THE HOST PLANT RANGE OF THE SWEDE MIDGE (CONTARINIA NASTURTII KIEFFER) WITH SPECIAL REFERENCE TO TYPES OF PLANT DAMAGE

Met een samenvatting: De waardplantenreeks van de koolgalmug (Contarinia nasturtii Kieffer) en de door deze galmug veroorzaakte beschadigingen

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INTRODUCTION

During 1950 and 1951 I made an intensive study [1]), under the direction of Dr H. F. BARNES at Rothamsted Experimental Station, of the host plant range of the Swede Midge (*Contarinia nasturtii* KIEFFER) and the type of gall it causes. Pending the publication of the details of this investigation, it can be stated that in England the Swede Midge was found to have a large number of hitherto unsuspected host plants. The conclusions of BOVIEN (1950) and BARNES (1950) were confirmed, i.e., that midges bred from flower galls would oviposit on leaves and vice versa.

The purpose of this paper is to describe the methods used in this type of biological investigation and to give an account of the results obtained during 1952 in the Netherlands.

Thanks to the courtesy of Dr. J. G. TEN HOUTEN, Director of the I.P.O., Dr. S. LEEFMANS, Head of the Entomological Laboratory of the I.P.O. at Amsterdam, whose interest and help in the problem I much appreciate, and Dr. C. J. H. FRANSSEN, Entomologist in Amsterdam, facilities were afforded me to work there during June and July 1952. In this connection I wish to mention the help given to me by Mr. W. C. NIJVELDT and other members of the I.P.O. staff. I also acknowledge with thanks a grant from the Agricultural Research Council which enabled me to visit the Netherlands. I am indebted to Mr. V. STANSFIELD of Rothamsted Experimental Station for the photographs in this paper.

METHODS

It is necessary to have a good supply of live midges for such investigations. An easily accessible source of material is provided if a plot of ground known to be infested with the midge is planted with host plants together with possible hosts and infestation is allowed to proceed unchecked.

The plants are inspected frequently for midge damage. When galls and full grown larvae are found, they are placed in standard emergence cages (Fig. 1). Each of these consists essentially of a pot of soil on which stands a lamp glass half full of damp horticultural fibre. The galls with the larvae are placed on the peat. The covering is of muslin sewn on to an iron ring. Emerging midges fly up and settle on the muslin where they can conveniently be caught alive in a small tube, or on an alcohol-wetted paintbrush and stored in alcohol if required for morphological examination.

[1]) The results are already embodied in a thesis submitted for the degree of M. Sc. in the University of Reading.

Midges thus reared are used in experiments. For preference, individual midges are selected for breeding. Tests can then be made to see if a midge bred from one host plant will mate with a midge from another host plant. The two midges are placed in a glass tube where they often mate quickly. They are then released on a host plant grown in a pot, covered by a muslin cage supported on canes (Fig. 2). Experiments without cross-mating tests are also made when midges bred from one plant are caged with another host plant, or with a host plant in a different stage of growth. Since the midges may live for as short a period as a single day, a close watch must be kept on their activity and oviposition. The development of galls resulting from the feeding of the larvae on the plant is then observed over the following days. Finally the newly emerging midges can be caught, counted and made into permanent slides or used for further experiments. The plants used in such experiments are kept in unheated insectaries or well-ventilated glass houses.

In this way it is possible to see, for example, if a midge bred from leaves will oviposit on flowers, to observe the type of damage caused and the length of time necessary for the development of the midges and their galls.

A close search of host plants and types of gall occurring in the field during the various stages of plant growth is also made, and galls with larvae from different localities are collected for breeding.

The investigation of the Swede Midge in the Netherlands broadly followed these lines. The I.P.O. garden in Amsterdam, already infested with the midge, was planted with crucifers, some of which were known to be hosts. The arrangement of the plot which was 45 feet long and 18 feet wide, with the rows approximately equidistant, is shown in Fig. 3. The midge was also collected from other localities in the Netherlands. Experiments were made on caged plants using midges bred from collected galls. Some experiments were also made in which ovipositing female midges were transferred from one host to others in different stages of growth.

