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**STUDIES ON THE BARLEY STEM MAGGOT,
MEROMYZA SALTATRIX (LINNÉ), WITH SPECIAL
REFERENCE TO THE ECOLOGICAL ASPECTS**

By

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I. Introduction

The economic importance of Chloropids has occupied the attention of agricultural entomologists in various parts of the world for many years and many valuable works have been done particularly on *Oscinella frit* (LINNÉ) in European countries and on *Chlorops oryzae* MATSUMURA in Japan. Another important species, *Meromyza saltatrix* (LINNÉ), which is one of the serious pests of the wheat in Hokkaido, has also been noticed in Europe, Asia and North America. Up to the present, several studies dealing with this stem maggot have been devoted to the bionomics in relation to the injury of the wheat and some taxonomic features (RAKHMANINOV, 1926; RAKHMANINOV *et al.*, 1930; TZUIGANKOV, 1930; ROCKWOOD *et al.*, 1947; NISHIJIMA, 1951, 1952). However, no attempt has been made to investigate ecological problem associated with physical and biological conditions, or to ascertain the manner and intensity of the attack on the host plant in relation to various agronomical measures of control. Extensive studies in those fields have been done since 1947 at the Hokkaido National Agricultural Experiment Station and have continued since 1954 at the Entomological Institute, Faculty of Agriculture, Hokkaido University, Sapporo. A mass of data have been accumulated and summarised in the present paper in order to contribute to the general knowledge of this insect.

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II. Geographical distribution

The range of distribution of *M. saltatrix* is given in Figure 1 having been referred to a variety of literatures and the present investigation. It shows that *M. saltatrix* has an extensive distribution, occurring over two continents locating between 30°N and 60°N Lat.: namely both in the temperate Eurasia and in the Pacific Northwest of America. According to the zoogeographical regions of WALLACE, it has been recorded from the following countries.

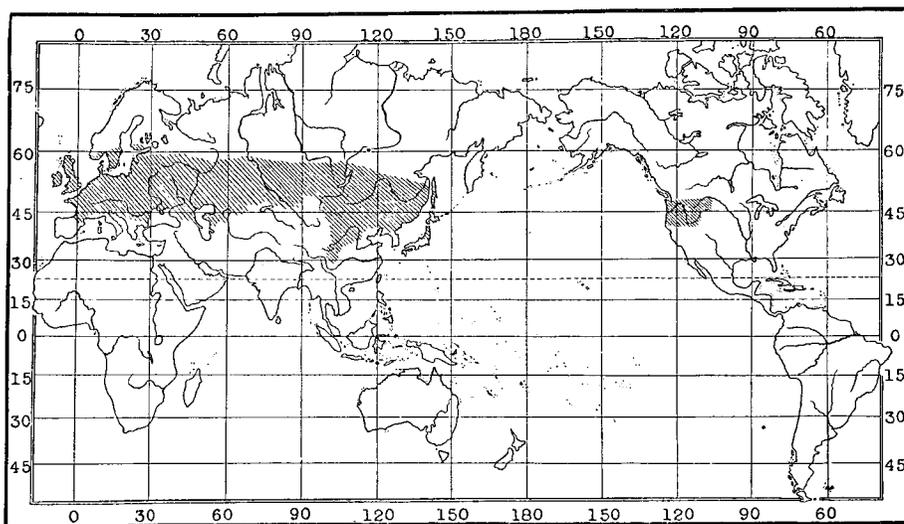


Fig. 1. The range of distribution of *Meromyza saltatrix* (LINNÉ) in the world.

Palearctic Region.

European Subregion: England; France; Germany; Swizerland; Sweden; Finland; Poland; Austria; Hungary; European Russia; Ukraina.

Siberian Subregion: Irkutsk; Omsk.

Manchurian Subregion: Inner Mongolia; Manchuria; Amur; Ussuri; Japan; Saghalin and Kurlies (New record).

Oriental Region.

Indo-Chinese Subregion: South China (Szetshwan).

Nearctic Region.

Californian Subregion: Oregon, Washington, Montana and Idaho.

In European countries, Ukraina and Smolensk districts have frequently been noticed as outbreak areas where the ears of winter wheat have been injured over 50 per cent by the maggot. In his work "Verzeichnis der schädlichen Insekten der Paläarktischen Region, Teil 1", STACKELBERG (1932) stated that recently, *M. saltatrix* spread across Central Asia to Ussuri district, and it attacks cereal plants almost anywhere in the territory of Soviet Union. Whether it has been widespread from Europe or was an original inhabitant in the Manchurian province is doubtful, but the distribution of the species over the whole of Eastern Asia suggests that it has been there for a considerable time. According to PLYATER-PLOKHOTZKAYA (1936), the serious injury of wheat in Russian Far East occurs extending from the surrounding districts of the community of quack grass, *Agropyrum repens* BEAUVOIS, which becomes the essential source of the second generation. In the Kurlies (Shikotan Is. and Kunashiri Is.), which are recorded as new habitats together with Saghalin, cereal crops have not been planted anywhere. However, a large number of adults were first discovered in the year of 1940. It may be indicated that the distribution of this species is not necessarily determined by the presence of cereal plants, but the climatic conditions associated with some original host plants are apparently favourable to the species.

In Japan, the main area where the fly occurs abundantly is Hokkaido, although it is found in northern prefectures of Honshu including Niigata, Fukushima, Iwate, Akita and Aomori. Inner Mongolia and Ussuri districts are also noted as outbreak areas in Eastern Asia. Southern China (Szetshwan) which is the only known locality in the Oriental Region, seems to be the southern limit of the species.

As the distribution in the Nearctic Region has been restricted to four states in the Pacific Northwest, there arises an interesting question, whether the fly has been introduced into North America or was originally holarctic. In this region, *M. saltatrix* and its related species, *M. americana*, occur in the same districts. The former was first recorded in 1912 by BECKER, while the latter has often been noticed since it was described in 1856. It would seem to favour the suggestion that *M. saltatrix* is not the native in North America unless it has been misidentified by early workers, because the species should had been discovered in earlier time for its injurious habits, if it was originally holarctic.

III. Taxonomy and Morphology

1. Taxonomic position

The barley stem maggot, *Meromyza saltatrix*, is one of the Acalypterate

Diptera belonging to the subfamily Chloropinae of family Chloropidae. It was first described by LINNAEUS in 1761 under the name *Musca saltatrix*, with his statement "Habitat in campis inter gramina, saliens more Cicade". In 1830, MEIGEN erected the genus *Meromyza* on the basis of three species including *Musca saltatrix* and two new species. Several years later, it was recognized by MACQUART (1835) who designated *M. saltatrix* as the genotype of *Meromyza*. Since that time, the genus has been well established by later taxonomists without any confusion, on account of the distinct character which can be easily delimited from the other genera of Chloropinae.

As the generic characters of the present genus, MEIGEN (1830) described as follows: "Fühler niedergedrückt, vorstehend, dreigliedrig; drittes Glied fast tellerförmig; an der Wurzel mit nackter Rückenborste. Untergesicht herabgehend, nackt; Stirn breit, vorstehend, feinhaarig. Augen rund, vorstehend. Hinterleib kegelförmig, nackt, fünfringelig. Flügel aufliegend; Queradern auf der Mitte genähert; Hinterschenkel verdickt". Although MEIGEN's original definition should be partly modified in the present sense, but his last mentioned note on the incrassated hind femur is one of the most important characters of *Meromyza*. This character is also found in three genera including *Platycephala* FALLEN (1820), *Chloromerus* BECKER (1911) and *Pachylophus* LOEW (1858) which belong to subfamily Chloropinae. However, the genus *Meromyza* may be clearly distinguished from *Platycephala* by the absence of the frontal puncture, from *Chloromerus* by the longer front which moderately projected forward the compound eye, and from *Pachylophus* by the slender arista. *Meromyza* is a small genus having only seven nominal species described from various parts of the world, and all the known larvae are recognized to be stem miners of the plant belonging to family Gramineae (Poaceae).

Although *M. saltatrix* is a typical species of *Meromyza*, its specific determination has had some confusion for a long while in Europe, as elsewhere, owing to the apparent lack of definite specific characters, the variability of the colouration of the species involved, or the presence of seasonal dimorphism.* In the Palaearctic region, however, DUDA (1933) has determined only three definite species, namely, *M. pratorum*, *M. saltatrix* and *M. inornata*, from many earlier descriptions given by several pioneers, but he has not been able to confirm the generic position of *Chlorops hordei*. Hereafter, two new species have been added to the genus, one being *M. nigrofasciata* named by HENDEL (1938) from Mongolia, and the other, *M. nipponensis*, by the author (1955) from Japan, although *Chlorops hordei*** has been merged into *M. saltatrix*

* The detailed features of this regards dealt with in the following section.

** However, this is the first exact record of *M. saltatrix* in Japan.

by the examination of the type specimens by the author (1952). Consequently, only five valid names have remained at present.

In this work which has been done with a large number of materials collected from various parts of the world, however, *M. nigrofasciata* and *M. inornata* are treated as new synonyms of *M. saltatrix*, because their mesonotal and abdominal colour pattern described as distinct characters is of no specific value in *Meromyza*. Moreover, no structural distinction, which is here considered valid, can be found between these species. The apparently valid species known from the Palaearctic region are therefore three in number, and their taxonomic differences are given in the following key.

Key to the Palaearctic species of the genus *Meromyza*

1. Front without short hairs at the anterior area. Frontal triangle distinct, smooth, extremely polished black. In profile, third antennal segment longer than the height. Scutellum entirely black, rugulose and pollinose. Third costal sector longer than the straight distance joining between the end of r_{4+5} and m_{1+2} *M. nipponensis* NISHIJIMA
- Front with a number of short hairs at the anterior area. Frontal triangle rugulose minutely, half-shining yellow to dark brown. Third antennal segment as long as the height. Scutellum yellow to dark brown, smooth and unpolish. Third costal sector approximately as long as the straight distance joining between the end of r_{4+5} and m_{1+2} 2
2. The anterior margin of front rounded apically. Palpi slender, rod-like, usually yellow, sometimes the tip slightly infuscated *M. pratorum* MEIGEN
- The anterior margin of front nearly straight. Palpi clavate, the apical half always black *M. saltatrix* (LINNÉ)

Meromyza saltatrix LINNÉ (1761), Fauna Svecica, p. 555 [*Musca*]; MEIGEN (1830), Syst. Besch., VI, p. 165; MACQUART (1835), Suites a Buffon, II, p. 589; SCHINER (1864), Faun. Austr., II, p. 210; WESTWOOD (1881), Trans. Ent. Soc. Lond., 1881, p. 608 [*Musca*]; ACLOQUE (1897), Faune de France, p. 488, pl. 216; BECKER (1902), Zeitschr. f. Hym. u. Dipt., II, p. 338; BECKER (1910), Arch. Zool., I (10), p. 43; MESNIL (1931), Rev. Path. vég. D'Ent., XVIII (7), p. 268; DUDA (1933), Die Flieg. der Palaearkt. Reg., 70, p. 119; ROCKWOOD *et al.* (1947), U. S. Dept. Agr. Tech. Bul., 928, p. 3; KATO (1950), Icon. Ins. Jap., p. 1676; NISHIJIMA (1952), Ôyô-Kontyû (Nippon Soc. Appl. Ent.), 8 (1), p. 22.

Syn. *cerealium* REUTER (1902), Medd. Soc. Fauna et Flora Fennica, XXVIII (B), p. 84; BECKER (1910), *op. cit.*, p. 42; MESNIL (1931), *op. cit.*, p. 269.

femorata MACQUART (1835), *op. cit.*, p. 590; MEIGEN (1838), Syst. Besch., VII, p. 396; BECKER (1910), *op. cit.*, p. 43; DUDA (1933), *op. cit.*, 70, p. 119.

- var. *hercyniae* DUDA (1933), *op. cit.*, p. 119.
- hordei* MATSUMURA (1927), *Ins. Mats.*, I, p. 127 [*Chlorops*]; DUDA (1933), *op. cit.*, 72, p. 223 [*Chlorops*].
- inornata* BECKER (1910), *op. cit.*, p. 44; DUDA (1933), *op. cit.*, 72, p. 228 [Syn. nov.].
- laeta* MEIGEN (1838), *op. cit.*, p. 395; SCHINER (1864), *op. cit.*, p. 210; BECKER (1902), *op. cit.*, p. 338; BECKER (1910), *op. cit.*, p. 42; DUDA (1933), *op. cit.*, 70, p. 120.
- marginata* BECKER (1912), *Ann. Mus. Nat. Hung.*, X, p. 25; CURRAN (1923), *Canad. Ent.*, LV (12), p. 279.
- minuta* GMEL. (1793), *Syst. Nat.*, I, p. 254 [*Musca*]; FABRICII (1794), *Ent. syst.*, IV, p. 361 [*Musca*].
- var. *nigripes* DUDA (1933), *op. cit.*, 72, p. 228.
- nigriventris* MACQUART (1835), *op. cit.*, p. 590; MEIGEN (1838), *op. cit.*, p. 395; SCHINER (1864), *op. cit.*, p. 210; BECKER (1902), *op. cit.*, p. 338; BECKER (1910), *op. cit.*, p. 43; BECKER (1912), *op. cit.*, p. 25; DUDA (1933), *op. cit.*, 70, p. 119.
- nigrofasciata* HENDEL (1938), *Ark. för Zool.*, 30 A (3), p. 12 [Syn. nov.].
- punctifer* BECKER (1912), *op. cit.*, p. 24; CURRAN (1923), *op. cit.*, p. 279.
- variegata* MEIGEN (1830), *op. cit.*, p. 165; MACQUART (1835), *op. cit.*, p. 225; BECKER (1902), *op. cit.*, p. 337; BECKER (1910), *op. cit.*, p. 43; DUDA (1933), *op. cit.*, p. 119.

The descriptions of adult and immature stages are given in the following four sections.

2. Adult stage

General feature: Head more or less broader than the thorax. Compound eyes with sparse white pubescence. Front pale to buff yellow, the length over three-fourths the width, the either side parallel, the anterior area with a number of short hairs and the margin nearly straight. Frontal triangle almost equilateral triangle in shape, half-shining with minute rugulose surface, the anterior corner ending three-fourths the length of front. Ocellar triangle black, distinct and well developed. Vertical bristles longest, ocellar and postvertical bristles relatively short. Two pairs of upper fronto-orbital bristles and three pairs of lower fronto-orbital bristles present. Antennae pale to buff yellow, the dorsal and apical parts somewhat darkened. In profile, the third segment as long as the height. Arista slender, the basal segment slightly thickened. Prefrons, cheeks and clypeus pale to dark yellow. Palpi clavate, at least the apical half always black. Thorax slightly longer than the width, pollinose, the dorsum

with three stripes. Scutellum rounded, the dorsal surface with sparse short hairs. Two pairs of anterior scutellar bristles weakly visible. Humeral areas, stenopleura, mesopleura and pteropleura with a small spot respectively. Abdomen slender than thorax, with brown to black band or stripe on either side and median part of each segment. Anal cerci with dense pubescence. Phallus rod-like and dark brown. Sternite lobes small, the surface with pubescence. Legs pale to buff yellow. In the hind legs, the femur extremely incrassate. Hind tibia strongly incurved. Wings hyaline, but the vein slightly pale. Costal vein ending to r_{4+5} . The distance from r_{2+3} to r_{4+5} on the costal vein nearly equal to the distance from r_{4+5} to the apical corner; m crossvein approximately two times the length of rm crossvein. Body length; In male, 2.6–3.8 mm, the average of 142 specimens is 3.18 mm and in female, 2.9–4.4 mm, the average of 338 specimens is 3.71 mm.

Variation: The colour pattern of the present species is very variable. As have been stated by MESNIL (1931), ROCKWOOD *et al.* (1947) and NISHIJIMA (1952), there are two distinct seasonal forms as follows.

Forma vernalis: Ground colour pale green or greenish yellow. Ocellar triangle large, the black spot occupying over one half of the frontal triangle. Occiput with distinct black stripe. Mesonotal stripes black, the median stripe reaching to the end of scutellum, sometimes three stripes fused into one. Pleural spot large and black, strongly marked. Abdomen black or dark brown. In Hokkido, the fly of this form always occurs from May to the end of June and represents the overwintered generation.

Forma aestivalis: Ground colour pale or buff yellow brown. Ocellar triangle small, the black spot within the confines of the ocelli. Occiput with indistinct black stripe. Mesonotal stripes dark to red brown, the median stripe slightly marked, not reaching to the end of scutellum. Pleural spots small and red brown, sometimes indistinct. Abdomen yellow, with three black stripes on each segment. The fly of this form occurs from July to the middle part of October and indicates the first and second generations.

Remarks: DUDA (1933) considered that *M. inornata* BECKER, having black mesonotal stripes and yellow abdomen, is a variety of the present species. However, the colour pattern has almost no specific value in *Meromyza* as described above. It is also difficult to recognize some specific characters for *M. nigrofasciata* given by HENDEL (1938). It is therefore considered that *M. inornata* and *M. nigrofasciata* are the same species with *M. saltatrix*. The present species is quite similar to *M. pratorum*, but it may be easily distinguished from the latter by the preceding key.

