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AMELIORATION DES PLANTES POUR RESISTANCE CONTRE LES INSECTES ET LES ACARIENS

BREEDING FOR RESISTANCE TO INSECTS AND MITES

BULLETIN SROP
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INTERNATIONAL ORGANISATION FOR BIOLOGICAL
CONTROL OF NOXIOUS ANIMALS AND PLANTS

EUCARPIA/IOBC WORKING GROUP BREEDING FOR RESISTANCE TO INSECTS AND MITES

EUCARPIA/OILB GROUPE DE TRAVAIL AMELIORATION DES PLANTES POUR RESISTANCE CONTRE LES INSECTES ET LES ACARIENS

REPORT OF THE 1st MEETING HELD AT WAGENINGEN, THE NETHERLANDS
FROM 7 TO 9 DECEMBER 1976
RAPPORT DE LA 1ère REUNION TENUE DU 7 AU 9 DECEMBRE 1976
A WAGENINGEN, PAYS BAS

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INSTITUTE FOR HORTICULTURAL PLANT BREEDING
AGRICULTURAL UNIVERSITY: DEPARTMENTS OF ENTOMOLOGY
AND PLANT BREEDING

BULLETIN SROP
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INTRODUCTION

I do not hesitate to call this Eucarpia/OILB Congress a historic moment as to my knowledge this is the first time that in Europe entomologists meet together with plant breeders to unite their efforts to obtain insect resistant varieties.

It is an amazing fact that although it was proved already over a 100 years ago by the use of Phylloxera resistant grape rootstocks that insect resistance may not only save production but even our spiritual welfare, that it was such a long time before breeding for resistance against pests aroused an interest comparable with that for resistance breeding against diseases. Undoubtedly some of the reasons for this were the impressive successes obtained by chemical control on the one hand and insufficient cooperation between plant breeders and entomologists on the other.

However, the rapid changes in our modern society also fundamentally affected our views on disease and pest control. It appeared that not everything in the garden of chemistry was lovely. Pests developed resistance against pesticides. People became more keenly aware of the dangers of chemical products to health and environment. Underdeveloped starved countries often lack the money, technical know-how and equipment to protect their crops effectively by chemical measures. These considerations caused a new reflection on the strategy of pest control. It was realized that we can live with insects, provided their number is kept below the economic threshold level and that an overkill is neither necessary nor desirable. Phytopathologists and entomologists became strongly interested in integrated and biological control. Plant breeders cast their looks, which had been focussed too long on disease resistance, on the possibilities of insect resistance. Both groups became aware of the mutual reinforcement which integrated control and pest resistance could bend to each other when combining the two.

I feel that now we stand at the beginning of a fascinating new era in plant breeding in which breeders and entomologists work closely together. In a large number of crops it has been proved how effectively resistance may control diseases. Some famous examples, mainly in

the U.S., prove that pest resistance opens up the same prospects. Breeding for pest resistance is by its complexity an intriguing challenge to the scientist. The many problems confronting him, such as the development of screening methods, the evaluation of data obtained and the translation of experimental results into the field situation require ingenuity and creativeness. I have no doubt that both being present to a high degree, this meeting has given all participants a strong stimulus to proceed with enthusiasm with their important research.

It is a praiseworthy achievement of the organizing committee, consisting of Miss H.D.M.Hollander, Ir.O.M.B. de Ponti, Ir.F.L. Dieleman en Dr.G.A.M. van Marrewijk, to provide the proceedings so quickly after the congress. This underlines the significance and scientific importance of the congress.

C. Dorsman

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THE SEARCH FOR RESISTANCE TO DELIA BRASSICAE IN CRUCIFERS AND PSILA ROSAE IN CARROTS

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INTRODUCTION

In recent years it has become increasingly difficult to obtain adequate levels of control of some dipterous pests of vegetable crops partly because the organo-phosphorus and carbamate insecticides do not appear to be as efficient as their predecessors used to be and also because consumers now demand such low levels of pest incidence and crop damage. In the 1960's a research programme was begun to search for alternative control measures for certain vegetable pests and, as an extension of this work, six years ago work commenced on studies of resistance in vegetable crops to root fly pests. Joint projects between the Entomology and Plant Breeding Sections at Wellesbourne were set up for these studies and in the initial phase we have concentrated on a search for resistance and the necessary development of methods for assessing this resistance. The approach to these projects has, to a large extent, been governed by the supplies of insects. Abundant supplies of both field and laboratory-reared Delia brassicae are available at Wellesbourne and so testing has been possible at all times of the year. In contrast, we have experienced difficulty in rearing large numbers of Psila rosae and therefore much of our work on carrots has been confined to field experiments.

RESISTANCE TO Delia brassicae IN CRUCIFERS

Cabbage (Brassicae oleracea L. var. capitata L.), cauliflower (B. oleracea L. var. botrytis L.), Brussels sprouts (B. oleracea L. var. gemmifera L.) and radish (Raphanus sativus L.) have been included in these activities. For the development of techniques for testing plants and assessing their resistance we have used radish extensively. Radish is valuable as an experimental tool because it is readily attacked by Delia brassicae, it is economical on space and soon reaches maturity. Generation times for this crop are much shorter than those for the Brassica species and so, in a relatively short period, it is hoped to gain experience with radish which may be of value in studies of Brassica crops.

Non-preference resistance. Non-preference resistance to Delia brassicae has been studied in radish and cauliflower in the laboratory and in Brussels sprouts, cabbage, cauliflower and radish in the field. The laboratory techniques were described by Ellis & Hardman (1975). Test plants were fully randomised on a turntable inside a large two-tiered test chamber containing a known number of

flies, the apparatus being housed in a controlled environment room. Delia brassicae eggs laid around test plants were collected at regular intervals, extracted using a flotation technique and finally counted. More than one batch of plants could be tested in an experiment by exposing them alternately in the chamber. Plants representing the extremes of the range of preference discovered in these tests were saved and seeded. With radish, three further cycles of selection and testing have been completed. The technique has given highly consistent results and shown that there are heritable differences both between and within cultivars of radish and cauliflowers in their attractiveness to cabbage root fly.

Soil samples collected three times each week for 2-3 wk from around plants tested in the field were processed to extract eggs by flotation. Consistent differences between and within cultivars of Brussels sprouts, cabbage, cauliflower and radish crops were detected and selections have been made of promising material.

In radish there is a cycle of changing attractiveness to egg-laying, one of the peaks of attractiveness being reached just prior to marketable size, when the hypocotyls of the plants are rapidly swelling. The changing pattern of egg-laying, illustrated for two cultivars in Figure 1, has been found to be similar in both

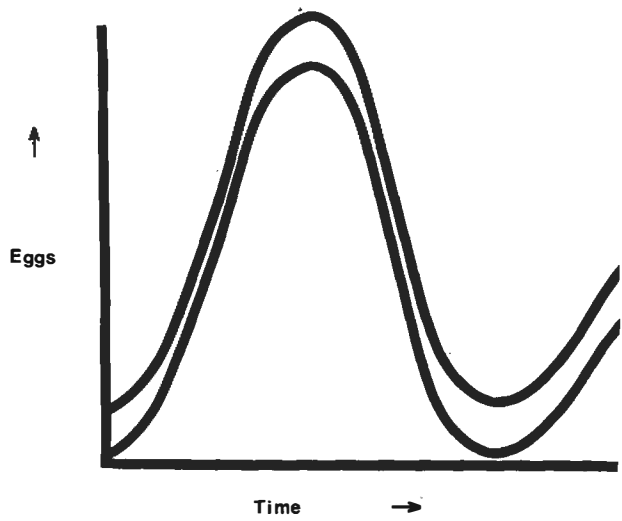

Figure 1. Cabbage root fly egg-laying around radish cultivars

laboratory and field experiments and for all the radish cultivars we have tested but the time scale varies according to the conditions of growth for the plants. It is clear that plant age, and therefore the physiological condition of the plant, is a critical factor in determining cabbage root fly egg-laying behaviour. Selection for the extremes of the range of preference in radish appears to have effected a shift in this cycle of attractiveness, the 'high' preference selections reaching their peak of attractiveness earlier than the 'low' preference ones (Figure 2).

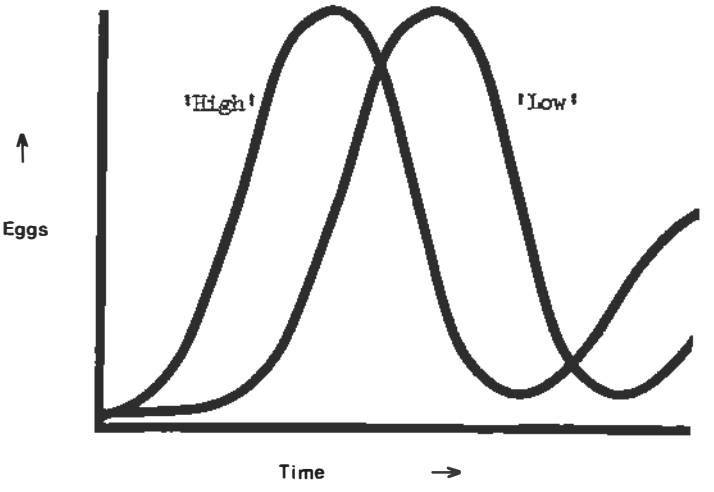

Figure 2. **Cabbage root fly egg-laying around radish selections**

The heritable non-preference resistance to Delia brassicae in one cultivar was maintained when the flies had no choice of host; three times as many eggs were laid on the susceptible selections as on the resistant ones.

It has not been possible to correlate any morphological characters or volatile isothiocyanate contents of the plants with the egg-laying preferences of Delia brassicae.

Antibiosis resistance. A technique for inoculating plants with Delia brassicae eggs and for assessing pupal numbers or damage to the plants has been developed. Test plants reared in the glass-house were inoculated with known numbers of eggs, samples of which were set aside for viability checks. Resistance of the plants was either assessed according to the time taken for 50% of plants

to wilt or from the numbers of pupae produced. Extraction of pupae from soil is very time-consuming and therefore it may be necessary to develop alternative methods of assessing insect performance on plants. A series of tests on radish to investigate damage to the roots and also plant survival has indicated the optimum number of eggs to be used for plants of a certain size. As with the non-preference studies plant age is a critical factor influencing the larval damage and thus plant survival. The damage to plants has been assessed by placing roots into one of five categories of root surface attack and then calculating a root damage index (Rolfe, 1969). Using this technique it is planned to compare the resistance of a range of cultivars of several crops.

Field Survival of Brassicas. Plots of cauliflowers, cabbages and Brussels sprouts not treated with insecticides have been exposed to field populations of *Delia brassicae* at Wellesbourne in the search for individual plants which are able to survive attack by this pest. This technique requires little attention and appears to be particularly valuable in sites where high populations of *Delia brassicae* regularly occur. In 1974, 2000 plants of one cauliflower cultivar, Asmer Hylite, were grown in the field at Wellesbourne and more than 95% had foliage symptoms of *Delia brassicae* damage eight weeks after transplanting. Forty survivors which appeared to have resisted attack 4 wk later were selected, lifted from the field, and seeded in the glasshouse. Further cycles of testing and selection are being done and may eventually result in cauliflower material resistant to cabbage root fly which is also not highly susceptible to other cruciferous pests.

RESISTANCE TO *Psila rosae* IN CARROTS

A high population of *Psila rosae* has been built up in part of the experimental ground at Wellesbourne and this site is used for the testing of carrots for their resistance to carrot fly. A wide range of carrot material collected from centres in many parts of the world has been screened for resistance in the field during the last 5 yrs. Carrots have been grown either as a maincrop or as stecklings, both being subjected to second generation attack of the flies. The plants were grown in rows 4.5 m long, 38 cm apart and sown at a density to achieve 110 plants/sq m for maincrop and 30 cm apart at about 160 plants/sq m for steckling trials. The carrot cultivars were randomised in three replicate blocks. Observations of plant condition and symptoms of attack were recorded during the growing season but assessment of resistance was based on examination of roots at harvest. Roots were lifted, washed, examined individually for carrot fly damage, and placed in one of five categories according to the area of root surface damaged by larvae. A root damage index was then calculated from the numbers of roots in each damage category to give a measure of the total amount of tissue affected.

Using this method, 84 different carrot cultivars or plant

breeders lines have been tested against carrot fly in the field. Many of the cultivars have been tested on more than one occasion. It has been possible to identify those which are consistently less severely attacked than others and also certain highly susceptible cultivars.

In 1974, thirty-one cultivars were grown in replicated trials both at Wellesbourne and at Cawood, Yorkshire. Carrot fly attack at Wellesbourne (94% attacked roots overall) was more severe than in Yorkshire (54% attacked roots). Certain cultivars performed consistently at both sites and were significantly different from each other, but a few others were inconsistent between sites.

Six carrot cultivars, Long Chantenay (Elsoms), St Valery (Sluis and Groot), Gelbe Rheinische (E. Luhn), Jaune Obtuse du Doubs (Clause), Sytan (Clause) and Vertou (Daehnfeldt) were consistently less susceptible than most other cultivars in the screening trials. The least attacked roots of these cultivars have been selected and seed produced for further study.

DISCUSSION

Much of our effort in the initial phase of these projects has been devoted to the development of reliable methods of assessing resistance. Ideally, the testing and breeding of plant material needs to proceed uninterrupted in field, laboratory or glasshouse. Certain inconsistencies in early experiments have indicated that environmental factors influence the interplay of plants and insects. At least with crucifers plant age is clearly a critical factor and needs to be taken into account. The behaviour of the flies when offered different degrees of choice of host crop also needs to be fully investigated.

Consistent differences occur both between and within cultivars of crucifers and carrot crops in their resistance to Delia brassicae and Psila rosae. Before breeding programmes can be set up to integrate the resistance to fly pests with other desirable characters, it is necessary first to investigate to what extent the differences discovered so far are heritable and whether a response to selection for resistance can be maintained.

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SOME PRELIMINARY DATA ON RESEARCH INTO CARROT FLY (PSILA ROSAE) RESISTANCE

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Introduction

The maggots of the carrot fly, which penetrate into the carrot roots, cause considerable damage to this crop in the Netherlands every year. Until now, control has been done with insecticides.

In 1973 it was decided to investigate the possibilities of breeding carrot cultivars resistant to this pest. This programme is carried out in close cooperation with the Institute for Phytopathological Research (IPO).

The following is a review of the results obtained in the last 3 years.

Material and methods

From 1973 to 1975 a large number of strains of carrot cultivars grown in the Netherlands and elsewhere were tested. Also a number of populations produced in other breeding programmes of the IVT were included.

Testing was done in the open on a plot of which it was known from experiences of the IPO that heavy attacks by this insect could be expected every year. The trials were in 8 replicates with plots of 4 rows of 1 m. length. Sowing was done in May. From each plot 50 roots of the two centre rows were harvested and checked for the incidence of maggots at the end of September or beginning of October.

Results

Infestation levels from 1973-1975

In Table 1 the % of infested roots of the different populations is demonstrated:

- In the first year of most strains 70-90% of the roots were attacked a small number showed a heavier attack, but a certain number showed a lower degree of attack. The lowest percentage of infested

roots found was 44%. Significant differences were assessed.
- In 1974 attack by maggots was more serious. No accessions with less than 90% infested roots were found. The differences were not significant.
- In 1975 the degree of attack was intermediate between 1973 and 1974. Significant differences occurred.

Table 1. Percentages infested roots in different carrot varieties tested in 1973-1975

Year	Number tested	% of infested roots				
		<50	50-70	70-90	90-100	100
1973	97	6	33	52	6	
1974	82				69	13
1975	47	2	5	35	3	2

The infestation of the more resistant numbers from '73 in '74 and '75

The most resistant numbers of 1973 were also sown out in 1974 and 1975. The results with some of them are presented in Table 2.

Table 2. Percentages of infested roots of the most resistant populations of 1973 in 1974 and 1975

Year	Vertou	Pioneer line	Rubica line	Rubica	Rialto line	Amst. forcing line	Nantes line	Tantal
1973	44	44	48	49	50	53	54	55
1974	98	100	93	97	99	99	99	99
1975	77	76	70	81	74	79	67	86

As can be seen from this table, in 1974 these numbers were heavily attacked. In 1975 the degree of attack dit not differ clearly from that of most of the other populations.

Results with S1's of healthy roots in 1975

From the most resistant strains detected in 1973 about 150 healthy plants were selected and selfed in 1974. The S1's obtained were sown out in 1975 and compared with the parent populations.

The average % of infested roots of the 148 S1's tested was about as high (76%) as the average % of attacked roots of the 17

parents (78%). However, a small number of the S1's showed a higher infestation than that of the parents: of a total of 148 S1's 11 showed an infestation more than 20% lower than that of the parents. The lowest % of attack found was 19.

Correlation between degree of attack and covering of the soil in 1973.

In 1973 it was found that the numbers with the highest percentages of attacked roots also gave the best covering of the soil by the foliage. It was precisely the most resistant numbers which showed the poorest stand. In 1974, in which much heavier attacks were experienced, no such relation was observed.

Table 3. Relation between % of infested roots and stand (1 = poor,----, 5 = good)

% of infested roots	Number	Stand			
		2	2-3	3-4	4-5
		frequency (%)			
<60	18	6	50	39	6
60 - 80	44	2	39	52	6
>80	34		5	68	26

Discussion

These are the main results so far. The question arises: are there prospects of breeding resistant cultivars in the way described? I think a definite answer to this question cannot yet be given. There are some indications that resistance can be improved by propagating healthy plants from the most resistant populations. But it is not sure that the most resistant S1's were indeed more resistant than their parents, as most of these S1's had a poor stand. And this factor decreases attack by maggots of the carrot root fly. A poor stand is caused by the fact that the germination capacity of the S1 seeds is sometimes low.

From the most resistant S1's healthy plants were selected and selfed in 1976. More information on the occurrence of resistance in our material will become available in 1977, when the S2's will be tested. In 1977 also the S1's from healthy plants selected in 1974 when the attack was very severe, will be sown out.

If we should not succeed in this way, more refined screening methods may be needed. In 1974 the infestation on the most resistant numbers of 1973 was as heavy as that on the more susceptible numbers, but it was only recorded if the roots were infested or not. It is conceivable that the most resistant numbers of 1973 also showed a certain degree of resistance in 1974, not in respect of the % of

attacked roots, but perhaps in respect of the number of maggots per attacked root. This aspect needs further study.

Are there any other sources of resistance ? In the tests mainly strains of normal varieties and breeding populations directly derived from them were sown out. Some white carrot varieties were also heavily attacked. Some sources of wild carrots, collected in the environs of Wageningen, showed some resistance. But this is presumably caused by the annual character of this material, by which the plants bolt directly after sowing, forming a woody root unattractive to maggots.

In conclusion it can be said: some first steps have been taken in the field of breeding carrot fly resistant carrot varieties, but much is still uncertain and unknown about the prospects of this breeding programme, and it seems not unlikely that more complicated selection methods must be applied in the future to obtain useful results.

RECENT STUDIES ON THE EFFECT OF PLANT VARIETY ON *TETRANYCHUS URTICAE* AND *PANONYCHUS ULMI* BIOLOGY

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In our previous work the hypothetical pattern of plant finding and acceptance by Tetranychus urticae Koch was described /Dąbrowski, 1976/. Certain amino acids, sugars, vitamins and phenolic compounds were classified as the feeding stimulants, inhibitors or deterrens.

Our present work was designed to find the differences in suitability of certain rose, strawberry and apple cultivars as the host plant for two species of spider mites: polyphagous Tetranychus urticae Koch and oligophagous Panonychus ulmi /Koch/. An attempt was made to explain the differences on the basis of chemical content of leaves of cultivars used in the test.

TETRANYCHUS URTICAE

The fecundity of T. urticae females on leaf disks cut out from four cultivars of Rosa hybrida as well as from foliage of five other Rosa species was analysed during the growing season of 1974 and 1975. Distinctly lower fecundity, especially in June and July was observed on Rosa rubiginosa /12.5-31.6 eggs per one female during a week/ and cv. Baccara /8.9-37.6/ than on other roses tested. The average fecundity of females on leaves of Super Star, Montezuma and Sutters Gold was 18.2-54.3 eggs per week, and on R. damascena, R. corüfolia and R. sweginzonii was 32.0-66.7.

Similar differences in fecundity and in the preimaginal development of this mite was found on foliage of three related species of Crataegus. On leaves of C. coccinea the fecundity was low /4.8-5.6/ and the mortality of larvae high. The T. urticae fecundity was higher on C. oxycantha /11.5-12.2/ and on C. monogyna leaves /20.8-34.0/. However, the fecundity of T. urticaefemales on leaves of Crataegus was significantly lower than on the roses.

Biochemical analyses of Rosa and Crataegus foliage are made to identify a mechanism involved in the resistance of Rosa rubiginosa and C. coccinea to this spider mite.

Distinct differences were found in the suitability of thirteen strawberry cultivars as food plants for T. urticae females. On leaves of sensitive cultivars Gorella, Cavalier, Tioga, Talizman and Purpuratka /American old cultivar. commonly grown during previous years in Poland/ the fecundity of T. urticae was higher than on foliage of Regina, Senga Sengana and Macherauchs Frühernte. The fecundity changed during the growing season. In May, at flowering time, the fecundity was highly undifferentiated between the cultivars. More distinct differences appeared in June, July and August. During the last two month the fecundity generaly decreased. Our earlier observations on the better suitability of old leaves for T. urticae development and fecundity during the whole growing season were confirmed in this experiment.

The suitability of 57 clones selected by the plant breeders from new crosses of certain strawberry cultivars for T. urticae was compared to the suitability of foliage of the cultivars used as the parental plants in the breeding programme. Cv. Purpuratka use as the male increased the sensitivity of progenies received from the crossings with other cultivars. The increase was high for the offspring of Asieta x Purpuratka and Senga Sengana x Purpuratka. The sensivity of progenies of Regina and Talizman x Purpuratka did not significantly differ in comparison to the sensitivity of the maternal plants. Results of reciprocally cross between sensitive cv. Purpuratka and moderately resistant cv. Senga Sengana depended from using Purpuratka as the male or as the female.

The offspring of Senga Sengana x Purpuratka always showed high sensivity to T. urticae /the fecundity was 16.8; 23.5 and 21.4 in July, August and September, respectively/ and the offsprin of Purpuratka x Senga Sengana - moderate resistance /8.9; 9.4 and 5.9, respectively/. However, only observations on wide plant material would demonstate if some extra-nuclear factors are involved in the strawberry suitability for T. urticae.

It was stated that the differences in suitability of strawberry leaves for T. urticae depended not only on the cultivar or time in the growing season but also on the kind of field where the cultivars was grown. Therefore a suggestion was made that a soil condition could influence the variation in suitability of strawberry cultivars for T. urticae.

In additional experiments we tried to estimate the role of N, P, K treatments on the nutritional value of certain

strawberry cultivars as host plants for T. urticae. Development and fecundity of the mites were measured on leaf disks cut out from plants of two sensitive cultivars /Purpuratka and Dixieland/, one moderate resistant /Senga Sengana/ and one resistant /Macherauch's Frühernte/ grown in pots under six fertilizer treatments. The data presented in Table 1 represents an average fecundity calculated from five values obtained monthly from May to September. Generally, the increased dose of mineral fertilizer has caused an increase of T. urticae fecundity and a developmental intensity, however, the increase depends upon the cultivar tested. There is not a simple correlation between an increase of fertilizer dose and the fecundity of this mite. It seems that the mutual ratio between N, P and K in the dose has influenced the female fecundity to the same degree as the level of fertilization of the plants. On the leaves of Dixieland plants grown under $N_3P_3K_3$ treatment the highest average fecundity /42.6 eggs per one female per week/ was observed.

Table 1. Effect of fertilizer treatment on four strawberry cultivars on the fecundity of T. urticae females / no. of eggs per female during week/.

Treatment	Purpuratka		Dixieland		Senga	Seng.	Macherauch's	
	no.	in%	no.	in%	no.	in%	no.	in%
$N_0P_0K_0$	18.6	100	17.0	100	17.2	100	12.5	100
$N_1P_1K_1$	21.2	113.8	32.0	188	20.8	120.8	22.9	182.7
$N_1P_3K_1$	32.0	172.0	35.4	208	33.2	193.1	29.8	238.1
$N_1P_1K_3$	23.6	126.5	29.2	172	29.2	169.7	21.3	170.2
$N_3P_1K_1$	27.9	150.0	29.5	173	21.5	125.0	27.3	218.5
$N_3P_3K_3$	33.4	179.1	42.6	251	34.9	202.6	31.8	254.2

The highest increase of T. urticae fecundity /above 250%/ was observed on Purpuratka and Macherauch's plants under $N_3P_3K_3$ treatment in comparison to untreated plants. The increase of nutrient dose from $N_0P_0K_0$ level to $N_1P_1K_1$ changed the T. urticae fecundity to above 180% on foliage of Dixieland and Macherauch's plants.

Strawberry cultivars tested differ in their sensitivity to the same fertilizer treatment. The same dose supplied to various strawberry cultivars could influence in a different manner the changes in their nutritional suitability for T. urticae development.

We could not estimate on the basis of our experiment described above if the increased mite fecundity after mineral fertilization of the plants was due to the increased intensity of T. urticae feeding on the leaves or due to the increased nutritional value of the treated strawberry plants. To explain this relationship an experiment using C^{14} was conducted under greenhouse and laboratory conditions. The intensity of T. urticae feeding on four strawberry cultivars grown under four fertilizer treatment was measured. Small plants were fed with 100 µC of C^{14} introduced with $Na_2C^{14}O_3$ and lactic acid for a period of one hour. Later fifty females were placed for three hours to feed on the leaves. The radioactivity of the females and of leaf disks taken from foliage undemaged by the mites was measured in a scincilation counter.

The data presented in Table 2 show that the fertilizer treatment and the cultivar of strawberry affect the feeding intensity, the fecundity of T. urticae females and the biology of preimaginal instars. The intensity of feeding

Table 2. Biology and feeding intensity of T. urticae females on leaves of four strawberry cultivars under four fertilizer treatments.

Cultivar	Treatment	% of adults obtained	No. of eggs per 1 o/7d	Radioactivity female	leaf
Purpuratka	5xoptimal	9.1	32.9	135.1	$5.3x10^6$
	1xoptimal	48.0	22.4	261.2	$4.2x10^6$
	0.5xoptimal	56.0	14.0	37.1	$4.3x10^6$
	untreated	1.3	0.0	11.0	$4.3x10^6$
Dixieland	5xoptimal	41.4	38.5	133.9	$3.8x10^6$
	1xoptimal	41.4	18.2	150.8	$3.7x10^6$
	0.5xoptimal	29.2	19.6	117.6	$3.1x10^6$
	untreated	0.0	0.0	-	$4.2x10^6$
Talizman	5xoptimal	60.0	31.5	49.0	$3.2x10^6$
	1xoptimal	21.3	17.5	201.6	$3.8x10^6$
	0.5xoptimal	16.0	18,9	114.6	$4.3x10^6$
	untreated	0.0	0.0	75.4	$4.1x10^6$
Macherauch's	5xoptimal	32.0	33.6	90.3	$4.0x10^6$
	1xoptimal	24.0	14.7	257.9	$3.6x10^6$
	0.5xoptimal	11.9	12.6	18.6	$3.3x10^6$
	untreated	0.0	0.0	35.4	$3.3x10^6$

usually was the highest on plants under optimal treatment. Lower doses or the suboptimal dose decreased the feeding intensity of the females. The fecundity, however, was higher on all cultivars treated with the highest dose. The development of preimaginal instars was better on all pla-

nts treated with suboptimal doses with the exception of Purpuratka cultivar. Only 9.1% of the initial population reached adulthood, wheras under the same combination, 60% of the mites reached adulthood on Talizman foliage.

Biochemical analyses on the content of the strawberry leaves has disclosed that the high content of nitrogen and phosphorous in foliage was not directly correlated with the high fecundity of the females. Some additional, not yet identified chemical components have modified the nutritional suitability of strawberry plants for T. urticae.

PANONYCHUS ULMI

Our laboratory experiments using nearly 70 plant species and cultivars showed that even between species belonging to the Rosaceae family differences occured in their suitability for the growth and development of the preimaginal instars of P. ulmi. Most of the plant species which were gustatorily rejected by P. ulmi females provided also poor nutritional conditions for mite development /Dąbrowski and Bielak, 1975/. Again, Crataegus coccinea did not allow larvae of P. ulmi to finish their development and the fecundity of females was also low / 5.6 eggs per one female during a week in comparison to 20.8 on C. monogyna/.

