

MEGADELPHAX SORDIDULA (STÅL) (HOM., DELPHACIDAE)
AS A VECTOR OF PHLEUM GREEN STRIPE VIRUS

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Megadelphax sordidula (Stål) transmits a hitherto unknown virus-like disease agent, referred to here as the *Phleum* green stripe virus (PGSV). It attacks spring cereals and timothy (*Phleum pratense* L.) producing light green to yellowish stripes and streaks of varying size in the leaves as well as weakening the growth of the plants and decreasing the grain yield. The proportion of vectors among *M. sordidula* in different aged timothy stands may exceed 40 %. The incubation period of PGSV in planthoppers was 28–33 days, and in plants 10–(18)–40 days. The shortest positive inoculation feeding time observed was 6 hours.

M. sordidula is most abundant in South and South-east Finland. The species is probably most harmful as a virus vector in old timothy leys on mineral soils in South and South-east Finland as well as in spring cereals in the same districts.

Index words: planthopper, *Phleum*, cereals, virus, economic significance.

INTRODUCTION

During 1955–65 studies were made at the Department of Pest Investigation of damage to spring cereals caused by different planthopper species. In laboratory trials during 1962 some hitherto unknown virus-like symptoms we discovered on oats sucked by the planthopper *Megadelphax sordidula* (Stål). The injuries differed from those of oat sterile dwarf (OSDV) (CATHERALL 1970, IKÄHEIMO 1961, LINDSTEN 1959, 1961 a, 1961 b, 1973, PRŮŠA 1958, PRŮŠA et al. 1959, VACKE 1960, VACKE and PRŮŠA 1959), european wheat striate mo-

saic (EWSMV) (IKÄHEIMO 1960, LINDSTEN 1959, 1961 a, 1961 b, PRŮŠA and VACKE 1960, SLYKHUIS and WATSON 1958, VACKE and PRŮŠA 1961, WATSON and SINHA 1959), oat pseudo-rosette disease (SUKHOV and VOVK 1938, ZAZHURILO and SITNIKOVA 1939, 1940), maize rough dwarf (MRDV) (HARPAZ et al. 1965, LINDSTEN et al. 1973), blue dwarf of tall oat grass (KEMPIAK 1972, MÜHLE and KEMPIAK 1971, VACKE 1966), *Dubia* disease of barley (KEMPIAK 1972), and cereal tillering disease (CTDV) (LINDSTEN 1974 a, 1974 b,

1975, LINDSTEN et al. 1973), all of which are transmitted in Europe by planthoppers, but none by *M. sordidula*. At the same time NUORTEVA (1962) announced some virus-like symptoms caused by *M. sordidula* in oats grown under unfavourable conditions. In our trials with spring cereals and ley grasses in 1963–65 it appeared that *M. sordidula* could cause similar symptoms in spring cereals and timothy (*Phleum pratense* L.). To date, attempts to infect timothy with viruses transmitted by planthoppers have been successful only with EWSMV (KEMPIAK 1972, VACKE and PRŮŠA 1961), MRDV (KEMPIAK 1972), and CTDV (LINDSTEN 1974 b, LINDSTEN et al. 1973). In

addition, LINDSTEN (1961 b) reported virus symptoms resembling EWSMV on timothy grown in the field.

Very few studies have been made of toxic injuries on gramineous plants caused by *M. sordidula* (NUORTEVA 1962), or its role as a vector of virus-like disease agents (BREMER 1974, RAATIKAINEN 1970, VACKE 1962).

The bionomics of *M. sordidula* were investigated in connection with disease studies. Some of the results of the ecology have been published earlier (e.g. RAATIKAINEN 1960, 1961, 1970, 1971, 1972, RAATIKAINEN and VASARAINEN 1971, 1973, 1976).

MATERIAL AND METHODS

Tests of injuries

Tests with planthoppers were made sowing the test plants in 430 × 250 × 120 mm wooden boxes lined with polyethylene film (Fig. 1). The bottoms of the boxes were perforated for to allow drainage. The boxes were filled to a depth of 110 mm with steamed and limed soil, fertilized with multiple fertilizer. Test plants' seeds were sown in 6

parallel rows, 4 seeds to each row, at equal distances from one another and at a depth of 30 mm. During test feeding times each planthopper was caged with one seedling under a cylinder of PVC plate, 30 mm in diameter and 250 mm tall, the upper end of which and two ventilation openings near the bottom were covered with gauze. Control plants were caged in the same manner. Observations were made at least once a week for any symptoms

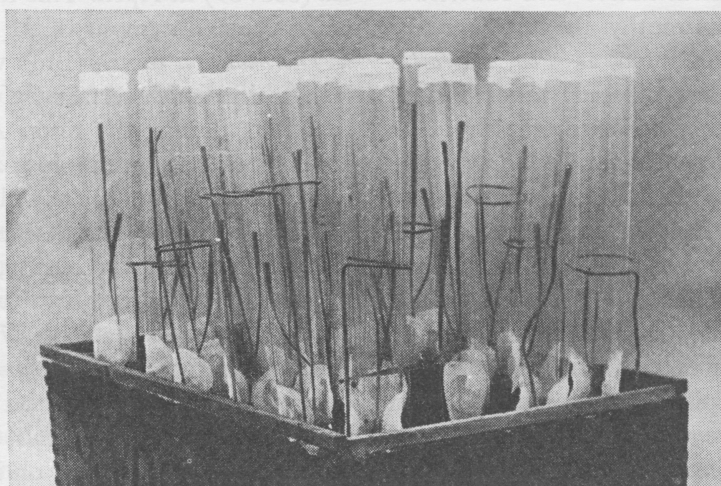


Fig. 1. Rearing box in the laboratory tests. Other explanations see text. Photo O. Heikinheimo.

of disease. Several characteristics noted on the test plants were measured against the mature plants.

The planthoppers used in the trials were either collected immediately before the trials from fields of timothy or cereals or they had been reared and kept on oats or timothy growing in 150 mm flower pots, and isolated by gauze (RAATIKAINEN and TINNILÄ 1959, Fig. 1).

In 1963, planthopper nymphs were collected in four different localities (page 43). From these localities, two sets of very poorly material were collected in April (Nos. 1 and 2) and consisted of hibernated 2–3 stage *M. sordidula* nymphs, and the other sets (Nos. 3 to 6) were collected on June 13, and consisted of distinctly more planthoppers, mostly adults. Using these materials, five successive tests were conducted in the greenhouse between June 14 and July 16.

