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AMELIORATION DES PLANTES POUR LA RESISTANCE CONTRE LES INSECTES ET LES ACARIENS

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EUCARPIA/IOBC WORKING GROUP BREEDING FOR RESISTANCE TO INSECTS AND MITES
REPORT OF THE SECOND MEETING HELD FROM 9 TO 11 APRIL 1980 AT CANTERBURY, U.K.

EUCARPIA/OILB GROUPE DE TRAVAIL AMELIORATION DES PLANTES POUR RESISTANCE CONTRE LES INSECTES ET LES ACARIENS
RAPPORT DE LA DEUXIÈME REUNION TENUE DU 9 AU 11 AVRIL 1980 A CANTERBURY, U.K.

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PREFACE

The Working Group Breeding for Resistance to Insects and Mites was founded in 1976 under the eagis of both the IOBC/WPRS and EUCARPIA to create a platform for discussion and coordination between entomologists and plant breeders. The second meeting has confirmed the benefits of this multidisciplinary approach. It was attended by 43 entomologists and plant breeders from 10 countries, including representatives of private breeding companies showing an increasing interest in breeding for resistance to animal parasites.

The 29 papers presented and included in these Proceedings cover a wide variety of arable, vegetable, fruit and fodder crops. These papers demonstrate that, thanks to a better understanding of the plant breeder's needs, since the first meeting much attention has been paid to improve the efficiency and reliability of test methods. This was achieved either by switching over from laboratory to field tests, or, the other way around, by background studies on host-parasite relationships in the laboratory.

During the time lag between the two meetings the Project Group Breeding for Resistance to the Carrot Fly and the Correspondence Group on Resistance to Cereal Aphids stimulated the activities in these particular fields. It should also be noted that recently some private breeding companies initiated programs on resistance to insects and mites, using the knowledge and sometimes resistant germplasm offered by some governmental institutes.

The above developments demonstrate increased activities in breeding resistance to insects and mites, which deserve further accompaniment by the Working Group.

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IMPLICATIONS OF INADEQUATE INSECT IDENTIFICATION

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Specimens of aphids collected around London in 1847 resemble the same species collected from the same plants today. The same aphid species can be recognised on the same plants over much of Western and Central Europe. Most species and some lower ranking taxa are consistent entities in terms of population genetics over useful periods and areas. Naming a specimen should ideally be the key to all that is known about that taxon and a means of conserving new information for the use of others. The name applied to a species (even at the BMNH) is not, however, always an accurate guide to all that is known. Many groups have not been adequately revised: probably less than half of the world's insects are yet described, let alone critically compared with their closest relatives. Species have been known by different names in different parts of the world or when feeding on different plants. Previous misidentifications assign biologies to the wrong species.

This paper draws attention to taxonomic uncertainties and errors concerning the published host ranges of aphid pests. Failure to recognise that several different species of aphids feed on closely related plants can conceal likely sources of genes for resistance.

Acyrthosiphon gossypii from cotton, A. sesbaniae (beans), A. skrjabini (Malva), A. paczoskii (Lepidium) and A. dubium (Papilionaceae) may really all be the same species, as characters said to distinguish them vary with size. However, in southern Iran where Malva is infested, specimens were not found on the common weed Lepidium draba. A. ilka and A. mordvilko from Russia may be the same as the more widespread and polyphagous A. bidentis which will feed on their respective hosts, poppy and Linum. A. malvae s.lat. lives on Malva, Geraniaceae and Rosaceae including strawberry. It is not known whether there is a distinct strawberry feeding species or whether any member of the complex feeding on it is consequently called A. rogersii. A. pisum, pea aphid, occurs on many herbaceous Papilionaceae and a distinct species, spartii, may occur on shrubs like Sarothamnus. Many populations from herbs are distinguishable from one another and it is possible that more than one taxon is called spartii when found on shrubs.

Amphorophora agathonica described from large specimens collected on wild red raspberry in the Rocky Mountains, is probably the correct name for American aphids (long confused with A. rubi) living on varieties derived from Rubus idaeus var. strigosus. A. rubi from brambles was until recently confused with both A. idaei from R. idaeus s.str. and A. agathonica from R. i. strigosus. R. i. peramoneus and R. i. aculeatissimus may also contain useful genes as

they are the hosts of A. tigwatensa and A. amurense in America and Japan respectively. A. rubicumberlandi described from R. leucodermis also lives on R. occidentalis; A. rubitoxica described from R. vitifolius also feeds on R. palmatus, procerus, ursinus and occidentalis on which it causes leaf symptoms; and both aphids have been misidentified as A. rubi.

Aphis craccivora described from Vicia cracca in Germany is now applied to a widespread pest of legumes and more rarely other plants in warm places, and was earlier confused with two other European aphids, A. laburni and A. medicaginis, which are more specific to the plants for which they were named. The distinct populations of the craccivora group which have been recognised by virus transmission or cytology are unlikely to be characteristic for the region from which they originated. A. fabae belongs to a poorly understood complex of species and A. gossypii is probably applied to at least two species with wide host plant ranges. A. nasturtii (= abbreviata, rhamni auct.) also belongs to a group requiring combined experimental, electrophoretic, cytological and morphometric study. A. pomi occurs mostly on Pyroidea while A. citricola (= spiraecola) with which it has been confused in warmer climates, has a much wider host range.

Aulacorthum solani belongs to a complex with different host plant preferences, life cycle characteristics and karyotypes.

Brachycaudus helichrysi alternates from Prunus to Compositae and more rarely other plants including Trifolium. It is not certain that the Crotalaria-feeding virus vector in South East Asia is really the same species.

Brevicoryne brassicae, the mealy cabbage aphid, has normal-looking resistance-breaking populations in New Zealand. Middle Eastern alatae tend to have more rhinaria than northern European specimens, but the taxonomic significance of this is not understood.

Capitophorus elaeagni (= braggii) alternates from Elaeagnaceae to various Cynareae, including globe artichoke. In Western Europe several other species living on Cynareae are separable by their abdominal chaetotaxy, but some exotic samples are more difficult to assign using these characters.