The differences in the fecundity of P. ulmi were also observed on six apple cultivars under field conditions in Poland. Foliage of Red Delicious and Golden Delicious was colonized more intensely by the mites, than foliage of Jonathan. However, on the leaves of the same cultivar the fluctuation in the P. ulmi fecundity were observed during the growing season under laboratory conditions. This suggested that the change of seasons affected the nutritional value of leaves as food sources for this mite /Table 3/.

Table 3. Fecundity of P. ulmi females on leaves of some apple varieties /no. of eggs per one female during week/.

Beginning dates of experiment	Starking	Fantazja	Red Delic.	Mc Intosh	Bancroft	Jonathan
June 3	4.1	3.7	3.8	2.0	1.8	3.3
June 27	5.9	4.0	4.0	3.2	2.6	4.1
July 10	5.3	3.4	4.5	3.9	7.6	2.6
July 25	6.3	4.7	7.4	7.9	3.8	3.0
August 8	8.0	6.6	3.9	7.3	5.6	5.3
August 22	17.1	13.3	6.7	8.6	13.8	8.2
Total	46.7	35.7	30.3	32.9	35.2	26.5

Our biochemical analyses of apple leaves showed the existance of only small changes with some tendency to de-

crease at the end of the growing season in total N content, protein N and soluble N. More significant seasonal changes were found, however, in the concentration of phosphorous. Generally, the highest amount was observed in August for all cultivars tested.

There was not a simple positive correlation between the content of nitrogen and phosphorous in leaves of apple cultivars and the fecundity of P. ulmi. These two elements play various role in the plants. Because our biochemical analyses described only total concentration of these two elements, we can not explain what part of them occures in various plant compounds in the cells or in various coenzymes.

Young apple leaves contained more N and P than old leaves and the fecundity of P. ulmi was lower on young leaves. The nutritional value of young leaves rich in N and P is, however, lower than fully deveped leaves. The actively growing young leaves have not fully developed a photosynthetic apparatus. They need a suppy of energy for the processes of biochemical synthesis which intensively takes place in the cells. To synthesize the nucleic acids, auxins or chlorophyll the young tisues need more N and P than old cells where specific proteins or phospholipids already occur.

The content of K decreased and of Ca increased in late season in comparison to spring time. The foliage of Golden Delicious contained about 50% less K and more than 20% Ca than other cultivars tested in autumn. These elements act as antagonistic compounds and their mutual proportion in leaves affect the water content in cytoplasm and in the plant. Such changes in the host plant could modify the suitability of food for P. ulmi. The young and old leaves contained similar amounts of K, but twice or threefold the amount of Ca. It suggests the high content of water in plant cytoplasm. The role of K as an activator in protein metabolism and an activator for several enzymes involved in carbohydrate metabolism can explain its high content in young leaves.

The concetration of Mg and Fe increased in moderately older leaves in late season. This phenomena is associated with their role in the plant. Magnesium is a constituent of the chlorophyll molecule and it functions as an activator of the enzymes later involved in carbohydrate metabolism. Iron has a number of important functions in the overall metabolism of the plant, especially in the synthesis of chlorophyll and as a component of various flavoproteins active in biological oxidations. The high content of these two elements in leaves in autumn suggest the dominance of break-down processes in such leaves and the increase of

compounds more easily assimilated by P. ulmi. The foliage of Golden Delicious showed higher concentration of Mg during the whole growing season than the leaves of other apple cultivar tested. We may conclude that this mineral element has a direct positive effect on the biology of P. ulmi. The young foliage contained less Mg and Fe than moderately old and old leaves.

The concentration of Mn and Zn fluctuated during the season in apple cultivar, but it is not possible to relate this fluctuation with the fecundity of P. ulmi.

Our present research is designated to find the coefficients of correlation between the concentration of certain macro- and micro-elements, seventeen amino acids and three sugars in the foliage of cultivars tested and the fecundity and the intensity of preimaginal development of Panonychus ulmi.

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BREEDING OF CUCUMBER RESISTANT TO THE TWOSPOTTED SPIDER MITE (*TETRANYCHUS URTICAE* KOCH)

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INTRODUCTION

In the Netherlands about 1000 ha of cucumbers are grown in heated glasshouses every year. The environment in these glasshouses highly favours the development of the twospotted spider mite. Because of the well-known objèctions to an extensive use of pesticides we started a research program at our institute some years ago in order to investigate the possibilities of breeding resistant varieties. This paper briefly reviews several aspects of these investigations.

METHODS FOR ASSESSING THE RESISTANCE

Based on a thorough study of the host-parasite relationship on cucumber varieties with different levels of resistance, to be published elsewhere, two resistance tests were developed.

1. The laboratory test, in which the degree of acceptance and of reproduction is scored. After greasing the petiole of the first true leaf with 'Tangle foot' 20 female deutonymphs are placed on this leaf. After 10 days the mites left are counted and this gives a measure of acceptance. From these mites (about eight days old adults) five are placed on separate leaf disks and after three days the oviposition is observed. This is a measure of reproduction. These tests are carried out under controlled environmental conditions.
2. The damage index test, which is carried out under normal growing conditions in a glasshouse. Ten adult female mites are placed on the third leaf of each plant. During about eight weeks the development of the spider mite population is observed using a damage index scale of 0 to 5 similar to the one developed by the Glasshouse Crops Research Institute at Littlehampton (Growers' Bulletin No. 1, 1972: 13 pp.). The economic damage threshold lies at 1.9.

Variety	ORIGIN	ACCEPTANCE (%)	OVIPOSITION (per 3 days)
PI 220860	Korea	26	11.7
PI 279469	Japan	80	16.8
VARAMIN	Iran	86	17.7
HYBRID LGP.	USA	38	18.9
ROBIN 50	USA	61	21.3
SUSC.CONTR.	IVT	86	27.0

Table 1. Degree of acceptance and of reproduction of five resistant varieties and one susceptible (control) variety.

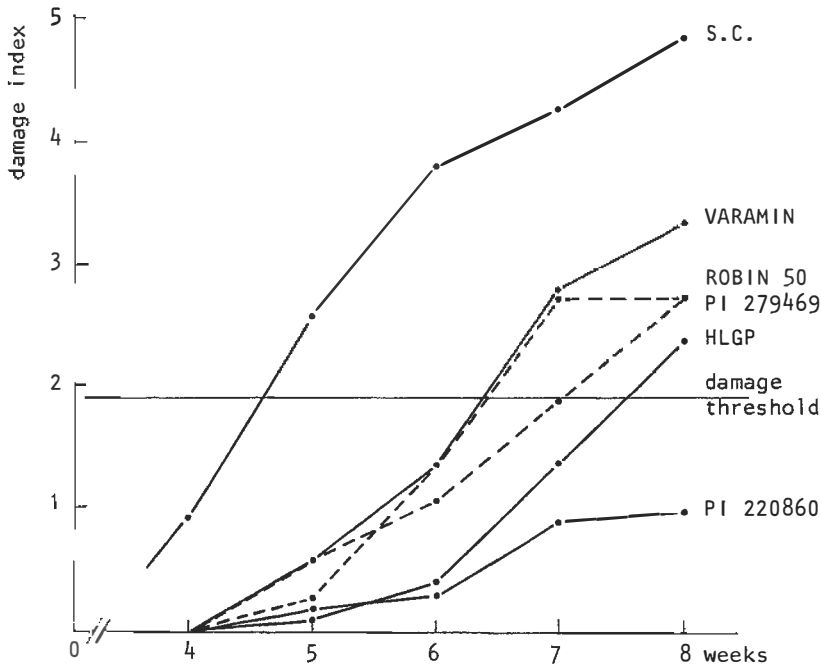

Figure 1. Development of populations of the twospotted spider mite during a period of eight weeks on five resistant and one susceptible variety, measured by the damage index.

SEARCH FOR SOURCES OF RESISTANCE

800 Varieties from the IVT Cucumis sativus collection were tested in a damage index test with one repetition of three plants. The 50 least attacked varieties were retested in a test with 3 repetitions of two plants each. These varieties were also tested in a laboratory test involving 15 plants per variety. Based on these tests the best 10 varieties have been selected for further breeding, genetic and other research. Table 1 and Figure 1 show the differences between five resistant varieties and one susceptible control variety in the tests described above. The outstanding results of PI 220860 and 'Hybrid LGP' in the damage index test are probably caused by the combination of low acceptance with low reproduction.

INCREASE OF RESISTANCE BY BREEDING

The above data demonstrate that only partially resistant varieties were found. Attempts were made to increase the level of resistance by crossing the most resistant varieties. Recently F_3 lines from selected F_2 plants were compared with their resistant parents. Some lines were selected which had a higher level of resistance than both parents. This was the case in the laboratory test as well as in the damage index test. In Figures 2 and 3 an example is given of the results of the cross 'Hybrid LGP' x 'Robin 50'.
These early results look promising and by continued crossing we will try to increase the level of resistance step by step to a very high level.

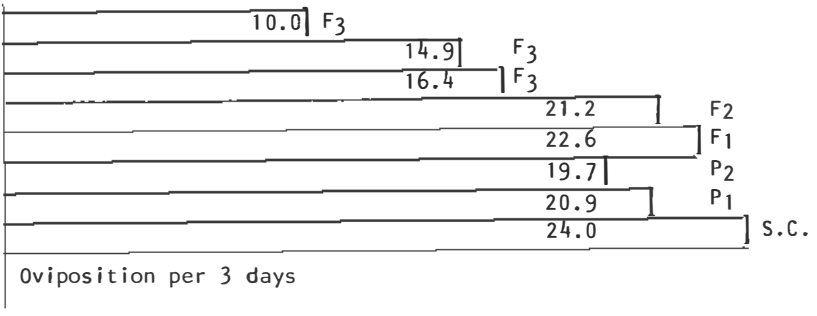

Figure 2. Degrees of reproduction of a susceptible variety (S.C.), two resistant varieties (P_1 = 'Hybrid LGP'; P_2 = 'Robin 50') and several generations originating from a cross between these two varieties.

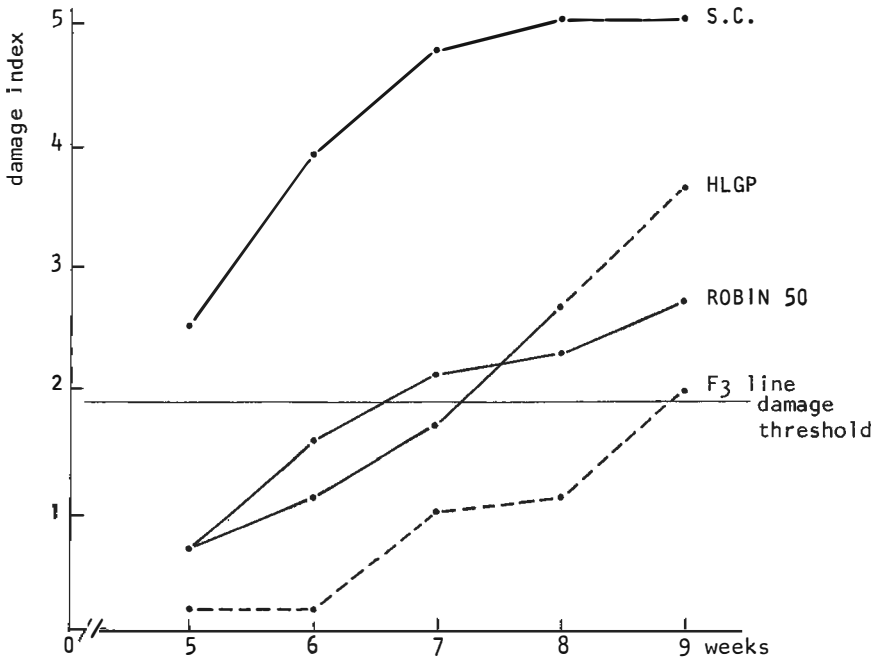

Figure 3. Development of populations of the twospotted spider mite during a period of nine weeks on a susceptible variety (S.C.), two resistant varieties and one F_3 line from a cross between these two resistant varieties.

THE SIGNIFICANCE OF CUCURBITACINE

DACOSTA & JONES (1971) have claimed that in cucumber the bitter principle is the main cause of resistance to the twospotted spider mite. Although this compound may contribute to the resistance, it is not the main factor, as appears from the following results obtained by us:

1. From the 800 varieties tested 799 were bitter and only one non-bitter. Only 10 varieties with an interesting level of resistance could be selected. The majority of the bitter varieties were susceptible.
2. With a semi-quantitative test the cucurbitacine contents of the true leaves of the 10 most resistant varieties were compared with those of 20 very susceptible varieties. The results shown in Figure 4 demonstrate that many of the resistant varieties contain the same amount of cucurbitacine as the susceptible ones. Only three resistant varieties are clearly more bitter.

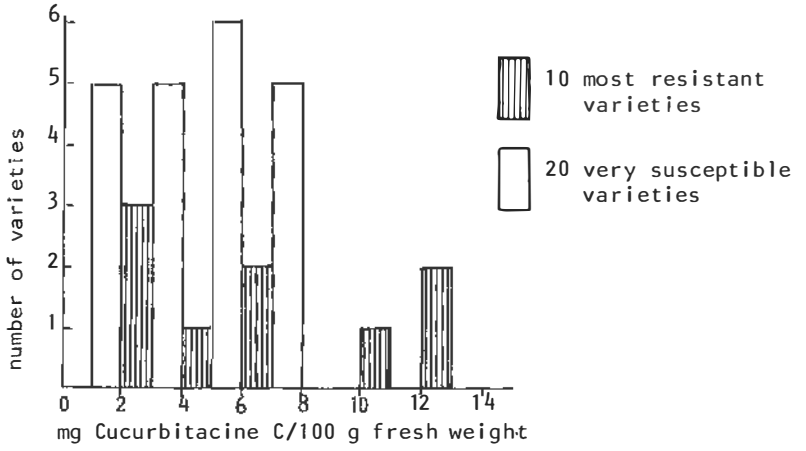

Figure 4. Comparison of the cucurbitacine content of the 10 most resistant and 20 very susceptible varieties.

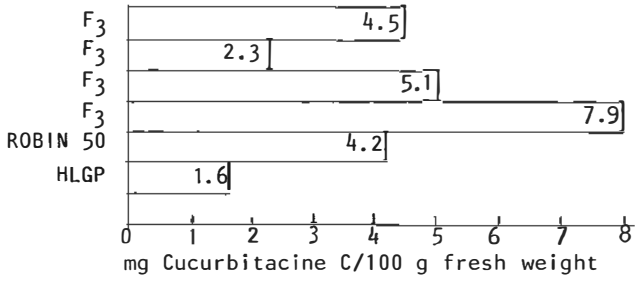

Figure 5. Comparison of the cucurbitacine content of two resistant varieties and four F_3 lines from a cross between these varieties.

3. The resistant F_3 lines mentioned in the previous chapter were selected without paying attention to the bitter content. If cucurbitacine were the main resistancefactor, selection for resistance with concurrent selection for cucurbitacine content should be practiced. The cucurbitacine contents of 4 F_3 lines of the cross 'Hybrid LGP' x 'Robin 50', which exceed both parents in degree of resistance, are compared with those of their parents. The results are shown in Figure 5. One F_3 line contained significantly more cucurbitacine than the most bitter parent, and one significantly less, whereas two

lines did not differ significantly. From these results it is far from certain that cucurbitacine is the main resistance factor.

FINAL REMARKS

The research will be continued along the lines indicated above. Much attention will be paid to the breeding of highly resistant lines. This might be facilitated by unravelling the genetic basis of the resistance, which part of the research is now in progress.

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EVALUATION OF DIFFERENT SCREENING TECHNIQUE FOR TESTING RESISTANCE IN BARLEY TO CEREAL APHIDS

by

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In the United Kingdom barley yellow dwarf virus (BYDV) (Oswald & Houston, 1951) is transmitted in the persistent manner by at least seven aphid species (Plumb, 1974). Normally the disease is widespread in cereals in the late summer with a minor effect on yield. However in south-western areas severe losses can occur, particularly in winter-sown cereals, due to infection caused by large numbers of infective vectors migrating in the autumn into the emerging crops, when the crops are most susceptible to virus infection (A'Brook, 1974, 1975). In this situation the main vectors, Rhopalosiphum padi (L.) and Macrosiphum (Sitobion) avenae (Fabr.), overwinter as apterous virginoparae on the cereal crop (George, 1974) and under favourable conditions can reproduce and spread the virus during the winter (A'Brook, 1974). This leads in some years to rapid reproduction and spread in the spring causing severe epiphytotics (Trow-Smith, 1976).

At the Welsh Plant Breeding Station, two approaches to this problem are being followed in barley, Hordeum vulgare L., the incorporation of tolerance to BYDV from Ethiopian cultivars into European backgrounds (Catherall & Boulton, 1976), and studies on resistance to the vectors, reported here. Both approaches are based on R.padi and the BYDV strains it transmits, these being the most important in the south-west.

In view of the situation described above we have decided to search for a number of sources of resistance in cereals, applicable to the persistent transmission of a virus by aphid vectors. Sources of non-preference would prevent the introduction of primary foci of infection by autumn migrants (a percentage of the autumn migrants of R.padi are

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alate exules, as well as gynoparae, in southern areas where the primary host. Prunus padus, is uncommon). Further sources of antibiosis (failure to settle, rapid probing and restricted feeding) would also inhibit virus transmission. Alternatively cultivars on which alatae settle, feed and remain would restrict infection to primary foci and if followed by an absence of secondary spread, would be a valuable attribute. Where secondary spread occurs during the winter and early spring, antibiosis in the form of low rates of reproduction and growth are required, with little interplant migration by apterae; these are parameters which probably conflict. Our initial investigations have been mainly in this area.

Three species of aphid were used, M. (S.) fragariae (Wlk.), Metopolophium dirhodum (Wlk.) and R.padi, chosen for ease of culture, their different feeding sites on cereals and local importance as BYDV vectors. Cultures were started from single apterae collected in the field and maintained on oats, Avena sativa L. Seven varieties of barley were tested, chosen for their widely different genetic background (Table 1).

Table 1. Barley varieties used in tests for resistance

Variety	Description
Mazurka	Spring variety on NIAB Recommended List
Sabarlis	Spring variety resistant to cereal cyst eelworm
DL 59	Indian variety resistant to R.maidis in India*
DL 107	Indian variety resistant to R.maidis in India*
DL 69	Indian variety susceptible to R.maidis in India*
Astrix	Winter variety on NIAB Recommended List
H.Roggors	Winter variety resistant to some strains of mildew

*J.D. Hayes, personal communication

Mature apterae were placed individually on each test plant and removed after they had deposited three nymphs. These nymphs were allowed to mature until they had produced up to a total of eight second-generation nymphs and the mothers removed. The second generation were weighed immediately on becoming adult apterae and dissected for counts of large and total numbers of embryos (we assumed that the large embryos represented nymphs deposited in the first few days, and the total number of embryos represented total fecundity). Irrespective of variety, a significant positive correlation was found between the live weight of

apterae and the number of large and total number of embryos in each species. This relationship of size of apterae and fecundity agrees with work on other aphid species, i.e., Aphis fabae Scop. (Dixon & Wratten, 1971; Taylor, 1975), R.padi (Dixon, 1976), R.insertum (Dewar unpublished) and for early nymphal production in Myzus persicae (Sulz.) (Lowe, 1974). The technique allowed aphids to develop naturally without crowding or disturbance and at population levels not affecting the physiology of the host variety. This technique required only one observation to be made thus allowing greater replication (a factor found important due to temperature and humidity gradients within the test area in the glasshouse). The technique does, however, suffer from the inability to make observations at a specific growth stage of the test crop and results can therefore be confounded with differential growth rates of the test varieties.

Table 2. Duncan's Multiple Range Test on mean weights (mg) of apterae on barley varieties

M. (S.) fragariae

Variety	Astrix	H.Roggors	Sabarlis	DL 59	Mazurka	DL 69	DL 107
Mean weight	0.5833	0.5900	0.6550	0.6983	0.7417	0.7733	0.8017

M. dirhodum

Variety	H.Roggors	DL 59	Astrix	DL 107	DL 69	Sabarlis	Mazurka
Mean weight	1.1500	1.2266	1.2366	1.2816	1.3283	1.4400	1.4683

R.padi

Variety	DL 59	Astrix	DL 107	H.Roggors	Sabarlis	DL 69	Mazurka
Mean weight	0.8016	0.8409	0.8800	0.9183	0.9300	0.9666	0.9866

Varieties connected by lines do not differ significantly at P = 0.05

Significant differences were found between the barley varieties in the mean live weights of apterae of each species. When subject to Duncan's Multiple Range Test the order of aphid weights on the varieties differed between species (Table 2), an expected result due to their different feeding site preferences. When varieties were scored for mean aptera weight and combined for the three species, the varieties fell into two groups, Astrix, H.Roggors and DL 59 having the lowest scores (i.e., lowest mean aphid weights) suggesting these to be more resistant. This effect may have been confounded with growth differences between the unvernalized winter varieties (Astrix and H.Roggors) and the spring varieties (Mazurka and Sabarlis) which do not require vernalization, but the results do suggest sources of resistance in the R.maidis (Fitch) resistant Indian varieties.

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SCREENING TECHNIQUES FOR THE DETERMINATION OF APHID RESISTANCE IN BARLEY

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In 1973 the departments of Entomology and Plant Breeding of Wageningen University of Agriculture started a joint project aiming at the detection and exploitation of aphid resistance in spring barley. The first objective was to develop simple efficient and reliable screening methods to detect differences in susceptibility between accessions.

Questions to be solved in the course of the experimental work, concern

(i) trial location: field, glasshouse or laboratory (single pots), cages.
(ii) inoculation: plant stage, inoculum size, inoculum composition, preconditioning, rearing.
(iii) assessment method: number of observations, sample size, sampling manner, counting, weighing or estimating.
(iv) trial lay-out: replications, plot size, number of accessions.

I. TRIAL LOCATION

This part concisely describes several methods of testing in the field and in the greenhouse, giving the pros and cons of each method and adding some of the results so far obtained.

1.1. Natural infestation in the field

This is the most simple way of testing. There are, however, some drawbacks, namely

(i) non-availability of the aphids at the right time and the right spot. Both in 1973 and 1974 our field experiments failed because of the low aphid densities in our trial fields.
(ii) unequal distribution over the field, which makes it necessary to introduce a high number of replicates. In 1975 we tested 30 Danish and Dutch commercial varieties for resistance to Sitobion avenae in a complete block design with four replicates by

counting aphid numbers in two 30-cm rows per plot. Though at the date the population density was highest, average scores ranged from 16 to 43 aphids per 30 cm, only a few cultivars could be traced that were significantly more susceptible than the others, as a result of the large intravarietal variation.

(iii) blending of aphid species. The occurrence of at least three aphid species in the same crop obstructs the testing procedures to some extent. As the species prefer different parts of the plants, at lower densities resistance assessments for separate species may be possible but not so damage (tolerance) assessment. Thus in 1976 in the absence of Rhopalosiphum padi it was possible to trace differences in susceptibility for both Metopolophium dirhodum and Sitobion avenae in the same plots of naturally infested spring barley varieties.

(iv) predators and parasites. These have free access and may reduce the aphid population.

(v) bad weather conditions. Strong wind and showers can destroy a population.

1.2. Field inoculation

This implies inoculation of test plots with reared aphids and may be significant when natural infestation holds off or is low. It has the disadvantages mentioned sub 1.1. (iv) and (v), the first even in a large measure because predators are likely to be attracted to this feed source. Thus, in an experiment conducted in 1976, five barley varieties sown in tussocks were inoculated with Sitobion avenae (10 aphids/plant) in six replicates. After one week, however, population density was not significantly higher than in the non-inoculated surrounding plots.

1.3. Field-cages

The use of cages in the field indisputably has a number of advantages:

(i) inoculation time, inoculum size and inoculum composition are under control.

(ii) contamination with other aphid species, predators and parasites is avoided or at least decreased.

(iii) weather influences (wind, rain) are reduced.

On the other hand, the introduction of cages creates many problems:

(i) trial expenses are high.

(ii) working with cages is time consuming and labour intensive, consequently the number of accessions or the number of replicates of a trial has to be diminished.

(iii) replicated assessment is difficult or impossible. An attempt to assess cage-contents more than once by lifting the cage and replacing it after counting in 1976 turned out to be a failure. Firstly because many aphids migrated directly after lifting and

secondly because it was impossible to replace the cage-pegs in the dried soil.

(iv) the environment (light conditions, humidity, temperature) is altered, which might affect the host-parasite relation.

Field cage trials were performed in 1975 and 1976. In these, use is made of modified Reitzel* cages, which are 150 cm high and 44 cm in diameter. The cages consist of a plastic-covered wire framework and a nylon gauze (monodur 300) cover which allows 80% of the light to penetrate. To consolidate the lower part of the wires can be pushed into the ground; an alternative way is the use of galvanized pegs.

One experiment included 30 commercial varieties laid out in a randomized block design with three replicates and one cage per plot. At ear emergence 100 Sitobion avenae adults and nymphs were put in each cage (ca. 1 aphid/tiller). The cages were lifted 24 days after infestation and aphid counts were made on 15 randomly chosen tillers. Total population amounts were determined by multiplying tiller number x average aphid number of the sample and adding the estimated number of alates concentrated at the top of the cage. Though aphid numbers per cage varied from about 300 to nearly 8000 no significant differences between varieties could be traced as a result of the tremendous within-variety variation. Besides, there was a very low correlation between the results of the cage experiment and those based on natural infestation of the cultivars concerned.

1.4. Greenhouse

Greenhouse experiments can be helpful in many respects. Apart from the pros of controlled inoculation and restriction of contamination, which they have in common with the field-cage tests, there are some specific advantages:

(i) influences of wind and rain are eliminated almost completely, and

(ii) trials can be performed in the off-season.

On the other hand,some doubt about the value of the results obtained under greenhouse conditions may be justified, because of the abnormal growing conditions which influence growth and development of the host, possibly resulting in an altered behaviour versus the parasite. In our experiments we observed different kinds of changed behaviour of the host:

*after Dr. J. Reitzel, Statens Plantepatologiske Forsøg, Lyngby, Denmark.

- plants stay vegetative. In a screening test with 600 barley accessions five accessions in the vegetative stage were among the seven that were the least susceptible to Sitobion.In a later experiment we found that susceptibility increased after heading. This is a strong indication that susceptibility depends on plant stage.
- the plants are rank and weak, which at least makes the evaluation rather difficult.
- plant development is accelerated. Consequently, the time between inoculation and ripening of the plants is short and assessments have to be done in a short lapse of time.

The crucial question is whether the results of glasshouse experiments are identical or comparable with those in the field. Hsu and Robinson (1962, 1963), who worked with Rhopalosiphum padi on barley, stated, that there was good agreement between glasshouse and field results; other literature data concerning this point are unknown to me.

2. INOCULATION

As for inoculation, many key-problems can be reduced to the simple questions - When?
- What?
and - How much?

The first question has a bearing on the plant stage in which inoculation should take place. Seedling tests appear very attractive. But it is at least questionable whether it is possible to evaluate properly the resistance to a parasite which prefers the ears and upper leaves like Sitobion avenae, in the seedling stage.

The next point concerns the nature and composition of the inoculum. In some of our experiments there were slight indications that the plant material on which the aphids are reared may influence the reactions towards the infested host (preconditioning). Concerning the composition of the inoculum it will be clear that in single plant tests this has to be as uniform as possible, otherwise differences in antibiosis might be suggested which are a result of differences in age or fitness of the individual aphids. In our detailed experiments L4 instars or young adults are generally used. In field cage experiments random samples of a fixed number of aphids in various stages of development are applied.

The size of the inoculum has been fixed at 1 aphid/tiller in most of our experiments. With this starting density population development is exponential and indisturbed by crowding-effects during ca. 4 weeks.

3. ASSESSMENT METHOD

Though the primary objective of the present investigations is searching for rapid screening methods, we have to take care that simplicity does not become the foe of reliability. Thus we can speculate about the question whether or not one assessment is enough. Single evaluations may suffice when the interrelation between host and parasite is well-known from earlier studies, e.g. when we know what plant stage is most suited for proper evaluation, or when we are assured that population density at a given moment provides a good reflection of the development in later phases. In other words, we have to know on what site on the population curve we are and that we can predict future or extrapolate former population size from the measured value. Apart from detail observations in single plant tests, these conditions will seldom be met.