In 1964, the tests were again conducted in the greenhouse but after inoculation feedings the test plants were kept in outdoor isolation chambers with screened walls, until mature. In the last series of trials, however, the plants were kept in the insectary the entire time. The planthoppers used were collected from a 3rd year timothy ley located at Kalanti (Grid 27°E: 675: 20, HEIKINHEIMO and RAATIKAINEN 1971). Besides timothy, the ley contained many other grasses such as *Poa*, *Agrostis*, *Deschampsia* etc. Two different series of inoculation tests were performed. Firstly, with the 231 2–3 stage nymphs collected on April 14, when the snow was in its final stages of melting. Two consecutive infection tests on oats were made on April 17 and 24, with 7 and 6 day feeding times. After this, the infective planthoppers were used in an infection time trial and a symptom trial with certain grass species. The planthoppers which proved to be non-infective were subsequently tested in an acquisition feeding test in the following manner: 22 of them were kept 10–11 days on infected oat plants, and 16 of them the same time on healthy plants. Wherever possi-

ble, the infectiveness of both planthopper groups was tested in 9 consecutive tests. Secondly, *M. sordidula* planthoppers collected on June 10 at the same place as before were divided into two groups. One group was kept 12 days for acquisition feeding on infected oat plants, the other, at the same time, was fed individually on healthy oat plants. Both groups were then tested as above, though they had not previously been tested for infectiveness before the trial. Seven consecutive infection tests were made with 165 planthoppers. The inoculation feeding times varied between 4 and 11 days. In addition to oats, barley and spring wheat were used as test plants. A symptom trial with the tested infective planthoppers was also performed on timothy. Toxic injury was determined by comparing apparently healthy oat plants fed on by one *M. sordidula* for 4–5 days with plants which had been caged without planthoppers for the same length of time. At the start of the trial, the plants were at the one-leaf stage. In this trial there was a total of 35 control plants, 45 plants fed on by female planthoppers and 34 by male planthoppers (Table 4).

In 1965, the planthoppers to be tested were sampled from a 3rd year timothy ley in Vantaa (668: 39) in April. This material consisted of 2–3 stage nymphs of *M. sordidula* as well as *Dicranotropis hamata* (Bh.), which could only be identified with certainty after they emerged to adults during the tests. Acquisition tests were made in a greenhouse, and after 9 days' inoculation feeding the test plants were grown in an outdoor isolation chamber with screened walls. For acquisition feeding, the planthopper nymphs were divided into two groups, as in 1964. From this material 37 nymphs of *M. sordidula*, and 15 of *D. hamata* were tested after acquisition feeding on PGSV infected timothy, and 29 *M. sordidula*, and 6 *D. hamata* were tested after feeding on healthy timothy. Besides oats, several spring wheat cultivars and ley grass species were used in 9 successive tests.

The bionomics of *M. sordidula*

The bionomics of *M. sordidula* were investigated in the years 1956—1975. Its life cycle, food, natality and mortality were studied between 1956—1960 (RAATIKAINEN 1960, 1961). During the years 1957—1964 species' migration was investigated in West Finland near the city of Vaasa with the aid of netting apparatuses, and fluctuations in the abundance of the species were studied using suction apparatus, sweep net, and netting apparatus (RAATIKAINEN 1970). The suction apparatus, sweep net and netting apparatus have been described by HEIKINHEIMO and RAATIKAINEN (1962) and RAATIKAINEN (1967). The occurrence of the species in different seasons and cereals as well as its migration from leys into cereal fields were also expounded during the same years (RAATIKAINEN 1971, 1972, RAATIKAINEN and VASARAINEN 1971, 1973).

The abundance of the species at the turn of June and July in oat fields throughout the country was investigated between 1962—1964. The material for this purpose was collected from 28 localities using sweep nets (Fig. 8). A sample of 60 sweeps from 14—26

fields was taken from each locality, 720 samples altogether. The material consisted of 68 932 adult leafhoppers, 1280 of which were *M. sordidula* (RAATIKAINEN and VASARAINEN 1976). At the turn of June—July 1966—1968 the netting samples were collected from leys in 54 localities (Fig. 7). Netting samples consisting of 60 sweeps were collected from 30 leys in each locality. The samples were taken from a total of 1080 hayfields. This material, also, consisted of more than 60 000 adult leafhoppers which included 2738 *M. sordidula*. In the years 1972—1974 netting samples were collected at the beginning of June from winter cereal fields in 18 localities. A netting sample of 60 sweeps was taken from 30 fields in each locality. Samples were collected from 540 winter cereal fields altogether. All of this material has not yet been identified. With the aid of suction apparatus and sweep nets, samples of leafhoppers were collected from 53 fields not under cultivation in Central Finland. This material consisted of 5 300 leafhoppers, including approximately 400 *M. sordidula*. In addition the species was being reared in the laboratory for several years. The whole material includes about 25 000 individuals of *M. sordidula*.

RESULTS

The injuries caused by *M. sordidula*

Symptoms of Phleum green stripe disease

The first symptom and the most distinct evidence of injury to oats produced by *M. sordidula* was the change in leaf coloration. On average 18 days after the planthoppers had been placed on oat seedlings at the two-leaf stage light green or yellowish green streaks and striations appeared, usually in the fourth leaf and often extending the entire length of the leaf (Fig. 2). Occasionally this discoloration appeared in the third leaf also, but never in older leaves which had stopped

growing. At the same time the fifth leaf either became striped or almost entirely light-coloured, with normal green or dark green coloured streaks of varying width. The sixth leaf and occasionally the seventh leaf were — as soon as they had emerged — entirely or almost entirely pale-coloured, yellowish green or greenish yellow, and their basal part had streaks of normal green or dark green colour. In certain instances these colour changes occurred only in the 6th and 7th leaves. Such discoloured leaves were not more rigid than the corresponding healthy oat leaves, rather more were thus somewhat indolent, and lacked a tendency to curl into rolls. Simul-



Fig. 2. Leaves of 'Tammi' oats (above left), timothy (above right), and 'Apu' (below left) and 'Selkirk' (below right) spring wheats, infected with PGSV. Inoculation feeding time by *M. egadelpbax sordidula* 2—3 days at 2—3 leaf stages of plant seedlings. Photo O. Heikinheimo.

taneously, pale green areas appeared in all the remaining leaves except the oldest ones on the plant and in the tillers. Such pale areas extended through the thickness of the leaf and were thus similar on both sides. Their size and shape remained unchanged from the time they first appeared. The injury was not accompanied by heavy tillering nor by premature death of the plant.

In the 6-rowed barley cultivar 'Pirkka' pale green stripes of varying width appeared in the upper leaves. The difference in colour between the normal green and the pale stripes was less striking than that in oats; in some cases it was somewhat difficult to distinguish colour differences.

In spring wheat 'Apu' the symptoms of PGSV were very distinct and marked (Fig. 2). The streaks and stripes appearing in the leaves were long, sometimes extending along the entire blade and pale green or greenish yellow in colour. In early stages, the injury resembled very closely the initial symptoms of EWSMV. The youngest leaf emerged, the growing point, and the leaves within the sheath which had not emerged withered and died imme-

diately after the appearance of the stripes. On the other hand, the old full-grown leaves, dark green in colour, remained alive for a long time, even longer than the uninfected plants. This phenomenon reveals a clear difference between the plants infected with PGSV and EWSMV, since the latter died within a short time, considerably before the wheat ripened. Since the growing point of the PGSV-infected plants was destroyed, no stem developed. In some of the plants, however, the injury remained so mild that a stem and spike developed. Such plants were only slightly shorter than normal, but with the exception of one spike in our trials, no grains were formed. The grains in this one spike were smaller than normal, and wrinkled (Fig. 3) but not shriveled (cf. PRŮŠA 1958, VACKÉ 1960), as are the grains of OSDV infected wheats and wheats mildly infected with EWSMV. When the injury caused by PGSV was severe, there were fewer shoots on the wheat plants than on healthy plants. In the other spring wheat cultivars tested, discoloration and inhibition of the growth were less pronounced (Fig. 2).

