.22	86—277
Oats		20	28.6±2.01	12—45	159.9±14.56	61—292

research years (Fig. 26). When Kanervo (1950) carried out his investigations, the development of the species was very late, for no adults of the new generation were found until June 29. In explanation, it may be pointed out that the observations by Kanervo were made at Ylistaro, where development is generally later than at Tikkurila. Moreover, in 1931, the year in which his studies were carried out, the spring was later than normal in South Ostrobothnia and the average temperature in June, when the development of this species is largely complete, was only +9.7°C there, while the normal figure at Tikkurila is then +13.5°C. In Sweden, the new generation begins to appear early in June (Johansson 1938).

The appearance of the new generation of *F. tenuicornis* on cereals can be seen from the occurrence of males. It seems, too, that the first eggs laid by the hibernated females usually develop into males. To ascertain this, hibernating females were put in culture tubes and each allowed to lay on a single shoot for 3—4 days, after which they were transferred to new shoots. It was found that 13 of the 14 laying females produced progeny of both sexes, and one produced males only. The progeny of this latter specimen were very few, i.e. 6 specimens, and later it might have produced eggs which would have developed into females. In the same investigations it could also be established that in each batch of eggs laid in the 3—4 days the first specimens to hatch were usually males, although there were exceptions. This would clearly suggest that males usually develop faster than females, although this could not be definitely confirmed in the investigations of the length of the developmental period (cf. p. 230). Not all the males came from the first-laid eggs, however, for males developed from later-laid batches of eggs, too, while numerous females hatched in the meanwhile.

The development of *F. tenuicornis* occurs concurrently in winter wheat and rye. For instance, on winter wheat the first eggs laid by overwintered females were found on May 16 in 1961 and on May 29 in 1962, while the first adults emerged on June 9 and June 24 respectively, i.e. only 2—3 weeks later than on rye.

A few *F. tenuicornis* specimens remain on the winter cereals, where they develop a second generation. The females may begin to lay soon after emerging. On rye, laying occurred on average 3.1±0.60 days after emergence, the average temperature being +22.0°C. There was a very great variation between the females in this respect, however, the variation being 1—10 days. On oats the females laid their first eggs on average 2.9±0.45 days after emerging, the variation being roughly as great as on rye. During the time these cultures were reared the average temperature was +24.0—25.0°C.

The females of the new generation may reproduce in two different ways, i.e. through fertilized or through unfertilized eggs. In the former case, a male has copulated with the female, and the progeny includes both males and females. In the latter case there has been no copulation, and reproduction is by arrhenotokous parthenogenesis, i.e. the progeny are exclusively males. To ascertain this, some females were reared separately from the larval stage onwards and were allowed no contact with males. Another group of females were reared from hatching onwards, each separately with a male. Of the 12 females reared singly, one died without laying, while the rest produced a total of 160 progeny,

Table 38. Durations of preoviposition period and oviposition period, and the number and sex of the progeny of *F. tenuicornis* Uz. specimens in different modes of reproduction

Mode of reproduction	Number of females	Preoviposition period, days		Oviposition period, days		Number of progeny	
		Average	Range	Average	Range	♀	♂
Reared singly	11	2.45±0.48	1—7	21.7±3.18	6—40	—	160
Reared in pairs	11	2.18±0.33	1—4	21.7±2.55	9—36	100	44

all of which were males. These females began to lay on average 2.45±0.48 days after emerging, and laying continued for an average of 21.7±3.18 days (Table 38). The females reared with males resemble the parthenogenetically reproducing females in respect of preoviposition period and time of laying, but there was a clear difference in the progeny, most of which were females. One such culture produced only males, a total of 10, which may mean that for some reason, the male and female had not copulated. To judge from the number of progeny of these two groups of females, the mode of reproduction does not seem to have a noteworthy effect on the number of eggs, although this was not thoroughly clarified in the present investigations.

On rye, the females of the new generation usually lay their eggs on the soft basal parts of the leaves and in the sheaths, which are conveniently open at about this time.

Most of the *F. tenuicornis* population, however, migrate from winter cereals to spring cereals. During the research years the first specimens on oats were found on June 10—26. The first eggs on oats were found simultaneously. Half of these were found on the leaves and half in the sheaths (Table 35), those on the leaves mainly in the first quarter, counting from the ligule, and those in the sheaths in the highest quarter closest to the leaf blade (tabulation on p. 233). It seems that the eggs are usually laid from the upper surface. The number of eggs laid on oats per female in the cultures was 159.9±14.56, and the oviposition period averaged 28.6±2.01 days, i.e. the averages were roughly the same as those for the hibernated and new generations on rye (Table 37).

From the end of June or beginning of July larvae were found on oats right up to the end of the growing season. At first they were on the leaves, later in the sheaths, and subsequently also on the panicles when these emerged from the sheaths. The prepupae and pupae prefer to hide in the sheaths and panicles. In 1963, when the weather during the growing season was favourable for the development of thrips, the first pupae were found as early as July 7 (Fig. 26). Thus the second generation may reach adulthood by mid-July, and even in years of later development it may do so before July is over. In 1931, Kanervo (1950) found the first adults of the second generation at the beginning of August. At this time, the emerged adults usually lay their eggs on the green adventitious shoots growing at the base of the oats.

The laying and development of *F. tenuicornis* on barley and spring wheat occur concurrently with its laying and development on oats. According to observations by Kanervo (1950), the second generation and some of the third generation of this species develop very vigorously on barley. The female may lay its eggs on this cereal not only at the base of the leaf blade and in the sheaths but also in the spikelets and even in the awns.

In September, when the rye puts out shoots, part of the *F. tenuicornis* population moves to the rye and hibernates there. It is possible, especially in warm autumns, to find damage caused to the rye by this thrips species, but there is obviously no egg-laying in the autumn, although females may continue laying in indoor cultures well into the latter half of September.

D. Haplothrips aculeatus Fabr.

Haliday (1836) placed this species in the genus *Phloeothrips* (*P. aculeata* Fabr.), Beling (1872) and Szaniszlo (1879) in the genus Thrips (*T. frumentarius* Bel.), Lindeman (1886) in the genus *Phloeothrips* (*P. frumentaria* Bel.), and Uzel in the genus *Anthothrips* (*A. aculeata* Fabr.). This species has been referred to its present genus since early in the second decade of the present century (Priesner 1927—28).

1. *Distribution*

H. aculeatus is found everywhere in Europe (Priesner 1927—28), in Caucasia (Schugurow 1907), Siberia and Khazakstan (John 1924, Tansky 1961) and in Japan (Kurosawa 1968). Von Oettingen (1955) regards this species as Palearctic. According to Hukkinen (1936 b, 1942), it is distributed in Finland all the way up to the Kemi district, in Lapland.

2. *Host plants*

H. aculeatus apparently feeds and reproduces on all species of cereals (Table 1, p. 206). In Finland, it is chiefly found on rye and winter wheat (Köppä 1967), on which most of the damage caused by this species has been observed (Brummer 1939). Elsewhere, the species is a common pest of all cereals (cf. p. 197).

Cereals apart, *H. aculeatus* is also able to reproduce on many other plants (Table 1, p. 206). Maize and Sudan grass, listed in the table, are also probably host plants of this species (Kurdjumov 1913 a, 1913 b, Reinmuth 1934, Blunck 1958), although this could not be confirmed, for it was not possible to obtain flowers or flower parts of these plant species in a suitable state for test. In addition to the plants mentioned in the table, *H. aculeatus* has also been found on other grasses, e.g. rice (Coidanich 1938), *Cynosurus cristatus* L. (Beling 1872), *Ammophila arenaria* L. (Priesner 1924 b) and *Holcus lanatus* L., *Phragmites communis* Trin. and *Glyceria* sp. (Tullgren 1917), all of which may be host plants of this species.

H. aculeatus is regarded as a highly mobile thrips species (cf. von Oettingen 1930, 1942, 1952 a, 1952 b) with a strong tendency to move from plant species to another. It is consequently understandable that specimens of this species have been found on a wide variety of plants, not all of which can be assumed to be host species.

Apart from being a plant pest, *H. aculeatus* is known to be predaceous. It may suck insect eggs dry (Znamensky 1914, Bremer and Kaufmann 1931). It may also kill insects and mites (Kurdjumov 1913 b, Knechtel 1931) in other stages of development, and even attack its own species. There are several other reports of predaceous behaviour in specimens of determined or undetermined species of the genus *Haplothrips* (Miles 1923, Gilliatt 1935, Listo et al. 1939, Lord 1949).

3. *Sex index*

In the present investigations the sex index of *H. aculeatus* on rye was found to average 81.1 % at Tikkurila and 84.4 % at Somero. On winter wheat the figure at Tikkurila was 81.8 % (Köppä 1969 b). Because of the sparsity of this species, the sex index on spring cereals could not be determined with certainty. Elsewhere, the proportion of males in the population has been considerably higher, and the sex index consequently lower (Körting 1928, Holtmann 1963 a, Wetzel 1964). Males occur throughout the year. The sex index of this species also seems to vary to some extent according to the food plant (cf. Holtmann 1963 a).

4. *Hibernation*

H. aculeatus overwinters in both its adult male and adult female form. Grassy forest edges and roadsides are very suitable overwintering sites for this species (Köppä 1969 a). Overwintering *H. aculeatus* can also be found in the shoots of winter cereals and in cereal stubble (Köppä 1969 a) and under tree bark (Priesner 1924 a, Körting 1930). According to Körting (1928),

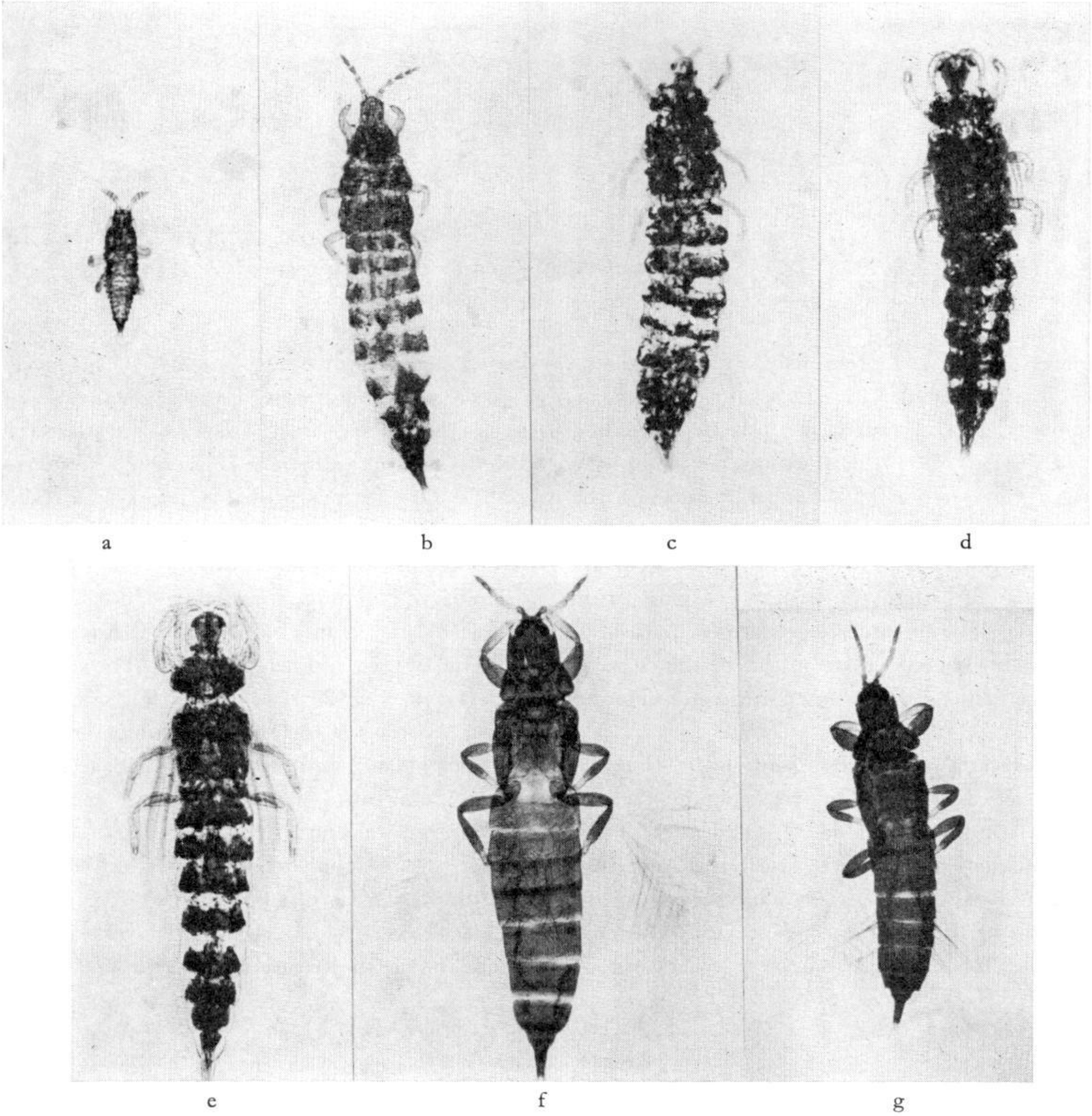

Fig. 27. Development stages of *H. aculeatus* Fabr.: a) 1st instar larva, b) 2nd instar larva, c) prepupa, d) 1 st instar pupa, e) 2nd instar pupa, f) adult ♀ and g) adult ♂. Photos: Institute of Photography, Helsinki.

this species seems particularly to prefer low-lying, damp and protected sites for hibernation.