In our experiments we have found repeatedly that the correlation between the aphid numbers in subsequent evaluations was low. As an example the behaviour of Sitobion avenae on 11 accessions in a greenhouse experiment with 38 varieties at three observation dates is shown (Table 1).

Accession	Assessment 1	2	3	Multiplication 1 → 2	2 → 3	Reaction type
T 7	39	7	72	0.2	10.3	
T 17	27	6	55	0.2	9.2	low-high
L114	35	12	133	0.4	10.9	
L 20	28	30	62	1.1	2.1	
L 19	32	36	84	1.1	2.4	high-low
0148	22	33	65	1.5	2.0	
D 72	23	25	72	1.1	2.9	
0 3	29	13	100	0.5	7.6	
N 24	28	16	69	0.6	4.4	average
0150	32	24	99	0.8	4.1	
T 10	24	24	89	1.0	3.8	

Table 1. Average aphid densities at threee assessments and multiplication factors of Sitobion avenae on 11 barley accessions in a greenhouse experiment in summer 1974.
1 = average aphid number/10 plants.
2 and 3 = average aphid numbers/plant.

This experiment suggested that there may be different "reaction types" relative to aphid resistance: Some varieties are very susceptible in the early stages and become more resistant later on, whereas others show the reverse reaction or have a constant level of susceptibility. Testing of this presumption failed to give conclusive results however.

A next point of importance is the method of assessment. With fungal disease use is often made of so-called assessment keys, picturally or otherwise standardized measures of disease or attack. As a result of the mostly irregular distribution of cereal aphids over the plant, we can not deal with it that way.

Estimating roughly the total aphid numbers per plant or tussock looks attractive at first sight, especially to trace big differences in susceptibility or to perform an initial selection in a large number of accessions. Thus, in 1973, we selected 38 varieties out of some 600 by scoring the aphid number after a scale ranging from 1 (low numbers) to 10 (extremely high numbers). Nevertheless,we have strong doubts about the value of the results. Apart even from the inoculation time (4 days after emergence), the evaluation was obscured by migration of aphids from overpopulated plants to less crowded neighbours and by the differences in developmental rate of accessions.

It is clear that to trace more subtle differences in susceptibility - which seems to be predominant in cereals as tested so far - we are thrown to counting or weighing of the aphids. The choice seems simple: weighing. Especially since we found out in an experiment under well-controlled conditions that the results of weighing and counting were in complete agreement. However, especially with larger numbers, collection of the aphids to weigh requires more labour (as a result of sticking of the aphids to the honey dew) than counting by a skilled person.

At this point the next problems turn up immediately: with how many tillers or plants do we have to do the counting (sample size) and in what way do we select the plants on which the counting is to be done (sampling manner)? As there is an absolute lack of conformity on this point between cereal aphid investigators and as sample size and sampling manner are often interrelated I confine myself to a compilation of the size-manner-combinations we have used so far:

(i) Randomly chosen plants according to a fixed pattern, e.g. four in each corner and the centre or seven on both diagonals of each plot.
(ii) One or two 30-cm rows per plot.
(iii) 10 tape-marked plants per plot.
(iv) Cutting off(different numbers) of randomly chosen tillers.

Methods (i) to (iii) have been applied in experiments with natural infestation, whereas method (iv) in many variants has been used in cage and glasshouse trials.

In the earlier mentioned field trial including 30 Danish and Dutch commercial spring barley varieties both methods 1 and 2 were tried out. Slightly significant differences in susceptibility between varieties were found with the aid of the 30-cm-row counts. In contrast to that, with the random-plant counts no significant differences were obtained. Besides, the correlation between the results of both assessment methods was low. It was thought first that differences in plant number in the 30-cm row might have affected the results, but from a covariance analysis it appeared that this presumption had to be rejected.

In the last summer aphid counts (of Sitobion avenae and Metopolophium dirhodum separately) were performed on tape-marked plants in a 6-replicates block design including 10 commercial and 30 non-commercial accessions. For both aphid species some accessions were significantly different, i.e. more susceptible to attack.

Cutting off tillers facilitates counting and this method is used in all cases where counting is impossible because of large aphid numbers, high plant density or bad attainability of the plants. The size of the sample is determined in dependence of the average total plant number, the number of observation dates planned, and the aphid density (less tillers at higher densities).

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TESTING FOR RESISTANCE TO APHIDS IN CEREALS AND SUGAR BEET

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Methods for assessing levels of resistance to aphids in sugar beet and cereals under glasshouse conditions have been developed with the aim that the tests should detect small differences in resistance, and that the methods should be sufficiently simple to enable large numbers of plants to be assessed. The breeding system of the crop exerts considerable influence on the development of test methods, and in this respect sugar beet and cereals offer a great contrast.

Sugar Beet

Infestations of Myzus persicae (Sulz.) normally occur on young beet plants in May and June, whilst infestations of Aphis fabae Scop. develop in June and may become large enough to damage beet in July. Potgrown plants are tested in the glasshouse for resistance to both aphids by the method which, outlined below, is described by Lowe (1974).

Young, vigorous plants are arranged touching each other in randomised blocks with at least 20 plants in each block. Apterous adults of M. persicae and A. fabae, from cultures on Brassica pekinensis and Vicia faba respectively, are released on the plants, three to five of each species per plant. After a few days the numbers of each species are recorded separately from each plant to give an assessment of resistance.

Sugar beet is an outbreeding crop which exhibits considerable diversity within varieties, and about thirty plants of a stock are considered necessary for assessment. A group of plants may be tested once for comparison of stocks or twice to allow selection (Lowe, 1974). In all cases the results are recorded before aphids born to the progeny of the introduced adults form a significant part of the population. Numbers of aphids of either species rarely exceed 200 on a plant, and are recorded either as counts, or as scores on a

0 to 9 system with intervals based on the residual variances in experiments where the aphids were counted (Table 1).

Table 1. Scoring for aphid infestation of sugar beet
For A. fabae and M. persicae, within 8 days of infestation. Scores are for aphids per plant - regardless of distribution.

Score	Descriptive estimate aphids/plant	Defined limits aphids/plant
0	5 or less	0 - 6
1	10 - 12	7 - 15
2	20	16 - 25
3	30 - 35	26 - 39
4	45 - 50	40 - 55
5	65	56 - 75
6	85	76 - 100
7	120	101 - 140
8	160	141 - 190
9	200 or more	over 191

This method has demonstrated resistance to both M. persicae and A. fabae amongst breeding stocks of beet (Lowe, 1974, 1975a). Resistance to one aphid species is usually associated with resistance to the other, and although a high degree of resistance has not been found, low levels of resistance are commonly observed. This resistance has been assessed on large plots in the field (Lowe, 1975a,b), and is judged to be worth inclusion in breeding programmes.

Cereals

Consideration of cereal aphids has been confined to Macrosiphum (Sitobion) avenae (Fabr.) and Metopolophium dirhodum (Wlk.), which are normally the most numerous species in summer infestations of wheat and barley in South and East England. S. avenae and M. dirhodum have been handled on these two crops in a similar manner; and, as with the aphids on beet, the two species have usually been placed together on the plants. For simplicity, the methods are described by reference to testing winter wheat with S. avenae.

Initially, as for sugar beet, plants were set out on glasshouse benches with considerable contact between plants, and numbers of aphids were counted a few days after release of adult aphids. Mean numbers (per plant) differed widely amongst varieties, but statistically significant differences were demonstrated only by using many replicates (Table 2). This approach has therefore been modified and

restricted to rough screening, for which the adult aphids are caged initially to ensure settling, and then left after release for three or four weeks before scoring aphid numbers on plants arranged with minimum contact.

Table 2. Mean numbers of S. avenae per plant on winter wheat. Aphids unrestricted, counted 3 to 5 days after introduction of 3 or 4 adults per plant, 16 replications.

	Wheat varieties				
	Joss Cambier	Nord Desprez	Maris Widgeon	Heines VII	Standard Error ±
Experiment 1 - in boot	19.8	18.4	9.2	14.8	2.7
Experiment 2 - ear emergence	16.4	6.9	3.2	4.9	1.9
Experiment 3 - anthesis	16.9	11.1	7.9	7.8	2.5

A preferred method assesses resistance from tillers caged between emergence of the flag leaf and the end of anthesis. Dialysis tubing is used to enclose the ear with one or two leaves, and has the advantage of permeability, which apparently minimises many of the effects of caging on plant physiology, although the tubing must be aged for some weeks before use to remove toxic vapour. Care is taken to grow the plants to a high standard of health and vigour.

Tests with caged tillers extend over approximately 1.5 aphid generations, with both the start-time and aphid densities controlled by conducting the tests in stages. First, adult S. avenae are held overnight on pieces of leaf of each variety in separate small boxes. Next day the leaf pieces with the new-born aphids only are placed on caged tillers of the same variety, 30 to 50 aphids per tiller. The young aphids are left to develop until the fourth instar when, except for dwarfed individuals, they are randomly redistributed three per tiller onto newly caged tillers of the same variety and age with eight to twelvefold replication. Counts are made after a further interval when groups of second generation aphids are evident.

Differences amongst wheat varieties in the mean number of S. avenae per caged tiller have been found to be statistically significant in most experiments using this method (Table 3), but the differences amongst varieties have often been inconsistent with successive batches of plants of the same varieties from serial sowings.

Table 3. Mean numbers of S. avenae per caged tiller of wheat. From 3 aphids/tiller, reared on the same variety.

	Wheat Variety				
	Joss Cambier	Nord Desprez	Maris Widgeon	Heines VII	Standard Error ±
Experiment A - Flag Leaf	32.4	32.9	46.7	47.8	4.6
Experiment B -Ear Emergence	30.0	13.6	13.5	12.2	3.6
Experiment C -Flag Leaf	24.0	43.0	46.0	28.9	4.7

However, results from experiments repeated with the same batches of plants have shown close agreement (Table 4). It is concluded that the method detects differences in aphid-resistance caused by variations of plant age or conditions of growth, and that such variations

Table 4. Mean numbers of S. avenae per caged tiller of wheat. From 3 aphids per tiller, reared on plants of the same variety and age

	Experiment 12		Experiment 13	
Wheat variety	Late milk*	Anthesis	Early dough	Early milk
Joss Cambier	45.8	16.8	72.5	26.7
Nord Desprez	44.3	19.0	62.3	22.5
Maris Widgeon	33.7	39.3	62.5	53.3
Standard Error (6 means)	±3.8		±6.1	

*At final observation

are large in comparison to the basic levels of inherited resistance in these varieties. In this situation assessment of resistance to S. avenae in a variety of wheat requires repeated tests. Since resistance must be effective in the field over a range of conditions, ~~consistent~~ performance in tests with some variation of growth is most likely to indicate useful resistance in a variety.

Discussion

It is worth considering the extent to which the nature of the plants has restricted the type of resistance detected. Sugar beet, a genetically heterogeneous crop, is tested at a stage when there is also great heterogeneity amongst the parts of the plant (Lowe, 1974).

Observations are made, therefore, on the whole individual plant and can be replicated only in repeated tests on the same plants. The movements of the aphids largely determine the results obtained and the resistance observed is mainly due to non-preference, or non-acceptance (van Marrewijk and de Ponti, 1975). In contrast, the method described for cereals depends on replicated plant units, supplied by the multiple tillers of genetically homogeneous plants. The restrictions imposed by the caging and manipulation of the aphids mean that any resistance is observed as antibiosis, the effects of which are accumulated over the test period. Other varietal properties, for example those related to preconditioning (van Marrewijk and de Ponti, 1975), may affect the percentage of aphids surviving the first stage, but the influence of these effects is not well estimated and is minimised by rejection of dwarfed aphids before the second stage. However, other forms of resistance may be effective, for instance non-acceptance in cereals (Table 2), whilst measurements of antibiosis, as relative growth rates (van Emden, 1969), have shown small but significant differences between beet stocks (Lowe, Biggerstaff and McCarthy, unpublished). There is a need therefore for methods to assess other aspects of resistance and thus make them accessible to the plant breeder.

The methods described here meet the requirement of testing plants in a condition near to that of the crop at the time of natural aphid attack (Lowe, 1974), and small differences in resistance can be detected by them in both beet and cereals. The number of beet plants tested is large enough to be useful in breeding work, but further work is needed before the testing of cereals can be simplified sufficiently for plant breeding.

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A CONTRIBUTION TO THE INFLUENCE OF FIELD SIZE ON THE DIAGNOSIS OF RESISTANT CULTIVARS

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The development of resistant plants against micro-organisms has been tackled more extensively than against insects. But now, as also can be concluded from this meeting, efforts are made to include the last-mentioned group. The hitherto existing trifling consideration using the difference of susceptibility of plants could be traced back to certain facts which have been gathered some years ago for typical insects. Therefore, it seems justified to point to this special case and to discuss at the same time respective proposals for solution.

In the cotton field of El Salvador from 1965 onwards the occurrence of the white fly Bemisia tabaci (Homopt., Aleyrodidae) increased. This insect is known to transfer a virus as well (KRAEMER 1966). As in the following years the yield reductions continued the investigations for solving the problem were supported by the Federal Republic of Germany since 1968. Based on experiments of MOUND (1965) it seemed to be possible that the damage was connected with differing cultivars susceptibility. According to own experiences (SCHÜTTE and BUHL 1968) with insecticide tests, larger plots should be used when the success of the control was not directly determined on the number of imagines migrating to the plots, but later on the descendants of the imagines. Therefore, the size of the plots used for testing the susceptibility of cultivars to B. tabaci should be about 1 ha. The performance of such tests was tried to dissuade me, on several occasions because resistance tests have been carried out since some years in El Salvador with the most popular cultivars. As all results obtained, however, based on experiments on small scale plots, tests

on larger ones seemed to be really necessary. Eventually the performance was granted. Probably because on one side the Government did not want to refuse a request of a guest, but on the other hand the size of the plots was reduced from 1 to 1/4 of a hectar. From Fig. 1 the arrangement and the size of the plots can be seen.

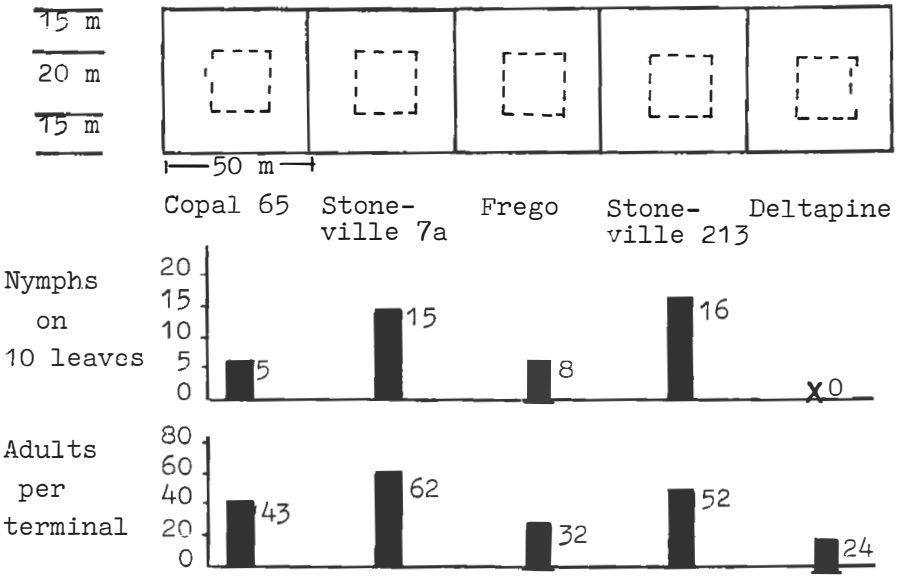

Figure 1 Size and position of the plots used and the population densities of Bemisia tabaci on five cotton cultivars.

Moreover it may be mentioned that the determination of the population density was carried out only in the centre of the plots. Furthermore, it may be recorded that at the time the cotton fields in El Salvador were sprayed about 30 times with insecticides during one season. As each of the 5 cultivars were grown on 1/4 ha the total experimental area amounted to 2,5 ha, including the corresponding large control plots. The experimental areas have not been excluded from the general spraying with insecticides because without using insecticides, the cotton plants, including buds and capsules, would have been destroyed completely by the insects. In consequence two results are only mentioned here:

1. the number of nymphs before applying the insecticides and

2. the number of imagines on shoot terminals at the end of the vegetation period when the number of insecticide applications was reduced.

From Fig. 1 can be recognized that both cultivars Stoneville 7a and Stoneville 213 were significantly (at p = 0,01 and p = 0,02) more infested than Deltapine, a cultivar grown extensively in former years. The differences are no doubt small in these short intervals of observation, but if the period for one generation of B. tabaci, which lasts only 14 days, is taken into consideration, it can be imagined that these small differences may operate a devastating effect during the course of approximately 8 generations up to the end of the vegetation period.

Investigations of MOUND (1965) revealed that the number of hairs of the plants was important for favouring or avoiding the cotton plants by the imagines, thus these cultivar differences are stated in Tab. 1 too. Both cultivars, Stoneville 7a and Stoneville 213 have more hairs than the others and especially more than Deltapine.

Table 1 Infestation of five cotton cultivars by Bemisia tabaci and number of hairs per leaf

	Cultivars				
	Copal 65	Stoneville 7a	Frego	Stoneville 213	Deltapine
Number of nymphs on 10 leaves	5	15	8	16	0
Number of hairs per leaf	27	80	27	47	18

This example which demonstrated the useful necessity of large plots for the determination of varietal differences, is to be opposed by another example in which very small plots were used.

In some still running investigations on the resistance of agricultural plants against the larvae of Melolontha melolontha L. preliminary results are compiled in Table 2. It has to be stated that single white grubs were placed in 100 ml polyethylene pots containing sugar beet plants. In spite of the short time these experiments are running, the cultivars caused an unequivocal different high mortality among the larvae of M. melolontha.

Table 2 Mortality of white grubs of Melolontha melolontha on sugar beet cultivars (4.10.76 -12.11.76)

Cultivar	Mortality (%)
1	20
2	20
3	60
4	90

These data have of course to be checked in the field before these differences may be used for practical purposes. It is, however, remarkable that such small experimental units were sufficient to demonstrate differences.

Considering again B. tabaci, the choice and the possibility of the imagines to fly towards the plants and also to leave them, was decident for the preference of the cultivars. To all probability the cultivars having more hairs were favoured. In the experiments with M. melolontha, there was no possibility for the larvae changing the plants. The differences were, however, pronounced that they could not be overlooked. Based on the results of the two experiments it is obvious that the determination of the resistance of cultivars has to consider the behaviour of the insects. Large plots are necessary when flying insects are to be tested which fly directly towards the plants and which also can leave them if they want to do so. Large plots seem also to be of advantage when the differences in resistance between the cultivars are relatively small.

When drawing up programs for an integrated control, the incorporation of cultivars is desirable which differ in susceptibility. In this case the height of the remaining population density of insects can be regulated. Therefore, it was to be our aim to find cultivars which offer only a slight protection against damage. The determination of such small differences after infestation with B. tabaci seems to be possible, if the cultivars are used on larger plots. As cultivar experiments with 1 ha plots per cultivar are quite expensive, the following procedure was tried with cereal leaf aphids. In the scope of a "reporting service" the density of leaf aphids was determined of fields up to 5 ha at one control point. In that area the mean infested lenght of 10 ears was measured.Furthermore, the used cultivar should be mentioned for each field.

Figure 2 Susceptibility of winter wheat cultivars to cereal leaf aphids

Cultivar	Number of fields	Mean lenght of infested ears (colonized) in cm
Benno	6	22
Kranich	9	13
Jubilar	11	9
Caribo	21	8
Diplomat	19	8
Perseus	6	4

From Fig. 2 it can be seen that the cultivar Perseus was less infested than Benno. If not infested fields are excluded from the calculation the difference between both cultivars was significant at a level of $p = 0,05$. It is, however, probable that this difference and perhaps also other differences may be higher significant if the experiments are carried on in future.

The last mentioned results seem to confirm as well that larger fields facilitate the finding of resistent cultivars, preferrably if the infestation of the cultivars is the result of the "selection" possibility and the flying capacity of the insects. Obviously smaller differences may be perceived and there is the opportunity to find cultivars with only slight differences of infestation which can be incorporated successfull in the integrated control program. In place of using expensive large plots for testing and comparing cultivars, it should be more suitable to test the new cultivars when they are grown for multiplication (breeding) on larger fields.

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RESISTANCE TO ROOT APHID (*PEMPHIGUS BURSARIUS* (L.)) IN LETTUCE

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Lettuce root aphid, Pemphigus bursarius (L.), can cause much damage to crops of outdoor lettuce in July and August, especially uner dry sunny conditions when badly infested plant are generally killed. It flies in late June and July from galls on poplar, Populus nigra and particularly var italica, to lettuce where in an hour or two each immigrant produces 20-30 young. These enter the soil to settle and feed on lettuce roots, undergoing two or three generations here before winged forms develop and fly back to poplar, on which the egg stage winters. All alternative summer hosts of this aphid are Compositae, sub-fam. Liguliflorae, but in England lettuce is preferred.

Lettuce varieties differ in their susceptibility to attack and several highly resistant to the aphid were found in a synonymy trial at Wellesbourne some years ago (Dunn, 1960). Some of the resistant varieties were practically immune and others seemed to be a mixture of resistant, less resistant and susceptible phenotypes. Among those with the highest resistance were a few lines of Imperial lettuce which Dr. T.W. Whitaker had bred, and one of these had been selected at Wellesbourne because of its immunity to the races of downy mildew, Bremia lactucae Regel, then present in the area. This line was Imperial 45634-M and it gave rise through selection over a series of selfed generations to the crisphead lettuce, Avoncrisp, and by way of a single cross with Borough Wonder and 7 generations of selfing and selection to the butterhead lettuce, Avondefiance (Watts & George, 1964; Haigh, 1965).

In 1967, these Wellesbourne-bred lettuces were being grown in a variety trial at Cambridge which was heavily attacked by lettuce root aphid and in contrast to most varieties which were either dead or dying, they stood out with certain others as showing no symptoms of damage (Dunn, 1968). Both Avoncrisp and Avondefiance,

as later work confirmed, had clearly retained the high resistance to root aphid of Imperial 45634-M to an extent which made them practically immune to attack. With Avoncrisp this finding was less surprising than with Avondefiance for with the latter, the relatively recent introduction into its parentage of Borough Wonder, a variety very susceptible to root aphid, could have led to the loss of root aphid resistance in the absence of selection for this character.

To answer the question - how had root aphid resistance been retained so successfully during this breeding for mildew resistant varieties of lettuce?, a study on its inheritance was undertaken (Dunn, 1974) and an investigation into its origin in Imperial 45634-M is currently being followed.

Resistance in Avoncrisp and Avondefiance

Winged root aphids from poplar do not discriminate between lettuce varieties. They alight in similar numbers on Avoncrisp or Avondefiance and on lettuces susceptible to attack, but the young they produce survive and multiply only on the roots of susceptible varieties. On Avoncrisp or Avondefiance roots these young may attempt to feed but they fail to develop and soon die. Thus, while their roots remain aphid-free, the root systems of susceptible lettuce in a few weeks may become infested with many thousands of aphids. The tops of Avoncrisp and Avondefiance, however, show no particular resistance to any of the four aphid species (Nasonovia ribisnigri, Macrosiphum euphorbiae, Myzus persicae and M. ascolonicus) which feed on the leaves of lettuce.

The resistance to root aphid can not be explained by morphological differences between the roots of resistant and susceptible lettuces and chemical analyses show that resistance is unlikely to be based on differences in sugar or amino acid compositions of the roots, but phenolic compounds in the roots remain to be investigated.

Inheritance of resistance and a search for its origin

Inheritance of resistance to aphid attack in crop plants was monogenic in the three examples given by Pathak (1970) and it was expected that this might also be so with resistance to P. bursarius in Avoncrisp and Avondefiance. However, from crosses between these two lettuces and the root aphid-susceptible varieties, Borough Wonder and Webb's Wonderful, it was apparent from the results obtained in the P_1, F_1, F_2 and BC generations, that the

inheritance was not a straightforward Mendelian type but was largely controlled by extranuclear factors (Dunn, 1974). Evidence suggested that a nuclear component was also involved, and in the absence of this the overall level of resistance to root aphid declined progressively in generations F_1, F_2 and F_3.

The nuclear component seemed not to be that which conditioned mildew resistance in Avoncrisp and Avondefiance, however, for lettuces like Calmar (mildew-resistant but root aphid-susceptible) and Imperial 19551-M (mildew-susceptible but root aphid-resistant) showed that resistance to mildew and to root aphid could occur separately. Now that more races of downy mildew have been identified (Crute & Johnson, 1976) some of the results from combined studies being made at Wellesbourne on *B. lactucae* and *P. bursarius* strongly indicate that the gene which conditions resistance to mildew race W3 is the nuclear component associated with root aphid resistance.

In their paper on the development of mildew resistance in lettuce, Whitaker *et al* (1958) gave the pedigree of Imperial 45634-M starting from an original cross between Imperial D and a Plant Introduction line of *Lactuca serriola* resistant to mildew. This *L. serriola* came from Russia and may also have carried resistance to root aphid but this can not be checked for its seed is no longer available. Other *L. serriola* from Russia have now been tested against root aphid and some show the same level of resistance to this insect as Avoncrisp and Avondefiance. The root aphid resistance of Imperial 45634-M, therefore, could have come from the Russian *L. serriola* PI line, but now having tested Imperial D and Imperial F (also in the pedigree of 45634-M) and found that both are highly resistant to *P. bursarius*, it could also have come from one or both of these Imperial lettuces. Imperials D and F lack mildew resistance and their root aphid resistance seems to be from a common source, a selection of a New York lettuce which originated from Iceberg (see Jagger *et al*, 1941, fig. 1). Iceberg is resistant to root aphid(Dunn, 1960)and some lines are highly resistant. Thus the resistance to *P. bursarius* of Imperial 45634-M and hence of Avoncrisp and Avondefiance could be from two sources, the Russian *L. serriola* and Iceberg, one with mildew resistance and one without. The implications of this situation in terms of inheritance have still to be worked out.

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RESISTANCE IN LACTUCA L. TO MYZUS PERSICAE SULZER

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Introduction

The green peach aphid Myzus persicae causes problems in glasshouse lettuce growing and has to be controlled by insecticides. Possible unwanted side effects of these could be overcome by the use of resistant varieties. Until now such varieties are not available. Therefore the following research programme was initiated:
1) search for resistance and development of testmethods;
2) research on the backgrounds of resistance;
3) transfer of the resistance into cultivated types.

Testmethods

For screening and genetic research different tests were developed.
Macrotest. To be able to test rapidly many genotypes a macrotest was developed. With this test of each genotype 4 replicates with 5 plants per genotype were placed in a glasshouse.
When the plants had about 8 leaves they were inoculated with aphids. This was done as follows. Aphids were reared on Chinese cabbage. A half day before inoculation leaves with aphids were detached and placed at 4°C. Then they were shaked off above plastic trays with leaf discs. On each plant a disc with 10-15 aphids was placed. Then aphid populations developed.
About 5 weeks after inoculation the aphids per plant were estimated. Because the aphids were rather evenly distributed over the older leaves of the plants, estimation of the number of aphids of one leaf was sufficient. For estimating, drawings of leaves with dots, representing aphids, were used (see Figure 1).
Hundreds of genotypes from the IVT Lactuca genebank were tested and various partially resistant genotypes were found.
The reliability and usefulness of the macrotest was investigated by experiments in which estimates of the number of aphids per leaf and counts of the number of aphids per plant of 19 partially resistant and susceptible genotypes were compared. It appeared that there was a good relationship between estimates and counts as shown in Figure 2.