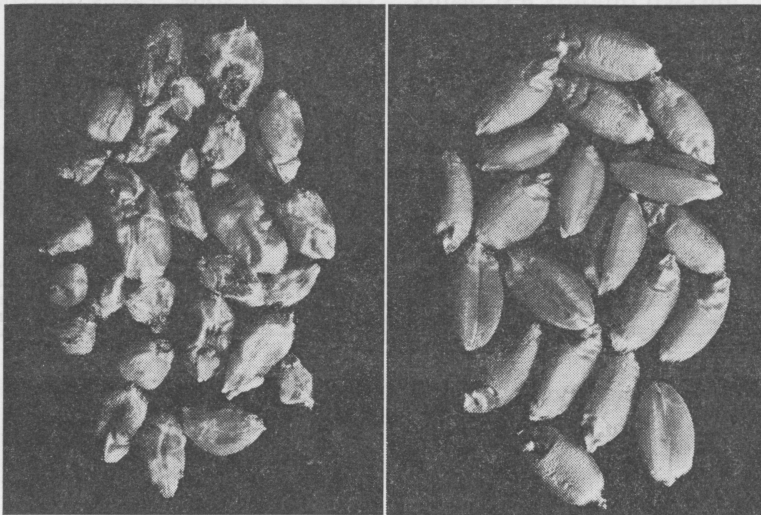


Fig. 3. The effect of the mildest PGSV infection on the grains of 'Apu' spring wheat. To the left wrinkled grains of an infected plant inoculated at 2-leaf stage, to the right grains of a healthy-looking wheat plant growing adjacently but also fed on by *Megadelphax sordidula*. Photo O. Heikinheimo.

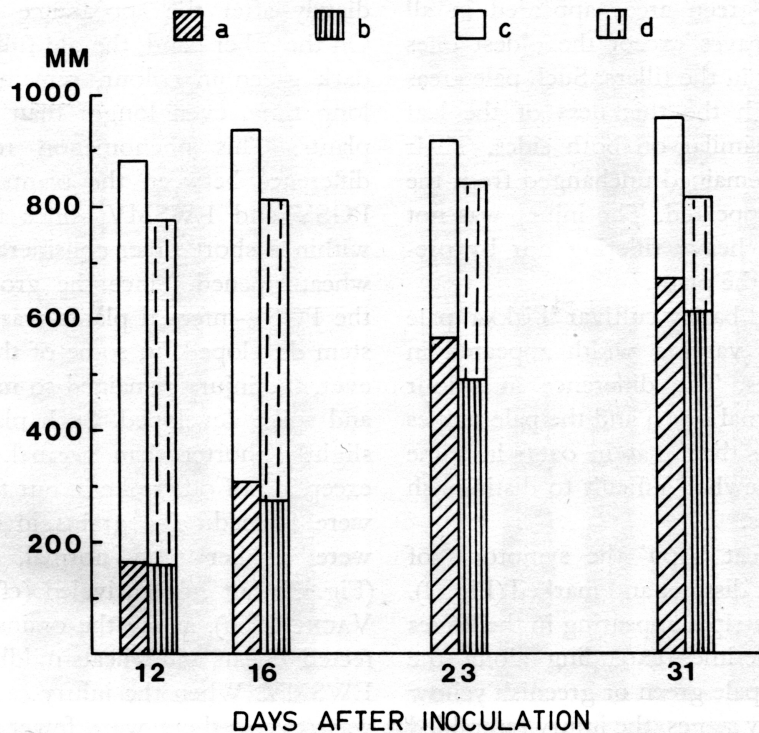


Fig. 4. Lengths of healthy oat plants compared with those of PGSV infected plants. Measurements made on different-aged plants sown on various dates. — a and c: healthy; b and d: PGSV-infected; a and b: measured July 17; c and d: measured from fully grown plants.

In the leaves of infected timothy test plants, the pale green stripes were more or less distinct, although the colour difference was somewhat less pronounced than in cereals

(Fig. 2). In some leaves the pale area extended throughout the entire width of the blade. In such leaves there remained narrow streaks of dark green colour at the base of the leaf

Table 1. Characteristics of PGSV infected oat plants compared with those of plants fed on by *Megadelphax sordidula* which remained healthy. Measurements made 1963. A total of 261 healthy and 111 PGSV infected oat plants were examined.

Characteristics measured	Means		Unbiased estimate of mean difference	F-value and its significance
	healthy	PGSV		
Total length of mature plant, mm	929	818	115	105.3***
No. of grains per spikelet on main shoot	1.5	1.1	0.4	75.0***
Grain yield per plant, mg	598	437	176	54.8***
% of light grains among total grains	21.2	36.9	-15.8	51.3***
No. of spikelets on main shoot	12.2	10.6	1.5	17.2***
Length of panicle stalk (tip of uppermost sheath to base of panicle), mm	124	107	17	12.5***
% of non-panicked shoots among total shoots	29.4	38.7	-7.8	7.4**
% of white spikelets among total spikelets	22.0	26.5	-3.6	6.0*
1000-grain weight, g	33.0	35.2	-1.3	4.7*
Time of panicle emergence; deviation of adjusted mean, days	0.39	0.80	-0.43	2.7
Total no. of spikelets on secondary shoots	5.85	5.59	0.58	0.4
Total no. of shoots	3.17	3.05	0.03	0.0

blades, such as often occur in the uppermost leaves of oats. In older timothy plants the pale green stripes were distinct only in some of the shoots. All the infected timothy plants grew much more weakly than healthy ones. This characteristic was very distinct in older plants.

Effect of injuries upon growth and yield

On July 17, 1963, the first length measurements of the oat plants were made simultaneously for the first four successive tests. In this manner parallel results were obtained from plants growing under the same conditions

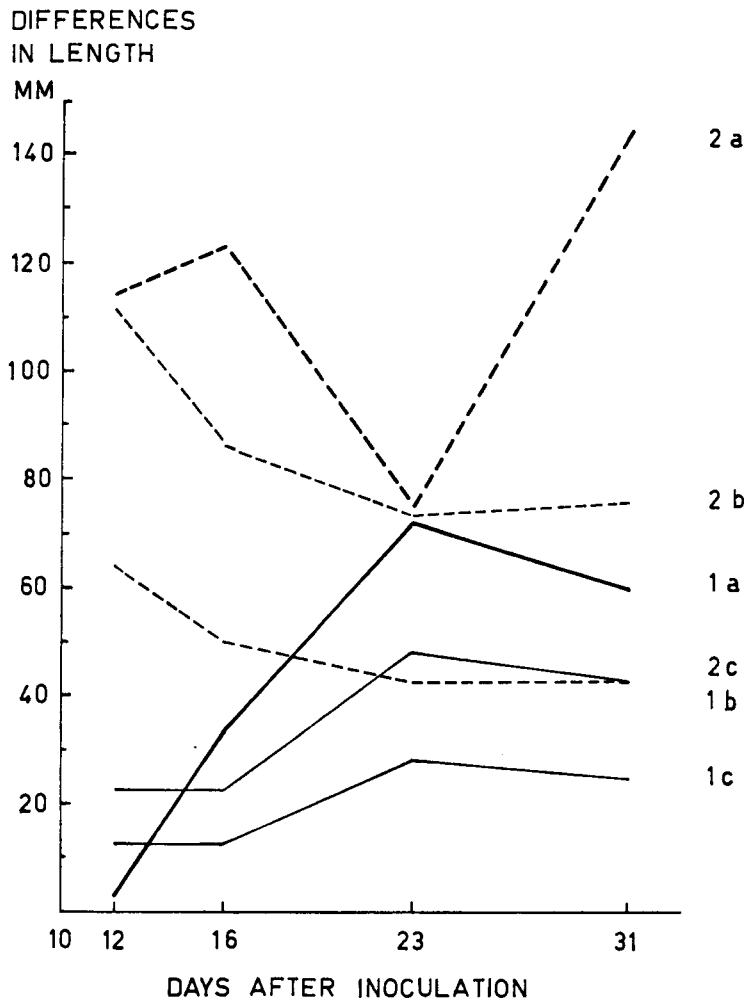


Fig. 5. Differences in length between healthy and PGSV-infected oat plants, the same material as in Fig. 4. — 1 a: Differences on July 17 due to the length of the time interval between inoculation and measurements. — 1 b: Statistically significant differences at the level of $P = 0.1\%$, and c: $P = 5\%$, respectively. — 2 a: Differences in the length of fully grown plants in successive tests. — 2 b: Statistically significant differences at the level of $P = 0.1\%$, and 2 c: $P = 5\%$, respectively.