5. Developmental stages

The development of *H. aculeatus* differs from that of the species previously described in that it has two distinct pupal instars. Fig. 27 shows the developmental stages of this species with the exception of the egg stage.

The egg is elongated and is usually only slightly curved (Fig. 28). When recently laid, it is yellowish white and translucent. Later it becomes slightly greyish red, and finally it turns bright red. The length of the egg varies from 0.360 to 0.468 mm, averaging 0.422±0.001 mm. The measurements for the breadth are 0.108 to 0.144 mm and 0.131±0.0002 mm respectively. A total of 281 eggs were measured. The egg is rather narrow in comparison with the eggs of the

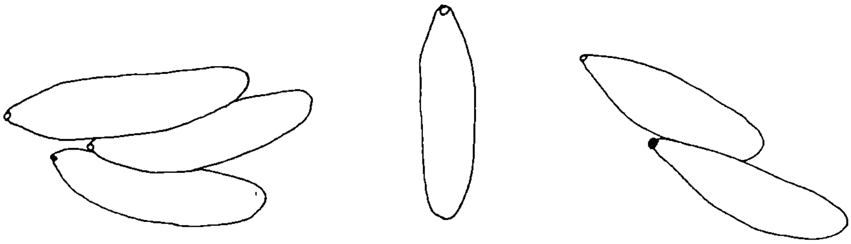

Fig. 28. *H. aculeatus* Fabr. eggs, about 80 times natural size.

species discussed previously, its length-to-breadth-ratio being 3.22. The results of the measurements are consistent with those presented by Körting (1934), according to which the length varies from 0.374 to 0.425 mm and the breadth from 0.125 to 0.135 mm. According to Holtmann (1963 a), however, the eggs are somewhat broader, the length varying from 0.339 to 0.446 mm and the breadth from 0.144 to 0.165 mm. The size distribution of the eggs by length and breadth is shown in greater detail in Fig. 29.

The duration of the egg stage of *H. aculeatus* varied between 5 and 13 days, depending on the rearing conditions (Table 39). The rates of development of individual eggs are shown in Fig. 30. The duration of the egg stage seems to vary more than that of the species previously discussed, but this is probably due to the lower outdoor rearing temperature. Znamensky (1914) gives 5—6 days as the duration of the egg stage of this species in Russia, and Franssen and Mantel (1965 a) as approximately 12 days in the Netherlands. The former probably refers to a result obtained in indoor cultures, and the latter to outdoor cultures or field conditions.

The larva hatching from the egg (Fig. 27 a) is yellowish orange in colour, only the rearmost segments of the abdomen being red. The second-instar larva (Fig. 27 b) also has the same colouring, except for the antennae, which are grey or almost black, and the legs, which are light grey. When fully grown, the larva measures 1.6—1.8 mm in length.

There is a considerable variation in the duration of the larval stage (Table 40, Fig. 30), and, as Körting (1934) has shown, this is dependent on the nature of its food (cf. Table

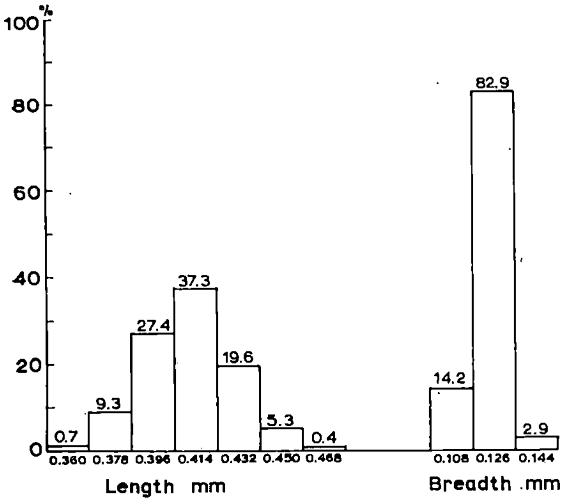

Fig. 29. *H. aculeatus* Fabr. eggs, size distribution by length and breadth.

Table 39. *H. aculeatus* Fabr., duration of egg stage on rye

Rearing place	Average temperature °C	Number of eggs	Duration of egg stage, days	
			Average	Range
Room	+24.7—24.9	10	5.4±0.16	5— 6
Laboratory ..	+21.2—21.3	11	6.3±0.14	6— 7
Outdoor culture	+14.8—14.9	8	12.4±0.19	12—13

Table 40. *H. aculeatus* Fabr., duration of larval stage on rye

Rearing place	Average temperature °C	Number of specimens	Duration of larval stage, days	
			Average	Range
Room	+24.0—25.0	10	14.3±0.63	10—19
Laboratory ..	+20.6—22.1	11	16.3±1.26	11—24
Outdoor culture	+16.7—18.7	8	18.8±2.04	12—29

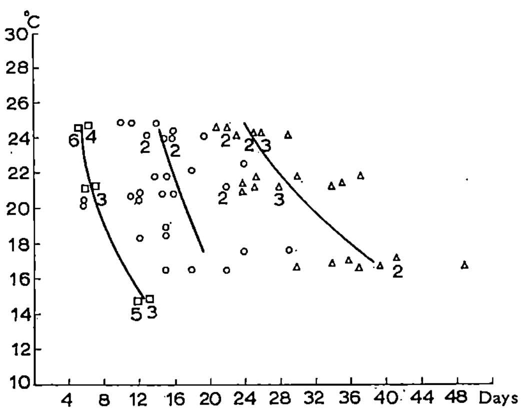

Fig. 30. *H. aculeatus* Fabr., individual rates of development of eggs (□—□) and larvae (○—○) and development from egg to adult (△—△), at various rearing temperatures. The curves indicate the average duration of the developmental stages.

41). If the larva obtains its nutrition from flowers of wheat or rye, its development is far quicker than it would be if the food were the grains of these same plants. According to investigations by KÖRTING (1934), the larval stage lasts 10—24 days on a diet of flowers and 19—47 days on a diet of grains. HOLTMANN (1963 a) gives 8 days as the duration of the first larval instar, and 18 as the duration of the second, bringing the total duration of the larval stage to 26 days. ZNAMENSKY (1914) gives 22—25 days as the duration of the larval stage, and FRANSSEN and MANTEL (1965 a) 16—30 days.

In the prepupa (Fig. 27 c) the colouring of the larva is retained. The tip of the abdomen is red, the other parts being orange-yellow or yellow. The antennae, legs and part of the head are translucent, and the eye spots red. The length of the prepupa varies between 1.1 and 1.7 mm, the shortest prepupae being males.

The prepupal stage of *H. aculeatus* is very short, and the variation in its duration is slight (Table 42). ZNAMENSKY (1914) states that the duration of the prepupal stage is 1—2 days, and KÖRTING (1934) gives it as 1—3 days at a temperature of +16.3—+23.8°C.

H. aculeatus has two different pupal instars (Fig. 27 d and e), which differ mainly in wing bud length. In a pupa of the first instar these do not extend beyond the second segment of the abdomen, while in the second pupal instar they are roughly twice as long. In colouring, the pupa resembles the prepupa, but the wing buds, which have appeared, are translucent. The length of the first-instar pupa varies between 1.3 and 1.7 mm, and that of the second-instar pupa between 1.2 and 1.6 mm.

The first pupal instar clearly lasted less long than the second (Table 43). The duration of the entire pupal stage is longer than that of the species discussed previously. KÖRTING (1934) obtained similar results, reporting that the first pupal instar lasts 1—3 days at a temperature of +16.3—+23.8°C and the second pupal instar 3—7 days at +17.0—+23.0°C.

Table 42. *H. aculeatus* Fabr., duration of prepupal stage on rye

Rearing place	Average temperature °C	Number of specimens	Duration of prepupal stage, days	
			Average	Range
Room	+24.3—25.0	10	1.0±0.00	1.0
Laboratory ..	+21.0—22.8	11	1.3±0.10	1.0—2.0
Outdoor culture	+15.6—22.5	8	1.5±0.16	1.0—2.0

Table 41. *H. aculeatus* Fabr., durations of larval, prepupal and pupal stages on various food plants and at various temperatures (KÖRTING 1934).

Average temperature °C	Duration of 1st larval instar, days		Duration of 2nd larval instar, days		Duration of prepupal and pupal stages, days		From hatching of larva to emergence of adult, days	
	Flowers of rye or wheat	Grains of rye or wheat	Flowers of rye or wheat	Grains of rye or wheat	Flowers of rye or wheat	Grains of rye or wheat	Flowers of rye or wheat	Grains of rye or wheat
+16—18	8—12	14—22	8—12	16	9—12	9—10	25—34	42—47
+18—20	6— 8	10—18	5— 8	15—25	8—10	8—10	19—22	31—42
+20—22	5— 6	10—13	5— 7	9—13	7— 8	6— 8	18—19	39
+22—23	?	?	4	?	?	5	?	?

Table 43. *H. aculeatus* Fabr., duration of pupal stage on rye

Rearing place	1st pupal instar				2nd pupal instar				Duration of pupal stage, days	
	Average temperature°C	Number of specimens	Duration, days		Average temperature°C	Number of specimens	Duration, days			
			Average	Range			Average	Range	Average	Range
Room	+24.3—25.0	10	1.0±0.00	1.0	+24.5—24.8	10	2.8±0.08	2.5—3.0	3.8±0.08	3.5—4.0
Laboratory ..	+21.0—23.0	11	1.3±0.08	1.0—1.5	+21.4—22.8	11	3.8±0.11	3.0—4.0	5.1±0.14	4.0—5.5
Outdoor culture	+16.8—23.4	8	1.2±0.13	1.0—2.0	+15.5—21.9	8	4.4±0.50	2.5—7.0	5.6±0.50	3.5—8.0

The figure of 4—5 days obtained by Znamensky (1914) for the duration of the pupal stage is again the result of indoor rearing. Holtmann (1963 a) gives 14 days as the total duration of the prepupal and pupal stages, which seems very long but may be the correct figure in very cool weather.

The wing buds of the pupa begin to darken shortly before the emergence of the adult. The length of the adult male (Fig. 27 g) varies from 1.2 to 1.5 mm, and that of the adult female (Fig. 27 f) from 1.5 to 1.7 mm. In this species copulation takes place between adults.

The development of *H. aculeatus* from egg to adult took 21—49 days, depending on the conditions (Table 44). The variation thus seems to be considerable, mainly owing to the great variation in the duration of the larval stage. Fig. 30 shows in greater detail the differences in the rates of development of individual specimens. In the Netherlands Franssen and Mantel (1965 a) found that a generation took 56 days to develop in 1962, 50 days in 1963 and 38 days in 1964. These results correspond closely to results obtained in outdoor cultures. Blunck (1925) gives 32—38 days as the duration of the entire development of *H. aculeatus*. Discounting the egg stage, the duration of development in this species varies from 18 to 47 days according to Körting (1934) and 29 to 44 days according to Holtmann (1963 a).