3. Egg stage

Snow white in colour and cylindrical fusiform. Micropylar area at the anterior end distinct, the posterior end slightly sharpened. The chorion is raised in longitudinal ridges, most of which extend the whole length but some end abruptly, and the space between the ridged being concave and marked off into rectangular areas by small transverse ridges. About 1.0 mm in length and 0.2 mm in diameter.

4. Larval stage

General feature: According to NYE (1958) and author's examinations, third instar larva, 6.8–9.0 mm in length and about 1.0 mm in diameter, blueish green with yellow patches particularly posteriad anal segment. A prominent brown crescentic dentate sclerite present but, apart from cephalo-pharyngeal skeleton which appears black, no other cephalic features visible. Anterior spiracles of rosette type, the posterior spiracles not borne on lobes and closely apposed.

Facial mask: Antennae small, well separated and distal segment light brown and partially retracted within the basal segment which forms a cup. A slight median groove present on either side of which are situated the light brown open type maxillary palps. Frontal palps consisting of three papillae on a small lightly tanned plate. Maxillary and frontal palps together with maxillary papillae mediad to maxillary palp; all lie on a large otherwise bare area, giving a characteristic appearance to the mask. Posterior to this area are two or three rami slightly crenulate on the outer edges running longitudinally, and joining two or three crescentic genal rami which are also crenulate. Dentate sclerite distinct, light brown and crescentic with the arms expanded to form wings the tip of which point anterolaterally. Cephalic papillae in the form of light brown rings.

Cephalo-pharyngeal skeleton: Apical tooth light brown, with two smaller teeth in first instar larva. It entirely black, with three and four smaller teeth in second and third instar larvae respectively. A single crescentic dentate sclerite as described above. Intermediate sclerites fused to the relatively long and narrow pharyngeal sclerite. Except for the parts of dorsal and ventral wings, whole skeleton densely tanned throughout.

Spiracles: A transversely elongate type, with 7–9 digitations in anterior spiracles. Posterior spiracles borne on very small spiracular lobes, separated only a slight depression; the spiracles themselves close and tending to incline towards one another. The four tufts of branched hairs present.

Spicular zones: Each consists of numerous irregular lines of overlapping

striae bearing minute spicules spaced throughout their length; the lines of each zone closer together anteriorly and extending the full width of the larva, but becoming more widely spaced and shorter posteriorly.

5. Pupal stage

Cylindrical type, fairly flattened, 5.0–7.2 mm in length and about 1.5 mm in diameter, blueish green with light brownish puparium.

It is formed from the larval integument and thus retains some of the morphological characters of the larva. Larval spiracles are present at the anterior and posterior ends respectively, and the larval segmentation and denticles are retained (Plate I).

IV. Bionomics and life history

1. Food Plants

In the course of the present investigation the larvae of *M. saltatrix* were observed feeding within the stems of the following species of plants.

Triticum aestivum hexastichon HACKEL (Wheat)

Hordeum vulgare LINNÉ (Barley)

Secale cereale LINNÉ (Rye)

Agropyrum repens BEAUVOIS (Quack grass)

Agropyrum semicostatum NEES

Festuca ovina LINNÉ

Bromus hordeaceus LINNÉ

In addition to the above food plants the maggot has been reported in the literature as feeding on the stems of *Alopecurus pratensis* LINNÉ, *Phleum pratense* LINNÉ (Timothy), *Lolium perenne* LINNÉ and a few species of undetermined wild grasses. Although *Avena sativa* LINNÉ (Oats) has been recorded as a food plant by European workers (REUTER, 1902; PLYATER-PLOKHOZKAYA, 1936), a closer examination of the host range in Japan suggested that the maggot does not attack that plant. It is highly probable that there exist two biological races among *M. saltatrix* showing some different host range as mentioned above. This may be an interesting problem in the light of ALDRICH's work (1920) that *Oscinella frit* has two biological races having different feeding range between North America and Europe. Among wild grasses *Agropyrum repens* has been frequently noticed from various parts of the world as the principal host plant maintaining the second brood of *Meromyza*. This is true in Hokkaido. A large number of the flies appear from spring sown cereals which are usually cut by the end of July and the oviposition is

chiefly concentrated on *Agropyrum repens*, as there is no available grain host until the middle of September when winter cereals begin to germinate. Furthermore, in the waste land of Hokkaido, quack grass serves as a main host throughout the life circle of the species. It is therefore probable that *Agropyrum repens* may probably be the original food plant of *M. saltatrix* and that it is playing an important role in the occurrence of the species. The conditions under which the food plants are attacked by the species will be dealt with in detail in the later chapter of this paper.

2. Behaviour of adult

Emergence: The emergence of the flies is always observed during the time from dawn to early morning both in the field and in the laboratory, even if the pupae are kept in darkness at various constant degrees of temperature and humidity. Under the humid conditions (70–100% R.H.), the flies appear in a moment from their puparia, while in the dry conditions (60–17% R.H.), they usually require more than ten minutes for the emergence. The pigmentation of the flies is not changed with the time of emergence, as it develops within eight hours.

Copulation: In breeding cages kept in an open air insectary the fly is polygamous. The mating takes place within two days after emergence. The posture of the mating is quite similar to other Acalypterate flies. The copulation lasts from 4 to 47 minutes, the male performing stroking movements with its hind legs on the five tergite of the female. The movement is vigorous and rhythmical. The frequency of the stroking per minute varies with the individual as shown in table 1.

TABLE 1. Lasting time of mating and frequency of stroking the male.

Dates of observation (1949)	26/V	28/V	30/V	31/V	1/VI	16/VII	20/VII
Lasting time of mating (min.)	22	37	18	25	12	4	11
Stroking number per minute	48	97	86	116	35	128	89
Dates of observation (1949)	21/VII	23/VII	25/VII	15/IX	16/IX	3/X	7/X
Lasting time of mating (min.)	28	33	20	13	18	28	32
Stroking number per minute	104	123	86	98	67	117	108

There is no correlation between the lapse of time of mating and the number of stroking as shown in the above table. The effect of this curious copulation behaviour on the physiology of their mating is not clear, but this is one of the interesting habits of the species.

Oviposition: Under cage conditions, the oviposition occurs usually within two or three days after the mating. The mated female reaches the lamina fairly close to the ligule walking about on the leaves or on the sheaths. At that place the female wanders around the base of the blade, shaking down her antennae with the behaviour which looks as if she is searching for a suitable site for the oviposition. Soon after the female directs her head upwards against the host plant so as to put her abdomen parallel to the long axis of the blade or sheath. From this ovipositional pose a single egg is deposited on the plant. Therefore, the eggs always lie between two adjacent longitudinal veins of the leaf surface, and their micropyles are situated towards the apical direction of the plant. The latter fact is interesting respect in relation to the larval behaviour which will be noted in the following section. The eggs are laid one by one on the leaves of the host plants, usually on the upper surface of the lamina, but occasionally on the under surface of the blade and on the sheathing part of the leaf. However, the egg-laying position on a plant varies with the growth of the host plants both in wheat and barley. This relationship is closely related not only to the occurrence of the host injuries, but also to the type of the symptoms as will be seen in detail in the later chapter.

3. Behaviour of larva

Hatching: Under various conditions of temperature and humidity in the laboratory, the author has not succeeded in getting the eggs to hatch during day time. Consequently, the actual hatching of the egg was always observed during from night to dawn. At the hatching the mouth part of the larva begins to appear from the anterior end near the micropyles of the egg and the larva starts the elastic movement with shaking its body right and left. The movement lasts usually for about ten minutes, occasionally more than half an hour and the larva escapes from the egg shell. However, the larva which is hatching from the egg in a dry conditions fails to escape completely and dies.

Entrance into the plants: After the hatching, the larva immediately enters into the plant by creeping. This behaviour finishing within one to three minutes is also observed during from night to dawn as well as hatching. When the larva appears from the anterior end of the egg which lies towards the apical direction of the plants, its head is therefore directed towards the apex of the

leaf. Supposing that the egg is on the upper surface of the leaf, the larva must therefore turn around before entering the shoot.

For the purpose of ascertaining that point, the following two experiments were carried out in the laboratory.

Experiment I: A small piece of wheat plant containing one egg was longitudinally glued on the outer surface of the glass tube (15 cm in height and 1.5 cm in diameter) which was uniformly covered with the membrane of vaseline by steeping it in the boiling vaseline. In this treatment the micropyle of the egg was directed upwards when the tube was set in the thermostat. The thermostat was kept at $22 \pm 0.3^\circ\text{C}$ and 100% R. H. with darkness. Then the trace of the larval behaviour left on the vasilinic membrane was examined distinguishing the three types: namely upwards (A), downwards (B) and downwards→upwards (C). The results are shown in table 2.

TABLE 2. The larval behaviour on the vasilinic membrane of the tube

Type of trace	Series of experiment												Total	Percentage	
	1	2	3	4	5	6	7	8	9	10	11	12			
A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B	13	23	20	18	4	5	5	4	3	6	5	6	112	56.85	
C	16	9	10	8	7	4	5	6	7	5	4	4	85	43.15	
Total number of hatching larva	29	32	30	26	11	9	10	10	10	11	9	10	197	100.00	

In the experiment no larvae appeared higher than the initial hatching point. This suggests that the larvae turned around before entering into the sheathing part of the leaves, if the suitable position for entering is not present. However, the larvae turns around again from the lower down to upper part, as shown by the result of symbol C.

According to the "critical leaf theory" of FREW (1924) the larva of *Chlorops pumilionis* BJERKANDER (= *C. taenioptus* MEIGEN) cannot penetrate into the ear-bearing internode if it hatches below the ear-bearing internode. However, the above experiment seems to indicate that all the larvae may be able to enter into the central shoot or ear-bearing internode by crawling up and down from their hatching point. The following experiment was carried out in order to ascertain the relation between the hatching position and the larval penetration into the ear-bearing internode.

Experiment II: Various growing stages of wheat stem after tillering were

collected from a field protected by a wire cage from the oviposition of the fly. After the ear-bearing position of each stem was measured, one egg was glued on the base of the laminae in each stem. The stems so treated were placed one by one in a small bottle. The following table was obtained from the result of observation by dissecting each stem.

TABLE 3. Experiment on the larval behaviour on the wheat stem.

Glued position of egg	Number of larva within;		Number of dead larva		Number of disappeared larva	Total number of hatching larva
	Ear-bearing internode	Other internode	Ear-bearing internode	Other internode		
Upper blade from the ear-bearing internode	40	0	2	0	4	46
Lower blade from the ear-bearing internode	0	6	0	28	17	51

On the upper surface of the leaf the larva immediately turns around from the hatching position and crawls down the ligule. Generally it crawls around between the ligule and the lamina until it comes to the slit in the overlapping edges of the sheathing portion of the leaf, and through this slit it enters between the sheath and the shoot or the culm. The larvae which hatch on the lower surface of the blade or on the sheathing part of the leaf, similarly enter the shoot in the approximated edges of the sheathing leaves. Therefore, in the case in which the egg was glued on a blade lower than the ear-bearing internode, no larva could be found in the ear-bearing internode. It is suggested that the first instar larva is subject to a definite taxis causing the first instar to migrate towards the base of the leaf upon which it hatches, and causing the larva to move downwards between the sheathing leaf and the shoot or the culm. In the majority of cases this taxis is beneficial and leads the larva to its food, but in a few cases the taxis will acts against the larva and destroys it by leading it away from suitable food. Actually it is observed that most of the larvae hatching on a blade lower than the ear-bearing internode die on attempting to enter the internode which is hard and probably unsuitable as the food. It is indicated that the first instar larva is unable to migrate into other internodes from the first internode which it has entered, because the first larval instar is apneustic and cannot, therefore, be expected to have a long existence. In the case of young tiller, however, the larva is not always unable to migrate from shoot to shoot. These phases should be noticed as a matter of importance concerning the relation between the egg-lying position upon the plant and the appearance of the injury.

Behaviour in the stem: By crawling downwards along the shoot the larva reaches the soft base of the shoot. It then gradually penetrates the successive sheathing leaves by cutting inwards and downwards in a spiral manner until it reaches the center of the shoot. Thus the larva feeds on the shoot or the young ear at the central shoot. In the boot stage of the host plant the larva reaches the culm directly below the young ear, but it never feeds the culm at that place. The larva turns around from the base of the culm and crawls up for feeding towards the young ear which is usually unable to grow out of its sheathing leaf as the culm has been cut in a spiral manner by the larva. It indicates that the first instar larva is, in fact, essentially in a migratory phase, although it undoubtedly feeds to some extent as shown by green chlorophyll coloured matter found in its gut, and again although it grows somewhat before moulting into the second instar. The primarily migratory nature of the first larval stage is a common feature among insect larvae.

The second and third instar larvae stay in the central shoot or in young ear to feed on them. However, in a few instances at the tillering stage of the host plant, the larvae which have entered into one shoot are found migrated into the adjacent tillers. In most of such cases the larva has bored directly through one or more of the inner sheathing leaves on its way to the center of the adjacent shoot which is newly sprouted from the base of the primarily injured tiller. This migration is probably caused by the lack of the suitable food for the larva because this is the only case in which the larva has entered into the young tiller. It may be indicated that all the migrations of the larval stage excepting the end of the third instar stage are strikingly connected with the search of the food, and that either the central shoot or the young ear is indispensable matter for the larval development.

Pupation: At the end of the third instar stage pupation takes place within the host plant. The mature larva, which heads downwards during the greater part of its life, turns around a short time prior to pupation so as to direct the head upwards. After turning round the larva usually migrates upwards a short distance before pupating. It pupates at that place. In the young tiller or in relatively slender ear-bearing internode, however, the larva is unable to migrate upwards because there is no space in the upper part of its food groove for its passing. In such case the pupation occurs in the spacious part of the host plant, usually in the base of the food groove, occasionally between the sheath and the internode near the outside of the food groove. But in a few instances the pupa fails to develop because the pupation occurs in a too restricted space and consequently the puparium are flattened. Adding to the probable necessity of finding the space for pupation, the migration of the mature larva

is probably connected in some way with some change in the physiological state of the larva. The answer for this needs a further investigation.

4. Duration of stadia

The duration of each stage is, of course, to be changed with various environmental conditions, especially temperature and humidity. These features will be discussed in a later chapter from an ecological standpoint, and here in order to avoid repetition the field observations including a few general points are considered.

To ascertain the duration of stadia in the field condition, the cage and marking experiments on the wheat plant were carried out from 1949 to 1950. The results are shown in table 4 and 5.

There are striking differences concerning the duration between the first and second broods, showing a definite tendency to make rapid development in

TABLE 4. The duration of stadia in the first brood.

Year	1949							1950						
Date of oviposition	28/V	28/V	28/V	30/V	30/V	1/VI	1/VI	20/V	20/V	20/V	24/V	24/V	24/V	25/V
Date of emergence	18/VII	15/VII	16/VII	16/VII	19/VII	23/VII	21/VII	13/VII	10/VII	15/VII	19/VII	17/VII	17/VII	16/VII
Sex	♂	♀	♀	♀	♂	♀	♂	♀	♂	♀	♀	♀	♀	♂
Egg stage (days)	12	11	12	12	11	10	11	12	12	13	13	13	12	13
Larval stage (days)	25	24	25	23	26	28	25	28	25	28	29	30	29	25
Pupal stage (days)	14	13	12	12	13	14	14	14	14	15	14	11	13	14
Total (days)	51	48	49	47	50	52	50	54	51	56	56	54	54	52

TABLE 5. The duration of stadia in the second brood.

Year	1949							1950						
Date of oviposition	26/VII	26/VII	26/VII	2/VIII	2/VIII	2/VIII	18/VII	20/VII	21/VII	28/VII	28/VII	2/VIII	2/VIII	2/VIII
Date of emergence	28/VIII	30/VIII	31/VIII	2/IX	3/IX	1/IX	19/VIII	24/VIII	24/VIII	28/VIII	31/VIII	30/VIII	28/VIII	29/VIII
Sex	♂	♀	♀	♂	♀	♂	♂	♀	♀	♀	♀	♂	♂	♀
Egg stage (days)	6	6	5	5	6	5	6	7	5	5	6	5	4	5
Larval stage (days)	16	19	21	15	17	17	19	18	18	16	17	15	15	15
Pupal stage (days)	11	10	10	11	9	8	7	10	11	10	11	8	7	7
Total (days)	33	35	36	31	32	30	32	35	34	31	34	28	26	27

the second brood. The duration from egg to emergence requires over 48 days in the first brood, while in the second it varies from 26 to 36 days. The mean values of the stages of egg, larva and pupa are 11.9, 26.4 and 13.4 days respectively in the first brood, and 5.4, 17.0 and 9.3 days in the second one. In September the egg laid mainly by the adult of the second brood requires more than 10 days for incubation as that in spring, and the larva hibernates until the middle of April in the following year. It therefore spends a long time covering at least 200 days for the larval stage. This owes probably to lower mean temperature in autumn.

5. Life history

From the rearing experiment as well as field observations for four years at several districts of Hokkaido it has been confirmed that there are no marked difference in the life cycle according to the year or to the locality. A typical life history of the insect in Hokkaido is noted below.