Table 2. Differences in some characteristics between 17 check plants, 8 PGSV-infected, and 12 oat plants fed on by planthoppers, but remaining healthy.

Characteristic measured	Weighted means of measured data			Unbiased estimates of mean differences and their significance between	
	check	healthy	PGSV	check - healthy	healthy - PGSV
Total length of mature plant, mm	1031	968	840	38	140***
No. of grains per spikelet	1.6	1.3	1.2	0.10	0.14
Grain yield per plant, mg	851	653	472	97	216*
% of light grains among total grains	17.2	32.4	36.2	-7.2	-6.7

but of different ages. When comparisons were made between PGSV-infected oat plants and healthy plants fed on by virus-free *M. sordidula*, it could be seen that a statistically significant difference in length became evident after an incubation period of about 16 days (Figs 4 and 5). At this time the average difference was 33 mm. In full grown oat plants the determinations showed differences in length in the different test lots ranging from 75 to 140 mm.

Among the characteristics investigated, the differences between injured and healthy oat plants were most distinct — in addition to the length — in the number of grains per spikelet, in the grain yield, percentage of light grains, number of spikelets on the main shoot, and the length of the panicle stalk (Table 1). There were, on the other hand, only slight differences in the relative number of non-panicled shoots, percentage of white spikelets, and 1000-grain weight, the latter determination revealing slightly greater grain weights in injured than in healthy plants.

Statistically significant differences were not found in the other characteristics investigated.

The grain yield of PGSV injured oat plants was on an average 27 % lower than that of healthy plants, and a similar difference was found in the number of grains per spikelet. The light grain content of infected plants was 74 % greater, and the number of spikelets per main shoot 13 % less than in healthy plants. Simultaneous emergence of the panicle in both groups shows that the difference in the length of the plants during growth was not due to a delay in development, but rather to a weakening in the vigour of the injured plants.

Some of the isolation cages contained check plants not fed on by planthoppers. The growth and yield of these plants was compared to that of both PGSV injured and healthy looking plants fed on by *M. sordidula*. This investigation concerned only those blocks (boxes) which contained oat plants belonging to all three of these groups (Table 2). Because of the limited size of the experimental material,

Table 3. Effect of PGSV on growth and yield of spring cereals. Insectary trial 1964. Measurements made at the same stage of maturity.

Companion crop	No. of plants	Means and 0.95 confidence limits			PGSV-infected	Unbiased estimate of mean difference	F-value and its significance
		Healthy	No. of plants				
Length of main shoot, mm							
Oats 'Tammi'	571	113.86	±0.73	198	101.39 ±0.35	13.09	295.0***
Barley 'Pirkka'	58	95.6	±1.8	11	77.9 ±5.0	18.41	54.5***
Spring wheat 'Apu'	99	97.5	±2.5	20	32.1 ±8.6	65.0	318.6***
Grain yield of main shoot, mg							
Oats 'Tammi'	552	1744.5	±0.4	191	1170.7 ±0.6	464.8	191.4***
Barley 'Pirkka'	58	1772	±83	11	961 ±156	769	48.3***
Spring wheat 'Apu'	99	1043	±44	20	18 ±27	1028	> 500***

Table 4. The effect of feeding by *Megadelphax sordidula* on the length of oat plants and their yield, 1964. No symptoms of OGSV were detected.

Test group	Average length of plants in mm		Average grain yield mg/plant	
		Difference		Difference
Male planthoppers	1089	56.4	1718	307
Control	1146		2025	
Female planthoppers	1091	55.2	1801	224
		F = 5.4*		F = 13.8**
		F = 10.0**		F = 12.4**

the differences between the test groups were statistically not as significant as in Table 1. When comparisons were made between all check plants (79 specimens), and the plants which had been fed on by *M. sordidula* females but remained healthy (20), an average difference in length of only 29 mm was found, which was not statistically significant.

In 1964, the effect of the PGSV-injury was studied in the same way as in 1963 (Table 3). The PGSV infection had caused an 11 % reduction in the length of oat plants, 8 % in barley, and 67 % in wheat. The reduction caused by PGSV in the grain yield was 33 % in oat, 45 % in barley, and 98 % in spring wheat. In all cases the reductions were highly significant.

There were distinctly less shoots and the shoots were markedly weaker on PGSV-infected timothy plants tested than on non-infected control plants.

The toxic injury of non-infective *M. sordidula* planthoppers manifested in the average length of mature plants, and in differences of grain yield between oat plants fed on by one planthopper for four to five days at one-leaf stage and control plants. A 5 % reduction in length growth, and 15 % reduction in grain yield were significant. No differences in injury caused by male and female planthoppers could be observed (Table 4).

Studies to determine the nature of the injuries of *M. sordidula*

Percentage of vectors of *M. sordidula* in the field material

The following table shows the numbers of *M. sordidula* planthoppers tested and the percentage vectors established in six planthopper populations collected in 1963 (cf. page 36):

Population No.	Grid 27° E	Locality	Age of timothy ley, years	No. of plant-hoppers tested	% of vectors
1	680:35	Pälkäne	1	1	0
2	699:23	Mustasaari	1	4	0
3	678:20	Rauma rural commune	old	11	9
4	675:20	Kalanti	1	11	45
5	675:20	Kalanti	old	37	41
6	675:20	Kalanti	old	48	38
Total				112	35

In 1964, a total of 231 second to third stage planthopper nymphs collected from a third-year timothy ley at Kalanti (675:20) in early spring, just after the snow had melted, were tested, 148 of them twice. The total percentage of PGSV-vectors was 17.6. Of these,

23 % caused symptoms in both the successive tests, 31 % in the first only, and 46 % in the second test.

17 % of young nymphs collected in Vantaa (668:39), 1965, from a third year timothy ley in early spring proved to be PGSV vectors.

The planthoppers collected in 1964 which proved to be PGSV vectors after two successive tests, as described above, were transferred to oats for different lengths of time ranging from 20 minutes to two days. One oat plant was infected after six hours' inoculation feeding time, one after one day's feeding, while the others remained healthy. The PGSV symptoms of these two infected plants were as distinct as in other tests.

In the five successive tests made in 1963 with the six populations mentioned above, a total of 39 specimens from all the 112 proved to be PGSV-vectors (Table 5). Depending on how many successive tests could be made with each planthopper, the positive PGSV-infection (+) results were distributed as follows:

No. of tests	Total no. of + results					Total no. of vectors	No. of planthoppers tested	Vector %
	1	2	3	4	5			
1	2					2	10	20
2	0	2				2	10	20
3	2	5	3			10	21	48
4	0	2	0	1		3	11	28
5	4	7	7	2	6	22	60	37
Total						39	112	35

Table 5. PGSV infection transmitted by *Megadelpfax sordidula* from different populations in successive tests with oats 1963. + = infected with PGSV, - = test plant remaining healthy. Further explanation, see text.