Table 44. *H. aculeatus* Fabr., period of development from egg to adult on rye

Rearing place	Average temperature °C	Number of specimens	Period of development, days	
			Average	Range
Room	+24.3—24.8	10	24.5±0.78	21—29
Laboratory ..	+21.0—21.8	11	29.0±1.40	24—37
Outdoor culture	+16.6—17.2	8	38.3±1.90	30—49

6. *Life cycle*

H. aculeatus does not leave its hibernation sites (cf. p. 236) to appear on cereals until the daily maximum outdoor temperature has reached +20°C (Wetzel 1962).

The first adults of this species were netted from rye between May 13—21, i.e. some 2—3 weeks before the rye came into ear. The first eggs of this species were found on the plants 1—2 weeks later.

H. aculeatus does not insert its eggs into the plant tissue, as do all the species of the *Terebrantia* group previously discussed, but attaches them loosely to the surface of the plant. The eggs are sometimes completely unattached. They are usually deposited singly, but may also be attached to one another in small batches (Fig. 28). During the research period, the greatest number of eggs found in a batch was 8, but Lindeman (1887) reports that he found a cluster of 27 eggs. The greater the number of eggs in a cluster, the smaller is the proportion of such clusters (Fig. 31). The same diagram also shows that most of the eggs are laid singly. A considerable proportion of the eggs occur in clusters of two, three or four eggs, although the number of these clusters in the total number of clusters is relatively low.

Before the rye comes into ear, *H. aculeatus* lays a few eggs near the base of the leaf blade. When the ears appear, the eggs are laid in them. Early egg-laying is also suggested by the asser-

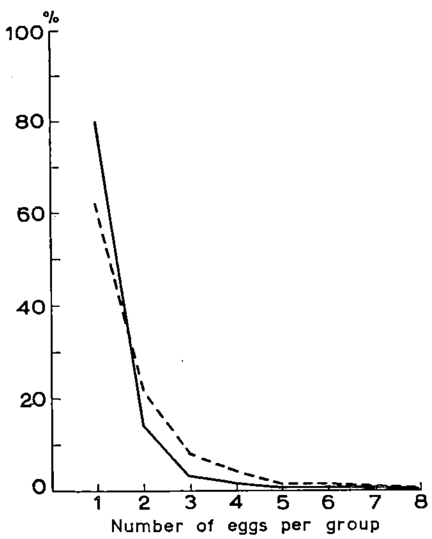

Fig. 31. *H. aculeatus* Fabr., size of egg clusters (———) and number of eggs (- - - -) in the various classes of cluster size.

tion of Trybom (1895) that the females lay their eggs on the ears while these are still inside the sheath. It is at this time that egg-laying begins, but it continues for a long period, and the report by Holtmann (1963 a) that the females do not usually lay eggs until the ear of the rye is entirely clear of the sheath, is consequently true in part.

H. aculeatus lays its eggs in different parts of the ear. At the stage when the floral parts are still tightly enclosed in the palea, eggs can be found on the surfaces of the spikelets. Many of these eggs occur between the flowers of a spikelet and, later, ventrally at the spikelet base. The eggs may sometimes be attached to the boat-shaped inner lip of the glumes enclosing the spikelet. If, at this time, the ear bears a drying flower or spikelet, the female prefers to force its way into it and lay its eggs there. While the flowers are still closed, a stray female may find its way to the inner surface of the palea around the flower and oviposit there.

With advancing development the flowers begin to open, and the *H. aculeatus* females will then usually lay their eggs inside the flowers of the spikelets. This became particularly evident in the oviposition cultures, where the ears had been cut short. Most of the eggs were then located inside the uppermost spikelets that had been cut. Eggs of this species have also been found (Holtmann 1963 a) inside the flowers, where they may be laid either in the furrows on the surface of the anthers or to the inner surface of the palea surrounding the flower. Eggs may also be found on the hairy coat of the stigma. Later, too, eggs may be found on the surface of the spikelets.

It seems that *H. aculeatus* lays fewer eggs than the species of thrips previously discussed. As the oviposition period is longer than that of the others, the number of eggs laid daily is very small. During the research period, females were reared and allowed to lay only on rye, and all the data on the oviposition of this thrips species consequently relate to this cereal. In the oviposition cultures the number of eggs per female was found to vary from 38 to 115, the average being 67.5±5.49. The oviposition period varied from 21 to 73 days with an average of 45.1±4.20 days. The average number of eggs per day was only 1.5, and the maximum number of eggs per day for any female 3.

Most of the larvae live on rye and winter wheat while the grains are developing, although some live on the spikelets immediately before or after flowering. On the ears the larvae prefer to remain between the spikelets, in the flowers and on the surface of the later-developing grains, which they damage. As the quality of the food of the larvae actually changes greatly with the development, from flower to grain, the specimens from the first-laid eggs develop more rapidly. In consequence, the period of adult emergence is longer than that of oviposition.

The earliest *H. aculeatus* larvae occur on rye at flowering time, and the number of larvae reaches its maximum when the grains are in milk-ripeness (Brummer 1939). During the research period, larvae were found from June 13 — July 3 onwards, and specimens occurred in samples netted right up to harvest time.

Prepupae and pupae were obtained from rye from June 24—July 27 onwards. In 1963, the adults of the new generation emerged quite early, i.e. on July 15. In 1960 and 1961 the first specimens of the new generation were found at Tikkurila on July 25, and in 1962 on August 12.

The females of the new generation do not usually begin to lay eggs until the following spring. In 1967, however, one female of the new generation laid 10 eggs some time after emerging. But in the cultures the females of the hibernated generation continued to lay until August 27, i.e. slightly later than the females of *L. denticornis.*

Lindeman (1887), Jordan (1888), Kurdjumov (1913 b) and Johansson (1938) assume that *H. aculeatus* is bivoltine. If this is the rule in some regions, the reproduction of the second generation may be associated with features similar to those associated with *L. denticornis* and *F. tenuicornis*. It is evident that apart from its bisexual reproduction the species also has the ability to reproduce by arrhenotokous parthenogenesis, in which event all the progeny will be males. In *Anthothrips verbasci* Osb., a species related to *H. aculeatus*, reproduction of this type has been confirmed experimentally (Shull 1914 c, 1917).

During the growing season *H. aculeatus* tends to migrate from one plant and plant species to another. It is consequently possible that part of the population will move from winter cereals to spring cereals. During the research period the abundance of *H. aculeatus* on spring cereals was low in all the trial localities. Thus the species was hardly able to establish populations at all on these plants, and certainly, very few specimens were netted in the early stages. Nevertheless, *H. aculeatus* has previously been found in great abundance on spring cereals in Finland, especially on spring wheat (Hukkinen 1934 b, Tiittanen 1954). Elsewhere, this species has also been found to be prolific on oats etc. (Holtmann 1963 a). Körting (1934) found early stages of this species on barley as well as on oats.

In Germany, *H. aculeatus* begins to move to its overwintering quarters after mid-August, and completes its migration there in the first half of September (Körting 1930). At Tikkurila, specimens were netted even during the last days of August; and in 1962, when the development of plants and thrips alike was later than usual, it was taken from rye fields at Somero on September 16.

E. Discussion

In the present study an attempt was made to investigate the biology of species of thrips living on cereals. For this purpose, use was made of laboratory and outdoor cultures, and the information obtained from these was supplemented where necessary with field investigations.

In investigating the duration of developmental stages in insects by means of laboratory and outdoor cultures kept in small rearing tubes, jars and bowls, there arise certain difficulties, which have received particular consideration from Franssen and Mantel (1965 a).

In the glass tubes (cf. p. 199) used as containers in the present study, which were tightly stoppered because of the small size and great agility of the thrips, moisture from the inserted shoots is apt to condense on the walls. Thrips in various developmental stages get caught up in this film of water, and their development may be disturbed or they may even die. If, however, the tubes are placed away from direct sunlight and the researcher is experienced in selecting a shoot of precisely the right size, this drawback can be eliminated or at least lessened. Another inconvenience in small glass tubes are the excreta of the thrips, which are deposited on the surface of the shoot and on the glass. The excreta are sticky, and thrips adults and larvae, which excrete and move a great deal, tend to get stuck in them. If the shoot is changed frequently enough, the excreta will not collect in harmful amounts. Small thrips larvae and the frequently colourless prepupae or pupae may be inadvertently lost when the shoot is removed. The new shoot introduced into the tube may easily crush a fragile thrips, of whatever stage, that happens to be in its way. In thrips cultures it is always safer to begin with abundant material, for losses will always occur; if not of the kind mentioned, then a moult may fail and the development of the specimen concerned thus be curtailed. During transfers, of which there must always be a number, thrips may likewise incur fatal injury.

Despite their drawbacks, small glass tubes have some great advantages over other types of culture vessel. First, they are easy to watch and examine. The thrips in its various developmental stages can be found in them without trouble. Thus counts of the numbers of eggs, for instance, are easy to carry out in such cultures even when the species is one of the *Terebrantia* group, the eggs of which may be difficult to discern within the leaf tissue under the microscope despite transillumination of the tissue. Such cultures also produce extremely accurate results, for they initially contain single individuals and can be checked with sufficient frequency. The development of thrips is very rapid, and the various stages follow each other in rapid succession. Extreme precision is necessary in such cases. Cultures in which the eggs are to be found within a very small space and can be counted daily when necessary are actually the only kind that can be employed for oviposition tests. Natural enemies of thrips are unable to enter small cultures of this type, nor will unfavourable weather conditions have the same effect on them as in the field. All this will ensure the accuracy of the result, although it must be admitted that indoor cultures, which in the present investigations were the only ones used to clarify points relating to the oviposition of the various thrips species, merely serve to reveal the potential egg number and oviposition period. In nature, however, numerous mishaps inevitably cause a decrease in the number of eggs laid and shorten the oviposition period and the life span.

In investigating the developmental stages of the thrips species living on cereals, an attempt was made to rear specimens continuously from egg to adult. The eggs with which the cultures were started were laid by several females of the species and can consequently be regarded as representative of a wider population.

The use of a detached shoot as substratum for egg-laying and rearing is justified in the sense that it is much easier to examine than the whole plant, and thus makes for accuracy in the results. A small shoot is a very suitable substratum for laying and rearing, provided that it is exchanged frequently enough for the freshness to be maintained. The shoot will stay fresh for 3—4 days in closed glass tubes. The development of the eggs and the determination of the duration of the egg stage, however, will not always be successful with this method, for the egg stage of the species studied usually lasts longer than 3—4 days. For this reason the duration of the egg stage, even of species that lay eggs in the leaves, was investigated by means of other types of cultures (cf. p. 200).

The rearing conditions have a very great effect on the rate of development of thrips, and these conditions must always be accurately described. Temperature is extremely important in this respect. In the present investigations the cultures were kept in three places at different temperatures. Two of these were indoors, where the temperature remained fairly constant. The third site was out of doors, where the changes in temperature were greater. An outdoor culture reflects the development of the species in field conditions, the sole difference being that a plant part is used as substratum in place of a whole plant. In similar studies carried out earlier (e.g. Hinds 1900, 1902, Znamensky 1914), the prevailing temperatures were frequently disregarded or, at least, were not reported. An exception is the study on *H. aculeatus* by Körting (1934), which was conducted in accurately controlled conditions.

The relative humidity in the cultures must be sufficient to prevent drying. Thrips usually do best in a relatively high humidity, although this requirement is less important towards the end of the growing season (Cederholm 1963). When prepupae and pupae are reared in a tube, a shoot is only necessary to maintain a suitable humidity. Humidity becomes an adverse factor in cultures only if it causes condensation on the glass surfaces.

The biology of the thrips species of cereals has been analysed on the basis of field studies (LINDEMAN 1886, 1887, HOLTMANN 1963 a, FRANSSEN and MANTEL 1965 a). In the investigation by HUKKINEN (1936 c) on *C. hamatus*, too, the passages on the biology of the species are based on field observations and on results from samples taken in the field at short regular intervals. Field studies of this kind do, indeed, clearly show the situation prevailing in nature at the time and indicate the developmental stages occurring in the species at the times in question. If, however, one begins to determine the duration of the individual developmental stages of the species in this manner, certain difficulties will arise. Firstly, samples will have to be taken very often, for development is very rapid in thrips, particularly if the weather is warm. Observation or sampling done too infrequently will give an erroneous picture of the development of the species. FRANSSEN and MANTEL (1965 a) made observations weekly, and this seems to be too long an interval. HUKKINEN (1936 c) took samples and made observations with considerably greater frequency. Another difficulty in conducting a field study lies in the taking of samples. Even a stand of cereal is always somewhat uneven in development, and so are the thrips fauna in it. To obtain a representative sample for investigation, the method employed should ensure the inclusion of both early developed and retarded plant specimens. The size of the sample should also be large. Even then, information is usually obtained on the development of the species on a certain plot only, and the situation elsewhere may be different. For greater reliability, the samples should be taken from cereals growing in various conditions.