The larva passes the winter in the shoot of the host plant fairly close to the ground. It begins to pupate during April and at the beginning of May. Actually the flies appear in the field towards the end of May, as shown by the following dates.

May, 17, 1948 (Sapporo)	May, 9, 1950 (Sapporo)
May, 28, 1949 (Sapporo)	May, 20, 1950 (Obihiro)
May, 29, 1949 (Obihiro)	May, 16, 1951 (Sapporo)
May, 25, 1949 (Kitami)	May, 22, 1956 (Sapporo)

The flies of the first brood congregate on the winter- or spring-sown cereals showing a small peak of their prevalence curve in the middle of June. After that, the flies decrease rapidly towards the beginning of July. The egg of the first brood can be found at any time at the end of May and during June. The larva which hatches early begins to pupate at the end of June. The first appearance of the adult of the second brood usually occurs before the middle of July. Their initial collecting dates are as follows.

July, 5, 1949 (Obihiro)	June, 27, 1950 (Sapporo)
July, 11, 1948 (Sapporo)	July, 11, 1950 (Obihiro)
July, 7, 1949 (Sapporo)	July, 13, 1951 (Sapporo)
July, 11, 1949 (Kitami)	July, 14, 1956 (Sapporo)

It has been reported that there are some natural aestivation periods lasting at least a month in the adult stage of the summer generation both in Ukrina (RAKHMANNINOV, 1926) and in North America (ROCKWOOD *et al.*, 1947), because of a long pre-oviposition period of the adult. However, such phenomenon

was never observed in the present investigation in Hokkaido. In the laboratory the adult of the second brood usually lays the egg within four days after emergence. In the field, the flies which are reliably identified by their clear colour pattern (cf. Chapter III) are collected without intermission from the middle of July until the end of September. The maximum prevalence representing the second brood appears at the early part of August. It shows a greater curve than the first one. Accordingly, numerous eggs are also found during August. They are restricted to volunteer cereals, to the second growth of cereals which are cut prematurely, and also to wild grasses as there are no chance for oviposition on the spring- or winter-sown cereals which are usually harvested before the end of July. As indicated in the preceding section, the duration of each immature stage in August becomes considerably shorter than that of spring. Actually, in the case in which the wheat is sown experimentally in August, a large number of eggs are laid on the young wheat and the larvae pupate within 20 days after hatching. Thus the emergence of the adult of the third brood occurs from the end of August until the beginning of September.

However, it is clear that since the later member of the second brood survive up to the end of September, the flies of the second and those of the third brood overlap for a time in autumn. These flies lay the egg on winter cereals until the early part of October. The larva on winter cereals continues the feeding until the beginning of November at which the larva grows usually to the third instar stage and hibernates within the young tiller of the host plant. Therefore, *M. saltatrix* repeats two complete generations in a year in Hokkaido as has been reported in Russian Far East (PLYATER-PLOKHOTZKAYA, 1936), though there occur a few group which has only one generation.

V. Fecundity and food requirement of adult

Since the eggs are laid singly and the oviposition period extends over two weeks, it is difficult to estimate the number of eggs laid in nature by a single female. In cage experiments, however, the females laid from 14 to 63 eggs during 12 days. The mean number of eggs for 16 females was 36.4. These results are similar to the data given by TZUIGANKOV (1930) and ROCKWOOD *et al.* (1947). However, it is noted that a number of eggs have been found remaining within the ovaries by dissecting the female which died in the rearing cage. In addition to this incomplete oviposition, the ovary of the adult is a typical polytropic form. These facts may suggest that the adult would have laid more eggs, if it had necessarily required the food for oviposition under a good supply of nutrient substances.

It has been well known that the ovaries of flies are totally undeveloped at the time of emergence and that female flies require a diet consisting of water, sugar and protein: water and sugar for maintenance of life and protein for egg-production. However, there have been conflicting reports concerning several members of Diptera in which the diet of adult stage seems to have little effect on the number of eggs produced. HORBER (1950) stated that the adult of *Chlorops pumilionis* feeds on pollen, nectar or other sweet substances, but these substances are not essential for the oviposition because a single female kept with water alone lays as many as 97 eggs. Thus an experiment was undertaken to ascertain whether the fecundity is controlled principally with feeding or diet and to determine the effects of different nutrient substances.

Experiment I: On the day of emergence, the flies of each sex were placed in the cage to permit copulation and were given only water for three days. After the repeated copulation five female flies were transferred into a glass chimney-like cage which is 20 cm in height and 9 cm in diameter, covered with a wire net on the top. They were fed with test solution. Green wheat was given to them for the site of oviposition. Since the female fly shows a definite site preference for oviposition which will be proved in a later chapter, 20 laminae of the wheat plant placed in a chimney. The contents of the test solution were as follows: egg albumin, glutelin, honey and dried yeast. Each substance was dissolved to make a 10 per cent solution or suspension and was soaked in a piece of absorbent cotton. The test solution and the wheat plant in the chimney were replaced each day. All tests were conducted in a thermoregulator at $20 \pm 1.3^\circ\text{C}$ and with 92-100 per cent R.H. and lighted for 12 hours each

TABLE 6. The effect of various diets on egg-production.

Diet	Number of the egg produced				Total	Mean no. of eggs per fly
	1	2	3	4		
Egg Albumin	61	143	129	92	425	21.3
Egg Albumin+Yeast	56	188	136	109	489	24.5
Egg Albumin+Honey	81	104	153	100	438	21.9
glutelin	94	127	104	133	458	22.9
glutelin+Yeast	93	120	128	145	486	24.3
glutelin+Honey	77	159	134	181	551	27.6
Honey	75	168	112	151	506	25.3
Honey+Yeast	73	113	147	162	495	24.8
Yeast	89	146	170	135	540	27.0
Distilled Water	62	140	115	138	455	22.8

day by 10 watt bulb. All tests were repeated four times and the egg was counted every day until the last fly died in the chimney. The result is shown in table 6.

Table 6 shows that the relation between the kind of diet and the fecundity is not clearcut and that no significant differences can be found between distilled water and the other treatments. The fecundity obtained is, in the strict sense, not an accurate index of the actual nutrient value of the food because there is no evidence that the equal quantity of the testing food is ingested during the experiment, although it is very difficult to arrange. However, no remarkable differences were observed either in preference or in feeding, as a coloured testing solution was found in the gut of each fly tested. Furthermore, no delayed oviposition could be seen in all the tests, since the oviposition began within two days after the treatment and lasted for 10–13 days. These facts suggest that the food of the adult stage is not essential for the oviposition. Thus a second experiment was necessary in order to ascertain whether the fecundity is controlled principally with the species of food plant during the larval stage.

Experiment II: The female flies used in this experiment were obtained from the pupae occurring in different hosts, namely, wheat, barley, naked barley and quack grass. Each of these flies was separately placed in a chimney together with the laminae of wheat and 10 per cent honey solution. The rearing conditions and the treatments were approximately the same with those described in the former experiment. The result is shown in table 7.

TABLE 7. The effect of the food plant during the larval stage on egg-production.

Food plant	Number of the egg produced				Total	Mean no. of eggs per fly
	1	2	3	4		
Wheat	173	148	122	190	633	31.7
Barley	121	166	175	134	596	29.8
Naked barley	139	127	152	118	536	26.8
Quack grass	156	113	169	146	584	29.2

Since the result given in table 7 shows no positive relation between the fecundity and the kind of plants, it may be postulated that the fecundity is not controlled by species of the food plant on which the insect feeds. This seems to suggest that inner nutritive conditions during the larval stage may decide the fecundity.

The third experiment was undertaken to determine whether the fecundity

is changed by the size of the female fly determined by the weight of the pupal stage.

Experiment III: The method and the conditions were the same to those described for the first experiment, excepting the following points. The experiment was set up for each female fly emerged from the pupa which was divided into four class by the weight, namely, 0.25–0.34, 0.35–0.44, 0.45–0.54 and 0.55–0.64 mg. In this case the weight of the pupa was measured immediately after pupation, since it may vary according to the rate of development. The female flies in the chimney were kept with distilled water alone. The result is shown in table 8.

TABLE 8. The effect of the body-weight of pupa on egg-production.

Body-weight of pupa (mg)	Number of the egg produced				Total	Mean no. of eggs per fly
	1	2	3	4		
0.25–0.34	83	77	91	64	315	15.8
0.35–0.44	105	112	98	107	422	21.5
0.45–0.54	116	134	125	102	477	23.8
0.55–0.64	140	118	152	139	549	27.5

The data obtained from the third experiment shows that the fecundity is increased accordingly with the increase of the body-weight of the pupae. The weight of pupa depends upon the size of the larva which is principally influenced by the nutritive value or conditions of the food. It is, therefore, obvious that the fecundity of this species is largely dependent on the nutritive condition during the larval rather fly stage. However, it has been well known that the fecundity of insect is influenced not only by the nutrient conditions of the adult, but also by some ecological factors such as the temperature, the parasite and the population. Therefore, a discussion concerning vitality or biotic potential of this species will be given later in this paper.

VI. Research of physical environmental conditions

The relation between the life of insect and the physical conditions of the environment would be of great value, not only for the explication of seasonal abundance of the insect, but also for the solution of many practical problems for its control. Although ecological studies dealing with the subject in Diptera have been accumulated, in the case of *M. saltatrix* little has been known excepting a brief note given by ROCKWOOD *et al.* (1947). Therefore, the purpose of this chapter is, at first, to present the results obtained in the laboratory

tests on the effects of temperature and humidity upon the life of *M. saltatrix*, and then to describe the nature of some physical environment in which the species occurs. The following experiment was primarily undertaken to determine the range of the thermal reaction of the adult and larva in rising and falling temperatures.

A. Laboratory experiments

1. Thermal reaction of adult and larva

Material and method: The principle used by MACFIE (1920), WRIGHT (1927), MOTOMURA (1938) and others was employed for this experiment. The adult was placed in a glass tube, 8.5 cm in height and 1.7 cm in diameter, with the bulb of a thermometer inserted through the cover of cork. This tube was fixed in the central part of a beaker which is to be filled to a capacity of about 800 cc with water maintained at 1–3°C. The test was commenced when the water was poured into the beaker and was heated by regulating a screened electric heater to raise the temperature in the tube at the rate of 1°C every 5 minutes. The falling temperature could be produced by cooling the water previously kept at 45°C in the beaker. All the tests were repeated three times for each sex on the same date of emergence. With the change of the temperature in the tube, the adults exposed showed specific response, showing a definite changing phases of the movement as follows:

1. Cold stupor; the fly becomes quite inert, showing no response to stimulus.
2. Spasmodic movement by cold; the fly turns upwards, showing only the twitching movements of their antennae and legs.
3. Sluggish movement by cold; the fly walks or moves with faltering steps.
4. Normal movement; the fly shows no difference in the movement in nature.
5. Violent movement; the fly walks quickly or wriggles excitedly.
6. Sluggish movement by heat; the fly shows the movement as indicated for the 3rd item.
7. Spasmodic movement by heat; the fly shows the movement as indicated for the 2nd item.
8. Heat stupor; the fly becomes quiescent, as indicated for the 1st item.

The observation was made for each testing fly by recording the temperature at which the phase of the movement was commenced. Since no difference in the data was recognized between sexes, the temperature range causing the

movement was determined by the frequency distribution of 60 individuals. The result is shown in table 9.

TABLE 9. The temperature ranges causing various phases of the movement of adult.

Changing phases of movement	The temperature ranges	
	Rising temperature (°C)	Falling temperature (°C)
Cold stupor	—	0.2—2.2
Spasmodic movement by cold	2.7—5.7	2.1—7.7
Sluggish movement by cold	4.6—12.5	8.2—19.6
Normal movement	12.3—24.8	19.7—31.9
Violent movement	24.9—32.0	30.6—33.6
Sluggish movement by heat	33.2—39.2	34.0—41.2
Spasmodic movement by heat	40.2—45.2	—
Heat stupor	42.3—46.1	—

For the larva, a similar experiment was carried out, excepting the following points: the larva used was the end of third instar stage without distinction of sex; the reaction to temperature was divided into seven steps of movement as indicated in table 10.

Results: In table 9 the temperature ranges were remarkably different between the tests. This difference was not so small as had been expected, although the movement was a little intensive at the beginning. This may be connected with some change of the physiological adaptation of the adult to the temperature. However, it can not be ignored that the gradients of temperature both in rising and in falling during a short period of time usually occurs in the natural habitat of the species. Therefore, the temperature ranges which cause the movement should be reasonably determined by combining the data obtained from two tests. For example, normal movement was observed in the range of 12.3–24.8°C in the rising test, while it was 19.7–31.9°C in the falling one. Then, we must consider that the broadest range, extending over 12.3–31.9°C, is a possible range for this movement. In this case, the overlapping portion which forms a peak of the frequency distribution, that is, 19.7–24.8°C seems to be optimum. Beyond this range, a varying number of the flies responded more or less to a given temperature. When exposed to the temperature range of 42.3–46.1°C, and also to that of 0.2–2.2°C, the flies became quite inert, but all recovered within 20 minutes. When exposed to the temperatures of 51°C and over for 5 minutes, none of the flies survived, but at low temperature reduced gradually to –17°C, most of the flies revived from 5 minutes to one hour.

TABLE 10. The temperature ranges causing various phases of the movement of larva.

Changing phases of movement	The temperature ranges	
	Rising temperature (°C)	Falling temperature (°C)
Cold stupor	—	0.1— 3.6
Spasmodic movement by cold	1.4— 8.9	2.6— 8.5
Sluggish movement by cold	8.2—14.1	7.4—16.3
Normal movement	14.2—26.2	16.4—28.6
Violent movement	26.3—35.4	27.0—38.7
Spasmodic movement by heat	40.6—44.7	41.5—45.0
Heat stupor	41.8—45.0	—

The behaviour of the larva differed a little from that of the adult. As was shown in table 10, the temperature below 3.6°C made the larva insensible. At 7.4–16.3°C the larva began to crawl slowly, showing a peak at 11.5–12.2°C. The violent movement as indicated by excited mining behaviour or quick crawling was observed at 26.3–38.7°C. The maximum frequency of this was at 35°C. The beginning of heat stupor occurred at 41.8°C and it continued to 45.0°C. Within the limits of these temperatures, all the larvae revived in a short time, but with an exposure to 48°C for 5 minutes, all died. Although normal movement was seen at 14.2–28.6°C, its optimum range seemed to fall into the temperature range of 16.4–26.2°C, showing a longer extent than that of the adult. It may be concluded that so far as this experiment is concerned, a possible temperature range of the normal activities of the species is fairly extensive, extending from 12°C to a little over 30°C.

The next series of experiments was undertaken to determine the effect of temperature and humidity on the rate of the development and mortality of the egg.

2. Effects of temperature and humidity on egg

Material and method: The eggs used in this experiment were obtained by placing the gravid fly in a cage together with fresh wheat for four hours before each test. Since these eggs were deposited singly on the surface of the wheat, a small leaf-piece with a single egg was cut away for the maintenance of constant humidity. Then, in order to avoid the disturbance of hatching rate, the egg was placed again under the original conditions. Therefore, the leaf-piece was longitudinally glued on a slender glass rod, so as to direct the micropyle of egg upwards. The rod was smoothly coated with vaseline, except

for a small area around the egg. By this treatment it will be demonstrated whether the larva has hatched or not. The rod was fixed in a small glass tube, 6 cm in height and 1.6 cm in diameter, containing a small quantity of water or salts to keep the desired relative humidity. After the whole tube was tightly corked, a batch of the tubes consisting of five different relative humidities was placed respectively under different temperatures, so that a whole set of experiments was carried out simultaneously. The combination of temperature and humidity was as follows.

Temperature (°C)	Source	Humidity (%)	Source
30.0	Thermoregulator	100	H ₂ O
25.0	Thermoregulator	70-80	NaCl
19.0	Low temperature room	50-60	Ca(NO ₃) ₂
15.0	Low temperature room	30-35	CaCl ₂
		17-20	ZnCl

The treatment of each tube containing 10 eggs was repeated 5 times under the same combinations of temperature and humidity. The examination of hatching was made every day after treatment. The result is shown in table 11.

TABLE 11. Hatching percentage and duration of egg stage at different temperatures and humidities.

Humidity (%)	Temp. 15.0°C		Temp. 19.0°C		Temp. 25.0°C		Temp. 30.0°C	
	Hatch (%)	Period (days)						
100	78.0	16.1	90.0	8.9	92.0	5.2	88.0	4.0
70-80	74.0	15.8	84.0	9.1	86.0	5.4	80.0	3.9
50-60	26.0	16.0	28.0	9.1	34.0	5.5	30.0	4.1
30-35	10.0	16.5	17.0	9.3	18.0	5.9	16.0	4.1
17-20	0	—	4.0	9.6	0	—	0	—

Result: The hatching percentage showed a marked decline in proportion to the decrease of relative humidity. This decline was especially remarkable below 70-80% humidity. At 17-20% R.H. the eggs did not hatch. Although the hatching was only slightly affected by temperature in general, it was reduced at 15°C.