Cerataphis lataniae has been confused with several other species, two of which, particularly C. palmae (= variabilis) from many palms and C. orchidearum from orchids, are much commoner than the true C. lataniae which lives in Latania and a few related palms.

Chaetosiphon fragaefolii (= fragariae), strawberry aphid, was distinguished from the North American rose-, potentilla- and strawberry-feeding species, C. thomasi and C. jacobi by chaetotaxy, but intermediate populations lead some authors to regard them as synonymous.

Diuraphis noxia from cereals in southern Europe and the Middle East is so similar to species described from various grasses in Europe and North America that the real number of aphid species and their host range is uncertain.

Dysaphis devecta: the preference for different apple varieties shown by different populations of rosy leaf curling aphid are interpreted as normal variation within species. D. plantaginea is regarded as a pest of apple in Europe where it is rarely collected from its secondary host, Plantago. Similar specimens are known from Plantago in Japan and Taiwan, where it has not been found on apple.

Eriosoma lanigerum has permanently parthenogenetic populations feeding on previously resistant varieties of apples. Discrepancies between host records for the E. lanuginosum, E. flavum and E. pyricola group from pear and close relatives and for the E. ulmi group may result from confusion between different aphid species.

Hyadaphis coriandri common on Umbelliferae in the warmer parts of the Old World may be known by another name on Lonicera. H. foeniculi is probably confused with another species alternating between Lonicera and Apium, Conium, Daucus etc. in Western Europe.

Hyalopterus pruni from Prunus domestica and P. spinosa differ from variable samples from almonds and apricots, often called H. amygdali. It is not known how many species are involved.

Lipaphis erysimi (= pseudobrassicae) is a pest of crucifers in the warmer parts of the world but, except occasionally in hot weather, is only found on a few wild species in Europe. Specimens from hot dry regions are green and from hot moist conditions are as densely wax covered as Brevicoryne brassicae. These differences may be environmentally induced.

Macrosiphoniella sanborni varies little and lives only on Chrysanthemum sinense and close relatives for most of its world wide range, but occurs on Artemisia in Japan. The chrysanthemum pest may be a parthenogenetic race of a more variable Japanese sexually reproducing species.

Macrosiphum euphorbiae was apparently introduced to Britain from America in 1917, and other genotypes have probably been introduced subsequently. Other American species such as the polyphagous M. pallidum will almost inevitably follow it. The genus is taxonomically difficult and many published records are based on misidentifications.

Melanaphis pyrarius alternates from Pyrus to Arrhenatherum in Britain and may also be found on other grasses. The exules are similar to M. sacchari (? = indosacchari, sorghi) but it is not certain whether all populations can feed on both Saccharum and Sorghum.

Metopolophium dirhodum and M. festucae have each been confused with similar species on grasses in Europe and some of the outbreaks on wheat in South Africa and South America attributed to Schizaphis graminum were in fact M. dirhodum.

Myzus cerasi-like aphids occur on both Galium and Cruciferae in the summer. As it is not certain whether two species of aphids are involved, cherry resistance should be tested with populations originating from both secondary hosts. A number of distinct species closely resemble Myzus persicae which contains both genetically isolated populations and recognizable karyotypes which are part of the main gene pool.

Nasonovia ribisnigri which normally alternates between Grossularia and the sticky flower heads of Compositae, also produces large colonies on Martynia, Nicotiana and Petunia. Protecting crops with sticky hairs could make them susceptible to a few aphids which previously did not colonise them.

Neotoxoptera species and some members of the Myzus persicae group have preferences for Caryophyllaceae, Viola and Allium. Some species colonise all three groups, while others are more restricted but there are taxonomic uncertainties in both groups.

Pemphigus species are specific to particular groups of Populus. American Populus are free from aphid galls in Europe and P. nigra in North America is colonised only by introduced European Pemphigus. While replacement of P. nigra by American species or hybrids could be useful in lettuce and carrot growing areas, it could lead to the establishment of American Pemphigus in Europe.

Pineus species have been described from many different Pinus, giving the impression of considerable host plant specificity. There are probably a few species with restricted host range but at least one Pineus has many hosts and probably many synonyms.

Rhodobium porosum from both strawberries and rose in North America is known only from rose elsewhere: possibly only part of the genotype has been widely distributed with roses. About forty species of aphids are known from roses in different parts of the world, and there has been confusion between some of them, particularly the Macrosiphum and Sitobion species from Asia.

Rhopalosiphoninus latysiphon varies little and is permanently parthenogenetic over most of the world, but sexuales may occur in Japan. Permanently parthenogenetic populations of R. staphyleae have been recognised as a distinct subspecies, R. s. tulipaellus. It is not known whether all populations have the same host range.

Rhopalosiphum maidis is permanently parthenogenetic over most of its range and a number of biotypes are known which, when reared under identical conditions, may be distinguished from one another by their degree of alatiformity. Different conditions may change and even reverse the structural differences. Permanent biotypes may be of less importance in Japan where sexual reproduction is likely. R. padi alternates from Prunus padus in the Palaearctic, but many populations are permanently parthenogenetic. Most North American records of R. fitchii from cereals apply to R. padi. Long-haired specimens from wet habitats key out as different species, but may really be environmentally induced forms of padi.

Schizaphis graminum with the ability to feed on Sorghum were only recently introduced to America, although long known from the Old World where yet other variants occur. S. hypersiphonata is a similar species from South Eastern Asia which prefers Digitaria.

Sipha maydis, an occasional pest of wheat, is recorded from many grasses, although in Britain it has only been found on Arrhenatherum elatius. The green form of S. flava is induced by low temperature, and the host range of S. maydis may also be affected by temperature.

Sitobion is taxonomically difficult. Records of S. avenae (= granarium) from eastern and S.E. Asia, Australia etc. mostly apply to other species, particularly to S. miscanthi, although genuine avenae appears now to be extending its range in India as well as Africa. S. fragariae is sometimes confused with avenae when found on cereals in Europe and west of the Rockies, and has recently been introduced to Australia and New Zealand.