Thus, in investigations on the biology of even those thrips species that live on cereals, it is safest to proceed from laboratory and outdoor cultures and to supplement these with field studies, as was actually done by KÖRTING (1934) in respect of *H. aculeatus*. The course of development of the various species in the present investigations was mainly studied from samples netted and taken by other means in the field and from field studies.

Investigations of the biological characteristics of thrips always involve, of course, measurement of the adults and the other developmental stages of the different species and sexes, especially if the investigation covers several comparable species, as in the present study. The measurements of the adults and other developmental stages, with the exception of the eggs of the species covered by the present study, were made on a score or so of specimens only and merely to gain a preliminary idea. For the eggs, however, measurements were made on a much larger material, comprising hundreds of eggs of each species. In addition, a fairly large number of macropterous and brachypterous specimens of *A. obscurus* were measured and their lengths compared.

In the determination of species, the length of the specimen merely serves to confirm the determination. Two different lengths were already given by PRIESNER (1926) for several species: the ordinary length and the extended length. Particular attention was paid to this point in the present investigations. Specimens kept in alcohol for a long time could not be used for purposes of measurement, for some of them had shrunk during preservation, while others had absorbed alcohol between the skin and the underlying tissues. For this reason, all the specimens were measured soon after they had been killed with ethyl acetate. The measurements were done in Canada balsam, onto which a cover-glass was gently lowered. Thrips stretch very easily. This could be ascertained by pressing the cover-glass down upon the underlying slide. The specimens in Canada balsam then became greatly extended before bursting. While 1.35 mm was obtained as the average length of the brachypterous specimens of *A. obscurus*, this became 1.62 mm when the specimens were extended to bursting point. The difference between these lengths was thus 19.3 per cent. In his measurements, PRIESNER (1926) found even greater differences with some thrips species.

Actual comparisons of lengths of adults were made only between the macropterous and brachypterous forms of *A. obscurus*. The method of measurement was the same throughout, and the differences in lengths were actual differences between specimens. The average length of macropterous specimens of this species collected from rye was 1.407 ± 0.007 mm and from leys 1.438 ± 0.010 mm (Table 11, p. 215). The difference in length between these groups was minute but statistically significant ($P < 0.05$). The average length of the brachypterous specimens of *A. obscurus* gathered from a first-year ley was 1.345 ± 0.015 mm, and that of those collected from a older ley 1.325 ± 0.014 mm (Table 11, p. 215). The difference in length between these groups was not statistically significant ($P > 0.05$). Comparison of the lengths of specimens of the different wing forms revealed that the difference was very significant ($P < 0.001$).

An analysis was made to find out whether it is possible to infer the species from the size of eggs found on the plants. Eggs of *L. denticornis*, *A. obscurus* and *F. tenuicornis* are alike in colour, may be situated in the same part of the plant and may even be similar in shape. It was anticipated, however, that the eggs might differ in size. The eggs examined were measured at the age of 24 hours at most, and the measurements were made directly on a slide without preparation. When sunk into Canada balsam, the eggs are not sufficiently distinguishable.

The average length of the eggs of *L. denticornis* was 0.331 ± 0.002 mm (cf. p. 206). For the macropterous females of *A. obscurus* it was 0.259 ± 0.0005 mm (Table 12, p. 217) and for the brachypterous females 0.258 ± 0.0005 mm (Table 12, p. 217) and for *F. tenuicornis* 0.276 ± 0.003 mm (cf. p. 228). The differences in length between the eggs of the various species are significant (*L. denticornis* and *F. tenuicornis* $P < 0.001$, *F. tenuicornis* and *A. obscurus* $P < 0.001$). But the lengths of the eggs of specimens of the different wing forms of *A. obscurus* do not differ significantly from each other ($P > 0.05$). A significant difference ($P < 0.001$) can also be seen between the breadths of the eggs of *L. denticornis* and *A. obscurus*, and between those of *F. tenuicornis* and *A. obscurus*. There are also differences in the shapes of the eggs. The eggs of *L. denticornis* are the most elongated, followed in succession by the eggs of *A. obscurus* and *F. tenuicornis*. The eggs of *H. aculeatus* differ from those of the above species in length and breadth ($P < 0.001$) and colour, and are, moreover, loose on the surface of the plant parts, mainly in the parts of the ear.

The thrips species studied lay their eggs on different parts of the plant. *L. denticornis* lays its eggs in the sheaths rather than in the leaves ($P < 0.05$), and its eggs in the sheaths are mostly located in the third quarter counting down from the ligule (Table 9, p. 212, cf. tabulation on p. 212). *F. tenuicornis* inserts its eggs in sheath or leaf indifferently; this could be clearly established in oats at least (Table 35, p. 233). Its eggs are located mainly in the first quarter of both leaf blades and sheaths; this first quarter of the sheath being the uppermost quarter, i.e. the quarter closest to the ligule (Table 36, p. 233, cf. tabulation on p. 233). *A. obscurus* lays its eggs chiefly in the leaf blades (in rye $P < 0.001$), mainly in the first quarter counting from the ligule (Tables 19 and 20, pp. 221 and 222). Eggs of *H. aculeatus* are found almost exclusively in the ears, where they occur in various parts.

The duration of the preoviposition period varies slightly with the species. With hibernating females of *F. tenuicornis* and *A. obscurus* the ovaries mature gradually during the winter (Fig. 18, p. 220), considerably more rapidly in the former species. The proportion of ovipositing females shows the same tendency of increase (Fig. 19, p. 220). From this it may be inferred that these species, or at least part of their populations, undergo a winter diapause, from which they emerge gradually. *L. denticornis* and *H. aculeatus* are in diapause throughout the winter, and do not begin to lay until the spring, after moving from their hibernation sites. The duration of the preoviposition period of the females of the new generation developing during the summer also varies with the species. The females of *F. tenuicornis* and *A. obscurus* may commence oviposition within a few days of emergency (cf. Table 18, p. 221, cf. p. 234). The ovaries of the females of the new generation of *L. denticornis* are slower to mature than the two former species, and do so only in part of the population during the same summer. Of the species examined *H. aculeatus* has the longest preoviposition period, the females only exceptionally laying eggs in the summer in which they emerge.

The several modes of reproduction in thrips were also clearly in evidence during the research period, and part of the investigation was specifically aimed at clarifying this phenomenon.

Thrips are able to reproduce bisexually as well as parthenogenetically. The copulation associated with the former mode of reproduction has been described in great detail by FRANSSEN and MANTEL (1964). Copulation usually takes place between adult specimens, *L. denticornis*, being an exception in which the adult male may copulate with females in the pupal stage.

Many thrips species are probably able to reproduce parthenogenetically as well. Parthenogenesis may be slightly different in character in different cases. POMEYROL (1928) distinguishes between three forms (1) the thelytokous and constant, or absolute, parthenogenesis, investigated by HINDS (1900, 1902), in which all the progeny are always females, (2) the thelytokous parthenogenesis, which alternates with bisexual reproduction, an alternating parthenogenesis, investigated by RAYMOND (1924), and (3) the arrhenotokous or facultative parthenogenesis, investigated by SHULL (1909, 1914 a), in which all the progeny are males.

L. denticornis, F. tenuicornis and *H. aculeatus* are thrips species whose chief mode of reproduction is probably bisexual, although the number of males is far smaller than the number of females. In bisexual reproduction the progeny are of both sexes. These species have an alternative mode of reproduction, arrhenotokous parthenogenesis in which the progeny are exclusively males. By means of arrhenotokous parthenogenesis the species is able to increase the number of males, and when the males are more numerous there are greater opportunities for copulation and bisexual reproduction, which makes the survival of the species more sure.

Among the thrips of cereals and grasses, *A. rufus* and *A. stylifer* are special cases in terms of reproduction. Very few males of these species have been found (WILLIAMS 1913, MORISON 1924, RADULESCO 1930, PUSSARD-RADULESCO 1931, SHARGA 1933, SPEYER 1935, HUKKINEN 1935). Considering this, and the fact that the male is locally occurring, SHARGA (1933) put forward the suggestion that these species have bisexually and parthenogenetically producing strains, of which the latter is the prevailing one, the question here being one of geographical parthenogenesis. In the opinion of PUSSARD-RADULESCO (1931), the bisexually reproducing strain is gradually disappearing. There are also very few males of *T. tabaci*, and this thrips probably reproduces in the same way as the *Aptinothrips* species (FRANSSEN and HEURN 1932, PRIESNER 1933, SPEYER 1934, GHABN 1948).

The male of *A. obscurus* is known only from North America. In Europe the species only reproduces by parthenogenesis, this being thelytokous in character. The significance of the sporadically occurring males in the life cycle of the species has not been explained as yet.

It is difficult, for more than one reason, to compare the durations of the developmental stages of the thrips species studied. First, temperature has a considerable effect on the rate of development. Consequently, comparisons of the respective developmental stages could only be made on cultures of the various species reared at the same temperature, and facilities for this were not available. However, the temperatures in both indoor cultures were relatively even. But the differences that occurred in the rates of development in these cultures were small for purposes of comparison. In the outdoor cultures, however, the temperature differences were occasionally very large. The value of data from previous investigations is reduced particularly by the fact that the rearing temperatures used have not been reported.

Second, the durations of some of the developmental stages in some species, especially *L. denticornis*, apparently also *F. tenuicornis* and possibly *H. aculeatus*, are dependent on the sex of the specimen, males developing more rapidly than females.

It may also be mentioned that the quality of the food seems to affect the rate of development of the specimen. This was found to be the case in the *H. aculeatus* cultures, in which the larvae developed at very different rates, according to whether they were fed on rye flowers or rye spikelets with already developing grain. Similar cases were not observed in the other species investigated, even when larvae were reared on different food substrata. The important thing seemed generally to be whether the larva obtained the nutrition it required from the plant. The effects of the various factors on the rates of development of the specimen are shown most clearly in the figures (Figs. 10, 17, 24 and 30, pp. 208, 218, 231 and 239) showing the development of the different species. The curves representing the average rates of development have slightly different shapes for the different species. This can be seen most clearly in the case of the longer developmental stages such as larval development and total development.

It might, however, be possible to draw some conclusions from the investigations on the rates of development of the various species. Thus it seems that the egg stage is shortest for *L. denticornis*. It could likewise be seen that the egg stage was shorter in *F. tenuicornis* than in *A. obscurus*, for these cultures were run concurrently. No clear differences in the duration of the larval stage could be detected between the different species, apart from the fact that it was much longer in *H. aculeatus* than in the other species. In all these species the prepupal stage was very short, and so was the pupal stage, which was longest in *H. aculeatus* on account of its two distinct pupal instars. The second of these instars was equal in duration to the pupal stages of the other species. Development from egg to adult was most rapid in *F. tenuicornis* and *L. denticornis*, and slowest in *H. aculeatus*.

Differences were also observed in the numbers of eggs of the thrips species studied, which are shown together with the test results. *F. tenuicornis* and *A. obscurus* apparently lay the largest numbers of eggs, and *H. aculeatus* the smallest number. The number of eggs is naturally highly dependent on the food plants, which in the present investigations were rye, oats and timothy, i.e. the host plants regarded as most suitable for these species. The rearing temperature, too, may affect the number of eggs. The oviposition cultures were run as indoor cultures at a relatively high temperature that did not vary much. It is possible that while a high temperature stimulates the oviposition activity of the specimen, it also places a strain on the organism which shortens the oviposition period and the life span. The number of eggs laid daily is obviously smaller in field conditions than in indoor cultures, although the oviposition period may be longer in field conditions, unless it is affected by adverse conditions. Among the species studied, *H. aculeatus* had a very long oviposition period.