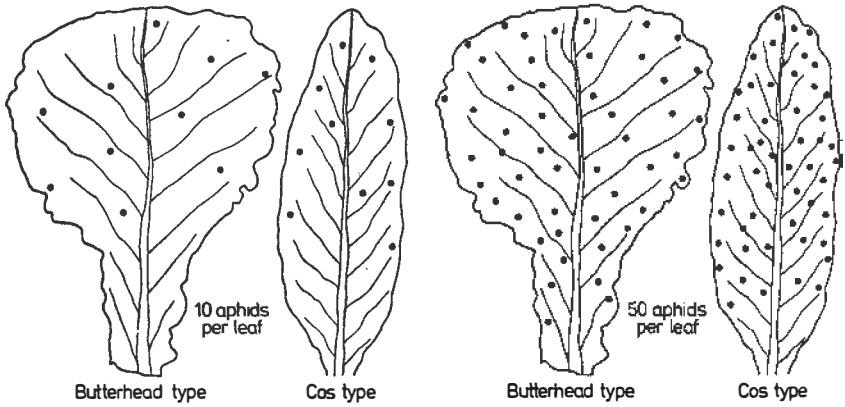

Figure 1. Drawings of leaves with dots representing aphids.

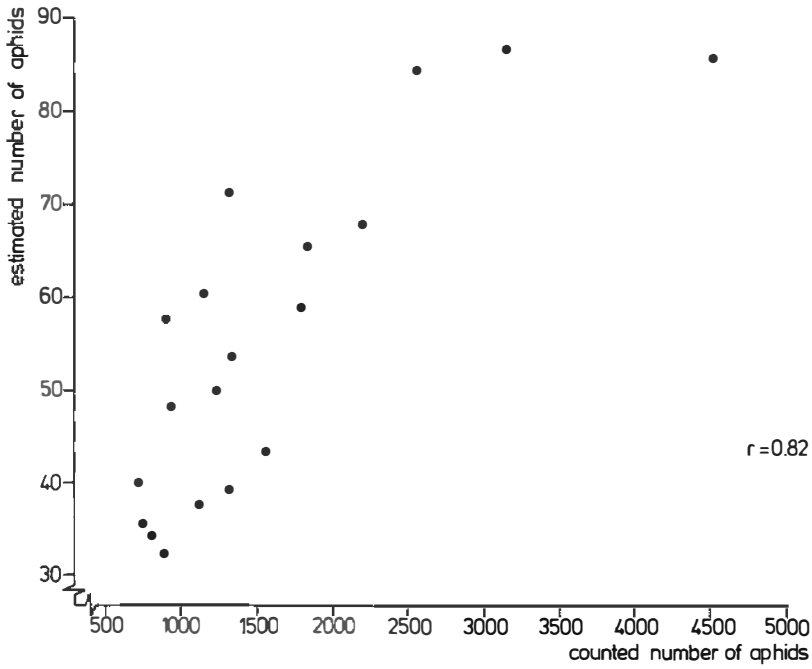

Figure 2. Relationship between counted and estimated number of aphids.

Microtest. For our research on the inheritance of resistance individual plants have to be tested. Therefore microtests were developed. In leaf cages 10 larvae were enclosed (less than 24 hours old) and after 8 days of larval development they were weighed (biomass) then larvae production of adults during the first four production days was determined. These two characters could function as criteria of resistance. It appeared, however, that there were significant differences between plants of the same genotype and also between and within leaves of the same plant.

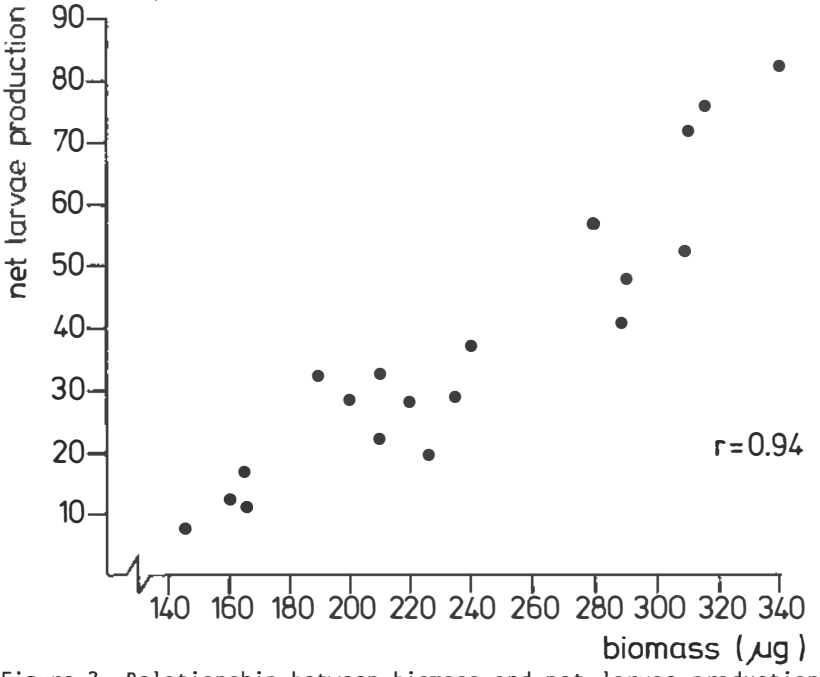

Figure 3. Relationship between biomass and net larvae production.

Table 1. Biomass (in µg) and net larvae production (in 7 days) for a partially resistant (PIVT 180) and a susceptible (PIVT 197) genotype.

Genotype	Biomass	Net larvae production
PIVT 197	400	21.7
PIVT 180	226	5.5

It was most suitable to place the cages on the middle of the lower leaf surface of moderately old leaves on both sides of the midrib. Nevertheless, for distinguishing resistance levels by using microtests, a rather great number of cages per plant should be used.
From experiments carried out with the 19 genotypes mentioned before, it appeared that there was a good relationship between macro- and microtest (see e.g. figure 4).

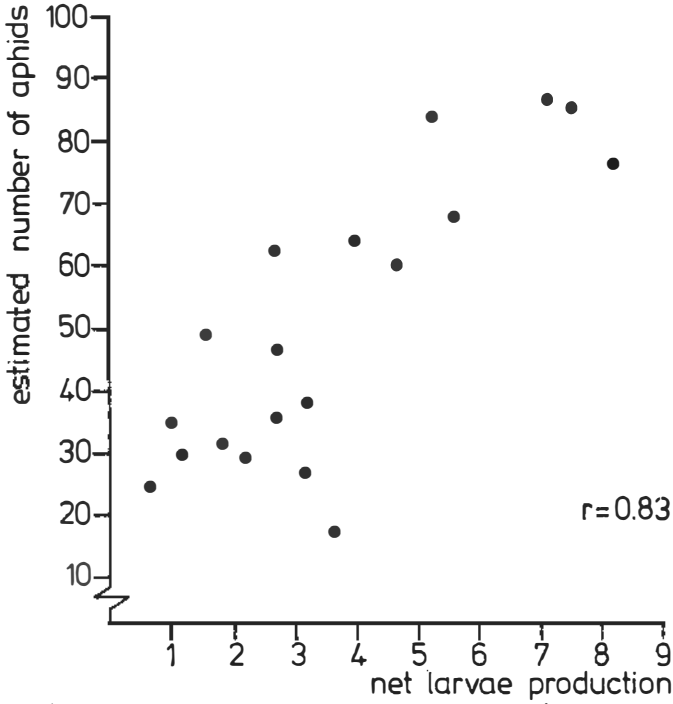

Figure 4. Relationship between the microtest (net larvae production) and the macrotest (estimated number of aphids).

Crosses

Diallel crosses were carried out between partially resistant and susceptible genotypes. Both parents and F_1's were tested for their resistance by using macro- and microtest. These crosses were carried out to investigate the inheritance of the resistance and to improve the level of resistance (partially resistant x partially resistant crosses). Some preliminary results suggest that at least in certain cases resistance inherites in additive fashion as is shown in Table 2.

Table 2. Net larvae production in 4 days of a partially resistant genotype (PIVT 180) a susceptible genotype (PIVT 197) and their F_1.

♀ \ ♂	PIVT 180	PIVT 197
PIVT 180	5.5	10.5
PIVT 197	9.7	18.9

Some final remarks

From the above it appears that different degrees of resistance to Myzus persicae occur in lettuce. By intercrossing and/or by further screening higher levels of resistance may be obtained. This means that in future resistant lettuce varieties will be available.

RESISTANCE IN LETTUCE TO NASONIVIA RIBIS NIGRI

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Lettuce is one of the secondary hostplants of Nasonovia ribis nigri (Mosley). Direct damage caused by an early infestation is less important than decrease in market value brought about by aphid contamination during the growing season. The control of N. ribis nigri in field lettuce needs several applications of insecticides. For this reason a program was started to trace resistance to N. ribis nigri.

A superficial screening of nearly 300 PIVT numbers of the IVT lettuce gene bank produced one accession with a very low field infestation. Selected material was retested in a greenhouse and only the none-accepted field number proved to be highly resistant. Crosses between the resistant Lactuca virosa and other Lactuca species resulted in resistant but sterile hybrids. In the meantime the test method has been modified to detect also partial resistant progenitors.

Improvement of the test procedure was brought about by quantification of some critical points in the aphid/plant relationship. From a close examination of behaviour and population growth on several varieties could be concluded that the frequently used criteria for resistance, probing behaviour choice tests, mean relative growth rate, larval mortality and larvae production of aphids of unknown origin have a limited useful value. Pretreatment of the aphids, foodplant mother and selection for quality in the initial population,

may sensibly influence the ultimate results.

Growing aphids on a susceptible standard variety only may reduce the discrimination power of fecundity as a criterium for resistance. For this reason larvae production and population growth was measured after one or more generations. On the other hand there was no indication for a modification in adaptation.

The aphid weight is a reliable criterium for quality. On a susceptible variety a good correlation has been found between adult weight and larvae production ($r = 0.90$). The adult weight range on this variety is 0.5 - 1.1 mg with a corresponding larvae production of 15 - 35 per six days. Selection for homogeneity is necessary to get comparable results.

The modified test procedure starts with an artificial infestation of seedlings with first instar larvae. The survival rate after six days is on a susceptible, partial resistant and resistant accession respectively 0.90 , 0.85 and nearly zero. Six days later the survival rate on the partial resistant variety is reduced to 0.50 but on the susceptible one still 0.85. Only a small difference in gross larvae production could be measured at that time. The relative small difference between birth- and death rate leads to a significant difference in population growth on both varieties after 1.5 - 2 generations.

The estimation of population growth over a short period of time is on certain conditions a reliable and easy to handle procedure to quantify resistance.

The production of alatae already at low larval density is a complication of this method. For this reason the infestation is carried out with first instar larvae born by selected winged virginoparae. After 12-16 days the number of aphids per plant on the resistant L.virosa, a partial resistant and susceptible variety is respectively, 0.90 and 400. Selected numbers or plants can be retested over another period of 10 days by infestation of individual plants with a small number of winged aphids. The same plant material can also be tested for resistance to Myzus persicae (Sulzer).

RESULTATS PRELIMINAIRES D'UNE ETUDE DE LA SENSIBILITE DU PECHER ENVERS LE PUCERON VERT DU PECHER *MYZUS PERSICAE* SULZER

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Collaboration technique P. MAISON

I - INTRODUCTION -

Le Puceron vert du Pêcher *Myzus persicae* SULZER commet des dégâts directs sur Pêcher (LECLANT et REMAUDIERE, 1970) et des dégâts indirects en tant que vecteur du virus de la Sharka (Bull. OEPP 1974). L'utilisation de variétés de pêcher présentant des caractères de résistance envers cet insecte devrait constituer une méthode de lutte d'autant plus séduisante qu'elle est compatible avec les objectifs de la lutte intégrée. La valeur de cette méthode est vérifiée par des observations effectuées en vergers de pruniers. (JORDOVIC, 1965). Aussi, nous avons réalisé un travail exploratoire axé sur l'étude de la résistance intra et interspécifique du Pêcher envers *Myzus persicae* SULZER.

II - METHODOLOGIE -

21 - Puceron

Quelques essais ont été effectués avec des larves de fondatrices, la plupart avec des adultes de fondatrigeniae aptera e. Ces dernières proviennent soit de prélèvements effectués dans un élevage de masse, réalisé à partir d'une ou de quelques fondatrices, sur semis du pêcher homozygote GF 305 cultivé en pièce climatisée (20 ± 2°, 10 000 lux, 16 heures de jour), soit de prélèvements effectués en verger sur diverses variétés de pêcher.

22 - Matériel végétal

Nos observations concernent une partie du matériel existant à la Station d'Arboriculture de Bordeaux : arbres, cultivés en collection variétale, de certaines variétés de *Prunus persica* (L) BATSCH, de *Prunus davidiana* CARR, d'hybrides *P. persica* X *P. amygdalus* L. plants de pépinières d'hybrides *P. davidiana* X *P. persica* Des études particulières ont nécessité la création de parcelles expérimentales avec des plantes cultivées en pots, en pépinière ou en verger. Ces études concernent les variétés Baby gold 6 et 7. Mac Kune 3200, Jungermann 3197, greffées sur le porte-greffe GF 305, les hybrides *P. davidiana* X *P. persica*, greffés sur GF 305 ou multipliés par bouturage.

23 - Réalisation des essais

Les essais ont été réalisés par contamination artificielle libre, ou, dans la plupart des cas sous manchons. Ces derniers en voile de nylon aéré isolent l'extrêmité ou la totalité d'un rameau. La contamination initiale des plantes est assurée par un nombre de pucerons variable, précisé pour chaque essai au chapitre résultats.

24 - Notation et analyse statistique des résultats

L'influence de la plante sur l'insecte est évaluée en notant le niveau des populations apparues pendant une période généralement comprise entre 15 jours et 1 mois.

La notation attribuée correspond à l'évaluation de la population aphidienne en fonction d'une progression géométrique d'ordre 5 (LECLANT et REMAUDIERE, 1970)

Six classes de notation ont été observées :

Classe 0 : pas de pucerons
- 1 : 1 à 5 pucerons
- 2 : 6 à 25 pucerons
- 3 : 26 à 125 pucerons
- 4 : 126 à 625 pucerons
- 5 : 626 à 3 125 pucerons.

Les résultats d'essais réalisés à la même date, dans des conditions expérimentales apparemment identiques, ont été comparés au moyen d'un test emprunté aux méthodes d'analyse statistique non paramétrique : le test 2 I (SOKAL et ROHLF, 1969).

25 - Histologie

Des coupes transversales de feuilles et tiges de pêcher ont été réalisées au microtome à congélation, colorées au Soudan III, puis observées au microscope photonique. L'épaisseur de la cuticule et la distance séparant l'épiderme des faisceaux libériens ont été mesurés à l'oculaire micrométrique.

III - RESULTATS -

31 - Variétés de *P. persica*

Les essais effectués avec des plants de pépinière indiquent l'influence des variétés sur le niveau des populations de *Myzus persicae* : Jungermann 3197 est la variété la plus sensible, Babygold 7 est la variété la moins sensible.

L'analyse statistique des résultats obtenus indique que la méthode des contaminations artificielles ne permet plus de mettre en évidence des différences significatives entre les variétés lorsque les essais sont réalisés après le mois de mai. Ainsi, nous notons 2 I = 24,606 et X^2 (0,05, 12)= 21,26 pour l'essai réalisé

du 18 avril au 15 mai 1975 ; 2 I = 28,848 et X^2 (0,01, 12) = 26,217 pour l'essai réalisé du 9 au 22 mai 1974 ; 2 I = 9,51 et X^2 (0,05, 12) = 21,26 pour l'essai réalisé du 5 au 20 juin 1974 ; 2 I = 9,906 et X^2 (0,05, 6) = 12,592 pour l'essai réalisé du 12 au 27 juin 1974.

Des fondatrigeniae apterae refusent, en nombre variable suivant les essais, de s'installer sur les plants de pépinière sur lesquels elles ont été déposées. Cette réaction de non-préférence est d'autant plus importante, quelle que soit la variété considérée, que la date de mise en place des essais est tardive. Ainsi l'effectif de la classe 0 représente, bien qu'il ait été utilisé 5 fondatrigeniae apterae pour les deux derniers essais et une seule pour les deux premiers : 21 % (n=70), 37 % (n = 72), 42 % (n=65) 50 % (n=40) des notations lorsque les essais sont mis en place le 18 avril, le 9 mai , le 6 et le 12 juin.

La technique des contaminations artificielles n'a pas permis l'installation de colonies de *M. persicae* sur les arbres des variétés peu sensibles : Baby gold 6 et 7 bien que cette technique permette l'installation de colonies sur les plants de pépinière contaminés aux mêmes dates : 18 avril et 9 mai. Des observations identiques ont été effectuées avec d'autres variétés de *P. persica*.

32 - Hybrides *Prunus davidiana* CARR. X *Prunus persica* (L) BATSCH.

Nous avons observé, début juin 1973, en pépinière âgée de 2 ans que les 10 plants de l'hybride 41.4.21 provenant du croisement *P. davidiana* X *Mesokomaron* ne présentaient aucun symptôme d'attaque par le Puceron vert, alors que le feuillage de quatre autres hybrides résultant du croisement de *P. davidiana* avec diverses variétés de *P. persica*, était fortement crispé, en particulier celui de 41.6.2, et abritait quelques colonies résiduelles de *M. persicae*.

Les hybrides 41.4.21 et 41.6.2. ont été greffés au printemps 1974 sur le porte-greffe GF 305. A l'automne 1975, des boutures de 41.4.21 ont été réalisées.

321 - Hybrides greffés sur GF 305.

3211 - Observations en pièce climatisée : 16 heures de jour, 10 000 lux, deux températures : 20 et 25°)

Plusieurs essais réalisés par contamination artificielle avec des fondatrigeniae apterae prélevées dans différents élevages de masse sur GF 305 indiquent que les pucerons ne parviennent pas à s'installer sur 41.4.21 alors qu'ils forment d'importantes colonies, provoquant une intense crispation du feuillage sur 41.6.2. La plupart des fondatrigeniae apterae quittent le feuillage de 41.4.21 après un temps de séjour compris entre 24 et 48 heures, aucune ne se maintient au delà de 96 heures. Cette réaction de non préférence ne peut être mise en relation avec l'épaisseur de la cuticule ou la profondeur du phloeme car l'étude histologique mon-

tre que ces caractères sont identiques chez les deux hybrides.

3212 - Observations en pépinière - Lors de l'essai réalisé du 2 au 29 avril 1975, par contamination artificielle sous manchons, toutes les fondatrigeniae apterae mises en place et appartenant à la descendance d'une seule fondatrice, sont à l'origine de colonies. Les colonies observées sur 41.4.21 ne comprennent que quelques individus dépigmentés, de taille réduite et de faible fécondité, installés sur les organes - tiges et feuilles - très jeunes. Par contre, les colonies florissantes observées sur 41.6.2 sont constituées par des pucerons normaux.

Plusieurs contaminations artificielles, par des fondatrigeniae apterae appartenant à la descendance de différentes fondatrices, ont été effectuées en mai 1975 sur 41.4.21. Le niveau des populations des colonies parvenues à s'installer est toujours resté faible. Le 21 mai, plusieurs plants de 41.4.21 ont été contaminés par 20 fondatrigeniae apterae prélevées dans les colonies installées sur 41.4.21 et sur 41.6.2. Les contaminations n'ont réussi partiellement (3 sur 5) que lorsque les pucerons provenaient de 41.4.21.

322 - Boutures de l'hybride 41.4.21

La survie des larves de fondatrices placées sur les boutures, lorsque les jeunes feuilles commencent à se développer, varie suivant les conditions de l'environnement. Elle est satisfaisante (46 %, n=50) et se rapproche de celle observée sur semis du Pêcher GF 305 (80 %, n=10) lorsque les essais sont réalisés en abri extérieur grillagé ; elle est faible (3 %, n=78) et très inférieure à celle observée sur semis de pêcher GF 305 (71 %, n=21) lorsque les essais sont réalisés en serre chaude. Les boutures sont d'autant plus sensibles à la descendance des fondatrices que leur nutrition azotée est satisfaisante.

33 - *P. davidiana* et hybrides *P. persica* X *P. amygdalus*

Ces essais par contamination artificielle libre et sous manchons, ont été réalisés au mois de mai 1976. Tous les hybrides de *P. persica* X *P. amygdalus* que nous avons testés, et , à un moindre degré la variété *P. davidiana potamini* se sont avérés sensibles. Par contre *P. davidiana alba* n'a pu être colonisé en dépit d'apports répétés et massifs de fondatrigeniae apterae prélevées sur des pêchers différents.

IV - DISCUSSION ET CONCLUSIONS -

Les différences de sensibilité des variétés de pêcher envers les fondatrigeniae aptera de *Myzus persicae* ne paraissent pas avoir une origine physique mais chimique. Elles proviendraient de réactions de non préférence et d'antibiosis (PAINTER, 1958). L'intensité de ces réactions varie non seulement en fonction de la phénologie et peut-être du développement des arbres, mais également en

fonction des conditions de l'environnement : température des essais, nutrition des plantes.

La réaction de non préférence est souvent observée, bien que les variétés soient favorables au développement des colonies en place. Elle pourrait résulter de l'inadaptation physiologique (ADAMS, 1967), ou comportementale (MONTGOMERY, 1974) des fondatrigeniae apterae envers leur nouvel hôte. Mais l'inaptitude d'une partie des fondatrices et fondatrigeniae à coloniser certaines variétés de pêcher provient vraisemblablement de la variabilité génétique de l'espèce *Myzus persicae* Sulzer (MASSONIE, à paraitre).

En raison des remarques précédentes, nos résultats doivent être considérés avec d'autant plus de prudence que la corrélation entre l'évolution des populations naturelles (HILLE RIS LAMBERS, 1946)et les résultats obtenus par contamination artificielle n'est pas établie. Cependant, l'on peut considérer que la sensibilité des espèces de *Prunus persica* (L) BATSCH envers *Myzus persicae* SULZ. n'est pas identique (BOGSANYI), que l'espèce *Prunus davidiana* CARR renferme des variétés à haut niveau de résistance.

REMERCIEMENTS

Ce travail a été réalisé grâce à la collaboration de la Station d'Arboriculture fruitière de Bordeaux. Nous remercions particulièrement MM BERNHARD, Directeur ; GRASSELLY, MARENAUD, MONET, Scientifiques, MAZY, OLIVIER, techniciens.

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SCREENING FOR RESISTANCE TO *RUBUS* AND *RIBES* APHIDS

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INTRODUCTION

In breeding for resistance to aphids in Rubus and Ribes, over the years we have evolved methods of screening large populations of very young seedlings, ways of testing mature plants for degrees of resistance, and techniques for checking the resistance status of elite selections already planted in the field. With four different aphid species as well as other pests and diseases to control, speed and simplicity are essential.
The species mainly involved are the rubus aphid, Amphorophora rubi, on raspberries, the gooseberry aphid, Aphis grossulariae, the lettuce aphid, Nasonovia ribisnigri, on gooseberry, and the currant sowthistle aphid, Hyperomyzus lactucae, on black currant. Although testing methods with all four species are basically similar, slight modifications have been introduced to allow for differences in activity and life style of the pests.

SCREENING SEEDLING POPULATIONS

Amphorophora rubi:- The basic essentials of screening large numbers of young seedlings were worked out in relation to the rubus aphid which is large, active, long legged, and quickly leaves plants it does not like. As it remains on Rubus throughout the year, screening can be done all through the growing season. Our methods of testing raspberry seedlings depend on the quick reactions of the aphid, enabling us to screen as many as 7,000 seedlings during April-June each year. The normal colour of the aphid is pale green, but most years we find in one or other strain a yellow form which we bulk up and use as much as possible as it makes counting small nymphs and recognition of strains much easier.
The method of testing young raspberry seedlings is as follows:-
The seed germinates in early spring and when the seedlings are large enough to handle they are potted singly into 3" (7.5 cm) plastic pots. About a month later when the first true leaves have fully expanded each plant is inoculated with three adult aphids. After 4-7 days the plants are examined, those with no aphids present being classified as resistant, while those with adults plus at least five thriving nymphs are classified as susceptible (Knight et al., 1959). Any plants not in these two categories, i.e. those with a few nymphs only, or with adult(s) present but no nymphs, are returned to the bench for a few days (re-inoculated with adults when required) until their reaction is clear.
Seedlings from progenies having known resistance genes in their parentage are placed on a bench for testing. At the beginning of

the season (when there is usually a shortage of adult aphids) the plants are placed with their leaves touching so that aphids repelled by the resistant plants may collect on the susceptibles and so increase in numbers. When the genetic control of resistance is under investigation, plants are completely isolated by spacing them on inverted pots in trays of water to prevent aphids moving from plant to plant. In these conditions the aphids will drown rather than remain on a resistant plant.

When a progeny is segregating for more than one race-specific resistance gene, the test is repeated with each appropriate strain. The seedlings are dipped in a solution of 5 ml Nicotine + 2 ml wetter in 2 gall water, between each test, to prevent contamination by aphids of the wrong strain. The plants stand for a minimum of 24 hr after dipping before being re-inoculated with a new strain. To prevent strains becoming mixed, tests are done in different glasshouses, or in well separated compartments in the same insectary.

Hyperomyzus lactucae and Nasonovia ribisnigri:- The method used for screening Ribes seedlings for resistance to these species is similar to that described above for A. rubi. Since both Ribes aphids migrate to herbaceous hosts the screening period is restricted to a few weeks in spring and early summer.

Aphis grossulariae:- This is smaller, short-legged, gregarious, and rather lethargic, and tends to remain on resistant seedlings longer than the other Ribes aphids. Short lengths of infested shoots from stock plants provide the most satisfactory inoculum and tests may extend over 2 weeks or more.

SCREENING MATURE PLANTS

Cut shoot tests:- Before elite raspberry selections go into replicated cropping trials, cut shoot tests are used to confirm earlier results in the insectary. This method is also used in initial screening of new plant accessions of both Rubus and Ribes (Keep et al., 1967; Keep et al., 1971). The tips of young shoots are placed in water in the shade in the insectary and inoculated with about 10 adults per shoot. As with seedling tests, absence of nymphs is used as a criterion of resistance. This method needs care, as the shoots are prone to wilt from high temperatures and resistance weakens after about 4 days in water. Nevertheless many shoots can be tested quite rapidly in a relatively small area of glasshouse.

Tests on pot plants:- When comparing the relative effectiveness of different resistance donors, insectary inoculation of mature plants in pots permits accurate counts of nymphs. The test extends over a period of several days. Pot plants are also used for testing the response of A. grossulariae since this species reacts too slowly to permit effective use of cut shoots.

Field tests:- In the absence of adequate natural colonization, it

may be necessary to determine aphid responses to mature Ribes plants by artificial inoculations in the field. Aphid infested shoots, taken from either stock or field plants in early summer, are attached to actively growing branches of test seedlings with plastic covered wire or small jewellers' tags. A week later the aphids will usually have started to colonize and breed on the susceptible, or have abandoned the resistant plants.

Field counts of A. rubi on mature plants are made periodically to confirm that the resistance conferred by known genes is still effective or to assess the relative strength of different resistance genes. For each plant the numbers of aphids are counted on one young expanding leaf from each of five actively growing random shoots (Knight et al., 1959).

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R RESISTANCE TO APHIDS IN R

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ION

s are important pests of both Rubus and Ribes crops, and at t Malling we have been breeding for resistance in raspberries o the rubus aphid, Amphorophora rubi (Kltb.), for about 20 years. Breeding for resistance to aphid pests of blackcurrants and goose- berries was started more recently and so far progress has been considerably slower for a variety of reasons, some of which will be discussed later.

The rubus aphid is widespread in raspberry plantations in Britain, but of itself causes little or no obvious damage. Its chief significance for fruit growers lies in its role as vector of four viruses, raspberry leaf mottle, raspberry leaf spot, rubus yellow net and black raspberry necrosis, which alone or in combination severely affect growth and cropping or even kill sensitive varieties (Murant, 1974).

In contrast, in currants and gooseberries the direct effects of aphid feeding - leaf curling or blistering, and checking and deformation of shoot growth - are most damaging, although some aphids are also virus vectors.

BREEDING FOR RESISTANCE TO THE RUBUS APHID

Sources of resistance

Early work at East Malling showed the old variety Baumforth A, its derivative Malling Landmark and the American Chief to be highly resistant to the aphid and these three cultivars were at first the main donors of resistance (Knight et al., 1959). When it became apparent that some strains of the aphid were capable of overcoming resistance of these origins, new sources of resistance were found, some of which were already in use in the breeding programme as donors of other characteristics. It has now become routine to screen new accessions for their response to the aphid. To date, resistance has been found in some seven red and black raspberry varieties and 13 Rubus species (Knight et al., 1959; Keep et al., 1970; Keep, 1972, and unpublished).