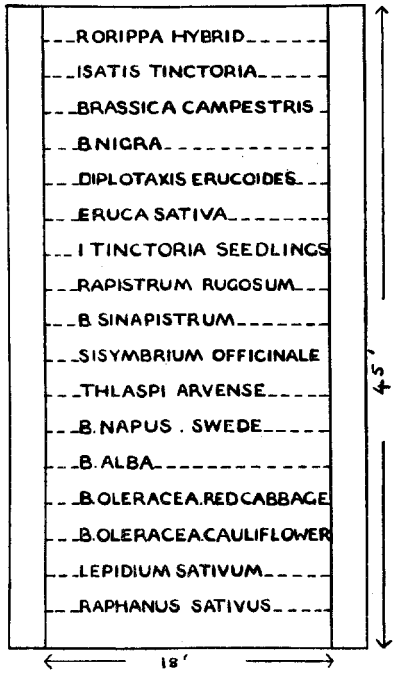

FIG. 3. The arrangement of the crucifers in the I.P.O. garden, Amsterdam

Schema van het Cruciferen-veldje in de tuin van het Entom. Lab. van het I.P.O. te Amsterdam

TYPES OF GALLS

The midge was found to cause four types of damage. These consisted of, first, closed, swollen flower buds, originally described by KIEFFER (1888), known as bellflowers (Fig. 4), and a second type of damage to flowering shoots, previously undescribed, which can be termed an inflorescence gall. In this, the inflorescence head consists of small buds with very short peduncles or none, the axis is very short

and the larvae live among the crowded flower buds (Fig. 5). Crinkling and puckering of the leaf tissue was also found (Fig. 6), and a fourth type of damage showed in infested shoots with swelling at the base of leaf stems and axils (Fig. 7). The last two were described by TAYLOR (1912).

The type of damage is not always clear-cut, for example several plants were found with both inflorescence galls and crinkling of the leaves most closely associated with the inflorescence. One plant of *Isatis tinctoria* growing in the I.P.O. garden exhibited all four types of damage at the same time, the older flowers were closed and swollen, small inflorescences clustered and short, individual leaves crinkled and leaf shoots up the flowering stem had swollen bases. In some plants flower heads were found with larger, outer buds swollen and closed and the central portion of very young buds clustered to form the typical inflorescence gall.

THE INCIDENCE OF THE MIDGE ON THE I.P.O. CRUCIFER PLOT

A natural infestation by the midge was found on fifteen different plants grown in the I.P.O. garden, Amsterdam. These are shown in Table 1, with the types of damage found. Host plants not previously known in the Netherlands are marked thus*.

TABLE 1. The incidence of *Contarinia nasturtii* on the I.P.O. crucifer plot

TABEL 1. *Het voorkomen van Contarinia nasturtii op het proefveld van het I.P.O., beplant met Cruciferen*

Host Plant *Waardplant*	Type of damage *Aard van beschadiging*
**Brassica alba* (L.) BOISS.	Inflorescence gall and crinkle-leaf
**B. campestris* L.	Bell-flower
B. Napus L.	Crinkle-leaf
**B. nigra* (L.) KOCH	Crinkle-leaf
B. oleracea L. (cauliflower)	Bell-flower, crinkle-leaf, leaf-axil
B. oleracea (red cabbage)	Crinkle-leaf, leaf-axil
B. sinapistrum BOISS. (*B. sinapis* VIS.)	Inflorescence, crinkle-leaf, leaf-axil
**Eruca sativa* GARS.	Inflorescence, bell-flower
**Isatis tinctoria* L.	Bell-flower, inflorescence gall, crinkle-leaf
**Lepidium sativum* L.	Inflorescence
Raphanus sativus L.	Bell-flower, inflorescence
**Rapistrum rugosum* (L.) ALL.	Inflorescence, crinkle-leaf
Rorippa hybrid	Bell-flower, inflorescence, leaf-axil
**Sisymbrium officinale* (L.) SCOP.	Crinkle-leaf, shoots
**Thlaspi arvense* L.	Inflorescence, crinkle-leaf, leaf-axil

THE OCCURRENCE OF THE MIDGE IN THE FIELD

The midge was found on a variety of cruciferous plants in other localities in the Netherlands. These are summarised in Table 2. A host plant not previously known in the Netherlands is denoted thus*.