Population no.	Successive tests					Total			%	Population no.	Successive tests					Total			%
	1	2	3	4	5	+	-	+			1	2	3	4	5	+	-	+	
3	+	-	+	-	.	2	2	50		6	+				
4	+	+	+	.	.						+				
	+	+	-	.	.						+	+	.	.	.				
	+	-	-	.	.						+	+	+	.	.				
	+	+	+	+	+	14	5	74			+	+	+	.	.				
5	+						-	+	+	.	.				
	+	+	.	.	.						+	+	+	+	.				
	+	+	-	.	.						+	+	-	-	.				
	+	+	-	.	.						+	+	+	+	-				
	-	+	+	.	.						+	+	+	+	+				
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	+	+	+	+	+						+	+	-	-	-				
	-	+	+	+	-						-	+	-	-	-	44	25	64	
	+	+	-	-	-														
	+	-	-	-	-	44	18	71											

Total + = 35 29 19 10 11 = 104
 - = 4 7 15 14 10 = 50
 Percentage mean of + = 90 81 56 42 52 68

The death of planthoppers during the course of tests was not due to less vigour in the vectors, since the relative number of positive infection results was as large with those specimens which lived during all the successive tests as with those which died soon after the first two or three tests. On the other hand, it is noteworthy that the percentage of positive results in Table 5 was considerably higher in the first two tests than in the following three.

In the transmission tests in early summer 1964 the grasses *Bromus inermis* Leyss., *Dactylis glomerata* L. *Festuca pratensis* Huds., *Festuca rubra* L., and *Lolium multiflorum* Lam. were used as test plants. Of these, only a single plant of *Bromus inermis* showed a paler green leaf colour differing from the other plants; no streaking, however, was visible. Such pale colouration could not be established definitely as a symptom of PGSV.

Infection of timothy (*Phleum pratense* L.)

Nine adult planthoppers were used in this trial, seven of which had been proved vectors in successive tests on oats. Of these latter,

four produced PGSV-symptoms in timothy after a five-day inoculation feeding period. In the comparison group five planthopper adults which proved incapable of infecting the test plants were transferred to young timothy plants. None of these infected, and no differences in growth appeared when compared with uninoculated check plants. On the basis of visible symptoms, the PGSV infection in timothy persisted in the greenhouse for at least one year.

Third stage *M. sordidula* nymphs collected from third-year timothy fields, and placed on healthy timothy seedlings for some days, caused PGSV-infection symptoms on these plants. Some of these planthoppers proved later to be PGSV vectors.

Acquisition trials

Rearing *M. sordidula* under laboratory conditions was not successful. Consequently, in the acquisition trials planthopper nymphs were used which had been taken from the field; some of the planthoppers were PGSV-vectors. In 1963, adult planthoppers which had pre-

Table 6. Results of inoculations made after 10–11 days' acquisition feeding by *Megadelpax sordidula* on PGSV-infected oat plants in successive tests. The planthoppers proved to be non-infective in two tests before the acquisition feeding. A = planthoppers fed on by healthy oats. B = acquisition feeding on PGSV oats. E = parasitized by *Elenchus tenuicornis* Kirby, + = test plant infected with PGSV, - = healthy test plant. Totally 16 (A), and 22 (B) planthoppers were tested.

Group	Vector	Successive tests, nos.								
		1	2	3	4	5	6	7	8	9
A	Male	+	+	+	-	-	-	-	-	-
	E	+	+	-	+	-	-	-	.	.
	Male	+	+	-
	Female	-	+	+	-	-	-	.	.	.
	Male	-	+	-	+	-
B	Female	+	-	+	+	+	+	+	+	-
	Female	+	+	+	-	+	-	-	.	.
	Male	+	+	+	+
	E	+	-	-	-	-	-	.	.	.
	E	-	-	-	-	+	+	-	.	.
	Female	-	-	-	-	+	+	.	.	.
	Female	-	-	-	-	-	+	.	.	.
	Female	-	-	-	-	-	+	+	.	.
	Female	-	-	-	-	-	+	.	.	.

viously been proved uninfected were placed for acquisition feeding on PGSV diseased oat plants. 19 planthoppers were tested on oats, some of them in 12 consecutive tests. It was found that not a single planthopper transmitted PGSV. In 1964, two acquisition trials were conducted, trial no. 1 in the spring with young nymphs, and no. 2 in June with 5th stage nymphs and adults which had not previously been tested for virus infection.

The planthoppers used in acquisition test no. 1 were kept on acquisition plants for 10 to 11 days, after which their ability to infect was determined in 9 successive tests on oats. The results (Tables 6 and 8) indicate that the vector percentage of planthoppers kept on

Treatment	Test no.								
	1	2	3	4	5	6	7	8	9
Without acquisition feed, A	60	100	40	50	0	0	0	0	0
Receiving acquisition feed, B	100	50	75	44	83	60	50	100	0

In the first four tests, an average of 60 % of the plants in group A fed on by vectors became infected, in the group B the figure was 67 %. In the fifth to ninth tests, the corresponding figures were 0 % in group A, and 67 % in group B. In group B there were five planthoppers (23 %) which had apparently no ability to infect in the first 4 tests but which caused infection in the fifth and sixth tests.

In acquisition trial no. 2, 1964, the fifth stage nymphs of *M. sordidula* were divided into two groups as before. Group A was kept for 12 days on healthy oat plants, group B on PGSV infected oat plants for the same period. Seven successive infection tests were made: 1 and 2 on oats, 3 on spring wheat, 4 on barley, and 5 to 7 on oats. Unfortunately,

Treatment	Test no.						
	1	2	3	4	6	7	
Without acquisition feed, A	84	69	34	17	50	0	
Receiving acquisition feed, B	76	81	34	47	67	29	

A much greater proportion of the group B vectors infected the plants in the fourth to seventh tests than of the group A vectors.

In 1965, the young nymphs were divided

healthy oats (check group A) was 31 %, and of leafhoppers feeding on PGSV infected oats (acquisition group B) 36 %. During the second to fourth tests the number of vectors did not rise. During the fifth and sixth tests, however, the number of vectors in group B doubled, while in the group A there was no increase, but instead, all the test results from the fifth onwards were negative. Among the planthoppers in at least the first five tests, 29 % were vectors in group A, and 47 % in group B. In the fifth to seventh tests, the corresponding vector percentages were 0 and 40 %. Of the test plants fed on by proved vectors the following percentages became infected during the consecutive tests (Table 8):

the oat plants in the fifth infection test were destroyed. The percentage vectors in groups A and B were 44 and 47, respectively, of the planthoppers tested (Tables 7 and 8). In the second and third tests, the number of vectors rose by only one in each group. In tests four to seven there was no vector increase in group A, while in group B there was an increase of two. Among those included in at least the first four tests there were 45 % vectors in group A and 48 % in the group B. On the basis of the fourth, sixth, and seventh tests, the vector percentage was 38 % for group A, and 78 % for group B.