Genetics of resistance and aphid strains

In the course of resistance breeding, more than twelve maj dominant resistance genes have been isolated. In parall this work, Briggs (1959, 1965) showed that samples of A collected from raspberry plantations all over Britain classified into four distinct strains on the basis of responses to plant resistance genes. The genes of ance in raspberry breeding at present and the res

strains are shown in Table 1.

Table 1

resistance genes in relation to strains of Amphoropho

ene	Origin	Response to A. rubi, strains				
		1	2	3	4	
A1	Raumforth A	R	R	R	R	R
A2	Chief	R	R	S	R	S
A5,6,7	Chief	R	S	R	S	S
A8	I. 518 R. idaeus strigosus	R	S	S	S	S
A10	Cumberland R. coreanus	R	R	R	R	R
Acorl	R. coreanus	R	S	S	S	R

R = Resistant
S = Susceptible

The gene A1 from Raumforth A provides strong resistance to the most common strains 1 and 3, while the American Chief supplies fairly strong resistance to the much less common strain 2. These fairly are now being replaced by the so-called universal resistance genes very rare strain 4 as well as the other three strains (Keep et al., A8, A10, and Acorl which provide effective resistance against the 1970).

At present most of our breeding lines carry A10, derived from the American black raspberry Cumberland, which was originally brought into the breeding pool as donor of fruit quality. A more recent donor of universal aphid resistance is the Asiatic R. coreanus (Mig.) which also provides resistance to five fungal diseases attacking the raspberry.

Value of vector resistance

The value of vector resistance in preventing or delaying virus spread has been proved by observations on segregating seedling progenies at East Malling, and by replicated trials, with aphid-stant clonal material interplanted with virus infector rows, at ottish Horticultural Research Institute. At East Malling, symptoms were recorded on four progenies comprising from 106 nts in which, exceptionally, the aphid-susceptible as well d-resistant seedlings had been planted in the field. years after planting, percentages of resistant plants symptoms ranged from 4 to 11, in comparison with a for susceptible seedlings. In Scotland, the on which carries A10, and the East Malling ch carries A1, remained largely free from both r four years, whereas the aphid susceptible

Lloyd George and Malling Jewel were rapidly infected, being 100% infected with 52V after four years (Jones, 1976).

Effective duration of resistance to A. rubi

Since the discovery of the four British raspberry races of A. rubi between 1952 and 1958 (Briggs, 1959, 1965), no new races have been found. In America, major gene resistance of the variety Lloyd George to Amphorophora agathonica Hottes, which until recently was considered to be identical with the European A. rubi, has remained effective for at least 40 years. It seems that A. rubi is a fairly stable organism and the universal resistance imparted by genes such as A_{10} is likely to be maintained for many years. Our policy will therefore continue to be to locate and utilize major resistance genes, since screening for these is simple and quick (Parker, in press). As an insurance against breakdown of resistance, we are combining major genes of different origins and already have a number of lines segregating for both A_1 and A_{10}, and more recently for A_{10} and A_{corl}.

Progress in breeding for resistance to A. rubi

Most of our breeding lines now carry one or more aphid resistance genes, and three of the raspberry varieties recently released from East Malling are aphid resistant. Malling Orion and Malling Delight, named in 1971 and 1973, respectively, are heterozygous for the gene A_1 conferring resistance to the common strains 1 and 3, while 'Malling' Leo (named in 1976), a fourth backcross from the black raspberry, carries both A_{10} and A_1 and is resistant to all four strains (Keep et al., 1972; Keep & Parker, 1974, and in press).

BREEDING FOR RESISTANCE TO RIBES APHIDS

The most common aphid pest of blackcurrants in Britain is the currant-sowthistle aphid, Hyperomyzus lactucae (L.), which overwinters in the egg stage on blackcurrants, produces a few generations on currants in the spring and then migrates to herbaceous hosts, returning to the currant in the autumn. On gooseberry, the most common aphid is the lettuce aphid, Nasonovia ribisnigri (Mosley), which has a similar life cycle. Aphis grossulariae Kltb., the gooseberry aphid, occurs more sporadically than N. ribisnigri but in some years infestations are very damaging.

Screening for resistance donors

Strong resistance to these three aphids has not been reported in blackcurrant and gooseberry varieties commonly grown in Britain. However, field surveys from 1967-70 of natural infestations in a Ribes collection revealed numerous potential donors of strong field resistance (Keep & Briggs, 1971).

To eliminate types whose field resistance depended solely on escape mechanisms likely to be vitiated in the course of backcrossing, plants considered suitable as donors from an agronomic point of view were artificially inoculated. Insectary tests with cut shoots were undertaken with the fairly active H. lactucae and N. ribisnigri, while the responses of the more sluggish

A. grossulariae were checked by inoculations in the field (Keep and Briggs, 1971; Parker, in press) (Table 2).

Table 2

Response of Ribes species to aphids following natural and artificial inoculation

Aphid species	Field observations on Ribes spp.		Artificial inoculations of field resistant spp.		% field res./ artificial inoculation susceptible
	No. of spp. examined	No. of spp. resistant	No. of spp. tested	No. of spp. resistant	
Hyperomyzus lactucae	56	51	40	22	45
Nasonovia ribisnigri	56	37	12	4	67
Aphis grossulariae	56	46	13	12	8

Plants found to be susceptible to artificial inoculation were excluded from further consideration as resistance donors, the percentage reduction in potential donor species achieved in this way being 45, 67 and 8 for H. lactucae, N. ribisnigri and A. grossulariae, respectively. In the final selection of donors, preference was given to species which were already in use as donors of other characters and which were aphid immune or very highly resistant to both natural and artificial inoculations. In this way, three North American species, R. cereum Dougl., R. glutinosum Benth., and R. sanguineum Pursh., the flowering currant, were selected as donors of resistance to H. lactucae; R. sanguineum for resistance to N. ribisnigri, and the North American R. watsonianum Koehne and R. leptanthum Gray for resistance to A. grossulariae.

Genetics of resistance

The precise genetic control of resistance to the three aphid species has not yet been determined, but data from F_1, BC_1, BC_2 and inbred progenies show that resistance to H. lactucae and to N. ribisnigri is recessive, regardless of the donor. In contrast data from F_1 and BC_1 show that the resistance of R. watsonianum and R. leptanthum to A. grossulariae is dominant and almost certainly oligogenic.

DISCUSSION

Progress in breeding for resistance to the rubus aphid in the raspberry has been relatively rapid and successful. The main reason for this is the occurrence of strong major gene resistances in old

cultivars and wild species which cross readily with modern varieties to form fertile hybrids with fairly good fruit quality. Screening of large populations of young seedlings is simple and rapid, and the response of mature plants in the field is identical with that of young seedlings in the insectary.

Of the Ribes aphids, resistance to A. grossulariae is likely to be the most easy to transfer to crop plants of commercial quality. As with the rubus aphid, donors are available which carry major gene resistance, have fruit of fair quality and form fertile hybrids with gooseberry. The transference of genetically recessive resistance to H. lactucae and N. ribisnigri will inevitably be slower and hindered by difficulties in selection with inbred progenies lacking vigour.

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BREEDING AND SELECTING BLACK CURRANTS FOR RESISTANCE TO THE GALL MITE *CECIDOPHYOPSIS RIBIS* (WESTW.) VECTOR OF REVERSION VIRUS

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INTRODUCTION

The gall mite is widespread in the Northern hemisphere and is a major pest of cultivated black currants (Ribes nigrum L.). It causes direct reduction in crop but is more important as the only known vector of reversion virus. Western European black currants are generally susceptible to the mite, although a few cultivars show slight resistance. Stronger resistance found in a number of R. nigrum sibiricum forms and in R. ussuriense (Jancz.) was attributed to a single dominant gene, designated P, by Anderson (1971). Resistance of this origin has been used by a number of Russian breeders.

BREEDING FOR RESISTANCE TO THE GALL MITE

Observations on Ribes species in a gall mite infection plot and insectary tests at East Malling in the early sixties showed that the black currant gall mite was unable to colonise and reproduce on gooseberry (R. grossularia L.). Very few or no mites were found on black currant x gooseberry hybrids suggesting that the resistance of gooseberry was dominant and probably oligogenic. In the course of a backcrossing programme a dominant, resistance gene, designated Ce, was isolated (Knight et al., 1974).
Transference of the gene Ce from the gooseberry to black currant was achieved by treating sterile F_1's with colchicine and backcrossing the allopolyploid to diploid black currants. BC_1 plants were resistant and usually triploid. All the BC_2 plants resembled black currants and five out of 297 were resistant. One of the resistant plants was aneuploid, the other four and all the susceptible plants investigated were euploid. Ce is not associated with any morphological marker genes and resistant plants in segregating progenies can be recognised only by their response to the gall mite.

SCREENING FOR RESISTANCE

Field tests. Gall mite response is assessed by exposing test seedlings to a bombardment of mites in an infection plot. Three rows of seedlings are planted at close spacing between pairs of established, heavily infested infector rows. Additional inoculum is provided during mite dispersal by placing infested twigs beside the test seedlings. Plants are examined during the winter, those with galled buds being discarded. The percentage of galled seed-

lings increases with time of exposure to migrating mites (Table 1) and four years are required for reliable classification. Individuals remaining free of galled buds for four years are classed as resistant.

Table 1

Percentage of galled seedlings following field exposure to mites

Year planted	No. of seedlings	No. of mite dispersal periods after planting			
		1	2	3	4
1969	1250	11.1	57.2	73.6	-
1970	1295	-	19.7	49.6	57.6
1972	556	3.3	24.0	62.4	73.7
1973	150	36.6	49.0	49.7	-
Mean		17.0	35.5	58.8	65.7

Insectary tests. Gall mite inoculations were made initially in the autumn, to minimise the risk of contaminating Ribes stocks in the glasshouse area. Also less glasshouse space and labour are available in the spring. In 1968 galled buds were chopped up, shaken in water, and a suspension of mites dripped onto the growing points of young seedlings (5 to 7.5 cm high) in 7.5 cm pots. These seedlings, plus approximately equal numbers of non-inoculated seedlings, were planted in a mite infection plot in spring 1969. By January 1971 29.8% of inoculated seedlings were galled compared to 9.7% of the non-inoculated seedlings.

In September 1972 seedlings were inoculated while still in the seed tray when between 2.5 and 7.5 cm high. Four inoculation techniques were used:

a) Chopped galled buds, spread on a gauze frame and watered until the water dripped through onto the seedlings below. Watered again for the next three days.
b) as a) with Agral wetter.
c) Chopped buds stirred in lukewarm water and 0.5 ml of the resulting mite suspension dripped onto the growing points. Inoculation repeated twice.
d) as c) with Agral wetter.

After 2 months 4.8% of seedlings had distorted leaves very similar to those described by Thresh (1963) as being associated with mites feeding in apical buds in the field. Thirteen seedlings with affected leaves were dissected and mites found on five. Mites were also found on one of ten seedlings without leaf symptoms. After one natural dispersal period in the field percentages of seedlings with galled buds were 38, 28, 35, 46 and 36 for treatments a, b, c, d and the non-inoculated control, respectively. None of the treatments caused a significant increase in the proportion of galled seedlings compared to the

non-inoculated seedlings, over the same period. Treatment (d) produced significantly more galls than treatment (b).
The following year an inoculation technique similar to (a) was used, again in autumn. Ten percent of the inoculated seedlings developed characteristic leaf symptoms and a further twelve seedlings developed galled terminal buds by early spring.
All seedlings were planted in the mite infection plot in the spring and examined for galled buds in subsequent winters. After two years in the infection plot, seedlings which had previously displayed leaf symptoms did not invariably have galled buds and the data presented in Table 2 suggest that leaf symptoms are not a reliable guide to mite susceptibility. Since planting in the field, nine out of the twelve seedlings with galled terminal buds developed additional galls, the remaining three failed to grow satisfactorily.

Table 2

Percentage of plants developing galled buds in the field following seedling inoculation

Year planted	No. of seedlings	No. of mite dispersal periods	% galled seedlings Leaf symptoms	Normal
1973	465	1	34.6	36.6
		2	45.6	45.5
1974	2790	1	15.6	5.4
		2	49.8	41.3

To determine if insectary inoculations nearer the time of the normal mite dispersal period are more effective than autumn inoculations, seedlings from crosses made in 1975 were inoculated as before soon after germination, in autumn 1975 or in spring 1976; 13.8% and 46.5%, respectively, displayed leaf symptoms. These seedlings will be examined for galled buds for the first time in winter 1976-77. Even if susceptible seedlings cannot be identified in the glasshouse, pre-planting inoculation would be advantageous if it speeded up field assessment. The results obtained to date (Table 3) suggest that this occurred with seedlings planted in 1969 but not in later plantings.

Table 3

Effect of insectary inoculation on subsequent galling in the field

Year planted	No. of seedlings	No. of mite dispersal periods	% galled seedlings Inoculated	Non-inoculated
1969	1395	1	50.4	11.1
		2	89.6	57.6
1973	389	1	38.1	36.6
		2	45.6	50.0
1974	3728	1	6.4	0
		2	42.1	47.4

EFFECT OF VECTOR RESISTANCE ON VIRUS TRANSMISSION

Smith (1962) showed that reversion can be transmitted by single mites. Early **observations** at East Malling suggested that most mite resistant seedlings remained free from reversion virus. A more detailed assessment of the effect of vector resistance on spread of reversion was made recently. Four hundred and fifty-two mite resistant seedlings, exposed to mites for four years, were propagated for agronomic selection in a situation where mites are controlled by endosulfan sprays. One year after planting, flower bud and leaf symptoms of reversion were recorded (Table 4).

Table 4

Incidence of reversion symptoms in gall mite resistant seedlings after 4 years exposure to mites

Family	No. of seedlings Healthy	Reverted	% Healthy
B1184	6	0	100
B1185	134	6	96
B1186	134	14	91
B1187	14	5	74
B1188	153	1	99
B1189	11	0	100
Total	452	26	95

With an average of 95% apparently healthy seedlings per family it appears that vector resistance is very effective in preventing virus transmission.

DISCUSSION

Progenies segregating for the gene Ce contain seedlings which are now approaching commercial quality. It would be extremely valuable to be

able to omit the present four year's screening in an infection plot and select immediately for agronomic qualities amongst the resistant segregants.

Insectary inoculations to date have not enabled mite-susceptible seedlings to be discarded prior to planting, although a very low proportion of seedlings have developed typical galled buds in the insectary. Autumn inoculations also failed to increase the rate of subsequent gall-in in the field in two years out of three (Table 3). Results from spring inoculations will become available over the next few years. Smith (1962) reported that mite transference was most successful during the normal spring and early summer migration period. The higher proportion of seedlings with mite feeding symptoms following the 1976 spring inoculation suggests increased transference. However at present the relative response of young resistant and susceptible seedlings to mite feeding is uncertain. The absence of galls after two years exposure on many plants which previously displayed leaf symptoms in the insectary (Table 2) suggests that mites may be able to feed and cause distortion without becoming established on plants carrying the gene Ce. The field screening of these progenies, however, is not complete.

Mites were not able to colonise and multiply on resistant plants but the occurrence of 5.8% of mite-resistant seedlings with reversion symptoms (Table 4) suggests that wandering mites, or mites which subsequently die, can sometimes transmit the virus, as with sprayed plants (Thresh, 1968). It may be significant that five out of six of these progenies were derived from a mite-resistant selection which appears to be tolerant to reversion virus (Knight and Manwell, in press) and the low incidence of symptoms may be due in part to virus tolerance. A sample of apparently healthy plants will be indexed by grafting to Baldwin to determine if they are in fact virus infected.

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RISK-RATING PLANTS IN RELATION TO APHID SUSCEPTIBILITY, USING ANALYSIS OF PLANT MATERIAL

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What is risk-rating?

The study of insect-plant relationships has long been subject to an unfortunate dichotomy of approach. On the one hand, plant breeders who have enhanced resistance to pest attack have given little attention to the underlying mechanisms. There is still a tendency to use Painter's (1951) classification of plant resistance into 'non-preference', 'antibiosis' and 'tolerance' as if these were mechanisms whereas they are really phenomena of resistance. On the other hand, entomologists have gone some way towards explaining the chemical basis of host selection by insects and their nutrition, and have shown how important the condition of the plant can be in insect population dynamics (vanEmden & Way, 1973). However, the concepts have rarely been directly utilised for pest control.

The two approaches converge in 'risk-rating' plants to insect attack on the basis of botanical characteristics as well as on pest performance (van Emden, 1972a).

An example of risk-rating research

We have tried to develop a progressive research sequence at Reading University to lead to risk-rating capability with respect to sucking insects, especially aphids. Field resistance phenomena often provide the researcher with a very limited range of variation, sometimes no more than a comparison between two plants or situations. Any difference between them could then be the resistance mechanism; the greater the number of possibilities, the less the likelihood of identifying the operative mechanism.

By increasing the plant variation against which insects are tested, the number of possible mechanisms which can be identified is paradoxically reduced. We have achieved this wide range of variation in seedlings from a single seed source. The development of risk-rating

equations for the peach potato aphid *Myzus persicae* began with 'treatments' of various kinds to Brussels sprout plants; the treatments included different balances of nitrogen, potassium, calcium and phosphorus in the fertiliser, watering regimes, different sowing dates, leaf excision and the application of plant growth regulators.

The next step was to identify a laboratory criterion of performance of *M.persicae* which was rapid and reliable and avoided the many snags associated with recording fecundity or population development of the aphid (Adams & van Emden, 1972). The measure chosen was the mean relative growth rate (RGR) of an individual aphid nymph caged on the plant for a few days; this measure appears meaningful and is correlated with fecundity and reproductive rate (van Emden, 1969). Non-clonal populations of the aphid were used so that results would not be unduly biotype - dependent.

As soon as RGR measurements had been completed, the plants were harvested and the leaves analysed, particularly for soluble amino acids and allylisothiocyanate (total mustard oil after enzyme hydrolysis). Emphasis was placed on these compounds following preliminary experiments (van Emden, 1966; van Emden & Bashford, 1969) showing a general but not reliable correlation between fecundity of *M.persicae* and total soluble nitrogen; mustard oils were also indirectly implicated in that *M. persicae* fecundity appeared to be highest per unit soluble nitrogen on leaf strata low in allylisothiocyanate.

Initially (van Emden & Bashford, 1971), a quantitative multiple correlation was established between the RGR of *M. persicae* and the concentration of only three amino acids; this has since (van Emden, 1972b) been extended to a prediction equation involving six amino acids and total allylisothiocyanate:

M.persicae RGR = 0.0038 + 1 1.0757(0.276 + 0.036 |amide| + 0.934 |methionine| + 0.332 |leucine| - 0.074 |α-amino butyric acid| - 0.564 |tyrosine| - 0.064 |proline<1.5|) - 0.4753 |allylisothiocyanate|.

The inputs into this equation are μ moles amino acid per 100 mg and per cent allylisothiocyanate, both on a plant dry weight basis.

Although there has been some progress in establishing causal links between the compounds in the equation and growth rate of the aphid (van Emden,1973), such work contributes little to any practical use of the equation. Cause and effect evidence does not demonstrate that the compounds determine the susceptibility of plants to the aphid in any general way beyond the range of plant variation from which the equation was developed.

Our philosophy is that the validation of such equation depends on testing their predictive power in different situations. We have therefore analysed a number of chrynsanthemum varieties and compared their predicted order of resistance to *M. persicae* (van Emden, 1972a), based on the amino acid component of the equation, with their known order in glasshouse experiments (Wyatt, 1969). Secondly, we have

picked five Brussels sprout varieties at random from a seedsman's catalogue and analysed the plants to predict their order of resistance. Following the prediction, the RGRs the aphid achieved on the varieties were obtained in the glasshouse. In both experiments, the results showed the usefulness of the risk-rating equation; it was especially successful at separating susceptible and resistant varieties, though some internal discrepancies of order occurred within the latter group. The most recent stage has been to screen some 43 commercial varieties of cabbage chemically, and we predict considerable resistance to *M. persicae* in 16 of these.
The trials testing this prediction have not yet been carried out, but it is encouraging that all but two of the varieties are predicted to gain rapidly in resistance with age, a phenomenon which has already been demonstrated with Brussels sprouts (van Emden & Bashford, 1971). We are also encouraged by the result that our equation for *Brevicoryne brassicae*, which predicted that two Brussels sprout varieties would differ in resistance to that species, was confirmed on a field crop scale following earlier confirmation in the glasshouse (Dodd, 1973).

What use is risk-rating?

Most workers on plant resistance are interested to know the fundamental mechanism behind the resistance they have observed, but many would query the practical use of this knowledge in crop protection. Certainly the late R.H. Painter (1968) was rather scathing about research on the mechanisms of resistance in terms of the contribution it can make to practice. One certainly has to admit it cannot be a substitute for field screening of genetic material because a) it relies on resistance phenomena first being discovered and b) it concentrates on single mechanisms of resistance to the exclusion of the many other mechanisms which may exhibit resistance phenomena in the normal field or glasshouse screen. However, there are some definite practical advantages in pursuing risk-rating in addition to the more conventional screening for resistance:

1) It enables very rapid screening of large germplasm collections for a particular resistance mechanism.

2) Knowledge of mechanisms can be put to practical use in ways other than incorporation into plant breeding programmes. Firstly, it can be used to project the likely effect of new management practices on pest problems. Secondly, it may lead to resistance being available 'out of a tin', for example. Such induced resistance could then be conferred on a variety with desirable characters such as disease resistance, or to add to a heritable mechanism to give the advantage of polygenic resistance.

3) It enables priority to be given in plant breeding programmes to those mechanisms which are sufficiently fundamental in the pest's metabolism that the problem of biotypic variation in the pest causing loss of resistance will be reduced. Similarly, the likelihood of resistance being sustained in spite of climatic or edaphic variation can often be predicted.

4) Finally, there is an increasing interest in utilising low levels of plant resistance in integrated control programmes. Such resistance lowers the selection pressure on the pest population and can be surprisingly effective in combination with natural control (e.g. Dodd, 1973) as well as reducing the dosage of insecticide needed to kill the pest (recent work at Reading and Ibadan, Nigeria). Such low resistance is often difficult to detect in field or glasshouse screening; in the latter situation adjacent varieties may have considerable effects on each other in terms of pest incidence and multiplication. Chemical screening allows the detection of much finer differences in resistance to pests than is possible with standard procedures.

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PREMIERS RESULTATS SUR L'ETUDE EN FRANCE DU COMPORTEMENT VARIETAL DE LA LUZERNE (*MEDICAGO SATIVA* L.) A L'EGARD DU PUCERON DU POIS (*ACYRTHOSIPHON PISUM* H.) (*HOMOPTERA APHIDIDAE*) ET DU PHYTONOME (*HYPERA VARIABILIS* H.) (*COLEOPTERA CURCULIONIDAE*)

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Les travaux entrepris en France sur la résistance de la luzerne à ses ravageurs, concernent la mise au point en conditions contrôlées de méthodes d'étude du comportement variétal de la plante, et la définition d'indices permettant de saisir rapidement et fidèlement les aptitudes des variétés. Les résultats que nous présentons portent sur deux espèces d'insectes, le puceron du pois *Acyrthosiphon pisum* H. et le phytonome *Hypera variabilis* H. Ces deux phytophages sont les principaux ravageurs de la luzerne-fourrage en Europe (BOURNOVILLE, 1976).

I - RESISTANCE VARIETALE AU PUCERON DU POIS

A - Critère de convenance du végétal pour les virginopares aptères :

L'analyse des caractéristiques biologiques d'*A.pisum* a fait l'objet de plusieurs études. Pour les résumer, à une température de 20° et une photophase de 16 heures, la période pré-reproductrice du puceron du pois varie de 7 à 9 jours selon les souches d'insectes et la plante étudiée. Elle est suivie d'un temps de reproduction durant de 13 à 16 jours. Une phase post-reproductrice, qui ne dépasse pas 10 jours termine la vie de l'aphide. La courbe journalière de fécondité débute par un accroissement rapide puisqu'elle atteint son maximum au 3 ou au 4e jour. Le nombre de larves nées quotidiennement décroît ensuite pour s'annuler environ 15 jours après. Partant de ces observations, afin de réduire la durée des expériences, nous avons utilisé le protocole général suivant (BOURNOVILLE, 1977) :

- on place des larves de 4e stade devant donner des aptères, sur le végétal, le jour J. Sept jours plus tard, on note la mortalité de ces individus et le nombre de leurs descendants. On remet en élevage les adultes survivants dont la fécondité et la mortalité seront à nouveau relevées sept jours plus tard. Ayant ainsi surveillé à peu près deux semaines de vie imaginale, on met en évidence presque toute la fécon-

dité des adultes. On calcule les taux nets de reproduction des aphides après 7 jours, de 7 à 14 jours et le total de 1 à 14 jours.

B - Premiers résultats acquis :

Nous avons évalué la réussite d'un biotype du puceron du pois trouvé dans une luzernière sur quelques génotypes de *Medicago sativa*. Nous avons utilisé 3 clones de luzerne d'origine française : 58 12, Europe. Tous trois ont dans leur parenté des populations flamandes. Nous avons également testé 3 variétés d'origine nord-américaine : Lahontan, Resistador (résistantes au puceron tacheté de la luzerne, *Therioaphis maculata* B.), et Anchor (modérément résistante au puceron du pois). On élève 45 aphides par lots de 5 par variété. Les plantes qui poussent dans des caissettes sont placées en chambre de culture. Les résultats sont les suivants :

Variétés	Resistador	58	Europe	12	Anchor	Lahontan
Taux net de reproduction à 14 jours	21,6	21,1	17,2	15,7	8,5	3,5
Analyse de variance	└----------┘					
			└----------┘			
					└----┘	

Les types flamands, cités dans la bibliographie nord-américaine comme présentant une bonne résistance au puceron du pois, ne s'avèrent pas particulièrement bien placés dans notre expérience. Quant à la variété Lahontan, elle est la plus résistante de notre essai alors qu'elle est sensible ou en position intermédiaire aux Etats-Unis.

La fidélité du test demande un respect de conditions thermiques et de stades phenologiques déterminés. Ainsi ISAAK et al (1963) ont montré que 3 clones de luzerne distingués selon leur résistance envers *A.pisum* à 21° n'étaient plus différenciés à 13°. De plus, en utilisant 3 stades phénologiques bien différenciés d'un clones de la variété Europe, nous avons trouvé que les taux nets de reproduction d'aphides s'alimentant sur les stades végétatif et fructifère sont la moitié de celui des aphides élevés sur le stade floral.

Stade	Végétatif	Fructifère	Floral
Taux net de reproduction à 14 jours	17,7	18,6	39,4
Analyse de variance	⌊----------	----------	----------⌋

II - RESISTANCE VARIETALE AU PHYTONOME

La résistance de la Luzerne envers *H.variabilis* peut concerner la ponte de l'adulte, l'alimentation larvaire ou l'alimentation imaginale. Nous avons analysé ces diverses éventualités en comparant la variété "Team", sélectionnée aux Etats-Unis pour sa résistance au phytonome, à la variété Europe. On trouvera dans BARNES et al (1970) les conditions de ces tests. Nous avons étudié l'influence de l'état du végétal (plante entière, brin coupé), de la densité d'élevage des insectes et de certaines conditions de photopériode.

A - Tests de ponte :

Après une période de conditionnement sur le nouveau végétal, on élève des femelles ayant hiverné et on dénombre leur ponte. Le nombre moyen d'oeufs pondus par jour est de 14,2 sur Europe et 10,1 sur Team. Les plantes entières reçoivent davantage de pontes que les brins coupés. Il est préférable de n'offrir qu'une variété de végétal au phytonome par cagette, plutôt que d'y mettre les 2 variétés. Ce résultat est contraire à celui de CAMPBELL et BUSBICE (1966).

B - Tests d'alimentation et survie larvaire :

A l'éclosion, les larves sont placées sur les végétaux. A chaque changement, on dénombre les survivants et on les pèse. La survie larvaire n'est pas différente entre les 2 variétés mais la densité des larves par cagette influe sur la mortalité. Team et Europe sont significativement différentes en ce qui concerne le poids moyen des larves à 14 jours qui sont respectivement 4,3mg et 5,1mg sur brin coupé. Là encore, la plante entière permet des croissances pondérales plus importantes.