Smynthurodes betae (= Trifidaphis phaseoli) occurs in the roots of cotton, beet, legumes and other plants. Some permanently parthenogenetic populations are readily separable from one another.

Therioaphis trifolii has various fractions of its genotype introduced to different parts of the world. The Medicago-feeding form maculata is recognisably distinct in America and Australia, but a different Medicago- and Trifolium-feeding form has been introduced to South Africa. Most Therioaphis prefer dry conditions and are seldom collected in North Western Europe, where only T. ononidis is at all common. As a result the 'spotted alfalfa aphid' was confused with T. ononidis until Central European literature was consulted. The search for natural enemies led to the discovery of further unsuspected species of Therioaphis in the Mediterranean region.

Toxoptera aurantii is a pest of citrus, coffee and tea and also occurs on many other shrubs in the warmer parts of the world. As only Camellia is infested in Britain, there may be many permanently parthenogenetic populations with different host plant preferences.

Uroleucon carthami seems only to feed on Carthamus glaucus and lanatus and not safflower on which the similar-looking aphid pest is U. compositae, which also feeds on many other Compositae in the warmer parts of the world.

Wahlgreniella nervata has long been known on rose and various Ericaceae in North America and host alternation was assumed. In Europe similar specimens were found only on Arbutus and Arctostaphylos and were regarded as a distinct subspecies W. n. arbuti. Recently W. nervata has appeared on rose in Britain, perhaps introduced from America. North American specimens called W. vaccinii are probably at least subspecifically distinct from this European species.

There are few aphid pests without attendant taxonomic problems, partly because the more adaptable, and hence often variable insects are better able to colonise newly available temporary habitats such as arable crops. Taxonomic concepts change, the earliest taxonomists were largely concerned with pigeon-holing similar looking things, and later with understanding macro-evolution. More taxonomists are now interested in gene flow between populations. New and outstanding applications of old technologies can, in a few years, revolutionise the knowledge of a group. Both known and unsuspected taxonomic problems concerning pests are likely to cause problems for plant breeders. The correct interpretation of resulting inconsistent results is more likely the sooner the taxonomic implications are considered. Voucher specimens eventually deposited in museums may explain the problems to later workers, but it is easier and more useful to understand the taxonomy while the breeding work is in progress.

Specimens should be identified during the early stages of a project, not after the experimental work is completed.

APHID GENETICS AND HOST PLANT RESISTANCE

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This paper is concerned, not with the genetics of host plant resistance-breaking mechanisms in aphids, about which we still know very little, but with those general features of the population genetics of aphids which need to be considered when we try to assess or explain the capacity of these insects to respond genetically to variation in their host plants. Unfortunately, our ideas about genetic variation within aphid species and populations are still rather poorly developed and based on very little factual information. It may be worth while, nevertheless, to juxtapose some of these ideas and see how they relate to experience in the cases of a few economically important aphids.

GENETICAL STRUCTURE OF APHID POPULATIONS

In spite of claims to the contrary (e.g. Cognetti 1961), the weight of evidence is against any regular mechanism of genetic recombination during maturation of the parthenogenetic oocyte (Blackman 1979), so that aphid parthenogenesis may be regarded as ameiotic, or apomictic. Populations on crops are therefore composed of a variable number of clones, the number present at any one time depending on (a) the number of different genotypes among the immigrants arriving on the crop and (b) differential selection and possible elimination of less fit genotypes from populations of mixed genotypic composition.

As yet we have very limited information about the clonal composition of aphid populations, and virtually none about the factors which are most significant in its determination. One overriding consideration must be the form of the life cycle. Cyclical parthenogenesis, involving the alternation of a series of parthenogenetic generations with a single annual (sometimes biennial) sexual generation, is found throughout the Aphidoidea, and is clearly a primitive feature of the group as a whole. The "typical" aphid holocycle (Figure 1) has sexual morph production in the autumn, with crossing-over during maturation of the sexual egg (spermatogenesis may be achiasmate, at least in some species - Blackman 1978), and segregation to produce overwintering eggs which are each of unique genotype. Parthenogenesis gives fit aphid genotypes tremendous potential for increase in numbers (or growth, looking at each clone as an "individual" in the genetic sense - see Janzen 1977). Environmental circumstances will dictate the extent to which the growth potential of each genotype is realised, or whether it survives at all. Figure 1 merely represents a guess about the possible course of events during one season, making the assumption that the number of genotypes entering the sexual phase remains

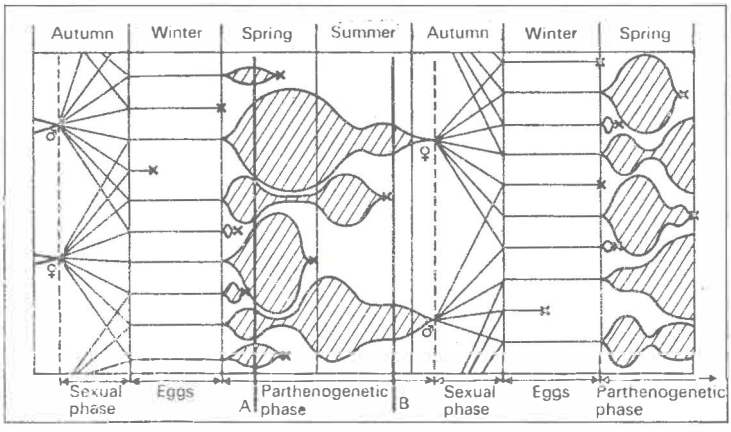

Figure 1: **Alternation of sexual and parthenogenetic phases in the aphid life cycle over two years. The width of each shaded area represents the number of individuals of one genotype. Sexual reproduction in the autumn generates a diversity of genotypes which spend the winter as eggs. In spring and summer many of these genotypes are eliminated (X); others build up large clones of genetically identical individuals, and some of these clones survive until autumn to contribute sperm or eggs to produce the following year's aphids. The genetic structure of a population at A is obviously very different from that of a population at B.**

about the same from one autumn to the next.