V. POPULATION SIZE AND SEASONAL FLUCTUATIONS IN ABUNDANCE

It has long been recognized that in some species of thrips several generations occur during a single summer (Lindeman 1886, 1887, Jordan 1888). Partly because of this, and partly because of the short life span of adult thrips, sizeable fluctuations can be found in their abundance even within a single summer. With the development of the new generation there usually occurs a period of great abundance, while subsequently the population begins gradually to decline once again on account of such factors as high mortality. Moreover, in species that overwinter in the natural vegetation and only migrate to the growing crops with the coming of spring, the amplitude of fluctuation is markedly increased. Because of their rapid development, however, the different thrips generations may overlap, and this may naturally have a considerable effect on the character of the fluctuation.

Previous investigators have devoted some attention to the size of thrips populations on grasses and cereals, and to the fluctuations in abundance. The most valuable studies on the subject are those of von Oettingen (1936, 1942), Weitmeier (1956) and Wetzel (1964).

The population sizes of the various thrips species investigated, and the fluctuations in abundance, are presented further on in graphs plotted from the results of samples netted in the various localities studied.

A. Limothrips denticornis Hal.

On rye *L. denticornis* usually has two peaks of abundance (Figs. 32 and 33). Only a few stray specimens of this species overwinter in rye (Köppä 1969 a). The bulk of the population does not usually move to the rye until the spring. The first peak of abundance occurs when migration is completed, while the second peak represents the new generation. In 1961, the first specimens of the new generation at Tikkurila were netted on June 18, in 1964 on July 3, and in 1966 on July 1. Admittedly, some of the new generation, as revealed by the first-appearing males, had already been noted earlier between two consecutive samplings. In 1966, for instance, the first specimens of the new generation were seen at Tikkurila on June 27, and at Somero on June 24. The numbers of *L. denticornis* in the samples decline between the peaks of abundance, partly because the overwintered females gradually begin to die off and partly because some of the specimens force their way into the sheaths when the ears are developing in the rye and are thus not so easily netted as specimens on the plant surfaces. Thus, in the latter case the decrease in the number of specimens is only apparent. The first generation of *L. denticornis* develops fairly early not only on rye but also on meadow foxtail and winter wheat, and the first specimens of the new generation are actually found on meadow foxtail, which in spring is the most rapidly developing grass species in Finland.

From winter cereals and meadow foxtail *L. denticornis* moves to the spring cereals, its preferred host in Finland being barley, while it occurs very sparsely in spring wheat or oats (Köppä 1967). Consequently, it is only on barley that this species produces any noteworthy amount of progeny that can be regarded as descendants, at least partly, of the generation that developed on winter cereals and meadow foxtail. In 1963, specimens of the new generation were found in a sample netted from rye at Somero on June 21, and there followed a distinct period of high abundance of this species (Fig. 33). The first specimens of the new generation on barley were found on July 7, and abundance reached a peak about one week later. As the first generation developed only about two weeks later on barley than on rye, the specimens that developed on barley are probably not progeny of the generation on rye. But on meadow foxtail the first specimens of the new generation were found on June 6, and these may well be parents, at least to some extent, of the generation that developed on barley, considering the rapid rate of development and maturation of the ovaries in *L. denticornis.* Thus it can be assumed that during their oviposition period overwintered females have moved into the barley from rye, winter wheat or meadow foxtail. This opinion has already been expressed by others e.g. by Pussard-Radulesco (1931).

Fig. 33 also clearly shows that on rye the population size of *L. denticornis* and the fluctuations in abundance reveal the same tendency at Tikkurila and Somero, while on barley it is

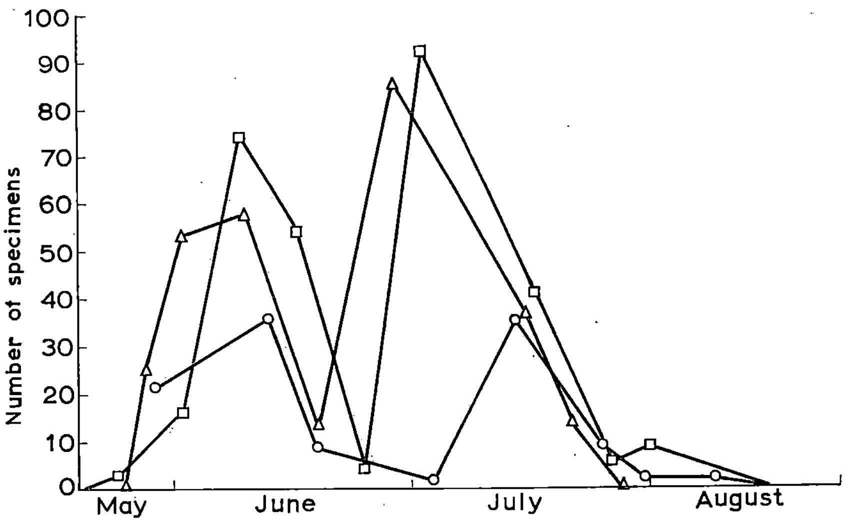

Fig. 32. *L. denticornis* Hal., population size and seasonal fluctuations in abundance on rye, Tikkurila 1961 (△—△), 1964 (○—○) and 1966 (□—□).

possible to discern considerable differences. The first males were found on barley on July 4 at Tikkurila and on July 7 at Somero, but at the former location males were not numerous until the turn of July—August and the peak abundance of this species occurred soon afterwards. It may be mentioned that at Somero in 1963 barley was growing immediately adjacent to rye, and this may have brought about an earlier movement of the species into barley.

One complete and another incomplete generation of *L. denticornis* occur annually in Finland:

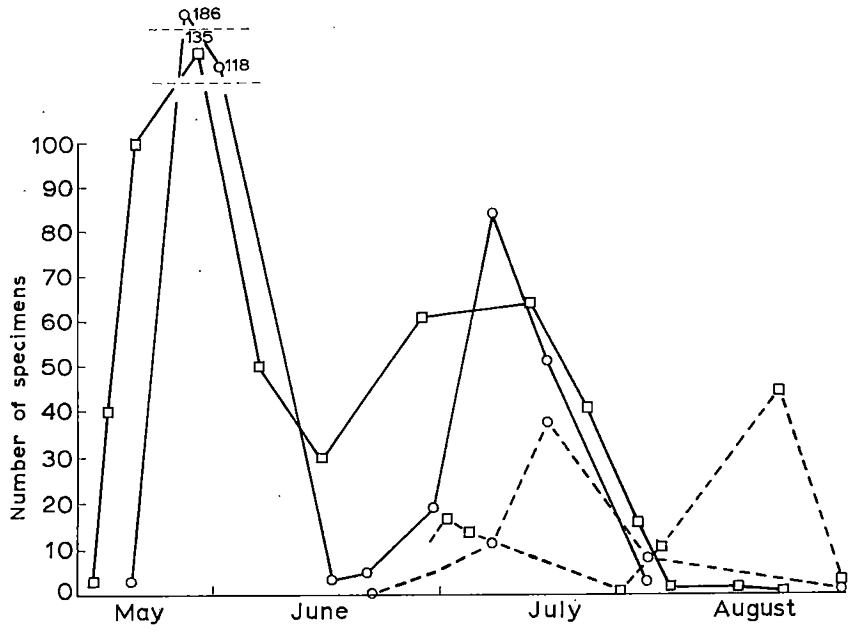

Fig. 33. *L. denticornis* Hal., population size and seasonal fluctuations in abundance on rye (□—□) and barley (□ - - - □) at Tikkurila and on rye (○—○) and barley (○ - - ○) at Somero, 1963.

not all the females emerging from the *L. denticornis* pupae introduced into cultures from rye and meadow foxtail achieved maturity during the same season. Similar observations in West and East Germany have been reported by HOLTMANN (1963 a) and WETZEL (1964). Some researchers (PUSSARD-RADULESCO 1931, von OETTINGEN 1936, WEITMEIER 1956) regard this species as characteristically univoltine, while others (LINDEMAN 1886, 1887, ROSTRUP et al. 1940, FRANSSEN and MANTEL 1965 a, 1965 b) regard it as characteristically bivoltine. BAILEY (1948) has actually expressed the opinion that 2—3 generations of this species may develop within one year, as is the case with the related species *L. cerealium.*

B. Anaphothrips obscurus Müll.

A. obscurus chiefly overwinters on leys and winter cereals (KÖPPÄ 1969 a). Thus no important migration to cultivated plants occurs in spring. The abundance of this species on rye does not reach a high level during the growing season, and no distinct fluctuations, similar to those found in *L. denticornis* or *F. tenuicornis*, occur in its numbers (Figs. 32 and 34). But on ley grasses (Fig. 35) a substantial increase in its population occurs in mid-June, while from the beginning of July the number of specimens begins to decrease. However, the numbers of *A. obscurus* and the fluctuations in abundance differed on the various grasses. On cocksfoot it was very sparse, in 1966 at least, and the abundance did not vary greatly during the summer. On timothy and English ryegrass, however, the population size according to the samples netted reached quite a high level in June and July. In 1966, the first period of abundance of this species lasted quite a long time on English ryegrass, where it was followed by another, lower peak of abundance at the turn of July—August. Cocksfoot and timothy were harvested fairly early, and it was consequently impossible to ascertain by netting whether there was any other peak of abundance.

The reduction in the *A. obscurus* population occurring from early July onwards was obviously caused by a considerable migration to spring

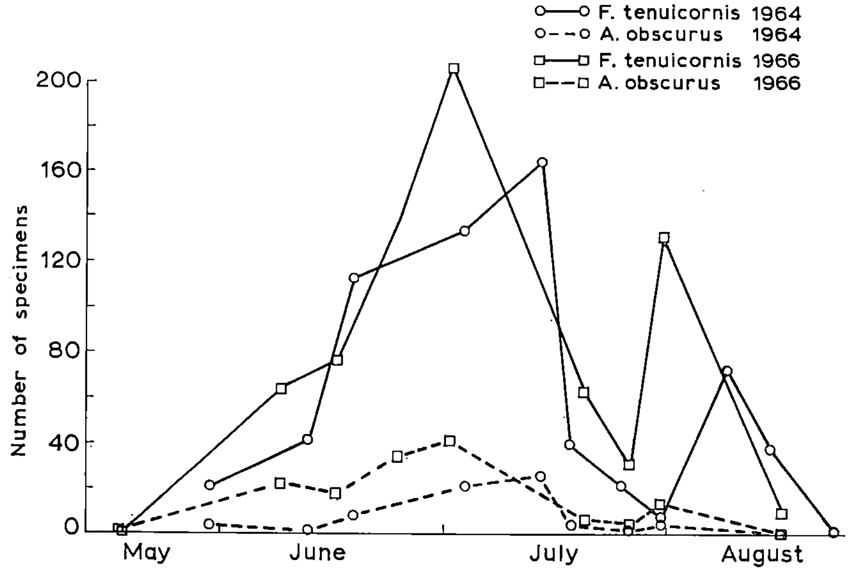

Fig. 34. *A. obscurus* Müll. and *F. tenuicornis* Uz., size of populations and seasonal fluctuations in abundance on rye, Tikkurila 1964 and 1966.

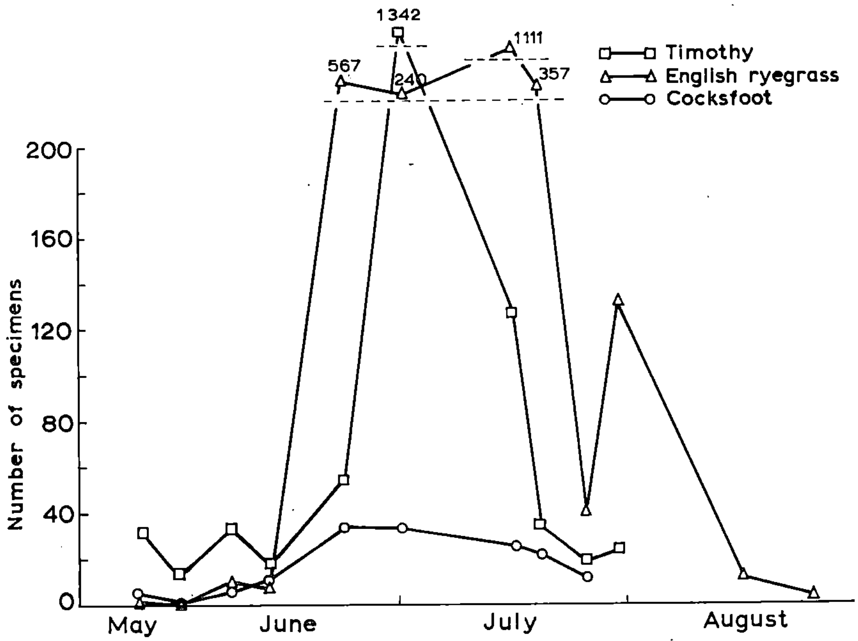

Fig. 35. *A. obscurus* Müll. population size and seasonal fluctuations in abundance on grass crops grown for seed, Tikkurila 1966.

cereals. In 1964 at least, when the population of this species was relatively high on oats grown on sandy clay containing organic matter, a distinct increase in abundance was noted in the latter half of July (Fig. 36). Thus in this species, two peaks of abundance occur annually on spring cereals, especially on oats of which the first and generally lower peak is primarily due to migration from winter cereals or from leys as a consequence of cutting. The second peak on spring cereals is chiefly due to the appearance of the new generation, but there may also be a migration to spring cereals of specimens of this species moving from seed leys when the grass there begins to ripen. From the very end of August onwards, specimens of *A. obscurus* again migrate from the spring cereals to the sprouting winter cereals, where they are able to overwinter (Köppä 1969 a).