On the contrary, the effect of temperature on the duration of egg period was evident, while that of humidity was not recognized at any temperature set in the present test. The duration of egg stage was gradually shortened by the rise of temperature, as shown in Figure 2 giving a linear regression formula

of developmental velocity (X) on temperature (Y). The zero point of theoretical development was determined at 9.4°C and therefore the total effective temperature was 87 day degrees. It is obvious that the hatching is largely controlled by humidity rather than temperature, whereas the latter will insert an influence upon the duration of the egg stage without reference to humidity.

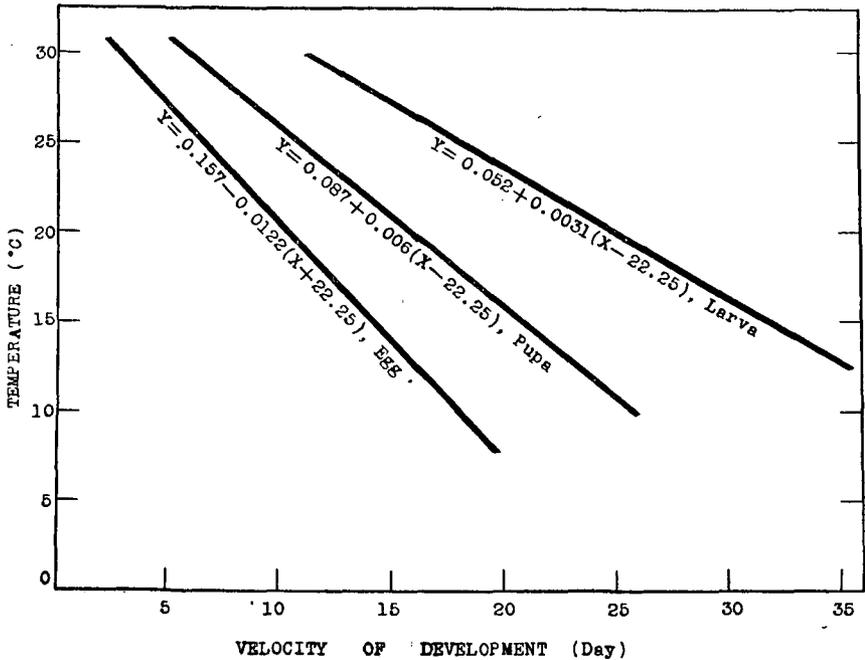


Fig. 2. Effects of temperature on the development of egg, larva and pupa.

3. Effect of temperature on larva

Material and method: The attention of the present experiment was directed towards the effect of temperature only, since it is clear that the larva living within the host plant where the humidity is completely saturated is probably impossible to survive under the condition of low relative humidity. Thirty larvae were placed in a glass bottle immediately after hatching, and were kept at 15, 19, 25 and 30°C respectively with 100% R.H. The young ear of wheat was supplied as food. The result is shown in table 12 and in Figure 2.

Result: In the course of this experiment a strong discolouration of the food plant occurred, but in a majority of cases the larva did not escape from the ear in which it entered, and it moulted into the pupa. This may neglect the effect of the change of food condition. Apart from this point, the duration

TABLE 12. Duration of larval stage at different temperatures.

Temperature (°C)	Duration from hatching to pupation (days)		
	Minimum	Maximum	Mean
15.0	31	37	34.7
19.0	21	25	23.1
25.0	14	18	16.4
30.0	13	15	13.2

from hatching to pupation varied with the fluctuation of temperature, showing a clear regression line as shown in figure 2. The zero point of theoretical development, 5.5°C, was considerably lower than those obtained for the egg and pupa. The value of accumulative effective temperature was 320 day degrees.

4. Effects of temperature and humidity on pupa

Material and method: In order to know the effects of temperature and humidity on the pupal period, an experiment was carried out under the same conditions as those described for section 2. When the larvae pupated, 10 pupae were placed on the wire gauze in a tube, which was divided a little below the center by a tightly-fitting ring of cork. On the upper part of the ring the wire gauze was placed, and below it a small quantity of water or salts was supplied. This tube was kept at desired temperature, and all the tests were repeated 5 times respectively. The result is shown in table 13 and in figure 2.

TABLE 13. Mortality and duration of pupal stage at different temperatures and humidities.

Humidity (%)	Temp. 15.0°C		Temp. 19.0°C		Temp. 25.0°C		Temp. 30.0°C	
	Mort. (%)	Period (days)						
100	21.1	22.9	17.2	14.6	10.6	9.0	16.7	7.4
70-80	23.1	22.5	10.8	15.0	8.3	9.4	10.6	7.4
50-60	42.2	22.7	29.0	15.2	16.3	9.0	32.7	7.7
30-35	79.5	23.0	72.5	15.1	46.0	9.9	67.4	7.9
17-20	74.5	22.9	77.0	15.1	51.1	9.7	64.5	7.6

Result: The mortality in pupal stage increased with low humidity at any temperature. The lowest mortality was recorded at 70-80% R. H., except a section of 15.0°C, at which the mortality was high. The highest mortality was observed at R. H. lower than 30-35%. Under these conditions, however, all the pupae reached the stage at which the cuticle begins to be coloured, and

several adults were able to emerge successfully even at 17–20% R.H. This clearly suggests that the resistance to low humidity is higher in pupal period than in egg period.

As in the case of the egg, the length of pupal period is affected by temperature, but not by humidity, showing a remarkable tendency of rapid development with the reduction of temperature. The ranges from the most rapid to the slowest development at each temperature were 20–26, 13–17, 8–11 and 6–9 days respectively. The zero point of theoretical development was at 7.8°C and the total effective temperature was 166 day degrees.

5. Effect of temperature on the rate of oviposition

Material and method: It has been well known that the number of oviposition varies with the change of temperature and humidity. In view of this, the flies emerged from the pupa in normal weight, 0.45–0.54 mg, were examined by the same method as those employed for the oviposition test at different temperatures as shown in table 14. However, the humidity could not be maintained at a low level because the tests were conducted by confining the flies in a chimney with fresh wheat and a honey solution in order to have sufficient oviposition. During the test the humidity of the chimney was 90–100% R.H. The data given in the following table was obtained by daily examination with 20 females in each temperature series.

TABLE 14. Duration and number of oviposition at different temperatures.

Temperature (°C)	Duration (days)	Total no. of eggs	No. of eggs per fly
15.0	6–24	310	15.2
19.0	3–13	496	24.8
25.0	2–16	561	28.1
30.0	2–14	518	25.9

Result: Table 14 shows that the increase of temperature from 19°C to 30°C brought about no significant difference either in the number of eggs deposited by a female or in the duration of oviposition at the second or third day after the treatment. A delayed oviposition with a few eggs was observed at 15.0°C. Therefore, it may be indicated that, so far as the oviposition is concerned, a difference of 15°C within this particular temperature zone made no difference in the ultimate efficiency of *Meromyza saltatrix* in attacking the host plant.

B. Field examinations

1. Data obtained by sweeping

In order to obtain a relative index of fluctuation in population, daily net-sweeping was continued during the whole flying season of the species in three consecutive years from 1949 to 1951. It was done in the wheat and barley fields, except the period from August to the early part of September, in which the cereals had been harvested. Consequently, it was conducted in a grass field where quack grass was predominant. This alternation of field swept may exert a little influence upon the number of flies caught by fifty sweeps with a net of 30 cm in diameter. Furthermore, even in the cereal field the environment is not of a uniform condition throughout the active season of the fly because of plant growth variation. Nevertheless, the *relative* variation of population among the years is possibly obtained, since the records were made at the same season with the same type of field. In order to eliminate variations due to unfavourable collecting conditions, the total number of spring and summer flies per month was used (table 15). The durations caught spring and summer flies are also given in table 16.

TABLE 15. Total number of flies caught per month during 1949-1951

Year	Spring form			Summer form					Total
	May	June	July	June	July	Aug.	Sept.	Oct.	
1949	4	382	25	0	1549	2037	99	54	4150
1950	72	270	0	3	768	2613	660	50	4436
1951	40	323	1	0	431	1044	702	35	2381

TABLE 16. Durations caught spring and summer flies during 1949-1951

Year	Spring form			Summer form		
	From	To	Total (days)	From	To	Total (days)
1949	28, May	8, July	42	7, July	17, Oct.	103
1950	9, May	31, June	53	27, June	18, Oct.	114
1951	16, May	4, July	49	13, July	14, Oct.	94

As shown in table 15, the mode of prevalence curve is almost the same in each year. It shows two peaks in a year, one in June and the other in August. In this case, a small peak in June indicates the first brood consisting

of the flies only of spring form, and the other one of a later season represents the second plus third broods being composed of the members of summer form which differs from the former by colour pattern (see, Chapter III). Thus, it is highly probable that the greater curves in August are due not only to actual increase of summer flies, but also to the duplication of two broods. From the same reason, a remarkable difference of the duration between spring and summer flies, namely 42-53 days in spring and 94-114 days in summer, does not indicate the proportional variation of longevity, though summer flies have a tendency to exist for a little longer than spring ones. The duration and the date of the first appearance on each fly differs a little from year to year. The total number of flies collected in 1949 and 1950 were closely comparable, but those of 1951 were conspicuously smaller. In 1951 the number of flies of spring form collected were by no means smaller than the other year, whereas a marked decrease occurred in the flies of summer form, especially in July and August. This indicates the presence of a special factor increasing the population normally from spring to summer, and then a question arises naturally as to what factors are concerned in this unusual case. Thus the results described above are to be compared with several climatic data in the following three sections.

2. Comparison between sweeping data and temperature conditions

Of the climatic data obtained in the sweeping field, those of the temperature are plotted graphically on the smoothed curve in figure 3. Each point on the curve indicates the mean, in a period of over ten days, of maximum and minimum temperatures.

On the whole, the fluctuation between max. and min. temperatures are fairly extensive, extending to about 10°C a little over. The curves show two noticeable facts: namely, minima are below 10°C during May and October, and maxima are not over 32°C throughout the active season of the species. These features may be of some interest, when we consider that the temperature requiring for normal activities ranges 12.3-31.9°C in the adult. The temperature in May, providing the temperature during the first pupal period, was high at the first decade in 1950, the second one in 1949, and the last one in 1951. In spite of these variations, no remarkable difference was seen in the sweeping data during June. Adding to this, the diversity of the swarming period of spring flies did not always coincide with the change of temperature. The temperature in the period from June to the early of July, during which the first generation is immature, was abnormally high in 1950, moderate in 1951, while it was

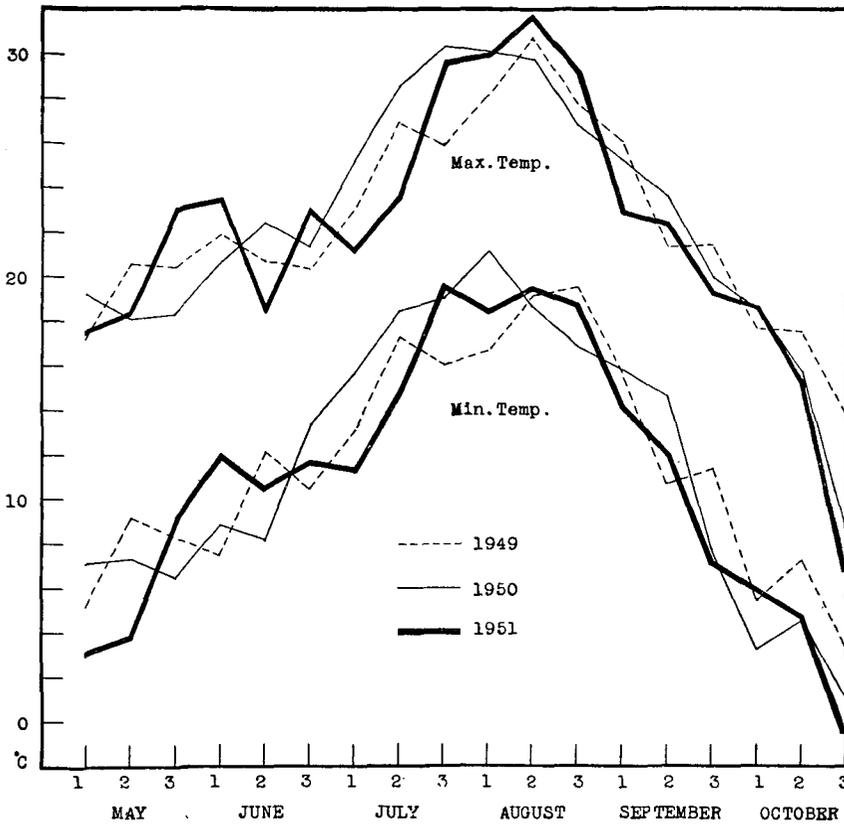


Fig. 3. Mean Maximum and Minimum temperatures in the field during the seasons in 1949-1951. 1, 2 and 3 indicate the first, second and third decades of every month respectively.

low through the whole period in 1949. The mean temperatures were 23.4, 21.1 and 20.9°C respectively.

Thus the appearance of summer fly would have occurred early in 1950, intermediately in 1951 and late in 1949, if the larval and pupal developments had been directly affected by the temperature of the field. But, actually the results of 1949 and 1951 were in reverse order, though a definite coincidence was seen in 1950, the year in which summer flies appeared early (table 16). This suggests that the field temperature, as expressed by the mean, is almost unavailable to indicate the variation of the swarming period of the flies unless it is extremely different. This may be responsible for the fact that the immature stage, the greater part of life being within the host plant, is not directly influenced by field temperature. In view of this, the wheat temperature at the

central part of the stem, the place where the larva has attacked, was measured by a thermopile in order to examine the relation between micro- and macro-temperatures on a biotope involved.

By comparing the results given in figure 4, we can learn an interesting fact: namely, the wheat stem temperature fluctuates correlatively with the change of the field temperature, but, the former is higher throughout a day than the latter, the average being 17.0°C while the latter shows 15.8°C . The fluctuating

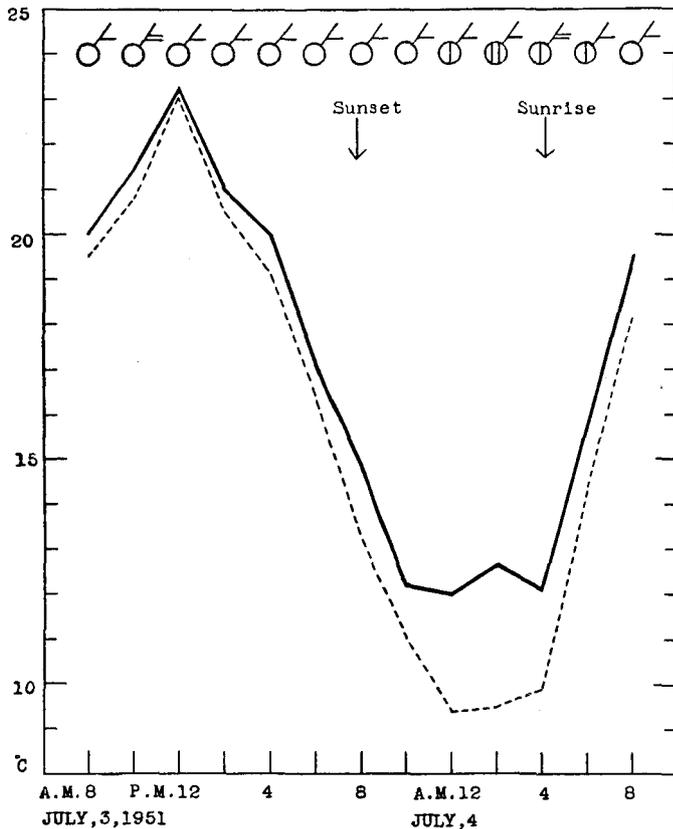


Fig. 4. A comparison between the temperatures at the rows of the wheat-field (broken line) and within the injured tiller (solid line).

range of the temperature in the wheat stem does not exceed 11.2°C , whereas it is 13.7°C in the field. This feature may be changed to some extent with various factors such as weather, sunny or shady site conditions etc. However, under the conditions of fine weather, the wheat stem maintained usually more monotonous temperature than the field. This condition serves not only to protect

the life of this internal feeder, but to favour the development in the immature stages. In other words, since the larval and pupal stages are not exposed to a stronger temperature fluctuation than in the field, their developmental period is less changeable than in the field. This suggests a tenable interpretation of the discordance of the relation in 1949 and 1951 between the swarming period and the mean field temperature.

As to the total number of summer flies, a profound decrease was recorded during the period from July to August in 1951. As the field temperature of the corresponding parts of this year was high, it may be supposed that the summer flies are influenced to some degree by high temperature. However, this is very doubtful because the max. temperatures during August in 1951 were always below 31.9°C, indicating the upper limiting temperature causing the normal activities of the fly. Furthermore, no other possible explanation can be given by the fluctuation of temperature alone, probably because of other various factors are concerned.