The population genetics of some other animals with cyclical parthenogenesis, Cladocera (e.g., Young 1979) and rotifers (e.g., King 1977), have received more attention. The species studied in these groups were pond dwellers, which are ideal for such studies as they exist in discrete populations between which there is little gene flow. Comparisons may be possible with some of those aphids which live on the same host plant all the year round, but the great majority of aphids, and certainly those which are pests of agricultural crops, have very well-developed dispersal mechanisms which seem to ensure a continual and highly efficient mixing of genotypes during the course of the parthenogenetic phase, resulting in uniformity of genotypic composition over a wide area. Janzen (1977) suggested that aphid genotypes spread themselves so thinly over the habitat that they are virtually indestructible for most of the parthenogenetic phase, as one mortality factor would be most unlikely to kill all carriers of any particular genotype.

The other complication to any consideration of the population genetics of aphids is the tendency, which is perhaps most pronounced in widely-distributed pest species, to lose the sexual phase and become partially or completely anholocyclic. Anholocycly can be due to genetic factors - so that holocyclic and anholocyclic genotypes of one species may exist within the same population - or it may simply occur when the environmental stimuli (e.g. low temperature, decreasing photoperiod), which would normally induce the production of sexual morphs, are absent - e.g. in tropical climates (see Blackman 1974). Such life cycle variability must have profound consequences for the population genetics of the aphid, because instead of a regular, obligatory termination of the parthenogenetic phase and genetic reassortment,

there is the prospect that the life of certain successful genotypes can be prolonged indefinitely.

Organisms which are permanently parthenogenetic generally have high levels of heterozygosity (see White 1978 for recent review). However, many parthenogens are thought to have arisen by hybridization between two bisexual species, in which case much of the heterozygosity could be due to hybrid origin rather than to any subsequent accumulation of mutations. Most permanently parthenogenetic aphids have probably arisen by loss of the sexual phase, and none are known to be of hybrid origin. Heterozygosity at the genic level has not yet been studied in any permanently anholocyclic aphid. However, chromosome studies have indicated a much higher incidence of structural heterozygosity in anholocyclic aphids than in those with a regular holocycle (Blackman 1980).

We must now move on from the general to the particular.

GENETIC CONSIDERATIONS IN PARTICULAR APHID SPECIES OF IMPORTANCE IN PLANT BREEDING

Amphorophora idaei Börner. The European raspberry aphid is, as far as is known, obligatorily holocyclic; although the close-related blackberry-feeding species A. rubi (Kaltenbach) can overwinter parthenogenetically. A. idaei perhaps provides the clearest example of a gene-for-gene relationship between an aphid and its host plant. In Britain, it has been possible for 15 years to classify A. idaei into four phenotypes according to their ability to colonise resistant raspberry varieties. Briggs (1965), on the basis of what are still the only experiments on inheritance of resistance-breaking genes in an aphid, postulated that the four phenotypes were the outcome of segregation at two loci. With annual genetic assortment and segregation the resistance-breaking alleles can presumably appear in any combination each year and it is therefore somewhat surprising that phenotype 4, with the ability to colonise more raspberry varieties than the other three, is consistently the least common. Phenotype 2 which, like 4, has the factor breaking the resistance of gene A_1 in raspberry, so perhaps there are deleterious factors closely linked to this allele (Briggs' "C_1") which make clones carrying it uncompetitive except on varieties with the resistance gene A_1. Briggs found that the sexual viability of laboratory cultures of these two phenotypes was low when inbred, but it is not possible to interpret this without knowledge of the clonal composition of his cultures. For example, if they had become virtually monoclonal, any apparent association between low sexual viability and resistance-breaking genes could be quite spurious.

Major resistance genes incorporated into R. idaeus from various sources, particularly North American Rubus species, continue to give protection against A. idaei, so that it begins to look as if the mutations to overcome such genes are not readily available to the idaei genome. Possibly the more likely event is accidental introduction of North American raspberry aphid, A. agathonica Hottes, into Europe.

Acyrthosiphon pisum (Harris). The pea aphid story is a very complex one about which much has been written, and there will only be space here for a few comments. In Europe, several speciation events seem to be currently in progress, with parts of the original pisum genome in the process of being separated off on Ononis, Lotus, Sarothamnus and probably on Pisum sativum itself (the latter form migrating to Vicia for the sexual phase). At the same time, the main pisum gene pool in north-west and central Europe is predominantly holocyclic

and generates each year a wide range of recombinants which may be differentially pre-adapted to Trifolium, Medicago, Lotus etc., but without the degree of specificity to any one host plant that would be necessary to restrict gene flow significantly.

A fragment of this gene pool has been introduced into North America, and thence, more recently, into Australasia. The pisum genome in North America lacks the dominant red allele found frequently in European populations, and is particularly well-adapted to alfalfa. North American workers have been especially inclined to describe and characterise "biotypes" of pea aphid on both peas and alfalfa, although as discussed first by Harrington (1945) and re-emphasised by Frazer (1972), A. pisum is predominantly holocyclic throughout the northern United States and Canada, so that the naturally-occurring "biotypes" will not be the same from one year to the next. Present indications are that the genetics of the interactions between pea aphid and its host plants is complex. For example, Frazer (1972) showed that different alfalfa varieties were resistant to different populations of pea aphid. On the other hand, differences in general vigour rather than specific preadaptations seem more likely to be determining the relative performances of A. pisum clones to different pea varieties (e.g. Cartier 1963). Recent studies of the variability in migratory tendency within and between pea aphid populations (Lamb & Mackay 1979) suggest considerable spatial and temporal fluctuation in genotype frequencies on crops. Taking into account both the apparent poly-genic character of resistance-breaking mechanisms and the genetic complexity of pea aphid populations, the recognition of biotypes in the pea aphid seems to have limited usefulness except where it can be demonstrated that populations are permanently anholocyclic.