TABLE 2. The occurrence of the midge on plants in the field
TABEL 2. *Het voorkomen van de galmug op planten in het veld*

Host plant *Waardplant*	Type of damage *Aard van beschadiging*	Locality *Vindplaats*
B. campestris L.	Inflorescence	Betondorp, Amsterdam
B. campestris L.	Inflorescence, bellflower and shoots	Botanic Gardens, Leiden
B. campestris L.	Shoot and leaf	Technical University gardens, Delft
B. Napus L.	Inflorescence, bellflower	Botanic gardens, Amsterdam
B. Napus L.	Inflorescence	Technical University gardens, Delft
B. oleracea L. (cauliflower)	Bell-flower	's-Gravenzande, Hoek van Holland, Naaldwijk
B. Rapa L.	Crinkle-leaf	Winkel, N.-Holland
B. Rapa L. var. *rapifera*	Crinkle-leaf	Technical University garden, Delft
**Eruca sativa* GARS.	Inflorescence	Botanic gardens, Amsterdam
Eruca sativa GARS.	Bell-flower	Botanic gardens, Leiden
**Isatis tinctoria* L.	Crinkle-leaf and shoots	Technical University garden, Delft
Raphanus sativus L.	Bell-flower	Technical University garden, Delft
**Raphanus sativus* L. var. *nigra*	Bell-flower	Technical University garden, Delft
Rorippa spp.	Bell-flower	I.P.O., Wageningen
Rorippa spp.	Bell-flower	River Maas, Grubbenvorst and Velden, S. Limburg
Sisymbrium officinale (L.) SCOP.	Inflorescence	Kruislaan, Amsterdam

EXPERIMENTAL RESULTS

Experiments were made to test the theory that biological races of the midge exist, restricted in their host plant range and causing only one type of gall. It is not possible to recognise such races by studying morphological characters. Tests for behaviour differences were made with midges caged with host plants in various stages of growth and differing from those on which the midges were bred.

Experiments with midges bred from leaves

Mating occurred between midges bred from leaves and others bred from flowers. The midge from *Brassica Napus* leaves cross-mated with the midge from bell-flowers of *Raphanus sativus*. One male from leaves of *Isatis tinctoria* mated first with a female from bell-flowers of *Raphanus sativus* and again with one from the flowers of *Brassica oleracea* (cauliflower). No breeding was made from these crosses.

A number of experiments was made with midges bred from the leaves of *B. Napus* var. *oleifera* (colza). They oviposited on flowers, leaves and shoots of seven different host plants: *Brassica alba, B. nigra, B. sinapistrum, Eruca sativa, Isatis tinctoria, Lepidium sativum* and *Rapistrum rugosum*. The developing larvae caused the typical bell-flower and inflorescence galls, crinkled leaves and swelling of young growing shoots. In some cases more than one type of damage was seen on a single plant. In each case midges subsequently emerged. Table 3 summarises these results.

Two experiments in which the colza leaf midges were placed on plants in leaf gave no result. The host plants were *B. oleracea* (red cabbage) and *B. Napus* (swede). Possible reasons for failure will be discussed later.

TABLE 3. Host plants of *C. nasturtii* bred on colza leaves and types of damage
TABEL 3. *Voedselplanten van C. nasturtii, opgekweekt op koolzaadbladeren, en aard van beschadiging*

Host plant *Waardplant*	Type of damage produced *Aard van beschadiging*
Brassica alba (L.) BOISS.	(*a*) Inflorescence galls with associated crinkled leaves (*b*) Inflorescence galls
B. nigra (L.) KOCH	Gall of young growing shoots
B. sinapistrum BOISS. (*B. sinapis* VIS.)	Inflorescence galls
Eruca sativa GARS.	Crinkle-leaves, inflorescence and bellflower galls
Isatis tinctoria L. (no flowers on plant)	Crinkle-leaves
Lepidium sativum L.	Inflorescence galls
Rapistrum rugosum (L.) ALL.	Inflorescence galls

Two experiments were made using midges from *B. Napus* (swede) crinkled leaves. Both were successful, in the one case the midges bred on *Rapistrum rugosum*, causing inflorescence galls, and in the other on *Diplotaxis erucoides*, where inflorescence galls and crinkle-leaf galls were made.

Experiments with midges bred from flowers

Midges bred from the two types of flower damage were seen to cross-mate when a male from the inflorescence of *Lepidium sativum* mated with a female bred from the bell-flower galls of *Raphanus sativus*.