The following percentages of test oat plants fed on by proved vectors became infected in the tests (Table 8):

into groups A, and B, as in 1964. Nymphs of group A were allowed to feed on healthy timothy plants, whereas nymphs of group B underwent acquisition feeding on PGSV in-

Table 8. Feeding times, numbers of planthoppers, and test results after acquisition feeding. Explanations see Table 6.

Test no.	Inoculation feeding time days	Numbers of planthoppers tested		No. of plants infected		Cumulative no. of vectors		No. of days from start of acquisition feeding
		A	B	A	B	A	B	
1. The test trial results presented in table 6								
1	4	16	22	3	4	3	4	14
2	5	16	19	5	2	5	4	19
3	5	16	16	2	3	5	4	24
4	4	14	15	2	2	5	4	28
5	5	14	15	0	5	5	7	33
6	8	11	11	0	5	5	9	39
7	6	8	8	0	2	5	9	46
8	5	3	1	0	1	5	9	54
9	4	3	1	0	0	5	9	63
2. The test trial results presented in table 7								
1	8	86	79	35	29	35	29	19
2	7	81	76	26	30	40	34	26
3	7	66	68	11	11	41	35	33
4	4	53	46	4	9	41	37	37
6	11	20	13	9	8	41	38	53
7	4	8	9	2	2	41	38	57

Table 9. Infection feeding times, test plants, and the numbers of planthoppers in successive tests of the planthopper groups A and B 1965. An acquisition feeding on PGSV-infected timothy. Other explanations as in Table 6. The ley grasses enumerated in the text.

Test no.	Inoculation feeding time, days	Test plants	Number of planthoppers tested and test results			
			Group A		Group B	
			PGSV	healthy	PGSV	healthy
1	5	Oats 'Tammi'	4	25	5	32
2	5	Oats 'Tammi'	3	26	7	29
3	4	Ley grasses	1	28	1	35
4	2	Spring wheat 'Apu'	0	7	1	5
		Spring wheat 'Svenno'	0	6	1	6
		Spring wheat 'Timantti'	0	6	0	9
		Spring wheat 'Selkirk'	0	5	1	6
		Spring wheat 'Norröna'	0	5	0	7
5	3	Oats 'Tammi'	1	26	6	29
6	3	Oats 'Tammi'	3	24		
		Ley grasses			0	23
7	4	Spring wheat 'Apu'	2	12	0	10
		Spring wheat 'Svenno'	0	13	0	10
8	2	Oats 'Tammi'	1	17		
		Spring wheat 'Apu'	0	7		
		Ley grasses			0	10
9	2	Oats 'Tammi'	1	23	1	9

Dicranotropis hamata (Bh.), 6 in the group A, and 15 in group B. One specimen from group B apparently acquired PGSV from the infected timothy plant, because its second ('Tammi' oat) and third ('Norröna' spring wheat) test plants were PGSV infected, showing typical and distinct symptoms.

Occurrence of *M. sordidula* vectors and PGSV

On the basis of the materials collected for the trials in 1962—1965, PGSV infective *M. sordidula* were found in three localities (cf. p. 43). In these materials the percentage of in-

Table 10. Number of *Megadelpfax sordidula* per 60 net sweeps in hayfields of different ages.

Age of ley, years	South Finland			Middle Finland			North Finland			Total		
	Total adults	Brachypters No.	%	Total adults	Brachypters No.	%	Total adults	Brachypters No.	%	Total adults	Brachypters No.	%
1	2.2	1.0	44.0	0.3	0.1	18.8	0.0	0.0	0.0	1.4	0.6	41.9
2	2.6	1.6	61.2	1.1	0.8	69.4	0.9	0.8	80.9	1.9	1.2	63.8
3	3.6	2.3	64.9	1.3	1.1	82.3	0.6	0.5	87.1	2.6	1.8	67.7
4	9.8	5.3	54.8	2.9	2.4	85.6	0.3	0.3	100.0	6.1	3.6	59.5
>4	5.4	3.4	62.3	2.1	1.9	91.3	5.5	2.1	38.5	4.4	2.5	56.5

fective planthoppers was high. Relatively speaking the proportions of vectors were equally large in the planthopper specimens collected from both first-year and third-year or older timothy fields. Among the nymphs collected in April the percentage of infected planthoppers was distinctly less than in June, e.g. in 1964: 18 % in April, and 44 % in June.

Specimens of *M. sordidula* which caused leaf striations in oats were collected by NUORTEVA (1962) at Bromarf (665: 27), South-west Finland.

According to Dr. Katri Bremer (oral communication), in timothy leys of different ages she found the same kind of symptoms as were produced by *M. sordidula* in our timothy infection trials. She suspected that it was a new virus disease, but the agent transmitting it was not found. The plants having pale green stripes in their leaves were weaker than normal plants. The symptoms were more pronounced in the spring and autumn. Such diseased plants were encountered by her in different locations in southern Finland, in the vicinity of Helsinki (667:38), along the west coast between Turku (671: 23) and Vaasa (700: 23), and in the region of Mikkeli (684: 51). We also discovered some timothy plants with symptoms similar to PGSV along the western coastal region between Turku and Vaasa, e.g. in Kalanti. Cereals with PGSV symptoms were found in the field on one occasion only in an oat field in Kalanti, and even there the virus infected oats were scarce although about 40–50 % of *M. sordidula* consisted of the vectors of PGSV.

On the bionomics of *M. sordidula*

M. sordidula is univoltine in Finland, and it hibernates as a nymph especially in leys, ditch banks, pastures, waste lands, and meadows. The adults emerge in June. More than half of the specimens emerging in leys are probably brachypters. Their proportion increases towards the north where the day is longer in summer, and the population density lower than in the south. In old leys the proportion of brachypters is also higher than in first-year leys (Table 10).

The brachypters usually stay in leys to reproduce, and only a few individuals move in the field layer to the edges of the cereal fields. The longest distance moved was found to be 25 m. On the basis of the material collected by netting apparatuses it seems that the macropters migrate in western Finland (63° N) between June 8 and July 18 (Fig. 6). Migration generally occurred only on days when the temperature was above average, i.e. when the maximum temperature for the day was at least 16° C. Migrating individuals descended mainly on spring cereals, but also on winter cereals, leys, and other vegetation.

M. sordidula prefers warm and dryish fields. Its abundance in leys on different soils was stated as follows:

Soil type	Adults/60 sweeps
Clay soils	4.06
Coarse mineral soils	2.63
Organic soils	1.32

The difference between clay soils and organic soils was statistically significant. As the leys aged, the density of *M. sordidula* increased up to the fourth-year but may have decreased

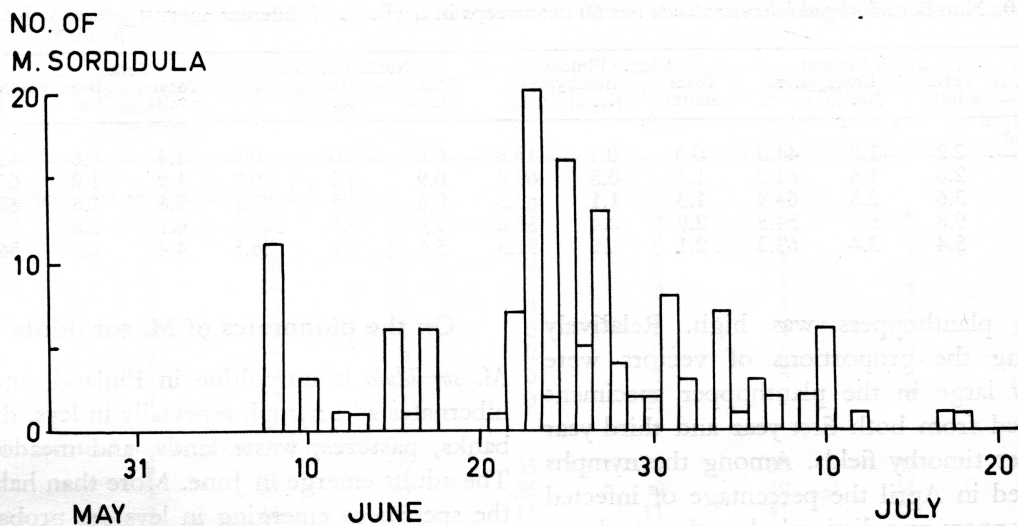


Fig. 6. Migration of macropterous *Megadelphax sordidula* in 1957-1964.

then (Table 10). This difference is statistically highly significant.