Therioaphis trifolii (Monell). Old World T. trifolii colonises a range of leguminous plants. There appear to have been two separate introductions into North America, both possibly limited to a single genotype and providing classic instances of the founder principle. The yellow clover aphid, introduced into the eastern states in about 1882, probably from north or central Europe, feeds almost exclusively on Trifolium pratense. The spotted alfalfa aphid was probably introduced into New Mexico in 1953. It differs morphologically from the earlier introduction, being most like Old World T. trifolii in the Mediterranean region, and it virtually restricts its feeding to Medicago. The spotted alfalfa aphid was apparently without a viable sexual phase until 1960, but then regained the ability to reproduce sexually and overwinter as cold-resistant eggs as it spread into northern states. Now both forms are sympatric over much of the United States but effectively isolated in their reproduction on separate host plants (Manglitz & Russell 1974).

Resistance-breaking biotypes of spotted alfalfa aphid have mainly been described from California and Arizona, where populations are still permanently thelytokous. The genetic mechanisms are little understood but Nielson & Don (1974) obtained results suggesting gene-for-gene relationships between aphid clones and clones of one alfalfa variety. Given the very large aphid populations on alfalfa in North America, one does not really need to look further than mutations, occurring at normal rates, to explain the genetic changes that have occurred in spotted alfalfa aphid since its introduction. Any mutant clone with a significant advantage over sympatric genotypes would spread rapidly through the extensive monocultures of alfalfa. Nevertheless, now that the holocycle occurs in the northern United States, the barriers to gene flow between biotypes may break down, even in the south-west; there is

substantial north-south movement of aphids annually in North America, and even anholocyclic clones of the spotted alfalfa aphid may in autumn produce some viable males which may mate with oviparae from holocyclic genotypes at intermediate latitudes to give new gene combinations.

Schizaphis graminum (Rondani). The "greenbug" is another Palaearctic aphid introduced into North America. Like T. trifolii, there appear to have been two separate introductions, both with severe economic consequences; one in about 1882 and the other about 1968. Here again, there were very obvious founder effects. The earlier introduction was of a highly virulent genetic stock, very damaging to wheat and barley. The form which appeared in 1968 differed from it morphologically in several respects, and was additionally a pest of cultivated sorghum. Resistance to disulfoton appeared in populations of this sorghum-adapted form of the greenbug in 1975.

Breeding for resistance to greenbug attack in North American cereals has generally been very successful, one or a few genes providing robust resistance, often with non-preference, tolerance and antibiosis all involved. However, the concentration of work in the Great Plains area, where S. graminum overwinters anholocyclically, has perhaps resulted in too much reliance being placed on the genetic isolation of biotypes. The holocycle described by Webster & Phillips (1912) presumably still occurs regularly in northern states, with overwintering as eggs predominantly on Poa pratensis (it may be significant that this grass, like the greenbug, is of Palaearctic origin). In Oklahoma Mayo & Starks (1971) obtained numerous sexual morphs and eggs from the sorghum-adapted biotype in culture; none of the eggs hatched, but this cannot be regarded as significant as aphid eggs very rarely do hatch under artificial conditions. One would not expect successful diapause development of the eggs in the field in the winter climate of the southern states, even if suitable host plants for oviposition were available. But long-distance migration of S. graminum regularly occurs from southern states into northern ones, and there is no reason to suppose that some recombination between biotypes does not occur at more northerly latitudes which will eventually result in a blurring of the distinction between them. This has probably been slow to occur because of the success of anholocyclic overwintering in the southern states, and because new recombinants produced in the north will rarely find their way southwards - and if they do they may often be unable to compete with the well-adapted genotypes already present. It is not known whether there is any reproductive barrier to gene flow between biotypes, but clearly host plant preferences do not constitute an isolating factor for S. graminum in the way that they do between the two North American forms of T. trifolii.

Rhopalosiphum maidis (Fitch). With the corn leaf aphid we appear to be on safer ground in describing biotypes, because although males occasionally occur there are no records of oviparae or overwintering eggs anywhere in the world, so genetic recombination, if it occurs at all, can be of little importance. Although first described from North America in 1856, R. maidis is probably Asiatic in origin, and if it has a holocycle anywhere then eastern Asia is the most likely area. In Kansas, Painter and co-workers distinguished four biotypes on the basis of differences in performance on resistant and susceptible sorghum, wheat, barley and maize; temperature relations; and efficiency of transmission of barley yellow dwarf virus (Painter & Pathak 1962). The differences were complex and must involve many loci, yet the four biotypes were sympatric over most of Kansas in 1956-57. A fifth Kansas biotype has since been described (Wilde & Feese 1973). If this is the situation in one

state in North America, then it is clear that on a world-wide scale there are likely to be immense differences in the response patterns of R. maidis to different varieties and species of host-plant, and local genotypes of this aphid must always be looked at in assessing resistance. Mechanisms of resistance may also differ according to the prevailing genotypes; resistance of maize to R. maidis seems to be polygenic in Kansas, but in Hawaii it may be controlled by a single recessive gene (Chang & Brewbaker 1975).

CONCLUSIONS

The few cases discussed here should serve to emphasize that the population genetics of each pest aphid is a different story, depending particularly on the frequency and extent of genetic recombination, and its consequences. There are basically three types of situation: (1) a regular holocycle, where each year brings forth a totally new crop of genotypes; (2) irregular sexual recruitment, where new recombinants are injected into populations composed of a variable number of old, well-tested genotypes; (3) permanent apomixis, resulting in one or many well-tested, probably highly heterozygous genotypes which may be adapted to particular niches in the habitat. These situations must inevitably affect the population structure, and consequently the genetic response of the aphids to differences in their host plants. Allozyme techniques will in time provide more information, and perhaps a better understanding, of the genetic structure of aphid populations. Such studies have so far concentrated on Myzus persicae, which is a very polyphagous aphid with complex life cycle variability, and therefore perhaps not the best starting point. In M. persicae, certain genotypes, identified by colour, allozyme variants or life cycle characteristics, seem to predominate on certain host plants (e.g. Takada 1979), but considerable spatial and temporal differences in genotypic composition occur within and between populations. The only possible general conclusion, in the present state of our knowledge, is that reliance on the occurrence of definable resistance-breaking strains or biotypes of aphids is liable to oversimplify the problem, and that tests for resistance of plants to aphids should usually involve as broad as possible a selection of the naturally-occurring aphid genotypes.