In Finland *A. obscurus* is bivoltine or, in part of the population, trivoltine. Wetzel (1964) considers this to be the case with the development of this species in East Germany. Morison (1943, 1957) states that this species is bivoltine in northeastern Scotland. Opinions diverging from the above have also been presented in respect of the voltinism of this species (Hinds 1900, Fernald and Hinds 1900, Bailey 1948). According to these researchers, this species has 8—9 generations per year in the USA. *A. obscurus* is cosmopolitan, and it is possible that such a great number of generations per year may occur in the tropics. The species is quite capable of producing several consecutive generations parthenogenetically.

C. Frankliniella tenuicornis Uz.

F. tenuicornis usually reaches two peaks of abundance during the growing season (Fig. 34). The first of these is formed by the new generation. In 1964, the first specimens of the new generation were found on June 12 in samples netted from rye, the respective date for 1966

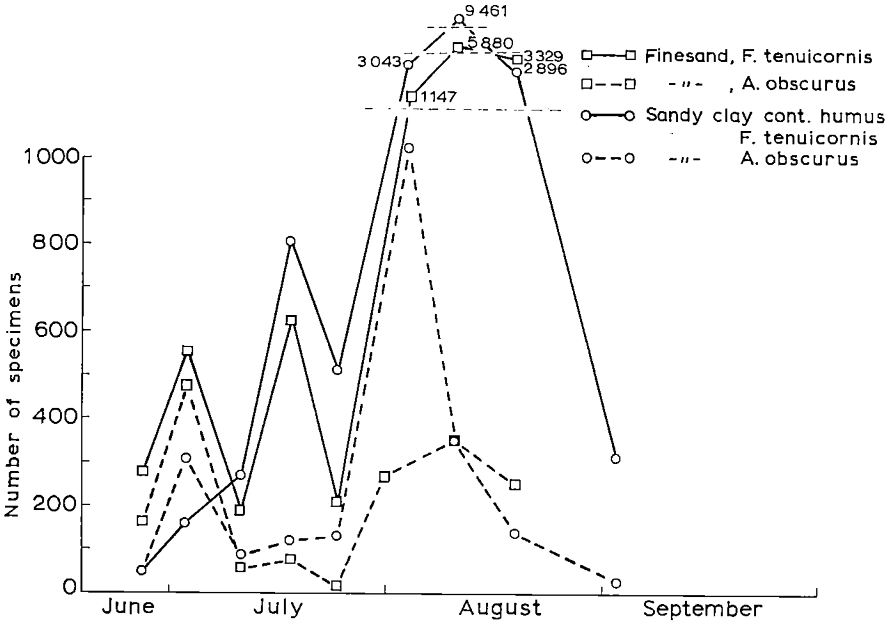

Fig. 36. *A. obscurus* Müll. and *F. tenuicornis* Uz., size of populations and seasonal fluctuations in abundance of oats growing on fine sandy soil and on sandy clay containing organic matter, Tikkurila, 1964.

being June 16. In the beginning of the growing season the increase in the *F. tenuicornis* population on rye may occur relatively slowly, for a large population has already overwintered on this cereal (Köppä 1969 a).

In 1964 and 1966, another period of great abundance of *F. tenuicornis* occurred on rye, this peak being composed of the second generation (Fig. 34). Most specimens of the first generation migrate to spring cereals but a few of them may remain on the rye and produce a new generation.

Two definite peaks of abundance of *F. tenuicornis* occur on spring cereals during the summer (Fig. 36). The first of these is seen when most specimens of this species have migrated from winter cereals to spring cereals. The second distinct peak occurs during August, when most of the specimens of the second generation have become adult, and adults of a third generation begin to appear.

In 1964, the peaks of abundance of *A. obscurus* and *F. tenuicornis* on oats almost coincided, although the second peak of *A. obscurus* on sandy clay with organic matter was slightly earlier (Fig. 36).

On other spring cereals, the populations of *A. obscurus* and *F. tenuicornis*, and the fluctuations in the numbers of these species were very similar to what they were on oats, but the magnitudes and shapes of the graphs showing the abundance of the specimens may differ greatly. Sometimes a peak may be entirely absent. Thus, on spring wheat in 1960 there was noted no second peak in the autumn.

In Finland, *F. tenuicornis* is bivoltine or to some extent trivoltine, as previously shown by Kanervo (1950). This species has been found to have 1—2 generations per year in Sweden (Johansson 1938), 2 in East Germany (Wetzel 1964) and 2—3 in Great Britain (Morison 1943).

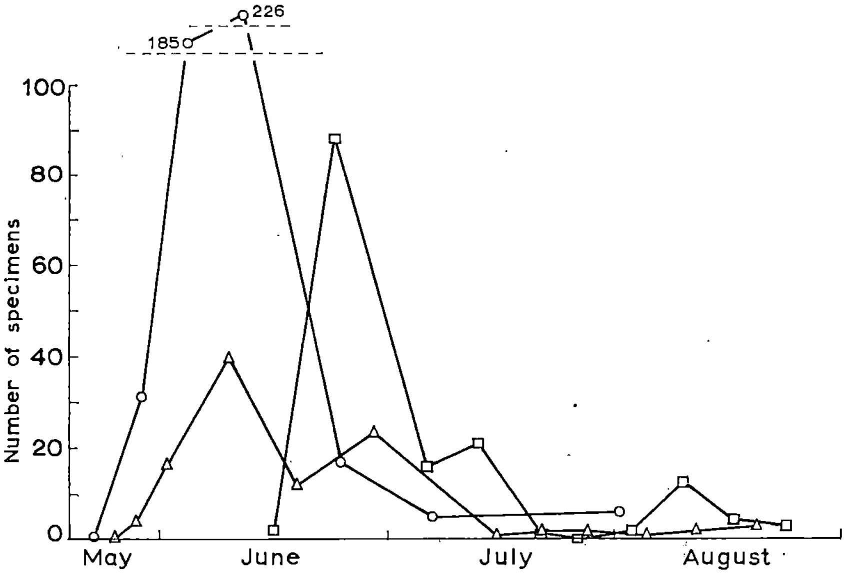

Fig. 37. *H. aculeatus* Fabr., populations size and seasonal fluctuations in abundance on rye at Tikkurila 1960 (□—□) and 1961 (△—△) and at Somero 1961 (○—○).

D. Haplothrips aculeatus Fabr.

H. aculeatus overwinters mainly in natural vegetation (Köppä 1969 a). Thus it does not move into rye until the spring, where it then reaches a distinct peak of abundance (Fig. 37). After this the size of the population decreases, or, at least, the thrips are more likely to elude the net. This species evidently shows another peak of abundance later or, when the new generation becomes adult. For example, von Oettingen (1942) observed such a peak in a stand of grass. However, nothing suggesting this could be clearly seen even in 1960, the study year in which this species reached its highest abundance on cereals. Relatively small numbers of *H. aculeatus* were netted throughout the research period, and it was not possible to produce graphs describing the fluctuations in abundance, such as shown in Fig. 37, except for the years 1960 and 1961. In the other years this species could be found only occasionally, even on rye, which is probably its most favoured host plant in Finland. At Somero, *H. aculeatus* was more numerous than at Tikkurila (Fig. 37, Köppä 1967).

In Finland, *H. aculeatus* is univoltine, and this is also the case in Germany (Körting 1930, 1934), East Germany (Wetzel 1964), and the Netherlands (Franssen and Mantel 1965 a, 1965 b). However, Lindeman (1886, 1887), Jordan (1888), Kurdjumov (1913 a, 1913 b), Johansson (1938) and Bailey (1948) state that this species is bivoltine.

E. Discussion

The abundances of thrips species that live on cereal plants, and the fluctuations in population size during the growing season, have been investigated by previous researchers, e.g. von Oettingen (1942), Weitmeier (1956) and Wetzel (1964). In all these studies, however, the plots examined were leys of cultivated grass or natural meadows. But the changes in the abundances of the various thrips species in the course of the growing season have not previously been studied closely on actual cereal crops. In Central Europe, where the investigations by von OETTINGEN, WEITMEIER and WETZEL were made, the growing season and hence the thrips season on outdoor crops are far longer than they are in Northern Europe, including Finland. This has a profound effect on the populations of thrips species and the fluctuations in their abundance. The longer season may allow additional generations in such species as thrips in which development is usually rapid. The appearance of a new generation usually causes a peak of abundance, although the overlapping of different generations may largely level out such peaks.

In leys and meadows composed of grasses differing greatly in such respects as earliness, there may be far more fluctuation in the abundance of thrips than in cereal crops, where, of course, only one plant species is concerned.

L. denticornis, which favours meadow foxtail and timothy, develops its first progeny on the early meadow foxtail, where the emergence of a new generation brings about a period of great abundance. Later on, progeny are also produced on timothy, and the size of the population. again increases.

A more complete picture of the course of development of the population can be obtained from leys and meadows than from cereals, for the stand is perennial on the two former. True, on leys for mowing or pasture the cutting or grazing of the stand may interfere with the normal development of the population and force the adults to move to other plants. During the growing season thrips may move to cereals from other leys also, and then return in the autumn, which, together with the formation of new generations, accentuates the fluctuations in the size of the thrips populations.

The weather conditions of the growing season have a considerable effect on the size of the populations of the thrips species and the fluctuations in their abundance, as was mentioned previously (cf. p. 198). A warm, dry summer usually speeds up the development of the species, and the new generations will reach peaks of abundance earlier than in cool, rainy summers. When favourable weather prevails, the thrips become adult at very much the same time too, and this naturally accentuates the fluctuations in population size. Thrips migration to new food plants, which also causes periods of great abundance, depends very much on the prevailing weather conditions too, and factors such as high temperature, low relative humidity, calm weather and, apparently, high light intensity, will increase the abundance (MORISON 1957). If favourable conditions do not occur, migration to the new plants may be delayed, as will, consequently, the period of high abundance, provided that the thrips are physiologically prepared for migration. Results obtained from netted samples were used in investigating the population sizes and fluctuations in abundance of various thrips species on cereals. To obtain a reliable picture in this manner, the samples must be taken in conditions as closely similar as possible. During cold, windy weather, thrips take shelter in protecting plant parts, often in the lower part of the plant, and are not so likely to be netted as they would be when in the upper parts. It is equally important that the samples should always be taken at the same time of day. If, moreover, samples are taken frequently enough and at regular intervals, it will be possible to date the periods of peak abundance with the greatest possible accuracy. In crops such as winter cereals and barley, on which *L. denticornis* and *H. aculeatus* occur in abundance, a considerable proportion of the thrips will take shelter between the parts of the ears after these are formed, *L. denticornis* forcing its way into the sheaths and *H. aculeatus* between and into the spikelets, with the consequence that they are less likely to be netted than they were before the ears had formed. This always causes a distinct and misleading decrease in the number of specimens in the netted samples.

By taking samples of cereal shoots concurrently with netting and counting the numbers of the different thrips species on them, it is possible to discover how great a proportion of the thrips in a field of cereal is obtained in samples netted at that time. It will then only be necessary to calculate the areas represented by the plant sample and by the netted sample. During earlier investigations on the thrips fauna of cereal plants (Köppä 1967, p. 41), it was established that during the early stages of development of the plants, only 1.5—5.0 % of the thrips specimens in a field — depending on the thrips species — are caught with a net. When the sheaths open, only about one-fifth of the *L. denticornis* and one-third of the *F. tenuicornis* specimens present prior to ear or panicle formation will be caught in netted samples. But there seems to be no marked decrease in the number of *A. obscurus* specimens, which is probably due to the different habits and habitats of this species on the plant. No investigations of this kind could be carried out in respect of *H. aculeatus*, because of the smallness of the population, but the situation is obviously the same for this species as for *L. denticornis*.