3. Comparison between sweeping data and humidity conditions

According to the laboratory experiments described in the foregoing paragraph, low humidity causes a marked inhibition both in hatching and emergence. Therefore, low humidity condition should have exerted some influences upon the numbers of the adult, if it occurred for a long time in the field. The mean field humidities representing the curves given in figure 5 showed a remarkable fall below 60% during May both in 1950 and 1951, and the first ten days of

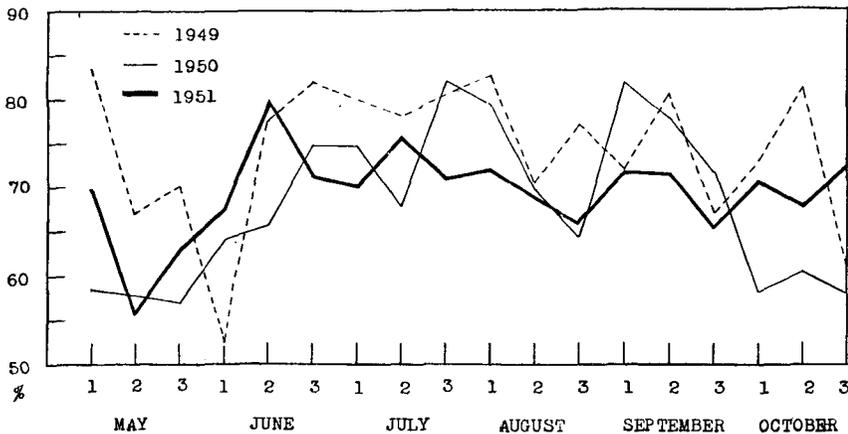


Fig. 5. The mean field humidities in 1949-1951. 1, 2 and 3 indicate the first, second and third decades of every month respectively.

June in 1949. Supposing that the pupa in May or the egg in June are severely destroyed by these conditions, the number of the flies is to be decreased in the following month, but its corresponding changes were not recorded in all occasions.

As already mentioned, there was a marked decrease in the summer flies in 1951. It is difficult to determine the cause of this decrease on the basis of the humidity conditions during the period concerned. During June in 1951, the spring fly which was closely matched in number with the other years has been exposed under the conditions of higher mean field humidities rather than the same periods of 1949 and 1950. Therefore, it is obvious that the field humidities during June are of little importance as a factor limiting the members of summer fly. The mean field humidities during July and August were on the contrary lower in 1951 than in the other years. Since at the same period in 1951 a marked decrease of summer fly was recorded, it is assumed that the condition of low humidity may act against the summer fly itself. However, this assumption is quite impossible to explain the adverse result obtained in the same year's September, showing lowest mean field humidity with a greater number of fly in comparing with other corresponding periods. If the summer fly and its progeny were harmfully affected by the condition of low humidity during August, their decrease should have occurred in September, whereas an actual result conflicting with this presumption will postulate that other undetermined factors causing the decrease of summer fly are present. Such being the case, it is concluded that the cause of abnormal decrease in 1951 cannot be explained by a prolonged period of low mean field humidity. What is the reason causing the conflicting results between the laboratory experiment on humidity and this field examination?

Evidence can be obtained on this point by comparing the relation between the life pattern of *M. saltatrix* and the daily change of the field micro-humidity, as observed by a self-hygrometer in a screen placed between the rows of wheat plant during June and the middle part of July in 1949. As shown in figure 6, the field micro-humidity was extremely changed between day and night, tending to rise to over 90% even when it was down to 50% in daytime. Each of the diurnal and nocturnal averages for 45 days were 78.6% and 96.5% respectively. This rhythmical alternation of the micro-humidity condition would almost certainly permit the larva to hatching because, presuming that the egg has not been destroyed by low micro-humidity for a short while in daytime, the larva should have hatched between dusk and dawn (*cf.* chapter IV). This seems to be true in many cases, considering the fact that low humidity in daytime is only an inhibitory factor for hatching, as proved by the laboratory

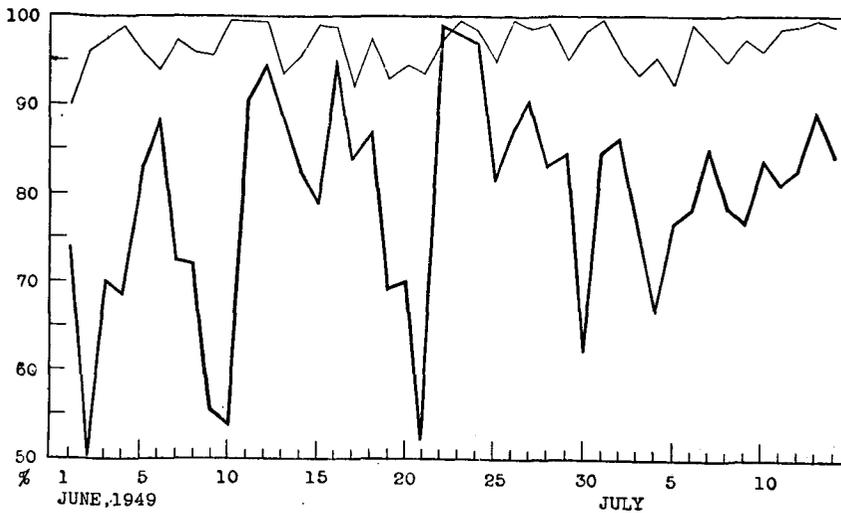


Fig. 6. The micro-humidities in the wheat field, showing at night (upper line) and at daytime (lower line).

experiment. This showed that the death of egg under low constant humidity took place not in the process of embryonic development, but resulted when larva was unable to escape from the egg shell after the completion of the body. Actually, the hatching percentages in the field were always over 90% in various marked experiments (*cf.* chapter VIII). This suggested that the nocturnal condition in the field was highly favourable to the first instar larva for hatching as well as for the entrance into the host.

After the larva has entered into the host for a short time at night, any external humidity condition is probably not concerned with this internal feeder, both in the larval and pupal stages. Of the adult stage, it should be noted that the fly is able to select freely various levels of humidities occurring at the same time in the field. Finally, the condition of the field humidity was almost unworthy to explain the cause of the prevalence of this species, owing to its alternative changeability regulating the hatching time which was, necessarily or behaviourly, in conformity with a higher counterpart of the field micro-humidity in a day.

4. Comparison between sweeping data and rainfall

The precipitation during the period concerned was apparently very diverse, as shown in figure 7. Its total per month in each of the years 1949 to 1951 was 36.5, 41.9 and 111.2 mm. in June, and 39.7, 248.5 and 46.3 mm. in August respectively.

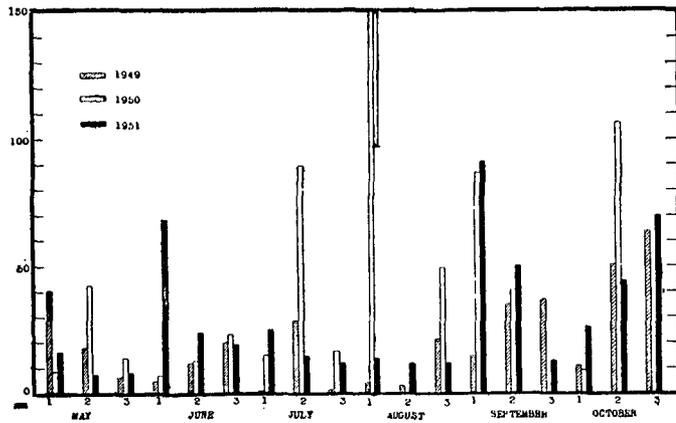


Fig. 7. Amount of rainfall during the seasons in 1949-1951. 1, 2 and 3 indicate the first, second and third decades of every month respectively.

During June in 1951, the weather was very dull and a long spell of rain was recorded at the middle of the month (10, 11, 13, 14, 15, 16, 17 and 19th), during which the eggs were laid or laying on the host plant. The field marking data concerning oviposition obtained at this period (table 17) showed that the number of new eggs deposited was considerably decreased under these conditions. This marked decrease was more than the variations due to a small difference

TABLE 17. Rainfall and the number of egg per 50 spring-sown wheat during 6th-20th June for 1949-1951*.

Year	Amount of rainfall (mm.)	Rainy day in daytime (days)	No. of initial egg marked at 6th, June	No. of new egg deposited	No. of egg hatched	No. of egg disappeared	Percentage of egg disappeared
1949	12.9	3	31	75	58	12	11.3
1950	15.1	4	43	82	74	17	13.6
1951	77.1	9	67	21	33	26	29.5

* Each sowing date of the wheat was 4/V, 26/IV and 27/IV: the mean extended plant height at 6th June was 26.9, 34.7 and 30.4 cm.

of fly population occurring in this period and the variation of plant growth relating to oviposition preference, since the wheat was in all cases in the stage favourable for oviposition when a majority of flies were ovipositing. It is therefore highly probable that under heavy rain the flies lay very few eggs. Under such conditions, the percentage of egg disappeared was highest as shown

in table 17. Regarding this, two possible factors may be considered, namely, the activity of predators and the direct effect of rainfall. The loss of the eggs caused by the predators including Carabids and small Red mites was, even in the conditions of fine weather, almost negligible. On the contrary, the direct effect of rainfall was of great importance in making it impossible for egg to hatch. As normal sown wheat is usually younger at the beginning of June in Hokkaido, a majority of eggs are laid on the plant surface fairly close to the ground, namely, coleoptile, the base of laminae and the leaf sheaths of the first or second leaf. Not a few numbers of these eggs disappeared either by washing away by a long spell of rain or by being covering with mud splashed by heavy rain. This indicates that a remarkable amount of rainfall during June will act not only to retard the adult pairing and oviposition, but also to destroy the eggs laid. A marked decrease of the summer fly in 1951 may be explained at least to some extent by the factor as stated above.

However, this explanation is not always possible in some periods. In 1950, a vast amount of rainfall was recorded during August, while it brought no corresponding decrease of the flies in September. It is difficult to interpret this case with the direct effect of rainfall only, though a number of eggs were destroyed by it. From the comparative observation done at the semiarid area and the humid one in the Pacific Northwest of North America, ROCKWOOD *et al.* (1947) demonstrated that unusually heavy rain in August causes the abundance of *Meromyza*, because it brought up the abundance of various host plants. This is also true in Hokkaido where the favourite host plants, being harvested or in the ripening stage to be unsuitable for the oviposition, are usually poor in August. But, heavy rain brings up an abundance of suitable host plants, namely, volunteer cereals, second growing cereals and newly growing grasses. Since these plants afford a greater opportunities for the oviposition, admitting that the direct effects of rainfall to the flies and their eggs are stronger than usual, more eggs will survive for the succeeding generation. It may be certain that rainfall factor to the population of the species will act as a deterrent in June, while it will be rather beneficial in August, owing to its great efficiency to the host plant production.

VII. Research of biological environmental conditions

A. Factors concerning insects

1. Parasites and predators

Several members of Braconids and Pteromalids have been recognized as parasites of the species, together with a few species of the predators including

Thrips and Red mites (TZUIGANKOV, 1930 ; ROCKWOOD *et al.*, 1947). However, neither these species nor the Nematode, such as *Tylenchinema oscinellae* GOODEY, which causes total or partial sterility in the adult of Frit fly (RIGGERT, 1935), have been found in Hokkaido.

In the present investigation, natural enemies such as a Braconid, *Coelinidea* sp., an unidentified hymenopterous ectoparasite, the Red mites and the Carabids have been obtained. These species, excepting *Coelinidea* sp., are observed to be of minor importance as the natural enemies on account of their low parasitism to *Meromyza* and their extensive feeding habit. *Coelinidea* sp. is the most important parasite and is very powerful biological control agent in Hokkaido as is *Coelinidea niger* (NEES) in Europe and *Coelinidea meromyzae* FORBES in North America. This parasite is distributed throughout Hokkaido and extends to the northern part of Honshu including Niigata, Iwate, Akita and Aomori prefectures. The taxonomy of *Coelinidea* sp. is omitted in this paper, as Dr. C. WATANABE is working on this as a new species. Only some biological features are noted below.

In the laboratory, the mating is observed usually on the day of the emergence. The male approaches the female with vibrating wings, stroking the female's antennae with its own for some time prior to copulation. After that the copulation is performed quickly, lasting about from 5 to 27 seconds. The oviposition takes place, with or without copulation, almost immediately on emergence if suitable hosts are present. When the females are placed in a glass tube together with fresh eggs laid on young wheat leaves, the oviposition usually occurs in the following day after the mating. The female shows great interest in these leaves, tapping along them with her antennae. When her antenna touches the egg, careful antennal examination is repeated three or four times over the whole surface of the egg. After such examination, the female bends the abdomen forward between the hind legs, beneath the body, and the ovipositor thrusts into the apical lower part of the egg shell. This process lasts only two or three seconds. Such a behaviour of oviposition is not repeated by the same female to the host eggs which have been already attacked, though it is done by the other female. When the host eggs, each of which contains one or more eggs of *Coelinidea*, are displaced experimentally on other space in the same plant, the displaced host eggs attract the interest of the female and cause the oviposition. This indicates that the behaviour of oviposition is not controlled by the host egg attacked, but the position of the egg unknown to her takes a role. Consequently, superparasitism seems to be fairly common, though only one egg is laid into the host as a rule.

The female feeds on some sweet substances, such as honey and sugar

water, but she shows no response to the fluid exuding from the stinging puncture for oviposition. The average longevity of the male is 11.2 days and of the female 15.5 days in glass tube with honey water alone, though the adults are collected continually from June to September in the field. The exact length of each immature stage has not been obtained. However the rate of development of the parasite larva seems to be determined by that of the host, since the parasite larva does not become fully grown until after the formation of the host puparium. Early larval stages of the parasite cannot be interfered greatly by the physiological process of the host, since normal puparium formation has already occurred. If conditions are to delay puparium formation, the parasite larva undergoes no further development. After puparium formation of the host, the parasite larva grows quickly, emerges from the shrunken host and finishes feeding the host within the puparial shell. It devours almost all the remaining tissues of the host larva and occupies nearly whole space within the puparium. At this stage a host puparium containing a *Coelinidea* larva has a characteristic appearance which distinguishes from unparasitic one. The parasitic larva is visible through the puparial shell. The parasite pupa is at first white, but darkens gradually to black prior to emergence. The adult emerges through a large irregular circular hole bitten through the puparial shell at the anterior end of the puparium, indicating that the parasitic pupa is always orientated in the same direction relative to the host puparium. The length of the pupal stage varies with the time of pupation, requiring about two weeks in July and ten days in August, and the adults of each generation emerge almost simultaneously corresponding to the host emergence. The parasite larva hibernates within the host. It is clear that the parasite has two summer generations according to the host and therefore there are three generations in a year.

To investigate the parasitism of *Coelinidea* sp., the host pupae collected in the field were reared during the period from 1948 to 1954. The results are shown in table 18.

During the succeeding seven years 1662 individuals of *Coelinidea* were reared from 3596 host pupae representing three generations. This was 46.6 per cent. However, the percentage of parasitism varies from the host generation to generation, indicating that it is highest in the second generation, next highest in the overwintered one and lowest in the first one. The percentage is most variable in the first generation, extending from 15.5 to 43.3. Within the limits from 39.6 to 53.3 per cent, the parasitism also differ with the year. The factors which cause these difference have not been determined, but it is suggested that the mortality in the adult stage of the parasite may differ from that of the host, since the immature stage of the parasite is quite protective without any secondary

TABLE 18. The parasitism of *Coelinidea* sp. according to the host generation.

Year	Overwintered generation				First generation				Second generation				Average percentage of parasitism
	Collecting date	Total no. of pupa	No. of parasitic pupa	Percentage of parasitism	Collecting date	Total no. of pupa	No. of parasitic pupa	Percentage of parasitism	Collecting date	Total no. of pupa	No. of parasitic pupa	Percentage of parasitism	
1948	20/V	159	87	54.7	26/VII	210	91	43.3	28/VIII	145	96	66.2	53.3
1949	19/V	87	53	60.9	10/VII	258	104	40.3	26/VIII	164	92	56.1	48.9
1950	22/V	147	76	51.7	10/VII	295	99	33.6	30/VIII	207	143	69.1	49.0
1951	20/V	102	70	68.6	12/VII	220	34	15.5	1/IX	135	77	57.0	39.6
1952	23/V	126	68	54.0	25/VII	239	75	31.4	3/IX	130	82	63.0	45.5
1953	18/V	155	79	51.0	30/VII	146	27	18.5	27/VIII	162	114	70.4	47.5
1954	20/V	93	60	64.5	26/VII	241	59	24.5	30/VIII	148	76	51.4	40.4
Total *		896	493	56.7	—	1609	489	30.4	—	1091	680	62.3	46.6

* The percentage of parasitism shows only the average.

parasite.

Many examinations have failed to discover the present parasite from the pupae of the other Chloropids and allied families of Diptera. This indicates that the host range of the parasite is definitely restricted to only one and the same species, that is, *Meromyza saltatrix* is an indispensable host of the parasite. From this and considering the percentage of parasitism, it is evident that *Coelinidea* is a predominant parasite playing an important role as the control agent of *Meromyza saltatrix* in Hokkaido.