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THE USE OF INSECT POPULATION SIMULATION MODELS IN BREEDING FOR RESISTANCE

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INTRODUCTION

Zadoks (1971,1977) suggested that simulation models could help plant breeders in assessing the partial resistance of varieties to particular diseases. This approach can be applied to insect pests as the components listed by Zadoks (1977) for disease-host plant interactions have equivalents in insect population dynamics (Table 1).

Disease-host plant	Insect-host plant	Type of resistance
Infection ratio	Immigration rate	Antixenosis[1]
	Survival rate	Antibiosis
Latent period	Larval period	
Lesion growth	Population growth	
Sporulation rate	Reproductive rate	
Infectious period	Longevity of adults	
Spore dispersal	Emigration	

Table 1. A comparison of the components of disease-host plant and insect-host plant interactions. ([1]Kogan and Ortman, 1978; equivalent to non-preference.)

Resistance in host plants, either antixenosis or antibiosis, could affect one or more of these components. For example, an increase in the duration of the developmental period of the larvae would reduce the rate of increase of the insect pest. A simulation model can be used to predict the outcome of this sort of effect and hence evaluate the usefulness of a particular variety against a pest. A simulation model of the population dynamics of the English grain aphid, *Sitobion avenae*, on cereals has been developed (Carter, 1978) and will now be used to demonstrate this approach.

DESCRIPTION OF THE MODEL

The model describes the population development of *S. avenae* on winter wheat and includes aphid mortality due to the action of coccinellids, parasitoids and fungal diseases. The major driving variable is temperature which is calculated hourly from daily minimum and maximum values using a sine curve. An estimate of aphid colonization of cereals is obtained from suction trap catches (Rothamsted Insect Survey), while the numbers of natural enemies are estimated from field samples. Laboratory results for aphid development, survival and reproductive rates together with estimates of adult longevity and the proportion of alatiform nymphs at birth are used to update, at hourly

intervals, aphid numbers present on the crop. Reproductive and survival rates of the aphids are dependent on the development stage of the crop (Watt, 1979), which is modelled using a polynomial equation. The dependent variable in this equation is the development stage of the crop (metric scale; Zadoks, Chang and Konzak, 1974) and the independent variable is the accumulated day degrees above 6°C.

As the aphid population model predicts trends which are similar to those observed in the field, both in Norwich (England) and Wageningen (The Netherlands) sensitivity analysis can be carried out to investigate the relative importance of the various components of the system. There are two types of sensitivity analysis; fine, which involves determining the consequences of small changes (increase or decrease) in the components and coarse, where components are omitted. The former type is more important to plant breeders as they are usually interested in partial resistance, which is likely to involve small changes in components.

SENSITIVITY ANALYSIS

As the model gave a reasonable fit to the 1976 and 1977 field results for Norwich, sensitivity analysis was carried out on the predicted population trends for these two years. Small changes were made to; the number of immigrants (± 20%), survival rate (± 6% - as survival is already high a larger change would result in more than 100% of the aphids surviving!), reproductive rate (± 20%), instar length (± 20%), and morph determination (the proportion of alatiform nymphs born, ± 20%).

Changing the number of immigrants had a directly proportional effect on the peak density attained,(20% change in the number of immigrants resulted in about a 20% change (for both years) in the peak density (Table 2, Fig. 1)). Reducing instar length by 20% (i.e. increasing development rate but reducing adult longevity), doubled the predicted peak population for 1977 while a 20% increase reduced the peak by almost 25% (Fig. 2). As the change in the size of the population predicted is greater than the change made to the component this is referred to as a super-proportional response. The response is also asymmetrical as a decrease in the value of the component had a greater effect on the peak population achieved than did the equivalent increase in this component. This is in contrast to the symmetrical response shown when the component changed was the number of immigrants. A 6% change in the survival rate led to a super-proportional and symmetrical response in the peak density for both years, as did changes to the reproductive rate. A 20% change in the proportion of alatiform nymphs at birth led to a subproportional response in both years and so it would not be useful for plant breeders to select only for this component when screening for resistance.

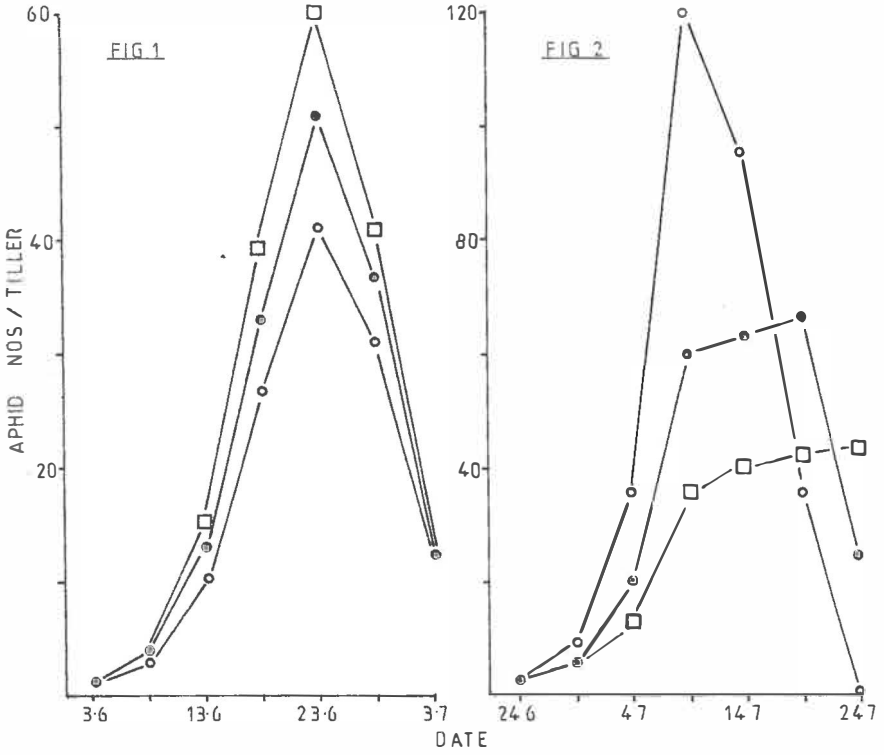
In general all these changes affect the size of the peak aphid density but not its timing. This latter factor is influenced by the timing of aphid colonization in relation to the developmental stage of the crop at that time.