Midges bred from flowers were found to cause more than one type of gall. A female from the inflorescence of *Rapistrum rugosum* bred successfully on *Raphanus sativus*, the larvae making both crinkle-leaf and inflorescence galls. A midge from the bell-flowers of the *Rorippa* hybrid oviposited on the leaves of *Isatis tinctoria* and one live larva was seen, though no midges emerged.

Midges from cauliflower bell-flower galls were seen to oviposit on the leaves of *Raphanus sativus*, and caused inflorescence galls on *Brassica nigra* and bell-flowers on *Rorippa*.

Some experiments with flower midges gave no result. No further developments were seen when radish flower midges were caged with *B. alba* and *B. Napus* and when cauliflower bell-flower midges were caged with cauliflower, red cabbage, swede and woad, all plants being in the leaf stage. Midges from inflorescences of *Eruca sativa* and *Lepidium sativum* did not breed when caged with radish and red cabbage respectively.

The transference of ovipositing females to different host plants

Fertilised female midges were placed on caged host plants and watched continuously. When oviposition was established, they were caught and placed on another host plant in a different stage of growth and watched again to see if oviposition continued. The process was repeated using as many different host plants as available.

Two midges, both bred from leaf shoots of colza were found to oviposit on

the flower buds of the *Rorippa* hybrid. When moved to flowering shoots of *Thlaspi arvense*, one of them continued to lay eggs on the flower buds.

Two more midges, also bred from colza leaf shoots were found to oviposit on the sepals of *Eruca sativa* flowers. One also laid eggs on the inflorescence axis. This female was caught and caged with *B. Napus* (swede) leaves, where it oviposited at the base of the leaves. It was then moved to the flowers of *Lepidium sativum* where it laid eggs among the buds, and when next caged with the leaves of *Isatis tinctoria* it laid eggs at the base of the leaves. It was then caught again and placed on the flowers of *Lychnis dioica* (Caryophyllaceae), never recorded as a host plant. It left the plant at once and rested on the muslin cage. This may have been because the host was unsuitable, or because the midge had no more eggs to lay.

In each case, egg-laying proceeded within a few minutes of being placed on the new host. This last experiment is illustrated diagrammatically in Fig. 8.

Galls did not develop in all cases as some of the shoots used, which had been picked and placed in water, died very quickly. Larvae and galls were found thirteen days later on the *Lepidium sativum* and *Thlaspi arvense*.

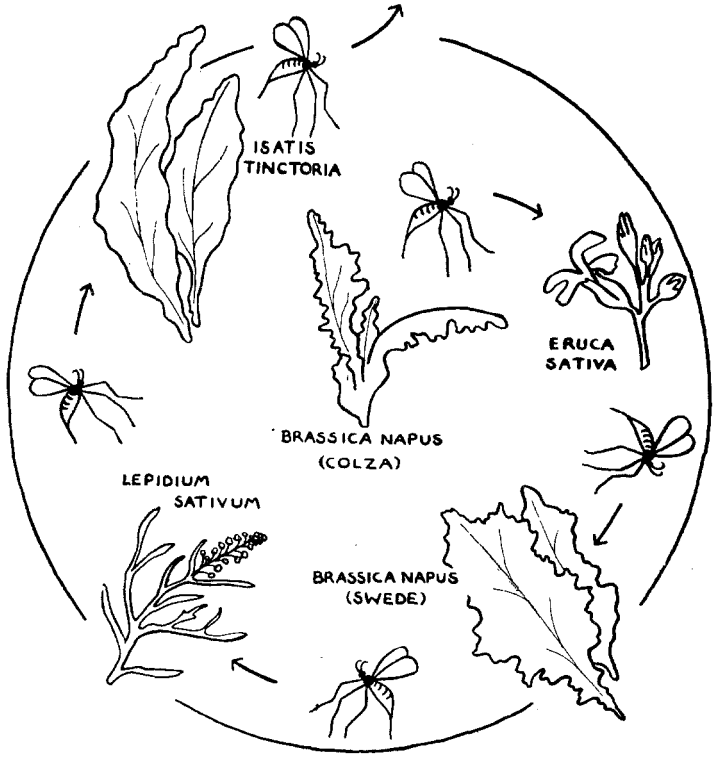

FIG. 8. Diagrammatic representation of an experiment in oviposition. A fertilized female (*C. nasturtii*) reared from Colza oviposited on several plants one after the other.
Schematische voorstelling van een ovipositie-proef. Een bevrucht wijfje van C. nasturtii, verkregen uit koolzaad, zette achtereenvolgens eieren af op de andere in het schema vermelde planten.