C - Tests d'alimentation imaginale :

Ils ont été réalisés sur les imagos issus des larves précédentes. La consommation des adultes est évaluée durant 24 heures sur des disques foliaires. Elle est mesurée par le poids de matière sèche consommée par unité de poids d'adulte initial (BARNES et RATCLIFFE, 1967) Les variables étudiées ici, en plus des variétés, sont la photophase et le sexe des individus. Les femelles, plus grosses à l'émergence imaginale, consomment davantage de végétal, mais lorsqu'on rapporte la quantité ingérée à l'unité de poids adulte, il n'y a pas de diffé-

rence de consommation. Avec une photophase de 16 heures, Team est significativement plus dévorée qu'Europe comme le montrent les résultats ci-dessous, exprimés en mg de poids sec de luzerne consommée par mg d'adulte.

Sexe	Mâles	Femelles
Variété		
Europe	0,26	0,30
Team	0,38	0,38

Les résultats des 2 variétés ne diffèrent pas significativement avec une photophase de 8 heures.

La variété Team, sur l'ensemble de ces 3 tests, ne présente qu'une résistance modérée au phytonome. Le critère qui traduirait le mieux un "antibiosis", à savoir la survie larvaire, n'est pas significativement différent dans les 2 variétés testées. L'utilisation de brins coupés de végétal ne perturbe pas les résultats. Cette méthode est moins astreignante que l'utilisation de plantes entières, mais les chiffres qu'elle permet d'obtenir sont plus faibles. Dans le cas des élevages larvaires, il convient d'éviter les densités élevées d'insectes.

III - CONCLUSIONS

La distinction de résistances variétales de la luzerne envers des insectes, en conditions contrôlées, semble être possible dans le cas du puceron du pois, mais plus délicate pour le phytonome. Le taux net de reproduction paraît être discriminant dans le cas d'*A.pisum*, mais la fidélité de ce test nécessite quelques précautions dans les méthodes utilisées. Les tests de laboratoire portant sur le phytonome ne font pas bien ressortir la résistance variétale. A ce propos, BARNES et al (1970) annoncent que la résistance de Team envers *H.variabilis* est essentiellement liée à la "tolérance" de cette variété en plein champ. Dans ces conditions, nos résultats ne surprennent pas. D'ailleurs, en ce qui concerne le puceron du pois, il conviendra de vérifier également en conditions agronomiques, les données obtenues. Les tests réalisés en conditions contrôlées doivent en effet être en bonne corrélation avec ce qui se passe au champ (GUY, 1975). Une étude en cours réalisée à l'extérieur doit nous permettre de conclure à ce sujet. Enfin, la discordance de certains de nos résultats avec des travaux nord-américains peut tenir à la variabilité des populations d'insectes.

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HOST PLANT SELECTION BY CRYTORRHYNCHUS LAPATHI L. (POPLAR WEEVIL)

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In this paper the conclusions of tests acomplished - some years ago are exposed. They discuss the clonal preferences of C. lapathi on feeding and oviposition, the clonal antibiosis and the invclved stimuli. A detailed account of the tests will be published in the Bulletin of the "Estación Central de Ecología" (ICONA).

1 - Standardization of laboratory tests

From the previous experiences for standardization of clonal multipreference tests, the conclusion was reached that they should be mounted the following way:

The cuttings should have 0.50 m. length with the same diameter in each block, and with the upper end covered with - paraffin so as to avoid dessication in the course of the test. The most suitable size for the cages is 50 x 50 x 50 cm. and - covered with a nylon mesh, and a tray at the bottom with earth where to implant the cuttings. Frequent water sprays are necessary so as to keep the suitable environment for the insects life. The duration of the test with the same cuttings should not exceed 15 days; thus, the factors derived from the drying and the chemical changes of the bark of the cuttings are avoided.

The number of adult insects in each test should be about a couple per cutting. These insects should be fed before starting the bioassay on fresh lettuce.

The number of replications or blocks of the experiences design, should be over 10, in order to obtain some statistical significance in the results.

2 - Clonal susceptibility on imago feeding

The feeding stimuli are of the chemical nature, and for C. lapathi they are compounds fairly common to all the clones, and even present in other plants and food. The content of these substances changes in the course of the vegetative cycle of each clone. It only appears to be more preferred, the clone 8; perhaps due to an optimum content of the mentioned substances, together with other permissive factors.

3- Clonal susceptibility on oviposition

The high agreement of the results from laboratory experiences carried out, allows for the conclusion that the factors influencing the oviposition are more definite than the feeding - stimulants and these are more specific for certain clones, preferred for oviposition.

The susceptible clones to C. lapathi oviposition, on - that order, are as follows:

P. nigra L. x P. balsamifera cv. 'manitobensis'; P. x euramerican (Dode) Guinier cv. 'Bayer B8 on mountain'; P.deltoides Marsh cv. 'Missouriensis Zeeland'; P. x euramerican (Dode) Guinier cv. 'Robusta Zeeland'.

P. alba L. cv. 'bolleana' Lauche; P. alba L.var. nivea cv. 'Palmata'. and P. simonii fastigiata C.S. may be considered as resisting clones.

The existence of a different oviposition in the various clones included in the experimental parcels was not registered may be due to an insufficient replications number. The location does not seem to modify the clone answer to oviposition but it has an indubitable influence on the insect oviposition.

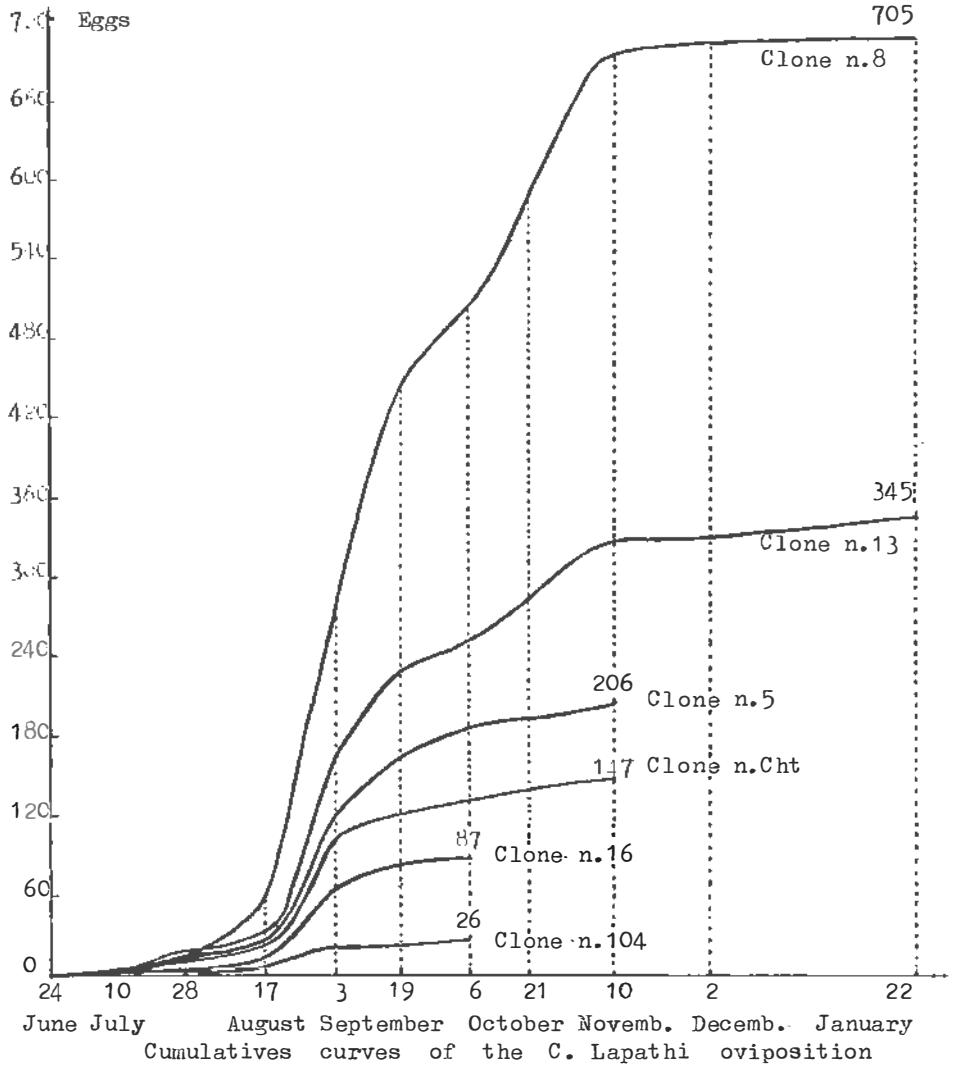
From these experiences it may be concluded that those factors such as irrigations and fertilizers, influence the - susceptibility of poplar plants to C. lapathi attacks, since - these factors affect their vigour. The oviposition is more abundant on trees of a better vegetative state. In the case of irrigations, there is besides, an interaction by this factor with the clones as for its susceptibility to the insect.

4 - Clonal antibiosis

Both C. lapathi male and female feeding on clone 8 and clone 13, have a longer mean life. Those feeding on clone 104 were those with a shorter mean life. Females mean life is always a little longer than males one, with similar feeding.

Clone 8 and 13 are the most suitable for the development of C. lapathi. The females feeding on clones 8 and 13 have a more abundant oviposition. The rate of C. lapathi reproduction (number of eggs per emerged adult) was 3.1 and 1.5, on those clones. Clone 104 rate was the lower, this outstanding with 0.1.

None of the tested clones has any influence on the extent of the pre-oviposition period. This period lasts from 30



Cumulatives curves of the C. Lapathi oviposition

to 40 days.

The larval feeding on different poplar clones does not show reliable differences neither on adults weight nor on sexual ratio.

5. Clonal preference causes

The olfactometers used proved the existence of olfactive stimuli with significance in food-plants recognition, acting on - the males, but not on females. They are not only present in - susceptible clones, but also in those with some resistance.

The hypothesis than the comparative resistence of clone 91 is due to the physical character of the tomentum lap or pruine of the stem, should be excluded.

From the realized poplar cuttings tests may be concluded that the acting stimuli for oviposition and feeding are not only coenesthesic, but they are of a chemical nature.

The realized experiences by using an artificial substratum including the clonal extracts or the assay chemical substances, proved their great possibilities in this kind of investigations.

The tests confirm the existence of a substance (X_1) - stimulating C. lapathi oviposition, which is perfectly determined by chromatography. It may be stated that this substance acts as - an "token" stimulus, and which is fit for the recognition of the most apt plant for the insect's offspring. Another substances (Y), existing in the clones with some resistance, may have an inhibitory significance. The salicin is present in all the clones under study; this glucoside acts probably as a "token" phagostimulant.

Clones included in the tests

Reference number	Clones terminology
68	P. nigra L. cv. 'gigantea'
102	" cv. 'Bordils'
104	" cv. 'Grenade white'
8	P. deltoides Marsh cv. 'Missouriensis Zeeland'
16	" cv. 'Carolin'
75	" from Kansas
77	" from Dakota
106	P. x euramericana (Dode) Guinier cv. 'pinseque'
107	" cv. 'Grenade dark'
108	" cv. 'White Canada'
Ch	" cv. 'Grenade Chope'
5	" cv. 'Robusta Zeeland'
37	" cv. 'Dolomiten'
49	" cv. 'Bayer B8 on mountain'
50	" cv. 'Bayer A5 on plain'
9	" cv. 'I-262'
10	" cv. 'I-488'
11	" cv. 'I-154'
12	" cv. 'I-455'
13	" cv. 'I-214'-'Italy Glory'
105	P. euramericana x P. euramericana cv.'Campeador'
Cht	P. euram. cv. 'Chopa' x P. euram. cv.'Negrito de G.' cv.'Chopita'
67	P. simonii fastigiata C.S. (Tacamahaca Section)
51	P. nigra L. x P. balsamifera cv. 'manitobensis'
91	P. alba L.cv.'bolleana' Lauche (Leuce section s.s. Albidae)
TxC	P. tremula L. x P. deltoides carolin
NP	P. alba L. var. nivea cv. 'Palmata

PROGRAMME D'AMELIORATION DU MAIS EN FRANCE POUR LA RESISTANCE A LA PYRALE *OSTRINIA NUBILALIS* Hbn.

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1 - LES RELATIONS ENTRE LES JEUNES CHENILLES DE PYRALE ET LA PLANTE-HOTE.

Selon les relations entre le déroulement de la période de ponte de la Pyrale, *Ostrinia nubilalis* Hbn, et la succession des stades phénologiques du Maïs, les séquences d'installation des jeunes chenilles sur la plante-hôte diffèrent et peuvent s'accomplir sur des organes divers. Classiquement, par référence à la situation dans le Corn Belt américain, les jeunes chenilles de la première génération s'alimentent sur les feuilles enroulées à l'intérieur du cornet, puis sur la panicule mâle en cours de montaison. Celles de la deuxième génération apparaissant après la floraison femelle, se nourrissent des tissus des gaines foliaires avant de pénétrer dans la tige ou l'épi.

Dans les nouvelles zones de culture françaises de variétés précoces, la situation apparaît très différente de ce schéma simplifié. Les populations, de caractère génétiquement polyvoltin, n'y manifestent le plus souvent qu'une génération annuelle dont les jeunes chenilles attaquent des plantes à des stades intermédiaires entre ceux subissant les attaques des 2 générations américaines. En 1975 par exemple, pour une période de ponte échelonnée durant tout le mois de juillet, le maximum d'éclosion des chenilles est situé du 15 juillet au 5 août. Si les chenilles précoces peuvent attaquer les feuilles du cornet, celles correspondant au maximun de ponte éclosent sur des plantes en floraison mâle (présence de pollen et apparition de l'épi femelle (tableau 1).

Dates	8 juillet	18 juillet	28 juillet	7 août
Nbre pontes/ 100 plantes	1.4	18.9	19.6	9.2
Stades du Maïs	Cornet Haut.90cm	fin de cornet 25% pani.visible	Floraison ♂ Pollen	Floraison ♀ 75% soies

Les dissections de plante à mi-août montrent des localisations préférentielles de ces chenilles au niveau des gaines foliaires et des épis (spathes, soies, grains) (MERLET, 1975).

Pour utiliser la résistance à la deuxième génération américaine de la lignée B 52, ce même type de sélection sera réalisé dans les descendances de croisements avec 14 lignées précoces dentées et cornées. On tente par ailleurs d'obtenir une transformation de B 52 en précoce, tout en conservant sa résistance.

Enfin, des synthétiques ont été crées ou sont en voie de création notamment par participation au programme du Groupe international de travail sur la Pyrale du Maïs à partir de lignées précoces européennes. Un programme de sélection récurrente pour accroître les fréquences des gènes favorables sera entrepris dans ce matériel

4.3 - Expérimentation : A partir des lignées jugées "résistantes" des essais diallèles sont mis en place en conditions naturelles d'infestation dans les zones à haut niveau de population de Pyrale et sous infestation artificielle à Bordeaux. Ils permettent de mieux connaître l'apport des lignées et de choisir des hybrides simples testeurs "résistants".

Les hybrides obtenus par la mise sur testeur des lignées provenant de la sélection pour la Pyrale sont éprouvés au champ en conditions naturelles ou en comparant des parcelles infestées artificiellement ou non par rapport à l'étalon du groupe de précocité correspondant à un témoin sensible. Les premiers résultats obtenus sont encourageants et des hybrides expérimentaux tolérants sont en cours d'étude.(tableau 3)

Variétés	Rendement du témoin	Rendement des parcelles inf.	Baisse de rendement
Témoin cultural n° 1	83.7	74.9	11 %
Témoin cultural n° 2	73.3	67.1	7 %
Témoin sensible W182ExW117	88.7	61.6	30 %
Hybride expérimental HS 1	93.7	88.5	6 %
Hybride expérimental HS 2	81.2	81.6	0 %

5 - CONCLUSIONS

L'installation,en cours,de populations importantes de la Pyrale du Maïs sur les variétés précoces, à base génétique étroite, largement cultivées dans les plaines du Nord de la Loire et le type nouveau de relation entre l'insecte et la plante hôte dans ces régions obligent à modifier les techniques et les programmes de sélection du maïs pour la résistance ou la tolérance à la Pyrale. Cet exemple met

2 - LES PHENOMENES DE RESISTANCE

Des phénomènes de résistance totalement différents ont été mis en évidence aux Etats-Unis pour les deux types d'attaque cités plus haut, sur des organes différents à des stades végétatifs nettement distincts , l'un en phase de croissance de la plante, l'autre après floraison (JENNINGS et al, 1974 ; RUSSEL, 1972).

La résistance à l'alimentation sur feuilles du cornet est polygénique, conditionnée par des gènes à plusieurs loci agissant sur le mode additif. Des corrélations ont été trouvées entre le degré de résistance apprécié visuellement, la survie larvaire et la teneur des tissus en DIMBOA (2,4-dihydroxy-7 methoxy-1,4 Benzoxazine-3-one),mais d'autres facteurs sont aussi en jeu. Ils agissent probablement comme descendants alimentaires condamnant les jeunes chenilles à une recherche continue de nouveaux sites de prise de nourriture réduisant ainsi la survie. Une gamme de matériel (surtout tardif), possédant cette résistance a été développée et peut être utilisée en amélioration.

Le mécanisme de résistance à l'alimentation à l'aisselle des feuilles et sur les gaines, avant pénétration dans la tige après floraison, n'a pas été totalement élucidé. Il s'agirait d'un mode d'action à plusieurs loci, non additif, avec dominance et epistasie. Très peu de matériel présentant ce type de résistance a pu être jusqu'à ce jour isolé, à l'exception de la lignée tardive B 52.

Le souci des sélectionneurs sera de combiner en une même variété les deux types de résistance si, comme aux Etats-Unis ou dans le Sud de la France, les cultures sont exposées aux attaques des deux générations ou lorsque, comme dans le Bassin Parisien, la première génération intervient tardivement par rapport au développement de la plante. Malheureusement, très souvent le matériel résistant sur la feuille n'est pas résistant sur tige et vice versa.

3 - L'ADAPTATION DES TECHNIQUES DE JUGEMENT DE LA RESISTANCE DES LIGNEES

Pour le jugement du matériel végétal en France, il est fait largement appel aux techniques d'infestation artificielle au champ à partir de pontes de Pyrale obtenues au laboratoire. On utilise les critères d'appréciation depuis longtemps expérimentés aux Etats-Unis ou plus récemment par le Groupe international de travail sur la Pyrale du Maïs, mais une adaptation est nécessaire pour répondre aux conditions françaises préalablement décrites.

A côté des notations classiques d'intensité de l'alimentation sur feuilles du cornet après infestation avant l'apparition de la panicule dans le cornet, il est largement tenu compte des dégâts ultérieurs en végétation ou à maturité appréciés selon un barême ana-

logue incluant les dégâts sur tige ou sur épi, ainsi que des résultats de dissection des tiges (nombre de larves et importance des galeries.) C'est la combinaison de l'ensemble de ces critères qui permet de trier les lignées étudiées par comparaison avec les performances d'étalons de sensibilité (par exemple W 182E) ou de résistance (actuellement PB 40 ou EA 2087 par exemple).

Par ailleurs, on prend en considération les résultats d'infestations artificielles réalisées à différents stades dans le cornet des feuilles ou à la floraison femelle sur la feuille de l'épi. On constate en moyenne une plus grande sensibilité à ce second stade, mais certaines lignées demeurent relativement peu sensibles quelque soit le stade de l'infestation. (tableau 2)

Comportement des lignées		Exemples de notes dégâts au champ à maturité			
Inf.précoce	Inf.tardive	Infestation précoce		Infestation tardive	
		Clt.	Note	Clt.	Note
"Résistant"	"Résistant"	2	1.4	1	1.7
"Résistant"	Sensible	4	1.8	9	5.2
Sensible	Sensible	8	3.5	8	4.0

4 - LES PROGRAMMES D'AMELIORATION POUR LA RESISTANCE ET LA TOLERANCE

Les programmes d'amélioration du Maïs pour la résistance et la tolérance à la Pyrale sont conçus et réalisés à l'INRA en collaboration entre les sélectionneurs et les zoologistes. Ils comportent des jugements systématiques de bonnes lignées fixées nouvellement obtenues par sélection ou par échange, des programmes de sélection sous infestation artificielle en pépinière, des expérimentations de variétés hybrides tolérantes.

4.1 - Comportement : L'examen du comportement, sous infestations artificielles précoce et tardive, de lignées comparées à l'intérieur de groupes précoces et tardifs à des étalons sans cesse plus performants permet soit d'éviter l'utilisation de matériel trop sensible, soit de détecter des lignées immédiatement utilisables.

4.2 - Sélection : A mesure que sont trouvées de telles lignées précoces "résistantes", les meilleures sont employées comme géniteurs et sont croisées avec les lignées sensibles entrant dans la composition des hybrides actuellement cultivés. Une sélection sous infestation artificielle en pépinière est réalisée pendant trois générations d'autofécondation à partir de la descendance F2 de tels croisements. De premières lignées "résistantes" à bon comportement en test de valeur hybride commencent à apparaître.

en lumière la nécessité d'études écologiques locales en vue d'une meilleure connaissance des relations insecte-plante hôte et souligne l'intérêt d'une collaboration étroite entre l'entomologiste et le sélectionneur pour la mise au point de variétés tolérantes de Maïs à cet insecte.

Remerciements : Le programme et les résultats rapportés ici sont dûs à une équipe de chercheurs et de techniciens des départements de Zoologie et d'Amélioration des Plantes de l'INRA comprenant notamment MM. PANOUILLE, RAUTOU, STENGEL et VIBLE.

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CHOICE OF OVIPOSITION SITE BY *CHILO*, THE SORGHUM STEM-BORER

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Selection of an oviposition site by the adult is the first stage in the Lepidopteran host selection process. Oviposition site selection has been shown to be influenced in *Plutella maculipensis* by a combination of physical and chemical factors (Gupta and Thorsteinson, 1960). Yamamota *et al.* (1969) divided site selection behaviour into two phases:-

(1) flight and decisions on host suitability at a distance;

(2) landing and final acceptance or rejection of the surface.

Phase (1) may be controlled by both visual and olfactory cues, whereas in phase (2) olfactory, tactile and gustatory cues may be important. The work to be described was carried out mainly in small cages where decisions at a distance involving visual and olfactory cues would be of reduced importance. This work was carried out at the Centre for Overseas Pest Research (COPR), London, and at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India. It forms a part of investigations intended to provide a basis for screening for resistance of sorghum cultivars to *Chilo partellus*.

At COPR it was observed that *Chilo* deposited its eggs freely after insemination and, in the absence of plant material, would lay its eggs on the surfaces of the glass cage. The eggs were laid, one overlapping the other, in batches of from ten to one hundred eggs each. If host-plant material (in the form of three-week old, seedling maize leaves) was made available, then the majority of eggs were laid on this, with only very few being laid on the cage surfaces (Table 1). This occurred despite the fact that the leaf-area offered was much less than the total

cage surface area.

Chilo females were offered leaves of a number of plant species on which to oviposit. These were offered alone, with only the cage surfaces as alternative oviposition sites, or with three-week old, maize seedling leaves. The leaf areas offered were made, as near as possible equal.

Table 1. Oviposition on plant surfaces

Oviposition surface	Replicates	Single plant expts		Choice expt with maize		
		% on plant	% on cage surface	% on plant	% on maize	% on cage surface
Cage surfaces	6				93±12	7±12
Agropyron repens	8	50±24	50±24	16±16	73±19	11±11
Holcus lanatus	8	3±5	97±5	4±7	85±17	11±7
Wheat seedlings	9	39±16	61±16	8±10	82±14	10±8
Leek	12	-	-	39±18	53±21	8±11
Onion	15	3±11	97±11	3±9	66±45	31±29
Eruca sativa	16	-	-	8±8	63±34	29±21
Daffodil	32	63±28	37±28	20±18	65±26	15±21

When the grass *Agropyron repens* was offered alone, 50% of the eggs were laid on the grass leaves, the remainder being laid on the cage surfaces (Table 1). When maize was included as an alternative to the grass, 73% of the eggs were laid on maize and only 16% on *Agropyron*. Wheat seedling leaves and the leaves of mature daffodil were also relatively acceptable without maize, but when maize was included, the majority of eggs were laid on it.

When leaves of the grass *Holcus lanatus* were offered with maize, very few eggs were laid on the grass. When the grass was offered alone, its acceptability did not increase. Similarly young onion leaves were not acceptable either with or without the presence of maize. Mature leek leaves were acceptable in comparison with mature maize leaves. Both young onion and the herb *Eruca sativa* increased the level of oviposition on cage

surfaces in cages with maize present.

The leaves of *Holcus lanatus* are distinctly hairy. The upper surfaces of the upper leaves of mature maize are also hairy as are the lower surfaces of the leaves of lupin and both surfaces of the leaves of nightshade. When mature maize or lupin leaves were offered for oviposition, either in a normal position, or reversed, virtually no oviposition occurred on the hairy surface (Table 2). No oviposition occurred on the leaves of nightshade when offered with maize seedling leaves.

Table 2. Oviposition on hairy leaf surfaces

Leaf type	Hairy surface	Leaf position *	% oviposition on:-		% maize comparison	
			Abaxial	Adaxial	Abaxial	Adaxial
Maize (81 days)	adaxial	n (11)	43±25	3±8	-	-
		r (7)	48±27	10±13	-	-
Lupin	abaxial	n (14)	1±1	36±25	-	-
		r (14)	1±2	27±26	-	-
Nightshade	both	n (14)	0	0	24±24	48±28

* n : normal r : reversed

The maize cultivar used produced fourteen leaves before flowering. After the cotyledon (leaf 1), leaves 2 and 3 have only indistinct mid-ribs. Leaves 4 to 7 have distinct mid-ribs and leaves 8 to 14 have distinct mid-ribs and hairy upper surfaces. In order to examine the effect of leaf ageing and changing morphology, *Chilo* females were offered the opportunity to lay on: (1) standard young leaves (leaf 2, three-week seedlings), (2) the oldest leaves of progressively older plants (leaves 2-5, weeks 5-14), (3) the youngest leaves of progressively older plants (leaves 4-10, weeks 5-14). The three-way choice was offered in stainless steel gauze cages which virtually limited oviposition to the leaf surfaces provided. The oldest leaves offered were selected as the oldest leaf on the plant which had not started to dry off. Equal areas of each leaf-type were offered.

Ageing of the leaves appeared to have little effect. Equal percentages of the total eggs laid were laid on the standard,

the oldest leaves and the youngest leaves (Table 3). However, the ratio of eggs on upper to lower surface did change so that, as the leaves became older, more eggs were laid on the lower surface. If the leaves were divided according to morphological type, not age, then this difference became even more distinct, with virtually no eggs on the hairy upper surfaces of leaves 8-10.

Table 3. Effects of ageing and leaf morphology on oviposition on maize

	% total on each leaf type	Ratio of eggs on upper to lower surface		Ratio of eggs on upper to lower surface
Standard (leaf 2, week 3)	36±7 (7)	1.0±0.4 (7)	mid-ribs indistinct (leaves 2-3)	1.0±0.4 (11)
Old leaves (leaves 2-5, weeks 5-14)	34±5 (7)	0.8±0.4 (7)	mid-ribs distinct (leaves 4-7)	0.5±0.1 (7)
Young leaves (leaves 4-10, weeks 5-4)	30±6 (7)	0.4±0.2 (7)	mid-ribs distinct upper surfaces hairy (leaves 8-10)	0.2±0.1 (3)

When offered the alternative of oviposition on a standard coarse nylon gauze and progressively finer gauzes, *Chilo* always selected the finer gauze, and progressively fewer eggs were laid on the coarse standard (Table 4).

At ICRISAT the opportunity was presented of observing *Chilo* oviposition on potted sorghum plants of a range of sizes in a net-house. Despite the presence of green leaves on the upper part of the plant and the greater area of green leaf, the

majority of egg batches were laid on the lowest, dried leaves (Fig. 1). When offered a choice between approximately equal areas of dry, brown leaves and turgid, green leaves of sorghum in small cages, the majority of eggs were laid on the dry, brown leaves. If green leaves were allowed to dry in the laboratory and then offered with turgid, green leaves, oviposition occurred mainly on the dry, green leaves (Table 5).

Table 4. Oviposition on nylon gauzes of varying mesh size

Test gauge			Open area%	Perforations per mm^2
	10N Standard	Test gauze	(10N=43%)	(10N=25.0)
12N	145±47	373±125	41	28.6
14N	85±65	369±157	35	37.2
16N	74±95	305±140	33	43.7
21N	49±55	364±164	29	53.0
25N	15±15	424±80	26	57.2

Direct observations of oviposition behaviour at the leaf surface suggested that the antennae, the ovipositor tip and possibly the tarsi were all used in actively sensing the oviposition surface. Scanning and transmission electron microscopy have shown that the ovipositor tip is covered with a large number of long mechanoreceptor hairs, but that among these there are two small groups of chemoreceptor type hairs. Chemoreceptor type hairs appear to be present on the antennal tip also.