The apparent decrease in the size of the population at the time when the plant forms ears and panicles depends on the fact that the estimates are based on netted samples. Such a decrease is seen mainly in winter cereals, on which *L. denticornis* and *H. aculeatus* occur in abundance, and in barley, where the former species occurs abundantly. But the apparent decrease is not so marked in the case of *F. tenuicornis*.

Despite its shortcomings the sweeping net method is quite important in the analysis of the thrips fauna of cereals. Thus, Heikinheimo and Raatikainen (1962) regard it as being superior e.g. to the suction method, especially in the study of thrips.

VI. SUMMARY

Investigations on the biology and abundance during the growing season of the most important species of thrips living on cereals in Finland (*L. denticornis*, *A. obscurus*, *F. tenuicornis* and *H. aculeatus*) were carried out in 1960—69.

To investigate the biology of these thrips species, cultures were set up both indoors in the laboratory and outdoors in controlled conditions. The information obtained from the rearing tests was supplemented by observations made in the field. Most of the tests were carried out at the Department of Pest Investigation at Tikkurila, but the studies were continued at the Ahlman Agricultural College in Tampere.

In the thrips species living on cereals the investigations on population size and the seasonal fluctuations in abundance are based on samples taken with a net at the Department of Pest Investigation at Tikkurila in 1960—66 and at Somero in 1961—65. The results for the cereal crops were supplemented in some localities with the results of samples netted on grasses grown for seed at Tikkurila in 1966.

Biology

Limothrips denticornis Hal.

During the research period *L. denticornis* occurred in abundance. It would feed and reproduce on all species of cereal and on several species of cultivated and wild grasses.

This species, i.e. adult females of this species, overwintered mainly on grass growing at roadsides and forest-edges. From there it migrated in spring to its first host plants: meadow foxtail, rye and winter wheat. After hibernating, the females underwent a preoviposition period and oviposition only began at the end of May or beginning of June. The females inserted most of their eggs within the lower parts of the sheaths. There were 58—142 eggs in the cultures, and the oviposition period lasted 14—33 days. The larvae hatched 3—9 days after oviposition.

Larvae were found on rye early in June. The duration of the larval stage on rye was 4—16 days. The subsequent prepupal and pupal stages lasted only a very short time. The entire development of *L. denticornis* from egg to adult took 10—31 days, depending on the rearing conditions. The males developed more rapidly than the females, apparently because of their shorter larval and pupal stages. The first specimens of the new generation emerged on rye in the field from mid-June onwards. On meadow foxtail its development was roughly one week earlier, and on winter wheat roughly two weeks later, than on rye.

Some specimens of the new generation began to oviposit in the same year. Most of their eggs were laid on barley, on which these females laid 20—156 eggs in 7—30 days. The species reproduced both bisexually and by arrhenotokous parthenogenesis. Males of this species were commoner than had generally been presumed previously. Adult males copulated with female pupae.

L. denticornis began to migrate to its overwintering sites at a fairly early date — the beginning of August — but migration continued till mid-September.

Anaphothrips obscurus Müll.

During the research period *A. obscurus* occurred in great abundance on oats, but it also lived and reproduced on other species of cereal and on several cultivated and wild grasses. Macropterous and brachypterous specimens of this species were found. They differ in size and colouring. In its macropterous form *A. obscurus* overwinters on sprouts of winter cereals, and in both wing forms on grasses of leys and roadsides and on cereal stubble. This species has a long preoviposition period, the ovaries maturing gradually during the winter. The ratio of ovipositing females also increases towards the spring. Oviposition on the plants usually began in mid-May, as was the case with *F. tenuicornis*, and eggs were laid both on winter cereals and on leys. Most of the eggs were deposited in the leaves, mainly at the bases of the blades. The number of eggs laid per macropterous female was 51—216, and per brachypterous female 54—232, but the average number was smaller in the latter. The average number of eggs laid per macropterous female was clearly greater than in *L. denticornis*. The females oviposited for 2—7 weeks. Development seemed to be slower in this species than in *L. denticornis* and *F. tenuicornis*. On oats the duration of the egg stage was 4—10 days, of the larval stage 6—16 days, of the prepupal stage 1.0—3.5 days, and of the pupal stage 2—7 days. Depending on the rearing conditions, the eggs developed into adults in 14—35 days. No definite difference could be found between the rates of development of the two wing forms, although it is possible that the brachypterous specimens develop faster.

The first females of the new generation appeared in the field in the early days of June, and a large proportion of the macropterous specimens migrated to spring cereals, where a second generation developed concurrently with *F. tenuicornis*. *A. obscurus* reproduced by thelytokous parthenogenesis, and the females of the new generation attained maturity a few days after emerging. The number of eggs was roughly the same as that of the generation that had hibernated. Adults of the second generation could be found on spring cereals already by the last third of July, and some of these laid eggs in the tillers. In autumn some of the *A. obscurus* population on spring cereals migrated to winter cereal sprouts and overwintered there.

Frankliniella tenuicornis Uz.

During the research period *F. tenuicornis* was the thrips species that occurred most abundantly on cereals, and its range of host plants was roughly the same as that of the two previous species.

The females of this species overwinter mainly in winter cereal sprouts and in cereal stubble. They have a long preoviposition period attaining maturity gradually during the winter, as in *A. obscurus*. The females generally began to lay eggs on winter rye in mid-May. Most of the eggs were deposited in the leaf blades, in the basal quarter. After the sheaths had opened, a number of eggs were also found in these, mainly in their uppermost quarter. In the cultures the number of eggs per female was 53—252, and the average number was clearly greater than the number of eggs laid by *L. denticornis* or *H. aculeatus*. The duration of the oviposition period was 13—50 days. In the cultures the egg stage lasted 4—8 days, and the larvae found on rye at the end of May and beginning of June became full-grown in 5—15 days. The prepupal and pupal stages were roughly as long as they were in the two previous species. The entire development from egg to adult took 12—29 days, i.e. roughly as long as in *L. denticornis*. It is evident that the males of this species develop faster than the females, although this could not be clearly demonstrated. The first adults of the new generation were found in field conditions on rye in the end of May and on winter wheat somewhat later.

Small number of this species remained on the winter cereals. The great majority migrated to spring cereals, where most of the second generation developed. The females of the new generation laid eggs a few days after emerging. The number of eggs per female was 86—277 on rye and 61—292 on oats, and the oviposition periods lasted 18—45 days and 12—45 days respectively. The females were able to reproduce both bisexually and by arrhenotokous parthenogenesis, as is the case with *L. denticornis*, but copulation only occurred between adults. On average, a quarter of the population was males. Adults of the second generation began to emerge on the cereals from mid-July. Some of the females of this generation laid eggs during the same summer. In September, part of the population migrated to sprouting winter cereals and overwintered there, while part remained in the cereal stubble.

Haplothrips aculeatus Fabr.

H. aculeatus, too, reproduced on all the cereal species and on several species of grass.

Adult females and males overwintered chiefly in grass on roadsides and forest edges. From there they migrated to the growing crops rather late, so that by the time the females began to lay eggs the rye was already coming into ear. Evidently, this species has to undergo a preoviposition period and does not attain sexual maturity until immediately before that time. The eggs were found unattached either singly or in clusters on different parts of the ear. The number of eggs laid was smaller than in the other species investigated. In the cultures it was 38—115. The oviposition period, however, was very drawn-out, being 21—73 days. The duration of the egg stage in the cultures was 5—13 days and that of the larval stage 10—29. The great variation in the latter was due to the rearing temperature as well as to the quality of the food. Larvae were found on various parts of the ear from mid-June until harvesting. This species was 1—2 days in prepupa, 1—2 days in the first pupal instar and 2.5—7.0 days in the second pupal instar. The whole development from egg to adult took longer in *H. aculeatus* than in any of the other species investigated, i.e. 21—49 days. In favourable summers the first adults of the new generation could be found from mid-July onwards. The reproduction of this species is probably as in *F. tenuicornis*, and copulation was observed between adults. Generally, the females did not begin to lay eggs in the same year as they emerged. During the research period this species occurred in very small numbers on spring cereals. It began to move to its hibernation sites at the end of August, and this migration continued until mid-September.

Dimorphism

Macropterous and brachypterous forms of *A. obscurus* are both very common. The progeny of each form include both macropterous and brachypterous specimens.

The development of the wing form was not affected by hereditary factors but was determined exclusively by external factors. A short photoperiod produced brachyptery. The wing form also seemed to be dependent on the food plant. On cereals almost all the specimens developed were macropterous, while on grasses there was a fairly large proportion of brachypterous specimens. Crowding may cause an increase in macroptery, although this was not clearly demonstrated in the tests performed. The wing form was most decisively determined immediately before or after the hatching of the larvae.

Population size and seasonal fluctuations in abundance

L. denticornis usually had two periods of great abundance on rye during the growing season. On barley, however, only one could be found. The species was mainly univoltine, but part of the population was bivoltine.

A. obscurus occurred in great numbers on grass leys and spring cereals. The first generation developed largely on leys, where at least one peak of abundance occurred. Two peaks of abundance could be found on spring cereals, the latter of these being composed of the second generation. A third generation had time to develop in part of the population.

F. tenuicornis was abundant on winter and spring cereals. On winter cereals it had at least one period of great abundance, this comprising the new generation. On spring cereals two peaks of abundance during the growing season could definitely be ascertained. The species was normally bivoltine, but part of the population was trivoltine.

H. aculeatus was chiefly found on winter cereals, where one peak of abundance of this species could be ascertained. The new generation may form another, smaller peak later in the summer. Only one generation per year was observed in this species.

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SELOSTUS

Tutkimuksia viljakasvien yleisimmistä ripsiäislajeista Suomessa

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Viljakasveissa elävistä ripsiäislajeista ovat Suomessa yleisimpiä viljaripsiäinen (*Limothrips denticornis*), ruohoripsiäinen (*Anaphothrips obscurus*), kauraripsiäinen (*Frankliniella tenuicornis*) sekä kahuripsiäinen (*Haplothrips aculeatus*). Näiden lajien biologiaa sekä kasvukauden aikaista esiintymisrunsautta koskevat tutkimukset suoritettiin vuosina 1960—69.

Ripsiäisten biologian tutkimista varten järjestettiin kasvatuskokeita sekä sisätiloissa että ulkona tarkoin kontrolloiduissa olosuhteissa. Lisäksi tehtiin kasvukauden aikana niitä täydentäviä kenttähavaintoja. Kasvatuskokeita suoritettiin Tuhoeläintutkimuslaitoksella Tikkurilassa, ja niitä jatkettiin vielä vuosina 1967—69 Ahlmanin maatalousoppilaitoksissa Tampereella.

Viljakasvien ripsiäislajien esiintymisrunsautta selvittelevät tutkimukset perustuvat Tuhoeläintutkimulaitoksella Tikkurilassa vuosina 1960—66 sekä Somerolla vuosina 1961—65 otettuihin haavintanäytteisiin, joita täydennettiin nurmiheinien siemenviljelyksiltä Tikkurilassa vuonna 1966 otetuilla näytteillä.

Kehitysbiologia

Viljaripsiäinen

Viljaripsiäisen isäntäkasveina saattavat tulla kysymykseen kaikki Suomessa viljellyt viljalajit sekä useat viljellyt ja luonnonvaraiset heinälajit.

Viljelysten ulkopuolella talvehtineet viljaripsiäisnaaraat siirtyivät keväällä toukokuun puolivälissä ensimmäisiin isäntäkasveihinsa, nurmipuntarpäähän ja rukiiseen sekä syysvehnään, joissa ensimmäinen sukupolvi pääasiassa kehittyi. Naaraat tulivat munintakypsiksi vasta talvehdittuaan ja laskivat munansa touko-kesäkuun vaihteessa lähinnä lehtituppiin, niiden alaosiin. Munamäärä oli rukiissa 58—142 kpl. Munista kuoriutui toukkia 3—9 vrk:ssa. Toukkana laji oli 4—16 vrk sekä esikotelona ja kotelona muutaman vuorokauden. Koko kehitys munasta aikuiseksi kesti rukiissa kasvatusolosuhteista riippuen 10—31 vrk.