The relationship between the type of gall and the stage of plant growth

Two preliminary experiments were tried. Four shoots of the *Rorippa* hybrid with yellow buds and well-developed flower stems, and four with green buds and scarcely developed flower stems were selected. Each bunch of shoots was placed in a jar of water in a muslin cage. One male and six female midges bred from the leaf shoots of colza were placed in each cage.

Fourteen days later conspicuous galls were seen. On the shoots picked with yellow buds seven bell-flower galls and one inflorescence gall were counted. On the shoots with less-developed buds, inflorescence galls were seen with one bell-flower gall. In both cases larvae left the galls six days later and the midges began to emerge after another week.

THRESHOLD TEMPERATURE OF OVIPOSITION

The minimum temperature when oviposition was observed was 16^0 C. Oviposition occurred up to 26^0 C but at this temperature the midges appeared less active than at lower temperatures. The most favourable temperature appeared to be about 22^0 C.

DISCUSSION

The host plant range of *C. nasturtii* among the Cruciferae is very wide and its extent is still probably not fully known. A change-over from one host to another can be made without any apparent difficulty.

It has been demonstrated that in Holland midges bred from leaves can cause bell-flowers, inflorescence galls, crinkle-leaf and leaf-shoot galls. Midges from bell-flowers have been shown to oviposit on leaves and cause inflorescence galls, but some experiments with these midges when caged with plants in leaf failed. The possibility of a race restricted to bell-flowers and living side by side with others capable of oviposition on other parts of the plant including the flowers must be considered carefully. It is impossible to ascertain whether midges bred out of bell-flowers collected in the field are really restricted to the flowers, or if they are derived originally from midges capable of causing a number of types of gall. Furthermore, as far as is known, the life-cycle of bell-flower midges does not differ from that of midges causing several types of damage, thus the question arises, what becomes of midges emerging from flower galls when cruciferous plants are not in flower? Do they die, or are sufficient host plants always in the correct stage of growth for oviposition to result in the production of more bell-flowers? No evidence of alternating generations from flowers to leaves has been found, but it is possible, however, that some such phenomenon, loosely depending on the natural growth cycle of the host plants does exist.

The experiments in which the midges from flowers did not establish a generation on leaves represent negative evidence for the existence of a specialised race and so too much importance must not be attached to them for the following reasons. Observation has shown that midges oviposit on young, actively growing tissue. The bell-flower midges emerged rather late in the season and the host plants were old. Further experiments are needed using plants in a series of growth from the first leaf onwards. Experiments may also fail because of adverse

external conditions, such as unsuitable temperature or the unsuspected presence of a predator.

Experimental evidence and observation under natural conditions point very strongly to the conclusion that the different types of gall depend on the stage of plant growth at the time of oviposition. If small, leafy shoots are available, eggs are laid and larvae develop on the protective base of the shoots, or at the base of young leaves causing crinkling. If the inflorescence is barely formed, eggs are laid on the axis and among the embryo buds, the whole structure then develops with a shortened axis and clustered buds. If individual flower buds are present when the midges emerge, eggs are laid on the buds themselves, which fail to open and exhibit the typical bell-flower. Galls are not seen on leaves if young flowers are available, or on open, mature flowers and very rarely on large, old leaves. This may be due to the physical condition of the plant in age, to a biochemical factor connected with senescence or because slowing-down of the plant growth makes protection for the larvae impossible, or to a combination of such factors. This matter requires investigation.

SUMMARY

1. A description of the methods used for obtaining a supply of midges and the technique of breeding is given. The methods used in investigating the host plant range of the Swede Midge (*Contarinia nasturtii* KIEFFER) are explained.

2. A short summary is made of the various types of plant malformation and the occurrence of several types of damage seen on single plants.