According to the netting samples taken at the turn of June and July, *M. sordidula* was fourth in abundance of the leafhoppers in leys, numbering 2 738 adults or about 4 % of adult leafhoppers. More abundant species were *Doliotettix pallens* (Zett.), *Diplocolenus abdominalis* (F.), and *Javesella pellucida* (F.). According to the material collected from oats at the turn of June and July, *M. sordidula* was fifth in abundance of the leafhopper species, accounting for 1 280 adults or 1.9 % of 68 932 adult leafhoppers. More abundant species were *Javesella pellucida*, *Macrosteles cristatus* (Rib.), *Doliotettix pallens*, and *Javesella obscurella* (Bh.). There were, however, great fluctuations in the abundance of *M. sordidula*. For instance, two- or threefold fluctuations in the density between different years were not exceptional. The density seemed to have been lowest in the years following cool summers, and greatest after warm summers. Also mortality during the winter was great and variable. For example, according to the suction samples caught in the field in autumn and spring average mortality during winter was 82 % but occasionally it could be as high as 90 %. The influence of natural enemies on the populations was

also considerable (RAATIKAINEN 1961, 1970).

The abundance of *M. sordidula* on leys according to the samples collected at the turn of June and July is presented in Fig. 7. The material caught by sweep net at the turn of June and July shows the density of the species in oat fields (Fig. 8). These figures, 7 and 8, show that *M. sordidula* has spread to South and Central Finland, and its density is greatest in Southeast and South Finland.

Variation in spatial abundance is influenced by several factors mentioned previously. Furthermore, tilling the fields is a very essential factor. The species remains in leys during the whole ley phase which lasts a little longer than 2.4 years on the average. On the other hand, descendants of the specimens migrating to cereals are destroyed in the nymphal stage, mainly during autumn ploughing, and those that remain perish during spring soil preparation. Only when the spring cereal has been undersown with grass will the species survive for some 3.4 years. The proportion of spring cereals undersown with grass of the whole cereal area varies from one cultivation area to another and is greater in eastern Finland than it is in western Finland. This factor explains partly the great abundance of *M. sordidula* in eastern Finland.

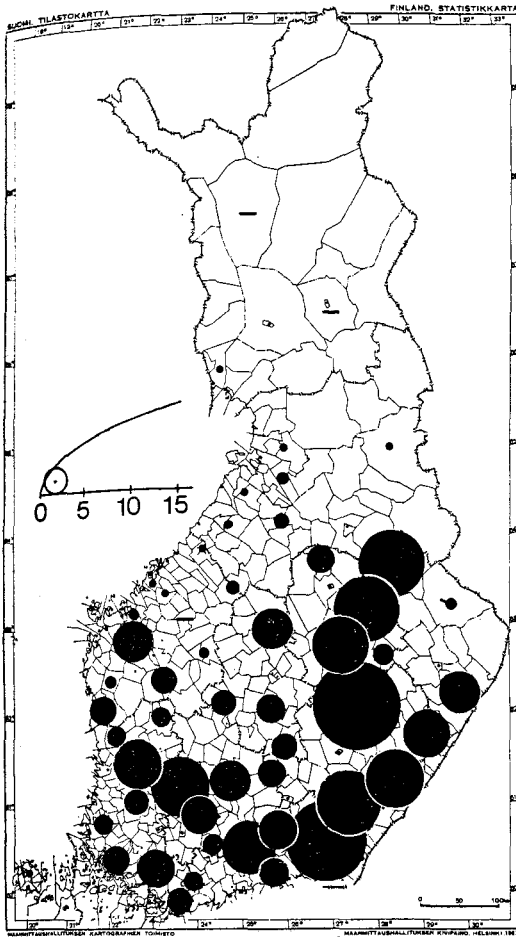


Fig. 7. Number *Megadelphax sordidula* per 60 sweeps in leys in 1966–1968.

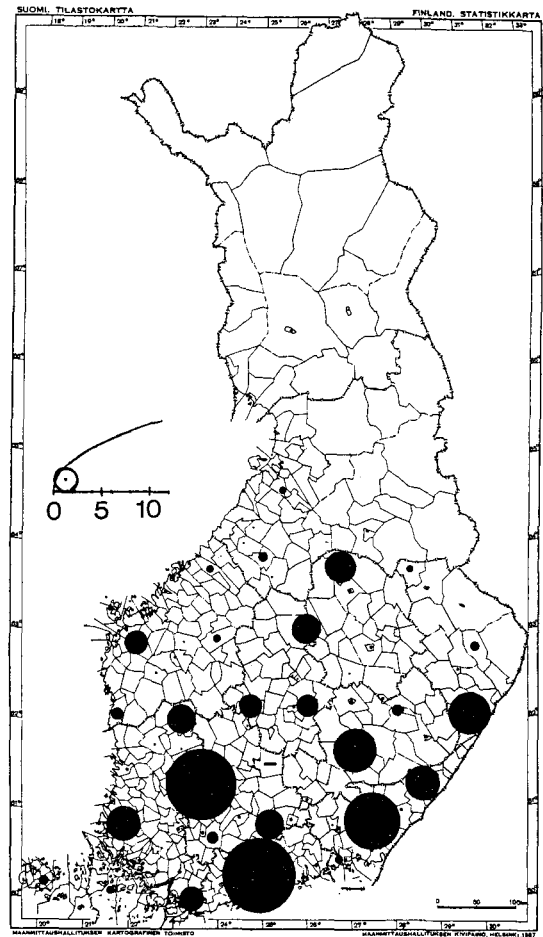


Fig. 8. Number of *Megadelphax sordidula* per 60 sweeps in oat fields in 1962–1964.

DISCUSSION

Toxic injuries of *M. sordidula*

Toxic symptoms of gramineous plants sucked by planthoppers is manifested in decreasing elongation growth and on increasing number of light-weight grains (NUORTEVA 1962) and, consequently, in the grain yield. No toxic injuries with chlorotic or yellow striations caused by planthoppers are known from gramineous plants. These are typical to most virus diseases on cereals and grasses.

According to the limited experimental material available, the results of the toxic effect

of feeding by *M. sordidula* show, that the species may have a mild influence in the elongating growth and yield of plants (Tables 2 and 4). The females did not differ in toxic effect from the males.