Uuden sukupolven yksilöitä ilmestyi rukiiseen kesäkuun puolivälistä lähtien. Nurmipuntarpäässä oli kehitys hieman aikaisempi kuin rukiissa, syysvehnässä taasen myöhäisempi. Kuoriutuneista aikuisista osa alkoi munia kuoriutumiskesänään. Munintakasvina oli tällöin pääasiallisesti ohra. Munamäärä oli keskimäärin lähes sama kuin rukiissa, ja munintaa saattoi jatkua aina elokuun lopulle asti.

Viljaripsiäinen lisääntyi sekä biseksuaalisesti että partenogeneettisesti. Jälkimmäisessä tapauksessa lisääntyminen oli lisäksi arrhenotookkista. Aikuiset koiraat, jotka ovat melko yleisiä, kopuloivat naaraskotelojen kanssa.

Viljaripsiäinen alkoi siirtyä talvehtimispaikkoihinsa, metsän- ja tienreunojen heinikköihin, verrattain aikaisin, elokuun alussa, mutta siirtymistä jatkui aina syyskuun puoliväliin asti.

Ruohoripsiäinen

Ruohoripsiäisen isäntäkasvit ovat lähes samat kuin viljaripsiäisen. Erityisen runsaasti sitä esiintyi tutkimuskauden aikana kaurassa.

Lajista tavattiin sekä pitkä- että lyhytsiipistä muotoa, jotka kokonsa ja värityksensä puolesta erosivat toisistaan.

Ruohoripsiäinen talvehti huomattavalta osalta viljelyksillä, joko viljoissa tai nurmissa. Naaraiden munintakypsyys kehittyi vähitellen talven aikana. Myös munivien yksilöiden osuus lisääntyi kevääseen mennessä. Naaraiden muninta alkoi yleisesti toukokuun puolivälin paikkeilla. Isäntäkasveina olivat tällöin syysviljat ja nurmiheinät. Pääosa munista sijaitsi kasvien lehdissä, lähinnä niiden tyvessä. Pitkäsiipiset naaraat laskivat timoteihin 51—207 munaa ja lyhytsiipiset 66—139 munaa.

Ruohoripsiäinen näytti kehittyvän hieman hitaammin kuin viljaripsiäinen ja kauraripsiäinen. Kaurassa sen kehitys munasta aikuiseksi kesti 14—35 vrk kasvatusolosuhteista riippuen.

Uuden sukupolven yksilöitä alkoi ilmestyä viljelyksille kesäkuun alusta lähtien. Pitkäsiipiset yksilöt siirtyivät huomattavalta osalta kevätviljoihin, joissa toinen ja osittainen kolmaskin sukupolvi kehittyivät.

Ruohoripsiäinen lisääntyi partenogeneettisesti, eikä lajin koiraita tavattu tutkimuskauden aikana lainkaan. Näin ollen partenogeneettinen lisääntyminen oli luonteeltaan telytookkista.

Uuden sukupolven naaraat aloittivat muninnan muutaman vuorokauden kuluttua kuoriutumisestaan, ja munamäärä timoteissa oli suunnilleen sama kuin talvehtineen sukupolven. Kaurassa munamäärät olivat selvästi suuremmat kuin timoteissa.

Syksyllä osa kevätviljojen ruohoripsiäiskannasta siirtyi syysviljojen oraisiin ja talvehti niissä.

Kauraripsiäinen

Kauraripsiäinen oli tutkimuskauden aikana runsaimmin viljoissa esiintyvä ripsiäislaji, jonka isäntäkasvivalikoima oli suunnilleen sama kuin viljaripsiäisen ja ruohoripsiäisen.

Viljelyksillä suureksi osaksi talvehtineiden kauraripsiäisnaaraiden munintakypsyys kehittyi vähitellen talven aikana kuten ruohoripsiäisenkin, joskin hieman nopeammin. Myös lajien muninta alkoi keväällä samoihin aikoihin. Pääosa kauraripsiäisen munista oli lehdissä, lähinnä niiden tyviosissa. Lehtituppien avauduttua naaraat munivat runsaasti myös niiden yläosiin. Munamäärä rukiissa oli 53—252 kpl, ja keskimäärin se oli selvästi suurempi kuin viljaripsiäisen ja kahuripsiäisen. Eri kehitysasteiden kehitysnopeudet olivat suunnilleen samat kuin viljaripsiäisellä, ja koko kehitys munasta aikuiseksi kesti 12—29 vrk.

Uuden sukupolven yksilöitä tavattiin rukiissa toukokuun lopulta lähtien, syysvehnässä hieman myöhemmin. Osa lajin yksilöistä jäi syysviljoihin suurimman osan siirtyessä kuitenkin kevätviljoihin, joissa toinen sukupolvi lähinnä kehittyi. Uuden sukupolven naaraat aloittivat muninnan muutaman vuorokauden kuluttua kuoriutumisestaan. Munamäärä kaurassa oli suunnilleen sama kuin rukiissa.

Kauraripsiäinen lisääntyi kuten viljaripsiäinenkin, mutta kopulointi tapahtui aina aikuisten yksilöiden kesken. Koiraita oli noin neljännes kannasta.

Toisen sukupolven aikuisia alkoi viljoissa kuoriutua heinäkuun puolivälistä lähtien. Osasta kantaa ehti vielä saman kesän aikana kehittyä kolmaskin sukupolvi. Syksyllä osa kannasta siirtyi orastuneisiin syysviljoihin ja talvehti niissä.

Kahuripsiäinen

Kahuripsiäinen lisääntyi lähes samoissa isäntäkasvilajeissa kuin edellä esitetyt ripsiäislajit.

Pääasiassa viljelysten ulkopuolella talvehtineet naaras- ja koirasyksilöt siirtyivät keväällä verrattain myöhään isäntäkasveihinsa, lähinnä rukiiseen ja syysvehnään. Naaraat aloittivat muninnan niihin yleisesti vasta viljan ollessa tähkimisvaiheessa. Munat olivat irrallaan joko yksitellen tai pienissä ryhmissä tähkän eri osissa. Munamäärä jäi pienemmäksi kuin muilla tutkituilla lajeilla, 38—115 kpl:ksi. Muninta-aika oli sitä vastoin pitempi, 21—73 vrk. Kahuripsiäinen kehittyi munasta aikuiseksi 21—49 vrk:ssa. Pitkä kehitysaika muihin lajeihin verrattuna johtui lähinnä pitemmästä toukka-ajasta. Toukka-ajan pituuteen tällä lajilla vaikuttivat paitsi kasvatuslämpötila ja sukupuoli myös ravinnon laatu. Myös koteloaika oli pitempi kuin muilla tutkituilla lajeilla.

Lajin kehitykselle edullisina kesinä voitiin uuden sukupolven yksilöitä tavata jo heinäkuun puolivälistä lähtien. Naaraat eivät yleensä aloittaneet munintaa kuoriutumiskesänään. Kevätviljoissa kahuripsiäistä esiintyi tutkimuskauden aikana hyvin niukasti.

Kahuripsiäinen saattaa lisääntyä kauraripsiäisen tavoin, ainakin kopulointi tapahtui aikuisten yksilöiden kesken.

Viljaripsiäisen tavoin lajin yksilöt alkoivat siirtyä talvehtimispaikkoihinsa viljelysten ulkopuolelle verrattain aikaisin syksyllä.

Dimorfismi (pitkä- ja lyhytsiipisyys)

Ruohoripsiäisen sekä pitkä- että lyhytsiipinen muoto ovat hyvin yleisiä. Kumpaankin siipimuotoon kuuluvien yksilöiden jälkeisöissä oli sekä pitkä- että lyhytsiipisiä yksilöitä.

Ruohoripsiäisen siipien pituus oli riippuvainen ulkoisista tekijöistä. Lyhyt valojakso sai aikaan lyhytsiipisyyttä. Myös ravintokasvi näytti vaikuttavan siipien pituuteen. Viljoissa kehittyi miltei yksinomaan pitkäsiipistä muotoa, nurmiheinälajeissa oli sen sijaan lyhytsiipisen muodon osuus kannasta melko suuri. Tiheyden lisäys saattaa lisätä pitkäsiipisyyttä, joskaan tämä ei tullut suoritetuissa tutkimuksissa selvästi esille.

Valojaksollisuuden vaikutus yksilöiden siipien pituuteen ilmeni voimakkaimmin juuri kuoriutuneissa toukissa tai välittömästi ennen toukkien kuoriutumista.

Esiintymisrunsaus ja sen vaihtelu kasvukauden aikana

Ripsiäisten esiintymisrunsaus viljaviljelyksillä vaihteli melkoisesti kasvukauden aikana. Vaihtelua lisäsivät lähinnä yksilöiden siirtyminen talvehtimispaikoista syysviljoihin sekä syysviljoista ja nurmista kevätviljoihin samoin kuin myös uuden sukupolven kehittyminen.

Viljaripsiäisellä ilmeni yleensä kaksi runsaan esiintymisen kautta syysviljoissa sekä yksi kevätviljoissa. Ruohoripsiäisellä sekä kauraripsiäisellä oli runsauden huippuja ainakin kolme, edellisellä yksi pääasiassa nurmissa ja kaksi kevätviljoissa, jälkimmäisellä yksi syysviljoissa ja kaksi kevätviljoissa. Kahuripsiäisellä ilmeni selvästi vain yksi runsaan esiintymisen kausi.

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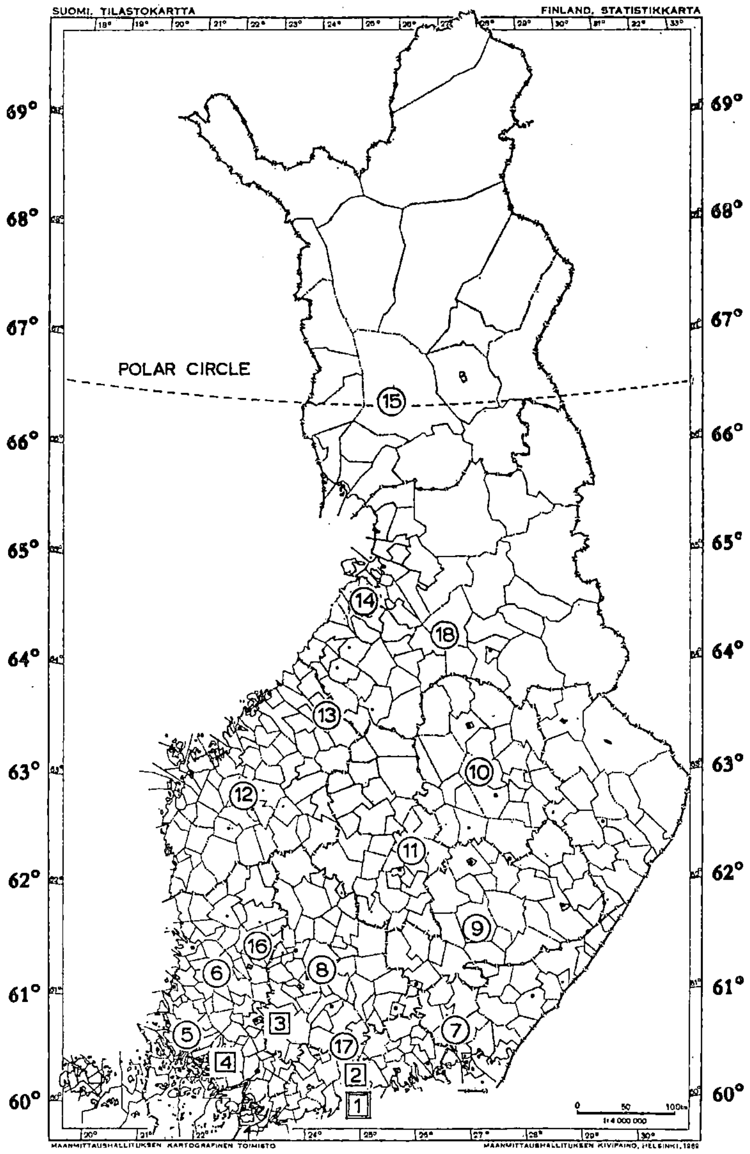

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