DISCUSSION

The results of the sensitivity analysis carried out with the simulation model indicate that it would be more advantageous for plant breeders to select for plant characters affecting antibiosis rather than antixenosis. As Gallun (1972) remarks antixenosis usually results in the pest moving to another crop, i.e. transferring from wheat to barley or from one variety to another, and so it does not solve the problem on a large scale. Antixenosis is however more likely to be race-non-specific (which is equivalent to horizontal resistance; Scott, Johnson, Wolfe, Lowe and Bennett, 1979) and hence might be more useful as the insect pest is less likely to overcome this type of resistance, as it involves more genes.

Component changed		% change in peak density	
		1976	1977
number of immigrants	+ 20%	+ 19	+ 19
	- 20%	- 19	- 16
instar length	+ 20%	- 31	- 23
	- 20%	+ 76	+100
survival rate	+ 6%	+ 15	+ 19
	- 6%	- 14	- 17
reproductive rate	+ 20%	+ 43	+ 54
	- 20%	- 35	- 40
alate determination	+ 20%	- 5	- 5
	- 20%	+ 5	+ 16

Table 2. Summary of the results of the sensitivity analysis.



The effect of altering the number of immigrant aphids for 1976 (Fig. 1) and the time taken to reach maturity for 1977 (Fig. 2). o - 20%; ◍ standard; □ + 20%.

A reduction in the survival rate of the aphids or in their reproductive rate would lead to a large drop in the peak population. An increase in the development period also leads to a lower peak population but the benefit (% change in peak: % change in component) is lower than for reductions in the survival and reproductive rates. Thus the effect of antibiosis will depend on the component affected. Plant breeders are frequently unable to choose which component is to be changed, but they can, using models, evaluate these changes. Very often partial resistance involves more than one component (Harrington, 1941) and although this was not studied with the model it could be done very easily. No consideration has been made for how easily a component can be changed - obviously a component which is easy to change is more attractive to plant breeders than one which is not, even though the benefit might be lower.

Models can also be used to screen new varieties as their susceptibility to a pest can be assessed once the basic components have been measured. Provided that sufficient is known about the growth of the crop under different conditions then by changing the weather data and other extrinsic variables (soil type etc.) a geographical pattern of the potential of the variety can be assessed without having to grow it over a number of years in different locations. Simulation models can, as Zadoks (1977) pointed out, also include other control measures, such as pesticide application, so that an integrated approach to crop management can be formulated.

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RESISTANCE OF LETTUCE TO MYZUS PERSICAE: FACTORS INFLUENCING THE HOST-PARASITE RELATIONSHIP

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INTRODUCTION

After screening the I.V.T. Lactuca gene bank for resistance to M.persicae, large differences for resistance between genotypes were found (Eenink & Dieleman, 1977a). Retesting selected genotypes has confirmed the existence of resistance in L.sativa, but also showed that the level of resistance should be improved.
The expression of the probably quantitatively inherited resistance can vary greatly under the influence of several different plant and aphid factors. This phenomenon may also interfere with the evaluation of the value of resistance for breeding purposes. This paper presents some results of investigations on the value of resistance to M.persicae as influenced by plant age, aphid biotype and aphid density.

EVALUATION OF RESISTANCE

Assessment of resistance was carried out according to the earlier described macrotest (Eenink & Dieleman, 1977a). Partially resistant and susceptible genotypes were retested. The selected genotypes were artificially infested with 10-20 aphids per plant. The number of aphids was counted and estimated 28 days after infestation. The level of resistance in L.sativa is illustrated in Figure 1. Besides the actual rate of increase, the intrinsic rate of increase was calculated for two selected genotypes.
Aphid reproduction and mortality on the selected susceptible and partially resistant genotype are shown in Figure 2. The calculation of increase (r) and multiplication factor per 7 days (λ) is based on the assumption of an exponential growth of an aphid population (Birch, 1948). Some results, together with the counted and predicted aphid density 18 days after infestation, are presented in Table 1.

Table 1. Intrinsic rate of increase (r) and multiplication factor per 7 days (λ) on a susceptible (S) and partially resistant (R) genotype.

genotype	r	λ	aphid density predicted	aphid density counted
PIVT 312 (S)	2,030	7,61	4970	3000
PIVT 227 (R)	1,379	3,97	800	1200

From the table it can be seen that the calculated multiplication factor

tends to overestimate the difference in resistance. Plant age dependent resistance and aphid density dependent factors, especially effective on the susceptible genotype, seemed to be interfering factors.

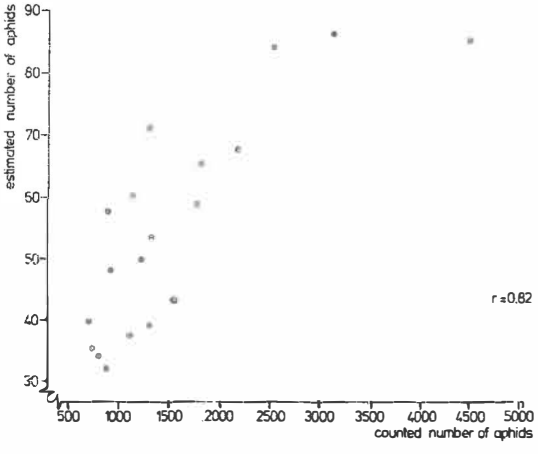

Figure 1. Resistance of 19 selected genotypes and relationship between counted number of aphids per plant and estimated number of aphids per leaf.