2. Larval mortality in host plants

Up to this time, no attention has been paid either to draw natural larval mortality of the species or to consider the possible factors concerned. Although the larva, being within the host plants during the greater part of its life, is able to survive free from the direct influence of climatic conditions as stated in chapter VI, it is destroyed to a certain extent by itself causing the host to become poor nutriment to support the larval development. This may be caused by (1) larval overpopulation within a restricted stem and also by (2) larval active feeding.

The number of larvae which are able to finish the stage within a tiller is variable, since suitable food for the larva, young ear or shoot, is changed with the growth of the plant in quantity. Judging from the number of pupae obtained from injured plants given in table 19, it is definitely shown that only one pupa is found per plant before the tillering stage of the host plant. After the tillering stage, the pupa increased from one to three. Although this result was more or less changed with the species of the host plant, especially in the quack grass having a smaller tiller than that of the rest, not more than four of the pupa was found in any host plant.

In the gout fly, *Chlorops pumilionis* BJERKANDER, FREW (1924) has supposed

TABLE 19. Number of pupae per plant and per tiller in different kinds of host plants (1950-1951)

Host plant	Before tillering stage				After tillering stage			
	No. of pupae obtained per plant				No. of pupae obtained per tiller			
	1	2	3	Total	1	2	3	Total
Wheat	345	0	0	345	2411	198	21	2630
Barley	211	0	0	211	1257	135	16	1408
Quack grass	76	0	0	76	1094	33	0	1127

that the feeding larva secretes some substances which maintain the attacked tiller in the green and sappy conditions necessary for the nutrition of the larva. In the case of the present species, however, such presumption is not admissible, since the injured tiller is almost or entirely inhibited to grow and it soon withers and dies. Thus the term "overpopulation" is considered to be applied when more than four larvae enter into a tiller, since it is clear that the larva can become mature when there are less than three in number.

The occurrence of such overpopulation is extremely rare from May to the middle of July, since this time is the principal growing season of the host plant and there is a plentiful suitable food in proportion to a very few of the flies. However, it seems to very common when the host plant is harvested, usually in the later part of July. The eggs of summer fly are necessarily concentrated on young weak plants, namely, volunteer cereals, second growing cereals and newly growing quack grass. The data in table 20 which were obtained from the observation on the field marked wheat plant sown the 20th of July and examined the 17th of August in 1951 will prove this.

Since the eggs are laid on the plant soon after germination and the larva severely attacks the central shoot of young plant, the plant is retarded sometimes to grow normally or sometimes to produce the tiller, showing 1.63 per plant in number. In spite of such poor food conditions, the number of eggs deposited on a plant is very numerous, showing 4.47 per plant. Occasionally, 12 eggs

TABLE 20. The larval mortality within the wheat in summer generation.

No. of marking plant per plot	Total no. of tiller	Total no. of egg deposited	Total no. of egg hatched	Total no. of pupa obtained	Larval mortality (%)
10	16	44	42	2	95.2
10	18	42	39	6	84.6
10	21	41	38	5	86.8
10	13	37	36	3	91.7
10	15	27	25	1	96.0
10	16	58	55	2	96.4
10	18	40	37	3	91.9
10	13	51	50	2	96.0
10	17	55	53	2	96.2
10	16	52	51	4	92.2
Average per plant	1.63	4.47	4.26	0.30	92.96

are laid. The frequency distribution of the egg on 100 plants is as follows: 43 plants with 1-3 eggs, 37 with 4-6, 13 with 7-9 and 7 with 10-12. This suggests that for some larvae probably due to the overpopulation within a tiller death may occur in about 60 per cent of the marking plants, because a majority of hatching larvae seem to enter successfully into the plant.

Beyond such presumption, the pupal number occurring in the plant is, in fact, extremely few, and consequently the percentage of larval mortality is estimated to be exceedingly high, the average showing over 90 per cent. The factors influencing the larval mortality may be climatic, parasitic and food plant conditions, but the former two may be almost neglected by the reasons already discussed. On the other hand, it is clear that the larva is unable to migrate from plant to plant and therefore it will be forced to die in the shoot which it entered, owing to the under-nurishment caused by overpopulation. This is not unusual at least in summer, as suitable food plants are extremely scarce as compared with a large number of the gravid females and consequently too many eggs are deposited on one plant. Therefore, for the summer generation, the food plant conditions are considered to be a principal factor causing high larval mortality.

Concerning the larval death caused by the feeding behaviour, some peculiar points have been demonstrated in the section of "Behaviour of larva" in chapter IV. Some important respects are that the first instar larva shows a definite "stem-down taxis", occasionally leading itself away from suitable food, and that the larva hatching on the lamina lower than the ear-bearing internode dies in the internode which it entered, as it is unable to reach to the ear-bearing internode where suitable food is found. From the above an interesting question may arise as to whether such larval death occurs commonly in the field.

It is well known that so-called "white ear", a type of the injury, appears when headed culm is attacked by the larva. A typical process of such symptom is represented diagrammatically in figure 8. The larva from the egg laid on the upper lamina crawls downwards along the culm or the sheathing part of the leaf until it reaches near its soft base. It then gradually cuts off the culm in a spiral manner and reaches the center. If the center is suitable for feeding, the larva remains for a short while before it migrates upwards. However, the culm is usually so hard that the larva turns away from the base of the culm without feeding and crawls up towards the young ear entering into or among the kernels. The larva at this status, first or second instar stage, is able to mature securely by feeding on the kernel and its surrounding tissues, if the head becomes "blindness". On the contrary, if the head emerges from the boot as shown in figure 9, the emerged ear containing young larva withers

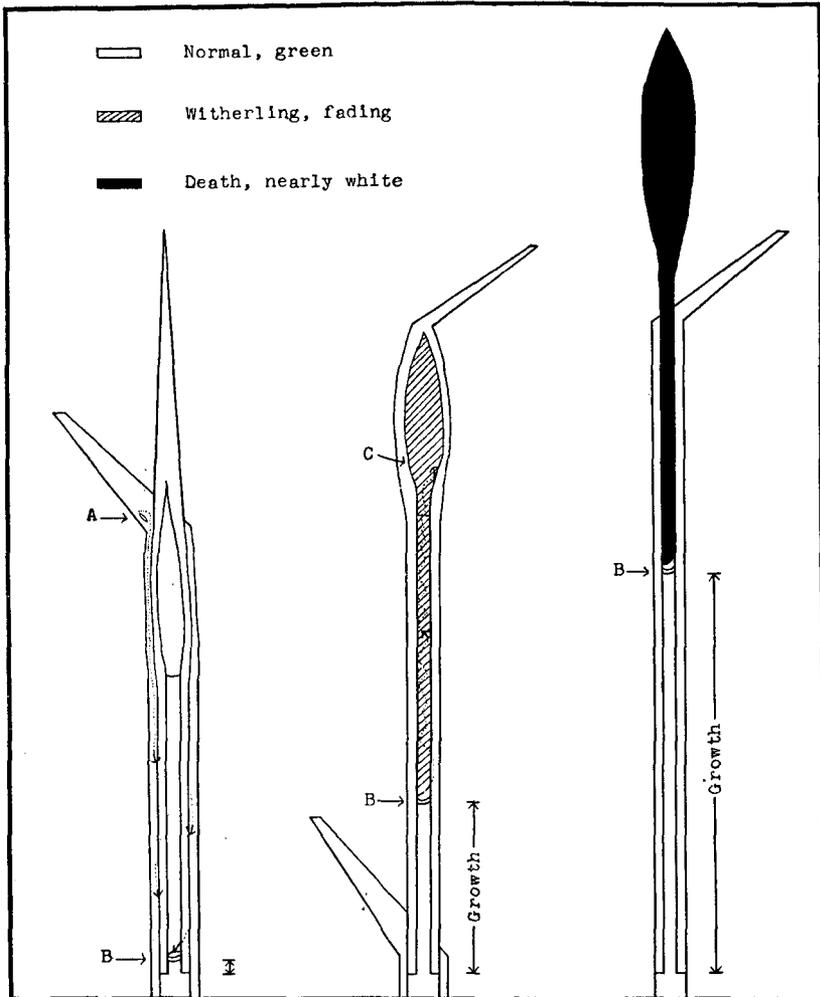


Fig. 8. Typical process of the occurrence of white ear. Hatching position (A), spiral cut of the larva in the culm (B) and enters into kernels in the ear (C).

and turns nearly white by drying up quickly, as the nutrient fluid for the ear-growth is almost entirely inhibited to circulate upwards from the place where the culm is cut off by the initial attack of the larva. This is a typical case causing white ear. Whether the growing point of the headed culm is injured or not will determine whether the attacked plant becomes white ear or blind. Apart from this, it is clear that for the young larva in such a white ear it is impossible to continue the feeding or to migrate to other tillers successfully.

During the present investigation, many white ears were examined, but neither the living larva nor the pupa could be found either in white ear or in the whole of such injured plant. In addition, dead young larva were observed between the sheath and the culm directly below the white ear in some occasions. It is therefore clear that the young larva in the white ear is forced to die by the death of the ear killed by the larva. Accordingly, the number of the white ears serves as an approximate index of the larval mortality in the heading plant, though it is not numerus, being below 12 per cent of the injured tillers.

The death of young larvae will not necessarily occur in the white ear only. When the egg is laid upon leaves arising from the shoot below the ear, the larva enters there, and it can not reach the ear to feed, as the larva moves downwards. Thus, it is necessary to consider the relation between the egg-laying place of the fly and the growing process of the plant. These aspects will be given in the following section.

B. Factors concerning plants

1. Oviposition and the growth of wheat

In 1950 an attempt was made to ascertain the above relationship. An experimental field, which consisted of six plots by replicate sowing three times according to randomized block design, was provided in the field of Hokkaido Agricultural Experiment Station. Three rows of the wheat* in a plot (2.0 × 1.5 m) were sown every week from 26th of April until 31th of May. The soil fertility for each plot was made as uniform as possible. After germination,

TABLE 21. Egg number on various places on the wheat.

Sowing date	Coleoptile	Sheath	Lamina	Culm	Ear	Total
26/IV	17	16	104	0	0	137
3/V	20	9	134	0	0	163
10/V	57	23	191	0	0	271
17/V	71	28	330	0	0	429
24/V	72	6	512	0	0	590
3I/V	62	21	657	0	0	740
Total	299	103	1928	0	0	2330
Percentage	12.83	4.42	82.75	0	0	100.00

* Hereafter, this means "Nōrin No. 29", a common variety of the spring wheat in Hokkaido, unless otherwise stated.

each row was divided into 10 subplots of 30 cm in length and some subplots were selected at random for successive examinations which were made at intervals of five days. In each examination, the place where the egg laid on the plant was recorded, then the egg was removed from the plant in order to avoid numerical repetition. The result is shown in table 21 and in figure 9.

As shown in table 21, the coleoptile, the lamina and the sheathing part of leaf are preferred for the egg-laying place by the adult, showing no significant differences with sowing date, but the culm and the ear are entirely avoided. A majority of eggs are deposited on the upper surface of lamina, usually on its base fairly close to the ligule. The eggs laid on the under surface or apical half of lamina are extremely rare. These facts are considered to be an evidence that the fly prefers the eggs-laying place on a plant. This may be also suggested by the change of egg-laying position at various growing stages of the wheat as given in figure 9.

As clearly shown in figure 9, the number of eggs deposited are necessarily increased with later sowing. In this occasion the growth of the wheat extended over the egg-laying period either in spring or summer flies. However, the egg-laying position on a plant, sorting from initial coleoptile (0) to 9th lamina (9),

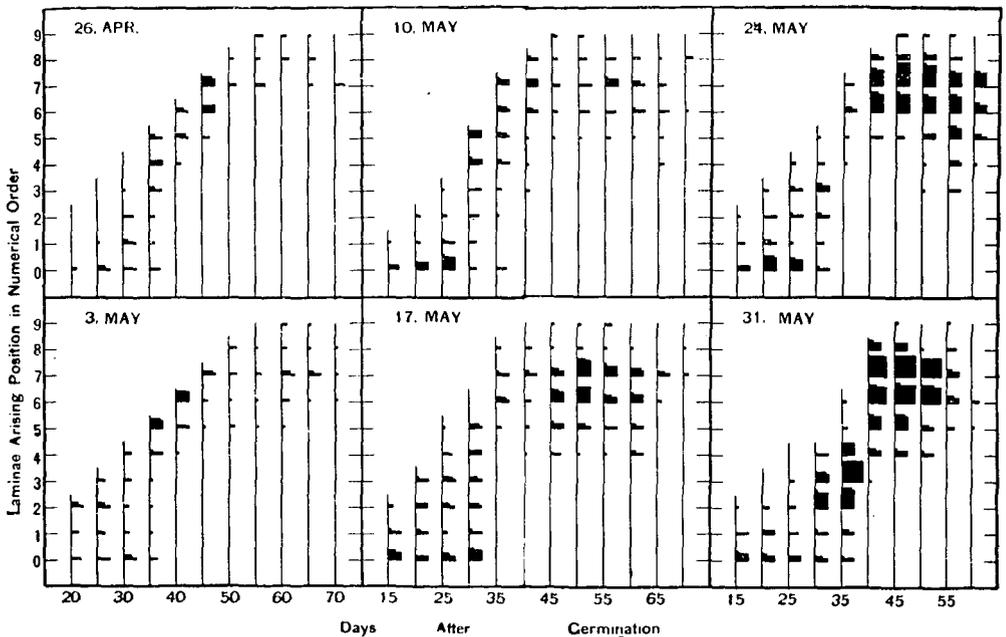


Fig. 9. The changes of egg-laying frequency and its position on various growth stages of the wheat obtained from six sowing examinations in 1950 (see, text).

shows a similar tendency in every occasion. In young wheat the egg is usually laid on the coleoptile and the sheathing part of leaves near the ground, as reported by ROCKWOOD *et al.* (1947), while it is laid on the upper lamina with the growth of the wheat. This tendency is also found in the result (table 22) obtained from a closer examination dealing with 50 tillers with eggs at various growing stages of the wheat.

TABLE 22. Egg number in each lamina-arising position on the wheat.

Leaf stage of tiller examined	Number of egg deposited on ***										Total	Correlation
	Coleo-ptile	1st la-mina	2nd lam.	3rd lam.	4th lam.	5th lam.	6th lam.	7th lam.	8th lam.	9th lam.		
1	91	35									126	1.000
2	35	67	30								132	0.125
3	9	34	41	24							108	0.484
4	9	10	24	29	21						93	0.774
5	0	0	3	8	37	36					84	0.895*
6	0	0	0	1	18	28	41				88	0.907**
7	0	0	0	0	5	7	26	44			82	0.834*
8	0	0	0	0	1	3	6	25	37		72	0.803**
9	0	0	0	0	0	0	3	12	46	5	66	0.557

* 0.05% and ** 0.01% level significant correlations.

*** A few eggs laid on the sheath were counted in the nearest lamina to them.

In the first leaf stage of the tiller, the number of eggs deposited is more on the coleoptile than on the first lamina, as compared with the second, third and fourth leaf stages in which the laminae are slightly preferred for the oviposition. From the fifth to the 9th leaf stages, however, no eggs are found either on the coleoptile or on the first lamina. Then the egg-laying position gradually shifts upwards, mostly to the top on the lamina or directly below the top. In each of these cases, high positive correlation between the leaf number of the tiller and the frequency of the egg-laying on each lamina exists with statistical significance except the 9th leaf stage. Thus it is obvious that the fly lays the eggs so as to prefer the egg-laying position according to the growing process of the wheat. This is an interesting phenomenon inasmuch as the larva hatched on a given place shall reach the center of the shoot or young ear to feed and its fate is primarily determined by the egg-laying position, as already ascertained by the laboratory experiment (*cf.* chapter IV).