3. The incidence of the Swede Midge on the I.P.O. crucifer plot during June and July 1952 and also in some other localities in the Netherlands is recorded.

4. The results of experiments to test the host plant range and the type of damage caused are next set out. It was found that midges bred from flowers cross-mated with those from leaves and from inflorescence heads of different host plants. The following host plants, new to the Netherlands, were found: – *Brassica alba*, *B. nigra*, *Diplotaxis erucoides*, *Eruca sativa*, *Isatis tinctoria*, *Lepidium sativum* and *Rapistrum rugosum*. Midges bred from leaves were found to breed successfully on flowers, inflorescences, leaves and shoots and those from inflorescences bred on leaves and inflorescences. Midges bred from individual flowers also caused inflorescence and flower galls and were seen to oviposit on leaves. It was found possible to transfer ovipositing females to a variety of host plant in different stages of growth.

5. The question of a biological race of *C. nasturtii* restricted to a particular type of gall is discussed, bearing in mind that, should such a race exist, it must be present side by side with the midges found to cause several types of gall. It has been demonstrated that the type of gall is largely dependent on the stage of growth of the plant.

SAMENVATTING

Een beschrijving van de methoden, die toegepast kunnen worden voor het verkrijgen van de gewenste hoeveelheden galmuggen, die nodig zijn voor het uitvoeren van experimenten als de onderhavige, wordt gegeven. Ook wordt de kweektechniek beschreven. De methoden, gebezigd voor het onderzoek inzake

de waardplantenreeks van de koolgalmug (*Contarinia nasturtii* KIEFFER), worden toegelicht.

Een overzicht wordt gegeven van de verschillende typen van beschadiging, die de aantasting kan verwekken nl. 1) de zgn. belknoppen (zie fig. 4); 2) een verkorting van de internodiën van de bloeiwijzen en een verkorting van de bloemstelen (fig. 5); 3) een rimpelen en plooien van het bladweefsel (fig. 6) en 4) een opzwelling van de voet van de bladstelen en de oksels (fig. 7). Het voorkomen van de koolgalmug op verschillende Cruciferen in de maanden Juni en Juli 1952 op het proefveldje van het I.P.O., dat speciaal ten behoeve van het onderzoek van Miss STOKES met verschillende soorten kruisbloemigen beplant was, wordt in tabel 1 vermeld. In tabel 2 wordt een opsomming gegeven van de waardplanten, waarop deze galmug te velde aangetroffen werd. Uit het onderzoek naar de waardplantenreeks van de galmug bleek, dat galmuggen gekweekt uit bloemen gemakkelijk gekruist konden worden met galmuggen, welke verkregen waren uit bladeren of bloeiwijzen van verschillende waardplanten.

De volgende waardplanten, die als zodanig nieuw voor Nederland zijn, werden gevonden: *Brassica alba*, *B. nigra*, *Diplotaxis erucoides*, *Eruca sativa*, *Isatis tinctoria*, *Lepidium sativum* en *Rapistrum rugosum*.

Galmuggen, verkregen uit bladeren, bleken met succes bloemen, bloeiwijzen, bladeren en scheuten te infecteren, terwijl de nakomelingschap zich hierin ook normaal verder ontwikkelde. Galmuggen, verkregen uit de bloeiwijzen, konden op dezelfde wijze met succes verder gekweekt worden op bladeren en bloeiwijzen. Galmuggen, verkregen uit afzonderlijke bloemen, verwekten een misvorming van de bloeiwijzen en ook bloemgallen; bovendien werd waargenomen, dat zij eieren afzetten op de bladeren. Het bleek mogelijk om wijfjes, die bezig waren met het afzetten van eieren, over te brengen op een reeks van waardplanten, verkerende in verschillende groeistadia.

Het eventueel bestaan van een biologisch ras van *C. nasturtii* in Nederland, dat gebonden zou zijn aan een bepaald type gal, nl. de belknop, wordt in discussie gebracht; hierbij moet men bedenken dat, indien er zulk een ras mocht bestaan, dit aanwezig moet zijn naast rassen waarvan de galmuggen in staat zijn gebleken verschillende soorten van gallen te kunnen verwekken.

Tenslotte werd nog aangetoond dat de aard van de verwekte gal in sterke mate afhankelijk is van het ontwikkelingsstadium, waarin de plant verkeert.

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