Table 5. Oviposition of sorghum leaves

No. of relication	% dry, brown leaves	% turgid, green leaves
6	79±15	21±15
	% dried, green leaves	% turgid, green leaves
5	71±8	29±8

From the observations described it would appear that the physical characteristics of the oviposition substrate are of major importance. Leaves with distinct mid-ribs (mature maize) or with elongate creases (dry sorghum) offer concave areas in

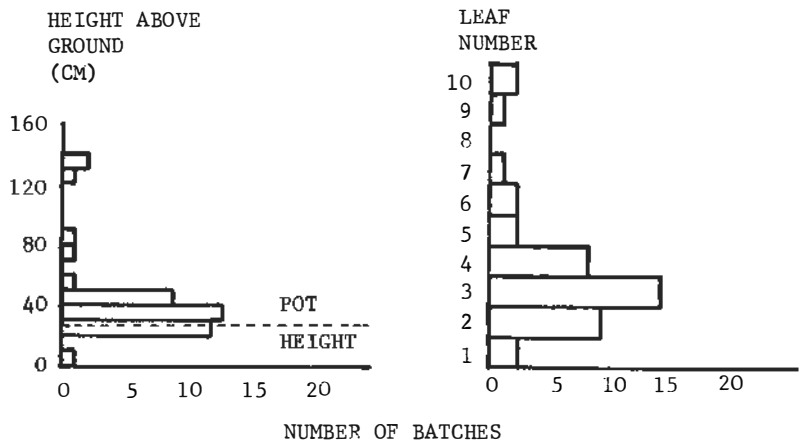

Fig. 1. Height and leaf chosen by *Chilo partellus* for oviposition in a net-house

which egg batches may be placed. Such leaves were favoured for oviposition. Surfaces with minor irregularities, such as hairs, were not favoured. More eggs were laid on fine than on coarse nylon gauze and *Chilo* could distinguish small differences in mesh size.

The form of the egg batch, with the eggs overlapping each other, suggests that prevention of desiccation is important. *Chilo* eggs are thin-walled with only very fine sculpturing of the chorion. Such egg batches could not be produced on a hairy or irregular surface. The formation of the batch in a concavity may increase its protection, while laying of egg batches low on the plant and on non-growing surfaces may prevent dislodgment by growth, distortion or wind movement.

Maize seedling leaves were preferred to all other plants offered, including those without hairy surfaces. In all cases there are physical differences between the form of the leaves which could account for these preferences. Thus the leaves of onion are round in cross-section and offer no concave surfaces. The presence of onion tended to increase the percentage of eggs laid on the cage as opposed to the maize, and the herb *Eruca sativa* had a similar effect. It is possible that the strong odours from these plants disrupted the normal preference for maize. However mature leek leaves had no such effect. Only by taking extracts of the leaf surfaces and offering these on a

surface of constant physical structure can the role of the chemical nature of the surface be resolved. The sensory structures observed testing the surface during oviposition carry sense organs of a chemosensory type. However the fact that *Chilo* chooses the lowest, dead leaves of sorghum, and has been observed at ICRISAT to lay on non-sorghum surfaces in the presence of sorghum, suggests that oviposition choice is for egg survival and a good place from which larvae can disperse, rather than directly for a suitable host for the larva. Choi *et al.* (1976) using *Chilo suppressalis* and rice, and Sharma and Chatterji (1971) using *C. partellus* and maize, have demonstrated oviposition preferences among cultivars in net-house tests. However they did not resolve the basis of the preferences shown, or demonstrate their presence in the field. While the physical structure of the oviposition surface is important to *Chilo*, a role for the chemical nature of the surface in oviposition site selection has yet to be demonstrated.

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CYANOGENIC GLYCOSIDES IN PLANTS AND THEIR RELEVANCE IN PROTECTION FROM INSECT ATTACK

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The ability of certain plants to produce HCN has been known for many years, but only more recently has the very widespread nature of the phenomenon been realised. Gibbs (1974) recorded over a thousand species with this capacity, and there have been several reviews on the associated plant chemistry (Miller, 1973; Tapper & Reay, 1973) and genetics (Jones, 1972, 1973). It is naturally assumed that this potential protects the plant against attack by animals since HCN is a potent inhibitor of respiratory enzymes, and certainly it is well known that cattle can be poisoned by feeding on cyanogenic clover or young sorghum. More recently it has been shown that voles and slugs prefer non-cyanogenic to cyanogenic plant forms (Jones, 1966; Crawford-Sidebothom, 1972). Sheep on the other hand show no preferences and are not poisoned by cyanogenic plants (Corkill, 1952). The situation with insects is equally variable.

There are a number of insects which habitually feed on cyanogenic plants: for example caterpillars of the burnet moths, *Zygaena* spp., feed on the cyanogenic bird's foot trefoil, *Lotus corniculatus* (Jones *et al.*, 1962), and the Mexican bean beetle, *Epilachna varivestis*, is actually stimulated to feed by the cyanogenic glycoside linamarin, which occurs in its host plant (Nayer & Fraenkel, 1963). Many other species feed occasionally on cyanogenic plants, for example the variegated grasshopper, *Zonocerus variegatus*, is a pest of cassava at certain times in southern Nigeria. Recent work at the Centre for Overseas Pest Research has demonstrated the protective role of cyanogenesis in plants in relation to grasshoppers and locusts.

Three cyanogenic glycosides occurring in plants were individually tested in the laboratory for their effect on feeding

by *Locusta migratoria* and *Schistocerca gregaria*. The compounds were prunasin, linamarin and amygdalin, and they were applied to highly palatable discs composed of either wheat flour or sucrose-impregnated glass fibre discs. In each case one insect was placed in a plastic box containing a disc with added glycoside plus a control disc. The experiment lasted 1-2 hours, when more than 30% of the control disc was eaten. The areas of each disc were measured and the amounts eaten of each were compared. There were 10 replicates for every different treatment. It is clear from Table 1 that such compounds had no deterrent effect on *Schistocerca* at dry weight concentrations comparable with those known to occur in plants, and although feeding by *Locusta* was reduced at high concentrations, these concentrations are higher than those normally encountered.

Table 1. The effect of cyanogenic glycosides on feeding by *Schistocerca* and *Locusta*. Results are expressed as % reduction of feeding compared with controls

	Locusta			*Schistocerca*		
Percent dry weight of disc	lina-marin	prunasin	amygdalin	lina-marin	prunasin	amygdalin
0.1	0	0	0	0	0	0
1.0	25	0	10	0	0	0
5.0	60	45	53	20	10	18
10.0	98	85	70	48	22	34

Longer term experiments were then carried out to investigate the effect of ingestion of a cyanogenic glycoside over a period of 10-14 days. Amygdalin was applied to the leaves of young wheat with a resultant concentration on the fresh leaf of approximately 0.1%. These leaves were then fed to nymphs of *Locusta* kept singly in jars for the length of the fifth instar, to the time of moulting to the adult stage. Insects were weighed daily, and the food intake and faeces production also monitored daily. Amygdalin ingestion had a beneficial effect on utilisation rate and on growth (Table 2), although preliminary experiments have shown that the digestive juices of *Locusta* contain enzymes capable of releasing HCN from amygdalin and linamarin.

Table 2. The effect of amygdalin ingestion on utilisation of food and growth rate of *Locusta* fifth instar males

	Number of insects	Mean length of instar (days)	Mean % weight increase	Utilisation of food (%)
wheat + amygdalin	19	10.3	128	44
wheat only	18	11.6	109	35

Cyanogenic species of plants however, commonly contain an enzyme which can hydrolise the glycoside and release HCN, and several plant species occur in four different forms associated with HCN production. They may contain the hydrolising enzyme alone, the glycoside alone, neither, or both (Jones, 1973). The last three of these four varieties of *Pteridium aquilinum* were tested for palatability with *Schistocerca*, and Table 3 shows that while *Pteridium* is not a highly favoured plant, only the variety containing both cyanogenic glycoside and the hydrolising enzyme was almost totally unpalatable (Cooper-Driver & Swain, 1976).

A number of plants have been shown to produce and release certain secondary compounds as a result of crushing and this is generally due to the hydrolysis of various glycosides (Miller, 1973). Such is the case with cyanogenesis: a glycosidase makes contact with a cyanogenic glycoside during tissue damage, with the consequent release of HCN. It seems likely that the same processes occur when an insect bites into a leaf, and that it is the HCN released which is the actual deterrent. The behaviour of acridids after biting into highly cyanogenic plants suggests a high level of deterrence with backward retreating movements. Similar movements can be induced with 2µl drops of prussic acid placed near the mouthparts during feeding, and the problem was studied in more detail with nymphs of *Zonocerus*.

Table 3. Amounts of different varieties of *Pteridium* taken in one meal by *Schistocerca* fifth instar males

Variety	Number of insects	Meal sizes as % of grass meal
cyanogenic glycoside, no enzyme	10	52
cyanogenic glycoside plus enzyme	10	4
no glycoside or enzyme	10	48

Table 4. Responses of fifth instar *Zonocerus* to cassava leaves producing different amounts of HCN (insects were deprived of food for the previous 24 hours)

HCN level	Number of insects	% rejecting	% small meals	% larger meals
low	14	21	7	71
medium	28	29	7	64
high	26	58	12	30

Individual insects which had been deprived of food for 24 hours were placed on cassava leaves and behavioural reactions after biting were filmed and later analysed. After each test, the leaf which had been bitten was tested for its ability to release HCN, using the picrate paper test (Jones, 1966) and the copper ethyl aceto-acetate test (Tantisewie *et al.*, 1969) modified to measure release over the first second after cutting into the leaf (Bernays *et al.*, in press). Rejection by the insects was associated with a high intensity of the reaction in different leaves (Table 4). Older leaves and certain 'low cyanide' varieties tended to give lower readings with both tests. It was also found that cut, wilted plants, which still produced large amounts of HCN as measured by the picrate test, but had a relatively low rate of release in the first second after cutting into the leaf, were quite palatable and gave maximum survival and fastest growth of the insects when given as the only food (Bernays *et al.*, 1975). Further experiments (McCaffery *et al.*, in prep.) have shown that individual insects kept on growing cassava eventually die, and that this death is due to slow starvation, although utilisation rates of ingested food are also low (Table 5). This is presumably due to the enfeebled state of the insects, since the cyanide intake on wilted plants is far in excess of that on growing plants.

Table 5. Consumption, weight and food utilisation by individual female *Zonocerus* adults on cut or growing cassava on day 20 of the experiment

	Number of insects	Mean daily consumption (mg)	Mean weight (g)	Utilisation rate (%)
cut cassava	5	135 ± 29	1.357 ± 0.172	55 ± 12
growing cassava	5	23 ± 8	0.768 ± 0.149	5.5 ± 2.3

Thus I suggest that cyanogenic plants gain protection from insect attack largely as a result of HCN release at the time of

biting, which strongly deters them from further feeding, and not from the presence of glycosides themselves. That some insects do feed specifically on such plants, indicates that they have very specific abilities. On the one hand they need to have sensilla which are relatively insensitive to HCN, and on the other hand they must be able to detoxify the material after ingestion. Both of these characteristics have been found in different species (e.g. see Levinson *et al.*, 1973; Parsons & Rothschild, 1964).

The case of *Zonocerus* is an interesting one. The highly cyanogenic plant, cassava, is relatively unpalatable probably due to HCN release, but in the absence of alternative host plants in the dry season this grasshopper can be a serious pest of cassava (Bernays *et al.*, 1975). There are probably two factors involved in this paradox. McCaffery (pers. comm.) found that a number of different woody plants were eaten by the insects in the vicinity of cassava plots, and that while each of them is to some extent unpalatable, the variety may allow survival. Probably more relevant is the gregarious nature of this insect, such that they concentrate on one plant. Small meals by numerous insects will cause wilting of the plant, with a consequent increase in its palatability. Thus the study of plant resistance to attack must be accompanied by a study of the insect in its ecosystem to provide the information required in the management of pest problems.

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MECHANISMS OF RESISTANCE TO *LYGUS* SPP. IN *GOSSYPIUM HIRSUTUM* L.

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Plant bugs in the genus Lygus are serious pests of cotton throughout the world. In the Southwestern U.S.A. their importance is revealed by the cotton fleahopper, Pseudatomoscelis seriatus (Reuter). In the Western U.S.A., Lygus hesperus Knight and L. elisus Van Duzee are of relative importance (Cassidy and Barber 1939). In the Eastern U.S.A. the tarnished plant bug, L. lineolaris (Palisol de Beauvois) and the clouded plant bug, Neurocolpus nubilis (Say) along with the cotton fleahopper are important (Pack and Lugwell 1976). The plant bugs L. hesperus, cotton fleahopper and tarnished plant bugs are of equal importance and exceed that of the other bugs depending on which part of the continent the cotton is grown. There is overlap of the range of those three species.

Resistance to plant bugs has been only recently sought, Gwynn (1938), Stride (1967), Laster and Meredith (1974), Schuster et al. (1976) and Tingey et al. (1973). Although resistance to plant bugs has been found in cotton the mechanisms of resistance have not been well defined. This presentation will attempt to identify these mechanisms of resistance based in part on a review of literature and in part on our own research.

Three morphological characters of cotton and two allelochemical factors have been suggested to impart resistance to plant bugs. From a theoretical standpoint, Beck (1974) argues that non-preference and antibiosis account for all situations in which the plant exhibits negative effects on the insect and are thus resistant in the classical sense of Painter (1951). However, tolerance of the plant to withstand insect attack and still produce yields seems a useful category from a practical standpoint, and we favor it usage. Relatively little information is currently available on the effects of plant bug feeding on the host plant, yet enough to suggest that tolerance may be an important consideration for plant breeders dealing with resistance to plant bugs (Strong 1970, Hori 1975, 1975a). Classification of observed plant resistance into the three categories of resistance is only the first step in understanding the exact mechanisms. In most cases, much additional work is required in order to understand the action of plant chemical and physical factors on the insects sensory receptors and/or metabolic pathways.

Glabrous

The relationship length and density of trichome hairs on cotton and resis-

tance to Jassid bugs was pointed out by Parnell (1928). Lee (1968) studied the genetic basis of trichomes in Gossypium hirsutum and designated three phenotypes as glabrous (no hairs), hirsute (medium normal hairs), and pilose (long, dense hairs). Knight (1952) described the alleles as Sm_1 for glabrous, H_1 for hirsute, and H_2 for pilose.

Glabrous genes from several sources were found to reduce cotton fleahopper populations in Texas by Lukefahr et al. (1968) and has been confirmed by our data for Mississippi. In 1970, Lukefahr and coworkers evaluated pubescent genes for resistance to the cotton fleahopper and found that plants with the pilose gene had more fleahoppers than plants with the glabrous gene. Lukefahr et al. (1976) showed that the reduction in fleahoppers was the same among plants containing several different glabrous genes. Their relative differences compared to plants with hirsute were nearly the same in all cases.

Although the glabrous gene imparts apparent resistance to fleahoppers, its presence appears to introduce a change in the overall tolerance of the plant bug feeding. Walker and coworkers (1973, 1974) and Niles et al. (1974) found that glabrous cottons limit fleahopper populations in central Texas, however, these cottons were often non-productive with low fleahopper densities. These authors postulated that glabrous cottons are hypersensitive to fleahopper feeding, and data from our field experiments support this hypothesis (Schuster et al. 1976). In greenhouse experiments we have shown that glabrous cottons are more sensitive to equal numbers of plant bugs as compared to hirsute types, while pilose types are unaffected. Tingey et al. (1973) have shown that L. hesperus prefers pilose cotton slightly to hirsute in "free choice" tests, but in "no choice" tests oviposition does not differ from that on normal hirsute cotton. We conclude that although fewer numbers of plant bugs are found on cotton plants with the Sm_1 gene, the hypersensitivity to feeding imparted by this gene resulting in increased damage dictates that according to the classical definition of resistance (Painter 1951), the glabrous gene does not confer resistance, whereas the pilose gene (H_2) does through the mechanism of tolerance.

Nectariless

Extra-floral nectaries received attention as potential feeding sites early in the study of cotton insects (Trelease, 1879). These nectaries are supplied indirectly by the phloem (Wergin et al. 1975) and may produce as much as 2.39 liters of nectar/hectare/day (Butler et al. 1972).

Identified components of cotton nectar include the sugars fructose, glucose, and sucrose as well as 20 or more

amino acids (Butler et al. 1972; Hanny and Elmore 1974). Sugars in the form of honeydew or nectar greatly improve survival of L. hesperus in alfalfa (Butler 1968) and L. disponsi grew only on diets containing surcrose and starch (Hori 1972). Work in our laboratory supports the idea that sucrose is a gustatory stimulant for L. lineolaris.

Laster and Meredith (1974) and Schuster et al. (1976) have found that tranished plant bug and cotton fleahopper populations are greatly reduced in nectariless cottons. Plant bugs were reduced by 60% in field studies, while adults laid 92% fewer eggs on nectariless cottons in the laboratory. We thus propose that the nectariless gene confers resistance through nonpreference and antibiosis, by virtue of a nutritional deficiency. Sucrose may be a feeding stimulant as well as a metabolic intermediate, thus alteration of this one plant compound may affect the insect at multiple levels. Delineating the contributions of individual nectar components in these proposed mechanisms requires further study.

High Gossypol

The dimeric sesqiuterpenoid gossypol, a constituent of both foliage and seeds of cotton is important in limiting insect utilization of cotton (Maxwell et al. 1972). Cowen and Lukefahr (1970) found that a primitive strain of cotton containing high gossypol reduced cotton fleahopper populations by 65%. Lukefahr and Houghtaling (1975) with improved strains showed that fleahoppers were reduced 50%, while nymphs were reduced more than 70%. Our field studies with L. lineolaris indicate that migrating adults show nonpreference for high gossypol (up to 1.3%) compared to normal cotton (.7%). Tingey et al. (1975, 1975a) found no differences in reproduction or growth rates of L. hesperus on glandless vs. glanded types, but did show increased survival on glandless lines.

Although they report differences on a high gossypol line, we believe this to be the result of its combination with nectariless. Our field data with cotton fleahoppers support that of Lukefahr and coworkers.

Although gossypol has been shown to affect feeding in Dysdercus spp. (Schoonhoven and Derksen-Loppers 1973) and is a minor attractant for the boll weevil (Maxwell et al. 1966; Parrott et al. 1969) other feeding inhibitors and stimulants for the boll weevil are known to occur (Keller et al. 1962; Maxwell et al. 1963). Also, recent identification of a number of gossypol intermediates in glands (Bell et al. 1975) indicate that a substantial list of candidate resistant compounds with varying modes of action have yet to be investigated with respect to plant bugs. It is quite likely that these compounds will exhibit activity for both nonpreference

and for antibiosis.

X-Factor

Lukefahr et al. (1974) reported a growth inhibiting X-factor from several stocks that is effective against Heliothis spp. This factor is thus a potential antibiotic factor for plant bugs, but its elucidation requires further study.

Normal Bract

The frego bract mutation was found in a Stoneville 2B cotton by Lincoln and coworkers (1971) who also found that is caused the plant to be resistant to the cotton boll weevil, but plant bug damage was greater than on normal bract. Our unpublished data indicate that plant bugs prefer frego bract for oviposition have a greater feeding rate, and develop more rapidly on it. Tingey et al. (1973) show that L. hesperus survive better on frego bract compared to Acala SJ-1, but our data with normal Stoneville and Deltapine varieties do not agree, perhaps due to varietal differences.

Tarnished plant bugs orient and feed preferentially on frego buds over normal. Removal of either antennae or rostrums abolishes the preferences. Differences in volatiles between frego and normal plants occur, but have not given reliable responses. Sucrose occurs at twice the concentration in frego as in normal, and Lygus appear to be stimulated to feed by sucrose. Studies with the recessive gene in 7 different backgrounds give similar results with preference bioassays and field damage trials. Apparently there is a link between sucrose and frego inheritance. We propose that sucrose stimulants feeding and results in faster growth and damage. The resistance in normal bract thus results from nonpreference and antibiosis through reduced nutrition.

Table 1.--Proposed mechanisms of resistance to plant bugs in Gossypium hirsutum.

Plant factor	Genes	Mode of resistance
Pilosity	5 major	Tolerance
Nectariless	2	Antibiosis and nonpreference
High Gossypol	3 major	Nonpreference(?) and antibiosis (?)
X-Factor	?	Antibiosis (?)
Normal Bract	1	Nonpreference and antibiosis (?)

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THE EFFECT OF PARASITISM ON APHID FEEDING

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Hymenopterous parasites of the family Aphidiidae are important natural enemies of aphids. As in other protelean parasites, only the immature stages of Aphidiids are parasitic, whereas the adults are free-living. The parasitic phase of the life cycle begins with the egg, which is laid, usually singly, into a suitable host aphid; the parasitic phase ends with the fully-grown larva. During this period the host remains active and generally shows little external signs of parasitism until shortly before death. For example, parasitism by *Aphidius smithi* had no significant effect on weight gain and development of the pea aphid, *Acyrthosiphon pisum*, until the developing parasite larva had reached a relatively advanced stage (Cloutier, unpublished). Similar observations were reported by Campbell & Mackauer (1975), who also showed that parasitized pea aphids continued to produce nymphs, though at a reduced rate, for 7 to 8 days following parasite attack.

Many aphids are classified as serious pests because they can damage plants either directly, through their feeding activities, or indirectly, as vectors of plant diseases. It is therefore of interest and of considerable practical importance to measure the effect, if any, that parasitism has on aphid feeding and food consumption. In this paper, we present data on the food budget of healthy pea aphids and compare it with that of pea aphids that were parasitized during the first, second, or third instar by the parasite *A. smithi*.

METHODS

In order to minimize variations in gustative and in nutritional qualities of the food, all experimental aphids were artificially reared on a chemically defined diet. First, second, and third instar apteriform nymphs were used as hosts and, when they were 1, 2 1/2, and 5 days-old, respectively, they were individually exposed to a single attack by a young and unmated *Aphidius* female.

The various components of the food budget including the feeding rate and the efficiency of food utilization were determined (Gordon 1972; Waldbauer 1968) for individual aphids from measurements of food uptake, weight gain, and honeydew production during three consecutive periods of 2-3 days each.

These periods were selected in a way so as to correspond roughly to the egg, early, and late larval stage(s) of the developing parasite. Healthy, unparasitized aphids maintained under similar conditions served as controls.

Aphid weight gain and honeydew production were measured gravimetrically. The amount of food ingested was determined by a radiotracer method; dietary phosphate was labelled with P-33, and the amount of radioactivity recovered in the aphid body and in cast skins, or excreted in honeydew was assayed using a liquid scintillation counter.

RESULTS AND DISCUSSION

Feeding rate.--The effect of parasitism on the rate of aphid feeding varied with the stage of the developing parasite (Table 1). During the egg stage, the feeding rate was reduced in parasitized aphids; this effect was statistically significant in second (= N2) and third (= N3) nymphal instars. A reversal of the effect was observed following the hatching of the parasite larva. The data show that during the larval stage the feeding rate was significantly greater in parasitized than in unparasitized control aphids of a similar age (Fig. 1). When the control values are used as a reference, the feeding rate of aphids containing a parasite egg was reduced by 18% in N2 and N3 hosts, whereas the feeding rate was increased by 35% in N3 hosts that contained a late parasite larva. Because parasitized aphids were then slightly larger than control aphids, this 35% increase in the feeding rate per unit of body weight actually amounts to a 40% increase in the feeding rate of the individual aphid.

Aphidius larvae, like most other endoparasites, feed on host haemolymph and eventually consume all host tissues; this feeding may affect the nutrient level, and in particular the level of metabolites which may play a role in the regulation of food intake (Barton Browne 1975; Gelperin 1971).

It appears unlikely that the parasite, during the egg stage, could have any direct influence on the host that would lead to a reduced feeding rate. More likely, the observed reduction in food turnover was due to an indirect effect of parasitism which caused a reduction in the food utilization by the host itself. Such a hypothesis finds support in the fact that parasitized aphids showed reduced weight gain, as a result perhaps of injuries caused by oviposition or by substances injected by the female parasite at oviposition in order to suppress or to impede host immune reactions (Salt 1968).

During the late larval stage(s), in contrast, the rapidly growing parasite larva probably removes significant amounts of nutrients from the host haemolymph and thus may have a direct influence on the homeostatic mechanisms which regulate food intake. If this assumption is correct, the feeding response of the host

TABLE 1. The effect of parasitism by *A. smithi* on the mean feeding rate of the pea aphid.

Parasite stage	Nymphal instar attacked N1	N2	N3
Egg stage	531.8	279.4	307.4
Control	535.5	342.2	373.3
Early larva	415.9	292.2	346.1
Control	340.8	253.4	286.2
Late larva	240.7	208.9	351.2
Control	208.5	163.1	260.5

All feeding rates are given in ug/mg x day.

TABLE 2. The effect of parasitism by *A. smithi* on food utilization of the pea aphid.

Parasite stage	Nymphal instar attacked N1 AD	N1 ECD	N1 ECI	N2 AD	N2 ECD	N2 ECI	N3 AD	N3 ECD	N3 ECI
Egg stage	75.5	16.4	12.4	76.1	32.2	24.6	75.5	18.6	14.0
Control	75.7	18.7	14.2	72.0	29.7	21.4	71.3	20.6	14.6
Early larva	80.8	21.2	17.0	75.5	30.1	22.6	69.8	16.7	11.7
Control	82.3	20.1	16.6	78.6	28.1	22.1	74.4	16.4	12.0
Late larva	70.3	16.0	11.4	66.9	25.4	17.3	60.3	17.0	10.3
Control	84.6	15.4	13.0	81.9	22.8	18.7	72.0	11.3	8.3

AD, percent assimilation of ingested food; ECD, percent incorporation of assimilated food; ECI, percent incorporation of ingested food.

TABLE 3. The effect of parasitism by *A. smithi* on the food budget of the pea aphid.

Instar attacked	Food intake	Honeydew excreted	Initial weight	Weight gain	Final weight
N1	2605.8	657.1	60.59	359.6	420.2
Control	2300.7	464.6	62.05	338.2	400.2
N2	1499.4	426.8	91.20	319.3	410.5
Control	1445.2	342.7	98.50	304.7	403.2
N3	2193.3	759.0	197.00	261.0	456.2
Control	1988.1	596.2	195.24	234.6	431.6

All budget elements are given in ug dry weight.

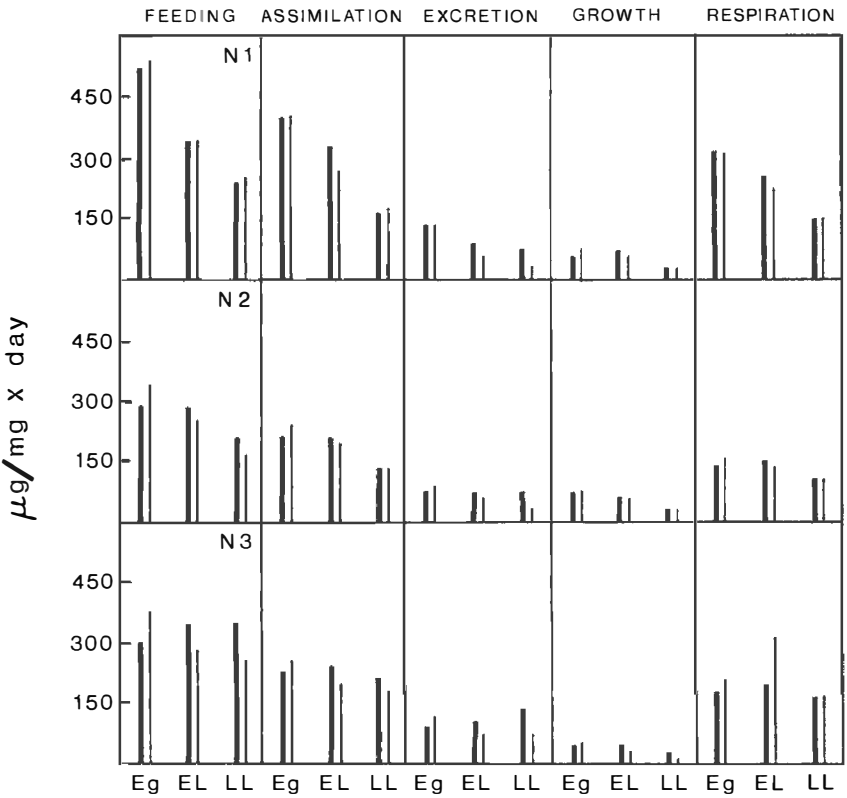

FIG. 1. The effect of parasitism by *A. smithi* on the rates of food utilization by the pea aphid. The solid and light bars indicate rates of parasitized and healthy control aphids, respectively. (Abbreviations: Eg = egg stage, EL = early larval stage, and LL = late larval stage of *A. smithi*; N1, N2 and N3 = first, second and third nymphal instar of the aphid at the beginning of parasitism.

should be expected to increase with parasite age. This could explain why the effect of parasitism on the feeding rate was quantitatively greater during the late than during the early larval stages of *A. smithi*.