Setting aside the factors which are concerned with the above fact, such phenomenon may be explained to some extent by the relationship between the

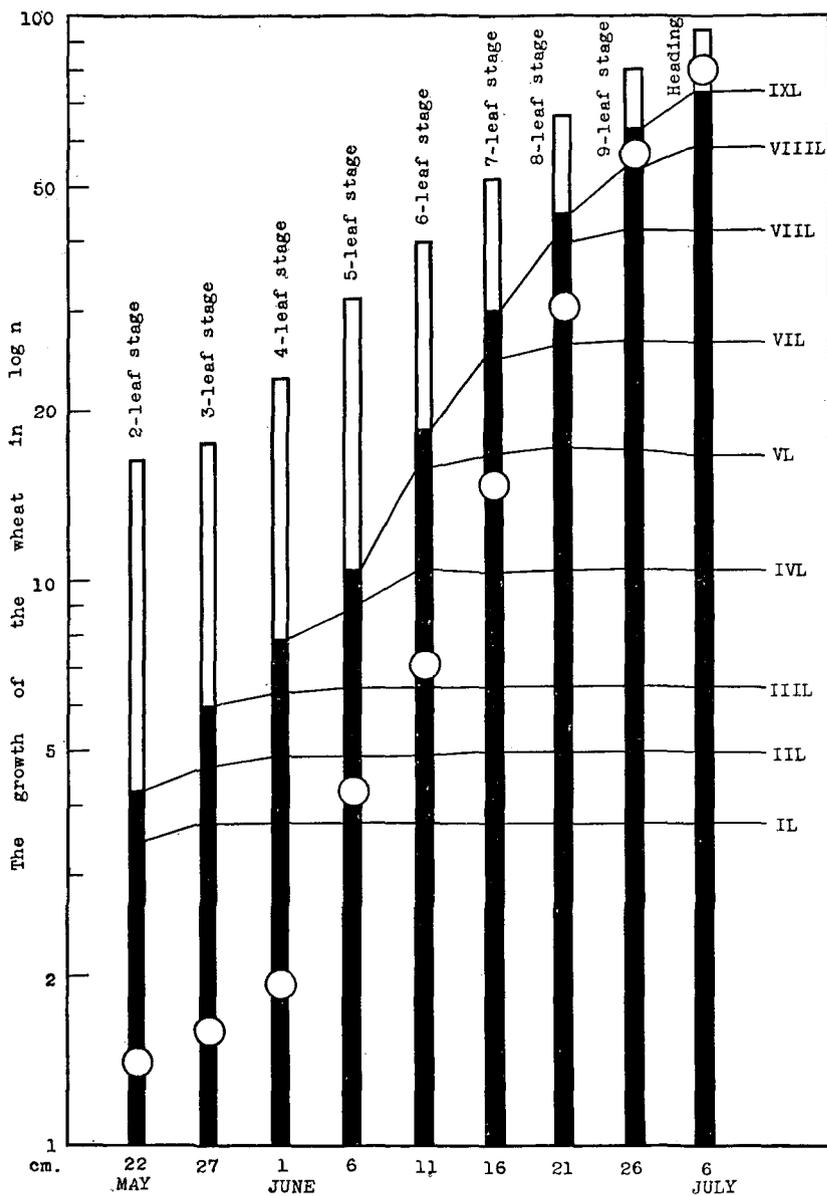


Fig. 10. The growth of the main stem of the wheat, showing extended plant height (rod line), standard plant height (black rod line), ear-bearing position (circular line) and lamina-arising position (cross line).

lamina-arising position and the ear-bearing site of the wheat as given in figure 10, designed under the following criteria: (1) a leaf stage is determined by the number of lamina which completely emerges from the sheathing part of the former leaf and (2) standard plant height is used to show the height from the base to the topmost ligule.

During the period from first to fourth leaf stages, the very young ear which is only seen anatomically in the center of the shoot is always situated below the first lamina-arising position (IL) near the coleoptile. This means that even though eggs were laid on any laminae until the fourth leaf stage, all the larvae would be able to reach the young ear successfully. At the end of the fifth leaf stage, the internode begins to grow quickly and the young ear is therefore pushed upwards, outrunning the lamina-arising position of the first leaf which has entirely finished its growth. In this case the first leaf may be considered to be a "non-critical leaf" as stated by FREW (1924), because the larva would be unable to attack the ear, assuming that it has hatched on the first leaf. As clearly shown in figure 10, the growth of the sheathing part of a leaf which determines the lamina-arising position usually finishes within 10 days after the emergence of the ligule, while the ear-bearing position gradually shifts upwards with the growth of the internode. Consequently, "non-critical leaf" is increased with the growth of the wheat, for instance, it ranges from the first to the 8th leaves at the middle of the 9th leaf stage. This relation is the same in every tiller diverging from main stem.

It is certain that the position suitable for the entrance of hatching larva is gradually limited according to the growth of the wheat. In the case of the 9th leaf stage, the possibility to allow the larval establishment is found only in a case in which eggs are laid on the 9th lamina. These eggs should be referred to "effective eggs", while "ineffective eggs" are those on the remaining leaves below the ear. Thus, assuming that the eggs are laid indiscriminately on any leaves regardless of the lamina-arising position, ineffective eggs would necessarily increase with the growth of the wheat.

In order to determine the actual occurrence of such ineffective eggs and to know what type of injury appears from the difference of egg-laying position, more detailed examination was undertaken in 1951. The method for the examination and the plot-design were almost the same as those described for 1950, excepting the following points: the wheat was sown in a group at a distance of 5 cm on the 27th of April; a total of 90 plants (30 × 3 blocks) were selected at random and extended plant height, tillering process, lamina-arising position, eggs and their laying position were examined successively at intervals of two or three days; the later two were also carefully studied individually.

After the examination which was continued until the end of heading stage, all the sampled wheat plants were dissected on the 4th of August in order to determine the number of pupae occurring in each tiller.

A brief description of the wheat at the ripening stage may be useful in interpreting the results. The extended plant height was 123.6 cm in average. The total number of tiller and that of efficient ear were 981 and 736, with a range of 7-17 and 5-14 respectively. Heading was almost completed on the 29th of June. These records indicated that the wheat had grown normally under suitable conditions.

On the other hand, 223 eggs including 57 which were inhibited to hatch were recorded. The resulting 166 larvae were entered into the sampled wheat and caused 171 injured tillers, while only 94 of the pupae were found. This suggests that about a half of the larvae could not finish their development. Some factors of such larval death will be explained in analyzing the result in five cases as follows (see, figure 11).

(A) This is a case in which eggs are laid on the coleoptile, first or second leaf before the 4th leaf stage of the wheat. As the young ear is soft and holds a lowest position, all the hatching larvae are able to feed on the ear, usually in a main stem, or occasionally in young tillers. A main stem and its young tiller diverging from the inner base of the node are so close that the larva is able to migrate to new shoot by boring directly through the successive leaves if it enters into a main stem and devours the shoot. It is likely, on several occasions, to attack initially a young tiller as shown in figure 11. The case A was observed in 6.6 per cent of hatching larvae.

(B) This is a case in which eggs are laid on various leaves during the period from the 4th to 5th leaf stages. The young ear is usually situated below the 1st lamina-arising position, occasionally between the 1st and 3rd on a main stem. Consequently, a few eggs found at lower leaves than the ear-bearing position may be supposed to be ineffective, but this is not always true as far as the period is concerned. The larva from these eggs attacks the young ear, sitting higher than the egg-laying position when it hatched, or sometimes destroys a new tiller sprouting from the base of egg-laying stem. This indicates that almost all of eggs laid at the present plant stage are effective because, admitting that they are deposited on any leaves, the larva is able to migrate easily from shoot to shoot on account of the softness and the closed position of each tiller. The percentage of the case B was 22.9. The folded central lamina of the injured tiller withers and before long turns nearly yellow and dies.

(C) When eggs are laid on a higher position than the ear and the larvae

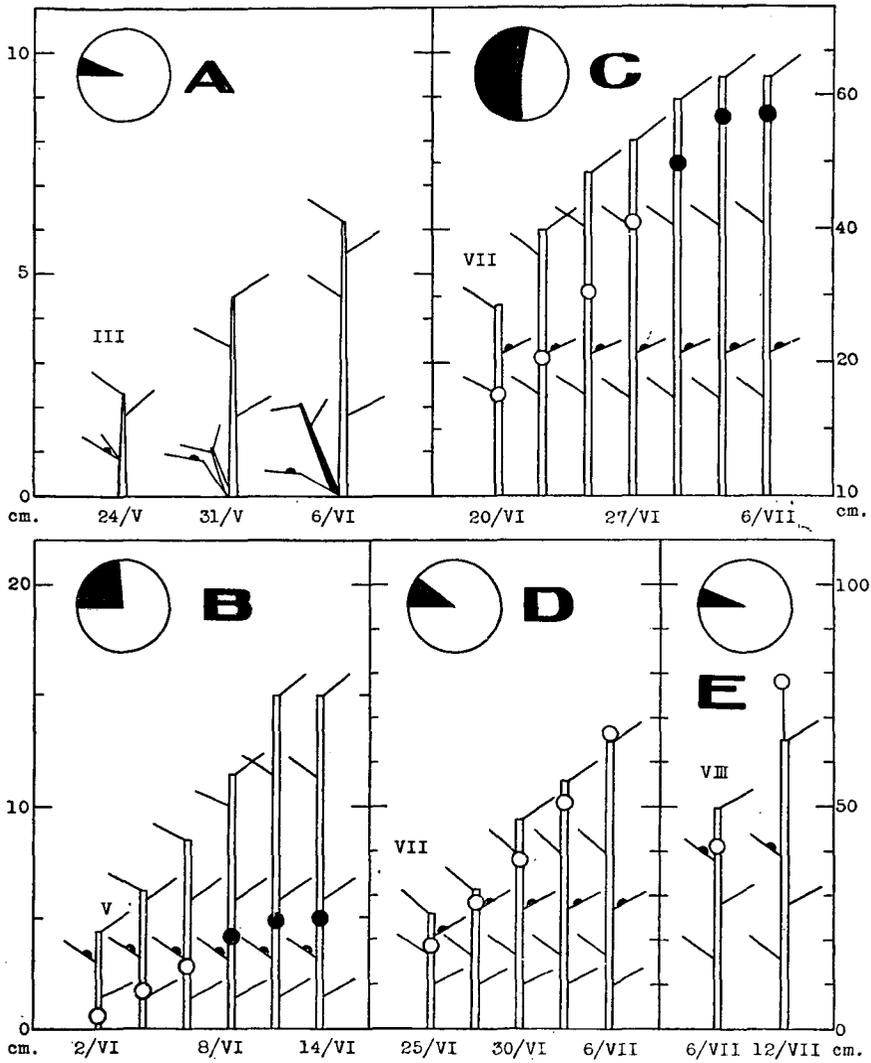


Fig. 11. The relation between egg-laying position on a lamina (semicircle) and ear-bearing position on the wheat (circle), with the resultant injured tiller (black) and the dead young ear (black circle). Black portion in the left upside circle shows the percentage of eggs in each case (see, text).

can attack the ear after considerable elongation of the internode, they belong to this case. Since the culm bearing young ear is cut nearly close to the base, the ear cannot be emerged from the boot or it becomes a "white ear". The eggs causing this case numbered 88, the percentage being 53.0.

(D) This is a case in which the ear has grown upwards over the egg-laying position within the period of incubation, though eggs were laid on a higher position than the ear. Thus the first instar larva enters between the sheath and the internode directly below the ear, feeding upon the internode where it is unable to obtain sufficient nutriment and commences to cut the tissue, as the internode is too tough, and it is therefore forced to migrate to some other suitable place to feed. However, it is almost impossible for the small larva to succeed in this migration, as the distance from the internode to the ear is too great. Consequently, the larva soon dies in the internode. Usually almost no damage to the internode is recognized, but occasionally very slight infestation occurs, the feeding trace being always less than 1.0 cm in length. The percentage of this case was 10.2 with 17 eggs.

(E) The eggs originally laid upon the leaves below the ear at the stage in which the internode is elongating rapidly are discussed in this case. The first instar larva is forced to die for the reasons as noted above, without any symptoms of the damage. These eggs were observed only in 7.2 per cent in the whole of eggs hatched.

The result of the present examination made in the field was in agreement with that of the laboratory experiment. It shows that the larva from the egg laid below the ear is killed by the lack of nutrient during its stem-down taxis movement, and the egg consequently becomes ineffective in the growing stage of the internode. Such ineffective eggs belonging to the cases D and E showed 17.4 per cent in frequency. This suggests in the first place that the ovipositing instinct of the fly is not faultless insofar as the position is concerned, though there is an apparent tendency to cause the fly to lay the egg on the upper position following the plant growth, and secondary that the internodal growth becomes the rapider, the more in number the eggs are left below the ear before the hatching. Thus the larvae will be destroyed in increasing numbers. Abnormally rapid growth of the internode may be expected when the plant is grown by late sowing or with a good supply of manure.

On the contrary, the eggs laid upon the leaves of the plant which is younger than the 5th leaf stage are all effective because the larva do not fail to get on to the ear to feed, even when the egg is laid below the ear-bearing level. FREW's critical theory seems to be unsuitable in this case. The soft plant and the close tillers are responsible for sufficient feeding and migration of the larva.

The egg-laying position is a principal factor to determine whether the larva is able to survive or not. Therefore, it is concluded that two biological factors, the plant growth and the insect behaviour, have exerted an influence upon the mortality of this insect.

2. Host plant selection

Since the larva is confined to live only on a given plant and does not migrate to other plants, the "host plant selection" in this case is in the problem of the oviposition of the adult. The intra specific preference for the oviposition has been noted in the preceding section, paying particular attention to the egg-laying place and position. Next the inter specific selection shall be considered.

Regarding this problem, the following experiment was undertaken. Ten gravid females were placed in chimney-like cage of glass (20×9 cm), covered with a fine wire net on the top. Each cage was planted with five different plants, namely, wheat, barley, oats, rice and quack grass, and set radially at equal distances. It was very difficult to have an equal surface area of each plant tested, but the leaf number was easily controlled. The eggs laid upon each plant were counted for a week after the females were set free. The test was repeated five times. The number of the eggs obtained was available as a relative index for the chosen plant, since no egg was laid on the place other than the given plant. The data obtained is shown in table 23.

TABLE 23. Number of eggs laid upon various plants in the laboratory.

Test	Wheat	Barley	Oats	Rice	Quack grass	Total
1	63	16	6	0	32	117
2	48	10	20	4	27	109
3	35	11	4	2	56	108
4	89	24	5	5	53	176
5	79	23	12	0	59	173
Total	314	84	47	11	227	683
Percentage	45.97	12.30	6.88	1.61	33.24	100.00

The experiment showed clearly that the eggs were laid mostly upon the wheat, and next upon the quack grass, the percentage being 45.97 and 33.24 respectively. The eggs laid upon the barley were 12.3 per cent. Furthermore, a few eggs were found even upon the oats and the rice. This is an interesting

result in the light of the fact that both plants do not serve as the food of the species in Hokkaido. Thus a question naturally arises as to whether such selection pattern occurs naturally in the field.

Evidence was obtained on this point by the following examination carried out in 1950. A randomized field consisting of three blocks, each containing four rows at intervals of 50 cm of the wheat, barley, oats and rice, was provided for the examination. The seeds of each plant were sown in the row (4 m in length) by drilling on the 28th of July. After germination, ten plants per row were marked at random and the number of eggs laid during the period from the 8th to 23th of August was examined. The result is given in the total in table 24.

TABLE 24. Number of eggs laid upon various plants in the field.

Block	Wheat	Barley	Oats	Rice	Total
I	138	82	0	0	220
II	106	95	0	0	201
III	154	90	0	0	244
Total	398	267	0	0	665
Percentage	59.85	40.15	0	0	100.00

During the examination, the attractive position for oviposition, namely, the coleoptile and the leave, was almost the same in every plant tested, and it was exposed to a number of the summer flies. In spite of such condition, eggs were found neither upon the oats nor upon the rice. It is obvious that these plants have not served as the food for the insect, though there occurred a few oviposition under laboratory conditions. The wheat and the barley were distinctly preferred, and the percentages between the two were significant. This result leads to the conclusion that the wheat is more readily preferred for oviposition than the barley. Then, a question arises as to whether the preference for oviposition occurs according to the plant varieties. No answer to this question was obtained, but it should be noted that there was a small difference in the number of eggs per tiller. Such difference seems not to be caused by the varietal external characters, but is determined by the case whether the period of the growth of plant is well matched with that of the peak-occurrence of the fly. Indirect evidence on this point is given in the following section.

3. Effect of sowing time

It is well known that the sowing time of a certain crop has a direct bearing upon the subsequent susceptibility of this crop to insect attack. Therefore, the purpose of the study of this section was to determine how the number of eggs laid on the host plant is changed with sowing time.

Field experiments were carried out in 1950 and 1951, using spring wheat and the winter wheat (Dawson No. 1). The method of examination employed for the spring wheat was identical with those described in the preceding section

TABLE 25. Number of eggs laid on the spring wheat sown at different times

Year	Sowing date	No. of eggs laid	Average no. of eggs per plant
1950	26/IV	137	2.67
	3/V	163	4.00
	10/V	271	5.42
	17/V	429	8.58
	24/V	590	11.80
	31/V	740	15.04
1951	27/IV	102	2.04
	4/V	145	2.90
	11/V	209	4.18
	18/V	362	7.24
	25/V	445	8.90
	1/VI	538	10.76

TABLE 26. Number of eggs laid on the winter wheat sown at different times.

Year	Sowing date	No. of eggs laid	Average no. of eggs per plant
1950	20/VIII	366	24.40
	27/VIII	190	12.67
	3/IX	85	5.67
	10/IX	61	4.07
	17/IX	22	1.47
1951	16/VIII	407	27.13
	23/VIII	249	16.60
	30/VIII	112	7.47
	6/IX	76	5.07
	13/IX	32	2.13

“oviposition and the growth of wheat”. In the winter wheat the eggs were counted during the period from germination to the early part of October by which time the flies had almost finished their oviposition. The results are shown in tables 25 and 26.

As shown in tables 25 and 26, it is obvious that the number of eggs laid is greatly increased with late sowing in spring, while this is quite reversed in autumn. In both cases, this may depend largely upon the fact that the attractive stage of plant for oviposition escapes the period of the mass emergence of flies. Synchronism between young plant stage and peak oviposition period results a heavy infestation. In practice, it is suggested that the earlier the date of sowing in spring and the later in autumn the better, if cultural and weather conditions admit such procedures.