The nature of Phleum green stripe disease agent

Typical for many gramineous plant viruses transmitted by leafhoppers and planthoppers are the yellowish streaks and striations of

varying length and width on leaf blades and sheaths. In this respect PGSV closely resembles EWSMV. However, in the latter the streaks are yellow, pale yellowish or tinged with red; no evidence of green is present. If these striations appear in seedlings at the 4–5-leaf stage, the plants cease growing completely and die long before maturity. The symptoms of PGSV, on the other hand, are more mild on oats and barley: the size of the stripes does not change and the plants do not stop growing at an early stage or die. On spring wheat PGSV symptoms resemble most those of EWSMV, but the plants do not die prematurely. When grains develop on wheat, they are not shriveled as in EWSMV, but wrinkled, and growth is checked. 'Apu' spring wheat proved to be more susceptible to PGSV than the other wheat cultivars tested.

Some confusion is possible in distinguishing PGSV symptoms on timothy from the toxic striations caused by the aphid *Cuernavaca mueblei* (Börner) (FRÖHLICH 1959/60). However, the distinct yellow striations caused by the aphid on timothy leaves and shoots are always limited to only such parts of the plants where the aphids are sucking, whereas the pale green stripes of PGSV are systemic, developing in several shoots and leaves of timothy, and the whole plants are weak in growth.

The investigations carried out to determine the nature of injuries produced by *M. sordidula* have shown that a disease agent most resembling a virus is involved. In our trials certain facts appeared which cannot be explained other than by stating that *M. sordidula* can act as a virus vector:

1. The symptoms of the injury are most likely some known planthopper transmitted gramineous viruses. The symptoms are systemic occurring as readily in the lateral shoots as in the main shoot which was inoculated.

2. The intensity of symptoms was relatively constant, when infected at the same developmental stage of a plant, quite independently of the length of feeding time. Six hours

feeding time was sufficient to produce all the symptoms typical of PGSV.

3. The length of incubation time for PGSV in plants (10 to 40 days, on average 18) is typical of persistent planthopperborne viruses.

4. A great number of the planthoppers in a population caused no PGSV symptoms at all, but of the infective planthoppers 70–82 % transmitted the disease more than once, and as many as 14–23 % caused injury in at least four successive test plants. If the infective ability had occurred at random in the entire leafhopper population, the above figures would have been much smaller.

5. In acquisition feeding trials some planthoppers originally incapable of causing injury, became capable of producing PGSV-symptoms only after receiving an acquisition feed, and this was manifested after an incubation period of 26–37 days. This is characteristic for persistent and circulative leafhopper and planthopper borne viruses (IKÄHEIMO 1961, IKÄHEIMO and RAATIKAINEN 1961, PRŮŠA et al. 1959, SLYKHUIS and WATSON 1958, VACKE and PRŮŠA 1961).

The gradual decrease in infective ability manifested in the successive tests may indicate that the concentration of the disease agent in planthoppers decreases if there is no new acquisition from infected plants, and that it cannot perhaps multiply in the vector (SLYKHUIS 1963) but only in cereals and timothy. In the latter case, the symptoms are visible at least one year, and the vector percentage of *M. sordidula* rises during nymphal development in the spring.

PGSV does not seem to be pathogenic to its vector.

Dicranotropis hamata, one specimen of which proved to be a PGSV vector, is known to be able to transmit OSDV (IKÄHEIMO and RAATIKAINEN 1963, LINDSTEN 1961 b), and CTDA (LINDSTEN et al. 1973), also. Because of the very limited material available, this species needs further studies to establish its ability transmit PGSV.

The significance of PGSV and *M. sordidula*

The name of this new virus-like disease agent, the *Pbleum* green stripe virus, was chosen to indicate the importance of timothy as a source of infection. Although detailed studies on the transference of the virus-like agent from the timothy by means of *M. sordidula* are lacking, the observations obtained reveal the significant position of timothy in the virus cycle. The rising of the vector percentage during the nymphal period of the development of the vector on timothy, and the high vector percentage in June, just before migration time for *M. sordidula* in both young and old timothy leys indicates timothy to be the most important source of PGSV infection.

The yield loss in infected timothy plants was very distinct, although it had not been measured. The decrease in grain yield of infected oats and barley were statistically highly significant, and the infection of wheat may lead to complete failure of crops. However, the numbers of infected plants in the fields have been small. This is due to the life cycle and low population density of *M. sordidula*.

PGSV hibernates both in the nymphs of *M. sordidula* and in timothy. The virus is transmitted into timothy leys and spring cereals

mainly by macropterous migrating plant-hoppers. The significance of *M. sordidula* as a vector of PGSV is probably greatest in old timothy leys in southern Finland, where the species occurs most commonly and where virus infected timothy plants are most often found. In such places the virus may be significant as a factor causing crop losses.

Considering the facts that the density of the macropterous individuals of *M. sordidula* is rather low and the migration period occurs later than that of the vectors of OSDV and EWSMV (*Javesella pellucida*, *J. obscurella*, and *Dicranotropis hamata*), it seems that PGSV cannot cause great damage in the form of crop losses.

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SELOSTUS

Kyttökaskas, *Megadelphax sordidula* (Stål) (Hom., Delphacidae) timotein viherjuovaviruksen (PGSV) vektorina

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Maatalouden
tutkimuskeskus

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Kyttökaskas, *Megadelphax sordidula* (Stål) todettiin entuudestaan tuntemattoman viruksen kaltaisen taudinaiheuttajan, timotein viherjuovaviruksen (*Phleum green stripe virus*) vektoriksi. Se aiheutti kaurassa, ohrassa ja timoteissa vaalean vihreitä juovia ja viiruja, jotka usein ulottuivat lehtilavan päästä päähän. Tauti aikaansai myös kasvien kasvun ja sadon heikkenemistä. Kevätvehnäajikkeessa 'Apu' vioitukset olivat samankaltaista, mutta huomattavasti ankarampia. Sen kasvu pysähtyi tavallisesti kokonaan ja kasvupiste tuhoutui jo aikaisessa vaiheessa. Juovat ja viirut vehnässä olivat väriltään keltaisia — vaalean vihreitä. Muissa vehnäajikkeissa vioitussymptomit eivät olleet yhtä ankaria. Vehnässä symptomit muistuttivat paljon vehnän juovamosaiikkiviruksen (EWSMV) oireita, mutta selviä eroja on todettu. PGSV alensi vioittuneiden kaurajen satoa 27—33 %, ohran satoa 46 % ja kevätsvehnän ('Apu') 98 %. Saastuneet timoteiskasvit kasvoivat paljon heikommin kuin vastavat terveet. Symptomit säilyivät timoteissa ainakin vuoden ajan.

Timotein viherjuovaviruksen inkubaatioaika kasveissa oli 26—37 vrk. ja kasveissa keskimäärin 18 vrk. Lyhin infektoitumiseen johtanut imentäaika oli 6 tuntia.

Timotei on ilmeisesti tärkein PGSV:n tartuntalähde. Vioitussymptomeja on todettu eri-ikäisistä timoteipelloista Etelä- ja Lounais-Suomesta. Timotein iästä riippumattomasti vektorien prosentuaalinen osuus *M. sordidula*-kaskaista voi nousta yli 40 %. Vaikka sairastuneissa kasveissa sadon aleneminen on huomattavaa, saattaa timotein viherjuovaviruksella ja kyttökaskaalla olla merkitystä vain paikallisesti timotein rehusadon alentajana. Tämä johtuu paitsi kaskaan alhaisesta populaatiitiheydestä, myös pitkäsiipisten kaskaiden melko alhaisesta suhteellisesta määrästä sekä myöhäisestä lentoajasta.

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