Efficiency of food utilization.--Parasitism caused an important reduction in the efficiency of food assimilation (= AD), that is, in the fraction of food which is not excreted but which is translated into weight gain and energy production (Table 2). A reduction in AD was evident already during the early larval

stage, but it became highly significant during the late larval stage(s) of the parasite. In parasitized aphids, the values of AD were in absolute terms 10-15% lower than in the controls.

As a consequence of reduced assimilation efficiency, the increased feeding rate of parasitized aphids containing a late parasite instar was balanced by a roughly equal increase in the rate of excretion and hence did result in little or no increase in the rate of assimilation. For example, aphids parasitized as N1 and N2 ingested, respectively, 32.2 and 45.8 ug/mg more food per day than the controls but also excreted, respectively, 39.4 and 40.3 ug/mg more honeydew per day. The observed increases in the rate of excretion, thus, are a measure of the significance of the reduction in AD; pea aphids that were parasitized as N1, N2, and N3, respectively, excreted 117, 129 and 84% more honeydew per unit of body weight per day than unparasitized control aphids.

The reduced assimilation efficiency perhaps suggests a fundamental difference between the nutritional requirements of the host-parasite system and those of the unparasitized aphid. If the various components of the diet are utilized in different amounts in the presence of a parasite larva, this could result in an apparent reduction in food quality and in reduced assimilation. Pathological, but unspecific, effects of parasitism of course could also explain a reduction in AD, with the exception that such effects would be unlikely to account for increased host feeding at the same time.

Total food budget.--The overall food budget during parasitism (Table 3) shows that parasitized aphids consumed more food, excreted more honeydew, and gained more weight than unparasitized aphids during equivalent periods of time. When tested statistically, only the differences in the amounts of honeydew excreted, however, were significant. (It should be noted that the first day after parasite attack is not included in the food budget).

Aphids parasitized during N2 and N3 were, respectively, 1.5 and 3.2 times heavier at the time of attack than aphids parasitized as N1. Because weight gain during parasitism was inversely correlated with the initial host weight (Table 3), little of the initial variation in aphid weight was expressed in the final weight. Thus aphids that had been parasitized as N3 were only 1.1 times heavier at the end of parasitism than aphids parasitized as N1 or N2.

The reduction in AD discussed earlier is reflected in the total food budget. Parasitized aphids were on average 5% less efficient in assimilating food than were controls. It is interesting to note that, given about equal food intake and reduced assimilation efficiency, weight gain was not reduced. Weight gain in fact was slightly but consistently higher in all instars of parasitized aphids than in control aphids. The only reasonable explanation of that phenomenon is that parasitized aphids incorporated assimilated food more efficiently into body

tissues than healthy aphids. This is born out in the values for efficiency of conversion of assimilated food (= ECD), which were high in aphids that contained a parasite larva (Table 2).

CONCLUSIONS

Some of the observed effects of parasitism on the food budget of the pea aphid can perhaps be interpreted as pathological; however, on the whole, the food budget of parasitized pea aphids does not suggest a disorganized system. For example, parasitized aphids gained as much weight as control aphids during the early stages of parasitism and, furthermore, this gain was achieved although the food ingested was assimilated less efficiently by parasitized than by healthy control aphids. In fact it is perhaps essential to the successful development of *Aphidius* that the host aphid remains largely functional with respect to food consumption and food utilization.

There is no obvious reason for assuming that parasitism by *A. smithi* would have a principally different effect on aphid feeding if the aphids had fed on a plant rather than on artificial diets. Our data thus suggest that, in nature, the parasitized aphid continues to convert valuable plant photosynthate into aphid and parasite biomass. The potential for plant damage as a result of feeding remains high until the aphid is killed by the parasite.

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THE MODE OF ACTION OF NON-PROTEIN AMINO ACIDS PRESENT IN PLANTS AND SEEDS ON INSECTS

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The diversity of an insects development on plants is qualified by its behavioural and metabolic response to a series of stimuli elicited by various physical factors and chemical components present in plants. High concentrations of non-protein amino acids and peptides frequently accumulate in dormant legume seeds and plant tissue (BELL, 1971) and are implicated in host resistance (APPLEBAUM and BIRK, 1972). Neurotoxic lathyrogenic amino acids are formed in certain seeds: 2,4-diamino butyric acid (DABA) accumulates in some Lathyrus species (RESSLER, REDSTONE and ERENBERG, 1961), while β-cyano-L-alanine (BCNA) is characteristically found in Vicia species (RESSLER, 1962).

This report deals with some observed effects of dietary DABA and BCNA on various insects and presents physiological and metabolic data explaining the relative insensitivity of locusts to DABA and the chronic toxicity manifested on exposure to BCNA.

EXPERIMENTAL AND RESULTS

The basic control diet for growth experiments with Tribolium castaneum, details of its preparation and experimental procedure were essentially as previously described (HARRY, DROR and APPLEBAUM , 1976). Where DABA or BCNA (0.1-1.0%) were added, the percentage of starch in the diet was proportionately reduced.

Mortality on control diet did not exceed 20%. 1% DABA increased mortality to 50%, but lower concentrations, up to and including 0.5% - did not. BCNA is more toxic: no larvae survived 1% BCNA and 80% died on 0.5% BCNA. These results were obtained by placing neonate larvae on the experimental diets. In order to assess the relative sensitivity of more advanced stages all larvae were first kept on control diet, and were later transferred at two day intervals from this basic diet to the DABA- or BCNA- supplemented diets. Control groups were concurrently transferred to new control diets. An initial period of 2 days on control diet decreased subsequent mortality on 1 % DABA to 30% while increasing the initial period to 4 days reduced mortality to control level. Sensitivity to BCNA was evident throughout larval development, but less pronounced at the later stages. 1% BCNA after an initial 4 days on control diet resulted in a final mortality of 80%. If transferred after an initial 6 days - 60% die and after 8 days, half die. Fig. 1 presents the subsequent weight gain and time of pupation for half of the population of

larvae transferred on day 8 to BCNA-supplemented, DABA-supplemented and control diets.

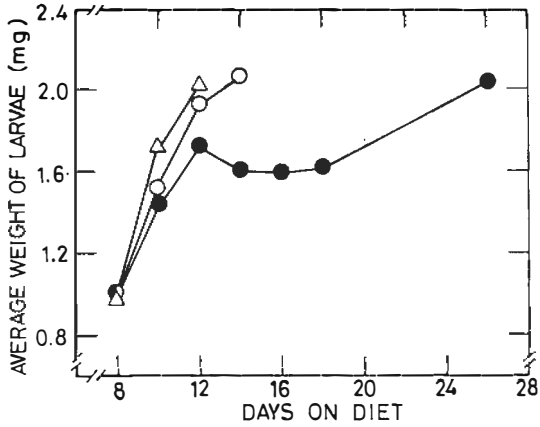

Fig. 1. Effect of 1% DABA or BCNA on 8 day old larvae of Tribolium castaneum. o——o = DABA; ●——● = BCNA; Δ——Δ = control.

Weight gain and pupation time of DABA-supplemented diets were similar to control diets, but none of the full-grown Tribolium larvae on supplemented diets succeeded in pupating.

Similar experiments were conducted with Tenebrio molitor larvae on a semisynthetic diet (cellulose - 40%; rice starch - 25%; casein - 25%; sucrose - 5%; yeast extract - 2.5%; salts mixture USP no. 2 - 2%; ascorbic acid - 0.4%; cholesterol - 0.1%). Where DABA or BCNA were added, the percentage of cellulose was proportionately reduced. Larvae of similar weight were placed in groups of three on 1 gr of control or experimental diet.

Tenebrio larvae are somewhat more sensitive to dietary BCNA or DABA than are Tribolium larvae (Fig. 2).

Larvae on 1% DABA increased in weight within the instar but were unable to moult, while larvae on 1% BCNA declined in weight and died, again without moulting. Death in both cases is not attributable to non-feeding: Tenebrio larvae of comparable weight are able to survive for much longer periods when starved.

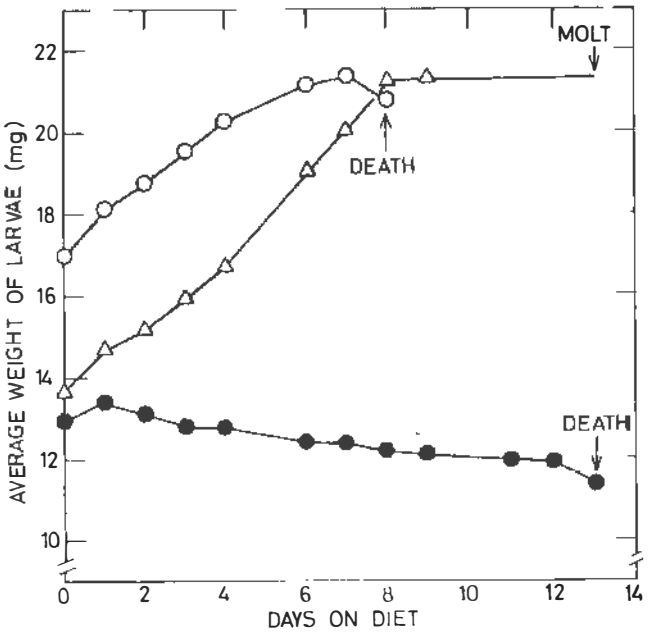

Fig. 2. Effect of 1% DABA or BCNA on larvae of Tenebrio molitor
O----O = DABA; ●——● = BCNA; Δ——Δ = control.

The toxicity of BCNA to Locusta migratoria has been shown to be due to impaired water resorption in the hindgut. A transient arrest of development of Locusta, soon compensated for, is evidenced on DABA-supplemented diets. Subsequent development is not retarded (SCHLESINGER, APPLEBAUM and BIRK, 1976).

Pharmacological observations on the mode of action of DABA and BCNA and related compounds, and metabolic studies on their fate, were carried out on Locusta. Injection of 2.5 mg DABA in 25 µl physiological saline into adult males caused immediate tremors of the appendages. These tremors subsided within one hour and ceased completely with full recovery, within two hours. No additional effects were noted on adults kept under observation for 8 more days. Response was similar to injection of 3 mg of γ-amino butyric acid (GABA). Injection of 2.5 mg glutamate or aspartate resulted in temporary paralysis with full recovery within 2 hrs after glutamate and 4 hrs after aspartate. BCNA (3 mg) had no apparent immediate effect when

injected into adult Locusta, but did elicit chronic toxicity which terminated in dehydration after several days. Addition of pyridoxal hydrochloride to the injected BCNA did not neutralize this toxicity. 3-aminopropionitrite a 'decarboxylated' derivative of BCNA, and asparagine, a 'hydrated' detoxification product of BCNA in other systems, elicited no acute or chronic response when injected into locusts. α-amino butyric acid did not elicit any response after injection similar to that obtained with DABA or GABA.

A steady state of DABA concentration in the haemolymph was attained within 6 hrs after the locusts were offered a DABA- supplemented diet. Turnover is attributed to the action of a diaminobutyrate - transaminase with an affinity for DABA 10-fold (K_m = 1.1 mM) that of GABA-transaminase for GABA (8-10 mM). Glutamate can be formed in vitro with α-ketoglutarate as acceptor and alanine with pyruvate as acceptor. Both these amino acids are metabolically labile and homeostatically regulated in locust haemolymph and may be regarded as intermediates in the detoxification of DABA (SCHLESINGER, APPLEBAUM and BIRK, unpublished data).

BCNA concentration increased linearly in the haemolymph of locusts offered a BCNA-supplemented diet. After injection of a 3 mg 'pulse' of either DABA or BCNA these compounds can be identified in the nervous system. Due to the relative stability of BCNA in the blood, in contrast to the rapid turnover of DABA, the ganglionic concentration of BCNA is 4-fold more than that of DABA. About 20% of injected BCNA is excreted unaltered into the hindgut but no DABA is apparent in the excreta.

DISCUSSION

BCNA has been described as a metabolic intermediate in the synthesis of asparagine in plants (RESSLER, GIZA and NIGAM, 1969). The enzyme responsible for final asparagine synthesis is impeded in certain legumes and this intermediate accumulates. BCNA is neurotoxic to rats, mice and chicks and is regarded as an antimetabolite in the synthesis of pyridoxal phosphate (vitamin B_6) (RESSLER, NELSON and PFEFFER,1964). A syndrome similar to BCNA toxicity is obtained on vitamin B_6 - free diets, and treatment with pyridoxal hydrochloride, a B_6 precursor, alleviates BCNA toxicity in vertebrates. We conclude that there are some specific differences between the action of BCNA in vertebrates and in insects. For one, pyridoxal hydrochloride treatment does not alleviate BCNA toxicity in locusts. BCNA is responsible for disruption of water balance in Locusta: Rectal fluid resorption is irreversibly impaired and the insect dehydrates (SCHLESINGER et al.,1976). This is clearly not the cause of BCNA toxicity in vertebrates, where water balance is regulated at other levels.

DABA is regarded to be a product of asparagine metabolism in

plants (RESSLER et al., 1961) and accumulates in Lathyrus. It has been shown to compete with, and inhibit binding of GABA to receptor sites in the synaptosomal fraction of rat brain (SIMON and MARTIN, 1973). DABA is metabolized in rats to β-alanine. In Tribolium and in Locusta DABA is relatively nontoxic and its effect does not essentially differ from that of GABA. β-alanine does not accumulate in locust haemolymph. The observed sensitivity of Tenebrio to DABA is of interest. It indicates a selectivity of toxicity presumably due to a lower turnover rate of DABA in Tenebrio. The γ-amino group is essential for the pharmacological activity of GABA and DABA, as α-aminobutyric acid lacks similar effects. Finally, an additional difference between the response of locusts and of vertebrates is that the former are insensitive to 3-amino propionitrite which elicits osteolathyrism in vertebrates. Insects of course lack a calcified endoskeleton, which is the basis for this differential response.

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WHITE FLY RESISTANCE IN CUCUMIS

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Introduction

Many wild species of Cucumis contain the genes for resistance to diseases, insects and nematodes. Sources for resistance to diseases were found in 192 resistant introductions of Cucumis, to virus in 79, to nematodes in 2 and to insects in 21, but none resistant to white fly /Leppik/.

Among the 19 Cucumis species which we tested in 1973 from different parts of the world, three were observed to be highly resistant to white fly.

We were trying to find out if this resistance can be related to the density and type of hairs on the leaves or to the cucurbitacins content?

Materials and method

Most of the samples from the 19 Cucumis species were obtained from South Africa, India, Nigeria, Ethiopia and some botanical gardens.

The plants were grown in big pots in the greenhouse from April to September.

The morphology of the hairs was observed by means of a Cornell Stereoscan electron microscope.

The density of the hairs and the number of eggs, larvae and pupae on the under surface of the leaves was measured by microscope.

The degree of infestation by white fly was evaluated by means of a 9- point scale, where 1- means no infestation, 9- very strong infestation.

Cucurbitacin content in the leaves was measured in the laboratory by using chloroform, Antimone Trichloride and ultraviolet light. The intensity of fluorescence corresponded to the levels of cucurbitacins content.

The Relation between the density of hairs on the under surface of the leaves and the degree of infestation by white fly and the number of eggs, larvae and pupae was calculated by means of a correlation coefficient /r/ and regression coefficient /b/.

Results

a/ Morphology of the hairs

One type of hairs was observed on the under surface of the leaves in the nineteen Cucumis species. The tops of the hairs are sharp and mounted on the stalk and on the wide base of the leaf. The hairs are long and short.

None of the Cucumis species tested had exudate in their hairs.

b/ The density of the hairs on the under surface of the leaves and their influence on white fly

Among the 19 species tested, Cucumis heptadactylus had the least hairs per unit leaf area. The most hairs were observed in Cucumis dinteri /Table 1/.

In the species where the mean number of hairs is 14 - 60 per unit leaf area we don't observe differences in the infestation by white fly. The distance between the hairs among this group of the species is

large enough that white flies have adequate room to feed on the blade of the leaves and to deposit their eggs there. The same is true with the larvae.

Table 1. The mean number of the hairs, eggs, larvae, pupae per unit leaf area and the degree of infestation by white fly in 9-point scale

Plant species	Hairs	Eggs	Larvae	Pupae	White fly infest.
C. heptadactylus	14	257	197	18	8,5
C. ficifolius	18	64	119	0	8,5
C. trigonis	24	175	236	148	9,0
C. metuliferus	26	82	119	63	8,0
C. pustulatus	30	46	70	19	7,o
C. myriocarpus	32	52	36	35	6,5
C. sativus	33	151	177	168	8,8
C. prophetarum	34	108	199	12	9,0
C. leptodermis	34	173	144	98	8,5
C. longipes	38	160	166	133	8,2
C. hookeri	40	102	144	72	8,0
C. zeyheri	43	106	121	40	7,1
C. anguria	45	234	226	74	7,5
C. africanus	52	107	103	38	5,8
C. melo	56	88	77	17	5,0
C. dipsaceus	62	123	99	28	7,5
C. asper	110	44	44	2	2,0
C. angolensis	117	44	86	13	2,0
C. dinteri	200	12	4	0	1,5

The species which have more than 100 hairs per unit leaf area are resistant to white fly. The hairs prevent the moving of white flies and larvae on the leaves.

Table 2 show the relation between the density of hairs and the degree of infestation by white fly, and the number of eggs, larvae and pupae.

Table 2. Correlation coefficient /r/ and regression coefficient /b/ between the density of hairs and the degree of infestation by white fly and the number of eggs, larvae and pupae

	r	b
White fly	- 0,89 *	- 0,05
Eggs	- 0,53 *	- 0,79
Larvae	- 0,61 *	- 0,89
Pupae	- 0,39 ***	- 0,45

* L.S.D at 1%
** " at 5%
*** " at 10%

Tables 3 and 4 show the relation between phases of the white fly.

Table 3. Correlation coefficient /r/ and regression coefficient /b/ between the degree of infestation by white fly and the number of eggs, larvae and pupae

	r	b
Eggs	0,63 *	17,1
Larvae	0,75 *	19,9
Pupae	0,53 *	11,3

Table 4. Correlation coefficient /r/ and regression coefficient /b/ between the number of eggs and the number of larvae and pupae

	r	b
Larvae	$0,84^{+}$	0,83
Pupae	$0,52^{++}$	0,41

The tests for cucurbitacins content did not show any correlation between the cucurbitacins content and infestation by white fly.

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INSECT INDUCED RESISTANCE AS A MEANS OF SELF DEFENCE OF PLANTS

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The phytophagous insect depends on its host plant, which in turn responds to challenges from the seasonally changing environment. The more specialized the association between the insect and its host, the greater is the insect's physiological dependence upon the plant and the risk when the chemical composition of the host changes. One of the environmental factors the plant must cope with is to stand the stress of injury and depletion caused by pathogens and phytophagous animals. Mechanical wounding often causes changes in the growth pattern of plants directed towards healing the wounds, setting up physical and/or chemical barriers against the causing organism and, sometimes, compensating for the losses. Astonishingly little is known concerning the basic mechanisms of injury reactions (GALSTON and DAVIES 1970; BECK and REESE 1976). The induced chemical changes in plant tissue may involve derepression of gene activity and cause cellular proliferation as well as the production of ethylene and peroxidase (LAVEE and GALSTON 1968; RÖTTGER & KLINGAUF 1976). The latter authors also demonstrated temporarily increased polyphenoloxidase activity in wounded as well as intact leaves of sugar beet plants infested by the leaf-mining beet fly *Pegomyia betae* Curt., with a maximum enzymatic activity 3 weeks after egg deposition. In some plants wounding results in the production of cinnamic, p-coumaric, caffeic, chlorogenic, and isochlorogenic acid, mediated by ammonia-lyases (URITANI *et al.* 1967). Chlorogenic acid is known as a growth factor in some insects (HAMAMURA 1970), and cinnamic acid is a precursor of the fungitoxic phytoalexin pisatin in sweet pea plants (HADWIGER 1967). The induction of fungistatic phytoalexin production in many plants by certain fungi is a well known example of induced plant resistance to an invading microorganism (CRUICKSHANK 1963; LIM *et al.* 1968). The system of the sugar beet plant infested by the beet fly can be taken as an example of an insect-induced increase of resistance in a plant. RÖTTGER & KLINGAUF found a 29% increase of larval mortality in beet plants infested 24

days previously. In some of these plants mortality of the L_1 reached up to 100%. This induced resistance faded away and became unmeasurable 42 days after infestation.

The question therefore arises whether or not injury by insects may induce similar mechanisms in other plant species, conferring them resistance to insects. A still hypothetical example has been offered by GREEN & RYAN (1972). From the fact that injury of potato or tomato leaves by *Leptinotarsa decemlineata* (Say) leads to the formation of a proteinase inhibitor inducing factor that spreads in the whole plant, causing the accumulation of a potent trypsin and chymotrypsin inhibitor in the tissues, they concluded that this might be a defence reaction of the plant, making it less digestible for insects. Experiments made in the author's laboratory designed to verify this hypothesis confirmed that wounding led to doubling of the concentration of the proteinase inhibitor in potato plants, but showed at the same time that development and weight gain of larvae of *L. decemlineata* on previously injured plants was not slower than on intact plants (T. JEKER, C. MUELLER & U. VOLKART, unpubl.). These results show that *L. decemlineata* is so well adapted to the conditions of the potato plant that the induced inhibitor does not harm the beetle. However, the results do not exclude the possibility that other insects might be inhibited by the proteinase inhibitor. Investigations by JEKER on the related beetle *Gastroidea viridula* Deg. feeding on the weed *Rumex obtusifolius* L. show metabolic changes in the host plant which slow down the weight gain of the developing larvae and stimulate oviposition less than leaves of intact plants. Whether or not these effects are of importance for the population dynamics of *G. viridula* has to be investigated.

Despite these still unsatisfactory results, the question of induced insect resistance as a more wide-spread phenomenon can be answered in the affirmative. STANDFUSS (1896), reporting on his experience with the rearing of lepidopterous larvae on coniferes and broad leaf trees, was probably the first to note that such rearing for several successive years on the same tree would not give satisfactory results, because the repeated defoliations would cause changes in the plant metabolism, leading to increasingly stunted shoots and thus to increasing malnutrition of the insects. He interpreted these facts as indication for the existence of self-protection mechanisms in plants.

It is evident that in nature such interference with negative feed-back must lead to cyclic population dynamics of the defoliating insect species. This is well demonstrated in the autoregulating life system of the European larch, *Larix decidua* Miller, in subalpine forests and the monovoltine larch bud moth, *Zeiraphera diniana* (Guenée), which defoliates the larch with a regular periodicity of 8-10 years (for details on the system see BALTENSWEILER *et al.* 1977).

The author has studied this system since 1960, but only part of the results have been published so far (BENZ 1974). In the subalpine larch forests the environmental resistance to Z. *diniana* is usually so low that the insect populations increase rapidly during a period of 4-5 years (generations) until the larch trees become defoliated. At this point the high density of larvae not only leads to strong intraspecific competition for food and space, increasing mortality of larvae and pupae and reducing weight and fecundity of the moths, but the feeding activity of the larvae also activates specific mechanisms in the trees, rendering them more resistant to further attack by the insect. Although defoliated larch trees will reflush during the same season, the flushing of the young shoots in the following year is delayed, which may reduce coincidence between the ideal needle length (or high quality food) and the eclosion of the bud moth larvae. Besides their late and slow growth, these needles never reach normal length (reduced nutritional base) and are sometimes covered with a layer of oleoresin. They contain an abnormally high amount of raw fiber (tough texture), a reduced concentration of nitrogen or raw protein, and are less palatable and assimilable for bud moth larvae than normal needles, as indicated by a reduction of the feeding rate and the index of nutrient utilization. The mortality of larvae is therefore high for one to several years after defoliation, and the fecundity of the surviving moths may be very low. The first of these parameters is positively, the second negatively correlated with the fiber contents of the needles, whereas the contrary is true for the protein contents. Thus the succeeding bud moth populations are depressed by negative feed-back.

There is evidence that the larch's reaction to the feeding activity of bud moth larvae is not simply a reaction to depletion, but also a reaction to being wounded at many points. Thus the reaction may be initiated already in the season preceding complete defoliation or it may be triggered in trees which become not visibly damaged. Essential for the induction of the reaction is probably the trespassing of a critical insect density in combination with certain environmental factors. The intensity of the reaction varies considerably, depending at the same time on the genetic constitution of the trees, their habitats, and the meteorological conditions. The latter are probably responsible for the fact that sometimes a primary defoliation causes only delayed flushing of the shoots, but no important chemical changes in the needles. The bud moth populations may then defoliate the tree a second time before full resistance develops.

Unpublished data suggest that the induced resistance of the larch wears out within 4-5 years. The cyclic numeric fluctuations of Z. *diniana* in its optimum area may therefore be regarded as the expression of an autoregulating life system in which the insect multiplies for

4-5 generations under favourable conditions and thus, transgressing the carrying capacity of the host, changes the quality of the nutritional base, so that the host resistance becomes high for 4 more generations, due to the induction of transient antibiosis factors.

Cycles of similar duration may be found in *Yponomeuta evonymellus* L. on *Prunus padus* L. Investigations concerning this insect/plant system as well as that of the chrysomelide beetle *Agelastica alni* L. on *Alnus* spp. are being conducted in the author's laboratory. It appears that the *Agelastica/Alnus* system has relatively short cycles. Another short type population cycle has recently been reported from the tropical island of Sao Tomé (DERRON 1977). There *Erythrina* spec. are used as shade trees in the cocoa plantations. Only in three localities with relatively poor and acid ferralithic soil (pH 4.5) the trees are defoliated every second year by the larvae of the pyralide moth *Agathodes bibundalis*. The insect has a short generation cycle of 45 days. For more than a year the populations overlap and reach only low density. However, when the local density of larvae becomes sufficiently high to cause defoliation of a whole branch, the larvae pupate and develop to moths within 20 days and, within the same time, the damaged branch produces fresh foliage, offering an ideal substrate to the moths for oviposition and to the eclosing larvae for food. Thus a larger population grows, which in turn defoliates larger parts of the tree crown, producing ideal conditions for a still larger larval population, which then starts to multiply exponentially. The populations become fully synchronized when all trees of a focus are defoliated. After four more consecutive defoliations the trees are so exhausted that reflushing is delayed and starts only after a lapse of 4-5 weeks, i.e. when most of the moths have died without having laid their eggs. By this incoincidence the insect populations are drastically reduced. The delayed refoliation of *Erythrina* may be joined with other physiological changes in the plant, since the insect populations become diseased and break down to such low levels as would not be expected from incoincidence alone. For several generations the insect populations develop again asynchronously; they will not rise to the critical density which starts the oscillating positive feed-back mechanism of population increase before the induced resistance of the damaged trees is worn out.

Mass multiplication of phytophagous insects has so far been interpreted as being provoked by the physiological weakness of the host, caused by adverse climatic conditions, old age or poor habitat, whereas the breakdown of the populations was considered to be due to the local destruction of the nutritional basis and/or natural antagonists such as predators, parasites, and infectious diseases. The examples of cyclic population dynamics described in this paper show that induced transient plant resistance offers a new aspect to their understanding and to the general theory of the break down of insect populations.

Induced resistance in insect/plant systems wears off within weeks or years, depending on the type of plant. Only long lasting resistance may be of practical value and only in extensive plant production systems, such as forests. However, a better understanding of the underlying biological and biochemical mechanisms might help to develop means to artificially induce resistance in plants at almost any time.

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