4. Effect of plant variety

Up to the present, many studies have been devoted to determine the varieties resistant or susceptible to the attack of certain species of Chloropids, particularly *Chlorops oryzae* MATSUMURA, *Chlorops pumilionis* BJERKANDER, *Oscinella frit* LINNÉ and *Meromyza americana* FITCH. In the study of the last named species, ALLEN and PAINTER (1937) reported that the difference in infestation depends not only upon the varieties, but upon the relationship between the peak occurrence of adults and a particular stage of maturity in which the plants are more attractive to the female or more palatable to the larvae. According to the recent paper of HORBER (1955), infestation has been demonstrated to be caused by the preference shown during oviposition. In *Meromyza saltatrix*, these features may be also agreeable, considering the results given in the preceding three sections. Therefore, the studies reported in this section are directed not only to bring together some evidences of the varietal difference in infestation, but also to reflect its influence on population change of the species.

The test was continued during four successive seasons since 1950 at the randomized block field. Six varieties of spring wheat shown in table 28 were planted on the 26th and 27th of April during from 1950 to 1953 respectively. After the heading had finished completely, all plants grown in the central row of each block were dissected for the examination of the infestation of plant, pupae and puparia. From the original data shown in table 28, some correlation coefficients are given together with their variance ratio in table 27.

The degree of infestation varied from year to year as indicated by the average percentage of injured tillers which showed an extremely lower level in 1951 than others. This variation seems to be principally responsible for the density of the fly population. However, the varietal differences of the infestation

showed a similar tendency without any relation to such annual variation. The early varieties, Nôrin No. 35 and No. 75, were always free from heavy infestation in comparison with the late varieties, such as Nôrin No. 3, Sapporo-Harukomugi No. 9 and No. 10.

On the contrary, the percentage of the pupation showed no significant difference among the years, the annual averages from 1950 to 1953 being 57.29, 60.22, 56.72 and 57.76 respectively. However, the difference among the varieties was not clearcut, though it showed a tendency to rise slightly with the late varieties having thicker more fruitful tillers as a rule.

TABLE 27. Correlation between the total number of injured tillers and of pupae and puparia.

Year	Correlation coefficient	Variance ratio tested	Variance ratio estimated
1950	0.986	139.864**	F (0.001)=74.14
1951	0.992	247.004**	F (0.001)=74.14
1952	0.857	11.137*	F (0.05)=7.71
1953	0.963	28.283**	F (0.01)=21.20

The relation between the total number of injured tillers and that of pupae and puparia showed a high positive correlation in every year together with its statistical significance as shown in table 27. These results indicate that the more the injured tiller appeared, the greater the pupae occur. According to comparative analysis given by the transformation from r to z , these correlations were not significant among combinations of four years. In this case, the number of injured tillers is considered to be an approximate index of the first instar larva which is able to reach the center of shoot, since the larva must cut primarily the culm or shoot to obtain suitable food, and consequently the tiller shows a characteristic symptom. Therefore, the fact that the total number of pupae and puparia are correlated with that of the injured tillers seems to postulate that certain antibiotic factors involved in the varieties are not considered, admitting that some larvae die during their essential feeding period.

In conclusion, it is suggested in the first place that the varietal differences of the infestation are not determined principally by the varieties involved, but by the differences of synchronism between the varieties and the flies as well as the sowing time of the plant, and secondary that the cultivation of late varieties may be favourable for the occurrence of the species, because these varieties are available to produce more pupae in the succeeding generation.

TABLE 28. Differences in infestation and pupation

Year	Varieties tested	Heading date	No. of injured tiller (A)					Average percentage of injured tiller
			1	2	3	4	Total	
1950	Nôrin No. 3	5/VII	179	166	145	165	655	20.11
	Nôrin No. 29	23/VI	184	159	172	160	675	20.74
	Nôrin No. 35	19/VI	126	105	113	117	461	12.21
	Nôrin No. 75	20/VI	88	81	114	144	427	11.96
	Sapporo Haru- komugi No. 9	5/VII	192	148	164	172	676	20.81
	Sapporo Haru- komugi No. 10	6/VII	170	153	161	174	658	20.55
1951	Nôrin No. 3	10/VII	121	121	107	99	448	14.49
	Nôrin No. 29	28/VI	60	74	91	71	296	10.88
	Nôrin No. 35	24/VI	59	58	38	48	203	4.89
	Nôrin No. 75	26/VI	65	59	63	55	242	7.09
	Sapporo Haru- komugi No. 9	10/VII	100	84	72	90	346	12.44
	Sapporo Haru- komugi No. 10	12/VII	113	87	84	77	361	11.88
1952	Nôrin No. 3	13/VII	207	201	172	196	776	31.31
	Nôrin No. 29	30/VI	158	224	183	177	742	23.45
	Nôrin No. 35	25/VI	198	183	186	192	759	21.99
	Nôrin No. 75	26/VI	181	187	210	190	768	22.09
	Sapporo Haru- komugi No. 9	12/VII	194	219	231	188	832	28.35
	Sapporo Haru- komugi No. 10	13/VII	180	195	227	208	810	28.67
1953	Nôrin No. 3	12/VII	182	169	171	154	676	36.73
	Nôrin No. 29	30/VI	156	121	165	143	585	30.05
	Nôrin No. 35	26/VI	163	116	150	128	557	26.79
	Nôrin No. 75	26/VI	137	137	115	132	521	28.89
	Sapporo Haru- komugi No. 9	11/VII	177	153	194	163	687	34.54
	Sapporo Haru- komugi No. 10	12/VII	189	211	178	196	774	35.30

VIII. Discussion and conclusion

From an ecological investigation carried out on the basis of taxonomy, a mass of informations on *Meromyza saltatrix* are presented in each foregoing section. The purpose of the chapter is to appreciate this information and to

on the six spring wheat varieties.

No. of pupae and puparia obtained (B)					Percentage of pupation ($\frac{B}{A} \times 100$)				
1	2	3	4	Total	1	2	3	4	Average
111	96	87	102	396	62.0	57.8	60.0	61.8	60.46
103	98	91	83	375	56.0	61.6	52.9	51.9	55.56
65	60	67	59	251	51.6	57.1	59.0	50.4	54.45
54	46	62	70	232	61.4	56.8	54.5	48.6	54.33
117	85	94	97	393	60.9	57.4	57.3	56.4	58.14
108	90	89	113	400	63.5	58.8	55.3	64.9	60.79
76	83	69	58	286	62.8	68.6	64.5	58.6	63.84
39	38	52	45	174	65.0	51.4	57.1	63.4	58.78
36	32	21	29	118	61.0	55.2	55.3	60.4	58.13
31	35	34	30	130	47.7	59.3	54.0	54.5	53.72
71	53	46	58	228	71.0	63.1	63.9	64.4	65.90
75	49	52	44	220	66.4	56.3	61.9	57.1	60.94
118	122	103	125	468	57.0	60.7	59.9	63.5	60.31
91	130	100	94	415	57.6	58.0	54.6	53.1	55.93
105	87	112	108	412	53.0	37.5	60.2	56.3	54.28
83	111	98	106	398	45.9	59.4	46.7	55.8	51.82
120	127	135	124	506	61.9	58.0	58.4	66.0	60.82
101	100	139	123	463	56.1	51.3	61.2	59.1	57.16
121	95	106	88	410	66.5	56.2	62.0	57.1	60.65
94	78	90	93	355	60.3	64.5	54.5	65.0	60.68
85	71	82	70	308	52.1	61.2	54.7	54.7	55.30
77	86	72	69	304	56.2	62.8	62.6	52.3	58.35
75	84	108	97	364	42.4	54.9	55.7	59.5	52.98
122	131	86	115	454	64.6	62.1	48.3	58.7	58.66

discuss some possible factors affecting the population regulation of the species in Hokkaido.

Since natality is a principal agent of population regulation, attention is directed mainly towards the power to increase in favourable conditions. The oviposition experiments suggested that the oviposition is not affected by the

food of the adult, by the host plants, or by the temperature and humidity in the field, though it is retarded by rainy dull weather in June. The average number of the egg output per female is 36.4. Now, assuming that the immature stage requires about 7 weeks, all the eggs laid within 3 weeks, the intrinsic mortality caused by the error of the egg-laying position is 20 per cent and the sex ratio of the survivors is unity. Then the self-multiplicative rate of increase, λ , as calculated by the method of THOMPSON (1931), is 1.146. The natural logarithm of this value, r , which is very use and is called "intrinsic rate of natural increase" (BIRCH, 1948; LESLIE & PARK, 1949; HOWE, 1953) is 0.268. However, this value is not applicable to the second generation. The summer fly develops in 4 weeks and is assumed to lay all of its eggs within 4 weeks. The ineffective egg seems to be rather rare, because the host plants are usually younger throughout the oviposition period. Therefore, assuming that the intrinsic mortality is 5 per cent during August and September, the value of λ for the second generation is 1.171. The intrinsic rate of natural increase is therefore 0.356, showing a higher value than that of the first generation. This calculation holds when the age distribution of the pest population is fixed and all stages of the insect are progressing at the same rate. Such a state is not considered to occur in nature, but the value of r gives an approximate index indicating how the population will increase under favourable conditions. Within the extent of such limited application, it may be concluded that the power to increase is greater in the second generation than that of the first one, though it will be greatly modified by various control agents in nature.

On the contrary, the factors which cause the mortality of the species in Hokkaido are summarized in table 29. The fact that the critical temperatures of the adult are over 40°C and below -17°C clearly suggests that the fly is not destroyed directly by the field temperature conditions, admitting that it cannot select various degrees of temperature. The rate of the oviposition shows no difference within the limits from 20°C to 30°C. This temperature range is recorded usually during the period of the oviposition. The first instar larva is extremely inhibited in hatching by continued low humidity, but such a state does not occur in the field for the reasons as already stated. Since the larva and pupa live within the host plants, being provided with more monotonous temperature than the open, they are able to survive free from the direct influence of the field microclimatic conditions. Heavy rain prohibits the hatching sometimes washing away the egg from the plant and sometimes covering it with splashed mud. This is the only possible mortality caused by the physical environmental conditions examined.

TABLE 29. The factors causing the mortality of *Meromyza saltatrix* in Hokkaido.

Factor	Stage	May	June	July	Aug.	Sept.	Oct.
Heavy rain	Egg	+	+	+	+	+	+
Rainless weather	Larva	-	-	±	±	-	-
Overpopulation	Larva	-	-	+	+	+	-
Erroneous oviposition	Larva	-	+	+	-	-	-
Larval stem-down taxis	Larva	-	+	+	-	-	-
Plant growing velocity	Larva	-	±	±	-	-	-
Parasite (<i>Coelinidea</i>)	Pupa	+	+	+	+	+	-
Predator (Red mite, etc.)	Egg	+	+	+	+	+	-
Interaction (Elaterids)	Larva	+	+	-	-	-	-
Interaction (<i>Gryllotalpa</i>)	Larva	+	+	-	-	-	-
Interaction (<i>Chaetocnema</i>)	Larva	-	-	-	+	+	-
Main host plant for <i>Meromyza</i>		Spring and winter cereals		Volunteer cereals and wild grasses		Winter cereals	

Since the spring cereals are cultivated abundantly in Hokkaido, the eggs are sparsely laid during the period from May to the end of June. After that, most of these plants are harvested, or grow into the heading stage which is unsuitable for the oviposition. Therefore, the favourable host plants are scarce until the middle of September. Since numerous summer flies emerge at that season, the oviposition is necessarily concentrated upon a few favourable host plants, namely, volunteer, new and second growth cereals and grasses. Thus the larvae suffer a very heavy mortality owing to their overpopulation or a density-dependent process which ANDREWARTHA & BIRCH (1954) called "relative food shortage". The mortality over 90 per cent in August (see, table 20) seems to be very important for the control of the insect. Since the essential feature of relative food shortage is that the food supply is too sparsely distributed, it may be changed to some extent with weather conditions such as a long spell of rain bringing up an abundance of the host plants. ROCKWOOD *et al.* (1947) have stated that the principal factors influencing the abundance of the species in the Pacific North West of America are doubtless climatic, because unreasonable early rain in August brings up an abundance of various host plants which afford the opportunities for the production of large numbers of *Meromyza* larvae. This is also true in Hokkaido, but the climatic condition refers to rather indirect factors, promoting or reducing the production of the host plants.

On the ethological features in the larval feeding, the stem-down taxis is a characteristic behaviour which has not hitherto been noticed in *Meromyza*, and has a great importance in destroying the young larva in relation to the egg-laying position. In most cases this is beneficial and causes the first instar larva to crawl downwards between sheaths, cutting the successive sheathing leaves in a spiral manner and feeding the shoot or young ear. However, owing to the taxis the larva sometimes runs away from the suitable food and destroys itself. This is always restricted in the case in which the larva enters below the ear-bearing internode after the plant grows into the node-elongating stage, usually during June and July in Hokkaido. Thus the "critical leaf theory" given by FREW (1924) is well applied to the species. According to his theory it must be postulated that the oviposition instinct of the fly is not perfect and the eggs are often laid below the ear-bearing internode.

The present investigation shows that a few eggs are laid below the ear and the first instar larva is forced to die. These ineffective eggs are about 10 per cent (see, fig. 17). This mortality is principally caused by the error of the oviposition site preference of the adult, and such a "intrinsic" loss may be considered as an inevitable consequence to some extent in nature. Furthermore, the plant growing velocity plays an important role in destroying the larva in certain cases, namely, the ear-bearing internode grows over the egg-laying lamina during the incubation period, and the young larva cuts the soft part of the culm and the resultant ear has turned white. The former case may be applied to the "semi-critical leaf" of FREW's theory. Both cases may be increased or decreased in some degree by variety, manural and cultural conditions etc., but these features are of little importance as a rule.

The parasite complex in the present species seems to be very simple in Hokkaido in comparison with those in Europe and North America. It includes only two species, *Coelinidea* sp. and an undetermined Hymenopteron. The life cycle of *Coelinidea* sp. is well matched with that of *Meromyza saltatrix* and destroys the latter probably as an indispensable host. The parasitism averaged 46.6 per cent during seven years. This indicates that *Coelinidea* sp. is playing an important role as a powerful control agent of the species. Another parasite and predators, such as the Red mites and the Carabids, are considered to have minor importance, granting their total agency gives a potential pressure to the population of the species.

In addition to the natural enemies, some other insects may be considered in the sense of the "interaction" among the biotype in the species involved. These insects are the Elaterids, *Ctenicera puncticollis* MOTSCHULSKY, *Melanotus caudex* LEWIS, *Agriotes fuscicollis* MIWA and the mole cricket, *Gryllotalpa*

africana PALISOT de BEAUVOIS, all of which are the serious pest of cereals in Hokkaido. During May and June, they attack the young cereals independently of *Meromyza*, by boring or cutting their shoot under the earth. The injured plant turns yellow and dries up soon after, being unable to supply food to *Meromyza*. In this case the larvae of *Meromyza* are always starved to death, because they are unable to migrate from plant to plant. Likewise, the larva of *Chaetocnema cylindrica* BALY attacks the shoot of volunteer cereals during summer season, and often interacts with *Meromyza*. The interaction between *Meromyza* and some subterranean insects mentioned above is a common feature seen elsewhere, and it is extremely difficult to estimate how the *Meromyza* larvae are destroyed by its influence. It seems to be doubtless that such interaction will be of importance among the mortality factors of *Meromyza*.

As is well known and as has been confirmed in this paper, temperature is a principal factor determining the length of the development of insects. It is therefore supposed that annual difference of temperature condition may change the number of generation of the corresponding year. In Hokkaido, the change in the number of generation cannot be found in *Meromyza* which has partially one and mostly two complete generations annually. This suggests that an accumulative total effect of the temperature in the field will not be so strong enough to change the number of the generation, but will exert some influences upon the appearing period of the species.

Eventually, the data given in this paper showed that, among the climatic conditions, the elements directly controlling the population of the species are very few though indirect effects on various aspects will need further investigation. On the contrary, the biological conditions concerning *Meromyza*, such as the natural enemies and the relationship between the host plant and the ethological aspects of its feeder, play many important direct roles upon the population regulation of the species. For instance, the relative food shortage in summer, operating in a density-dependent manner, brings up a heavy mortality in *Meromyza*, and is effective in limiting the species to low numbers until the following spring. Thus the population of the species is always low in spring and then increases extremely until the summer to decrease again in the autumn. In such a pattern no considerable annual change, such as periodical or sporadic occurrence, can be found. According to the classification of the fluctuation-type of insect population, this refers to the "parmanenter type" given by SCHWERDTFEGER (1954, 1957) or to the "balanced population at high density" expressed by GRAHAM (1939). Such a chronic occurrence indicates that an insect is maintaining its prevailing population within a certain balance, as a result of firm adaptation to the biotype concerned. The present paper dealing with *Meromyza*

saltatrix gives evidence that the balance will be maintained directly by biological conditions rather than climatic ones. In other words, it demonstrates that the essential factors controlling insect population in a chronic type are doubtless biologic, though climatic conditions will exert some indirect influences upon the biotype.

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Explanation of plate

- A: Adult (summer form) B: Adult (spring form)
C: Larva D: Egg E: Pupa
F: Eggs laid on wheat
G: Infested part at the base of node