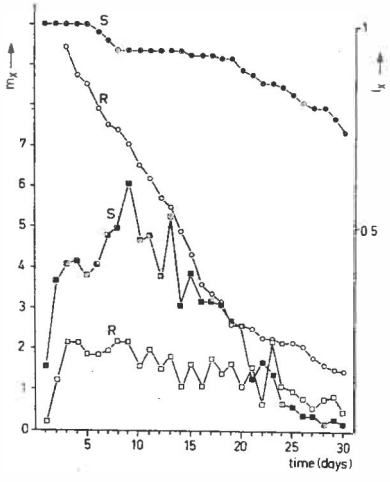

Figure 2. Aphid performance on a susceptible (S) and partially resistant (R) genotype. (Mx: larvae production per aphid per day; lx: age dependent mortality).

IMPROVEMENT OF RESISTANCE LEVEL

In spite of the pronounced differences in resistance to M.persicae it is clear that the level of resistance has to be improved to meet consumer demand for almost aphid-free lettuce heads. Combining ability analysis of variance for the degree of resistance of over 60 F2-populations obtained by diallel crosses and earlier data on the inheritance of resistance (Eenink & Dieleman, 1977b) suggest that the main component of genetic variation is determined by additive genes.

Combination of different genes to improve resistance is hampered by low selection responses, as was concluded from parent offspring comparisons for certain populations obtained by crosses between resistant genotypes. Nevertheless, early results of crosses between some resistant parents suggest the possibility of transgression of resistance.

VARIATION OF PLANT FACTORS

Host plant quality of a certain genotype is influenced by several factors, including plant age and growing conditions. The polyphageous aphid M.persicae is well equiped to detect small differences in food plant quality with the ultimate result of quality dependent differences in larval weight gain, generation time, mortality, reproduction and frequency of produced alatae. These factors were also used in our experiments as criteria of resistance.

The influence of plant age on some of these criteria is shown in Table 2.

Table 2. Influence of plant age on larval mortality, insect weight and number of larvae produced per aphid in four days for a partially resistant and a susceptible genotype. Plant age 22 and 15 days at the time of infestation.

Character	PIVT 313 susceptible		PIVT 339 partially resistant	
	22 days	15 days	22 days	15 days
larval mortality (%)	23	23	50	58
insect weight (µg)	566	502	398	304
number of larvae per aphid in 4 days	18.6	16.4	9.9	7.8

The measured difference in resistance is hardly influenced by plant age, but the degree of resistance seemed to be age dependent. The colonizing capability of M.persicae is higher on older than on younger leaves (Eenink & Dieleman, 1980 in press), so older plants seemed to be generally more susceptible than younger ones. For the assessment of resistance account has to be taken also of the possible interference of a variation in host plant condition caused by several different environmental factors.

VARIATION OF APHID FACTORS

The outcome of resistance measurement depends on virulence genes of the aphid used and may also be influenced by aphid density and conditioning of individual aphids.

Aphid biotypes.

From the initial population of M.persicae two biotypes have been selected. Differences between the two biotypes in insect weight, larval mortality and proportion of adults 7 days after infestation with first instar larvae on a susceptible and partially resistant genotype, are presented in Table 3.

Table 3. Comparison of two biotypes of M.persicae (WM1, WM2) on a susceptible (S) and partially resistent (R) genotype.

Plant genotype	insect weight after 7 days		larval mortality %		proportion of adults after 7 days	
	WM-1	WM-2	WM-1	WM-2	WM-1	WM-2
PIVT 313 (S)	637	268	4	48	84	24
PIVT 339 (R)	326	110	22	96	53	0

Most tests were carried out with biotype WM-1 and selected genotypes are now also tested with other biotypes. Up till now the WM-1 partially resistant genotypes have been found to be almost fully resistant to biotype WM-2.

Conditioning.

Short-term physiological adaptation can interfere in several ways with the measurement of the degree of resistance.

A transition or conditioning effect may influence especially the outcome of the microtest (Eenink & Dieleman, 1977). To avoid the conditioning effect only first instar larvae were used in the microtest.

Long-term adaptation of biotype WM-1 to the partially resistant genotype could not be established, at least for a period of 12 generations.
Aphid density.
A prerequisite for a reliable calculation and use of the rate of increase as a criterion of resistance is the absence of density dependent factors. Therefore, the newly born larvae were removed daily from the chip cages used in the microtest. The influence of aphid density on larvae production and aphid weight is shown in Table 4.

Table 4. Influence of aphid density on larval weight and larvae production on a susceptible (S) and partially resistant (R) plant genotype.

genotype	cage diameter (cm) 5 adults per cage	larval weight after 7 days (µg)	Cumulative larvae production per aphid after 5 days
PIVT 313 (S)	2	454	15
	5	494	20
PIVT 339 (R)	2	245	7
	5	278	8

Unlike the usual method, larvae were not removed from the cages over a period of 5 days. The negative influence of density on larvae production is the most pronounced on the susceptible genotype, but the ultimate effect on resistance difference between the two plant genotypes is very low.

Aphid density may also influence the outcome of the macrotest because of the earlier expression of density dependent factors on the susceptible plant genotype compared with the partially resistant plant genotype..

CONCLUDING REMARKS

A high level of resistance to the most frequent biotype of M.persicae has been found. The existence of a more virulent biotype makes the improvement of the resistance level for practical purposes necessary. Improvement of the level of resistance depends on the availability of different sources of resistance.
Manipulation and usability of resistance is hampered by a large number of factors.
Accurate knowledge of different resistance mechanisms, colonizing ability of aphids and several other factors is therefore essential for the development of highly resistant lettuce genotypes.

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RESISTANCE TO THE APHID MYZUS PERSICAE (SULZ.) IN POTATO CULTIVARS

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INTRODUCTION

This research was initiated as a result of concern that resistance in Myzus persicae (Sulz.) to organophosphorous and carbamate insecticides detected in sugar beet (Needham and Devonshire, 1975) and in potatoes (Devonshire et al., 1977) could cause increasing problems in the potato crop. Very little was known about host plant resistance to M.persicae in existing potato cultivars or of the potential of wild Solanum spp. in providing resistant genetic material.

The aim of this work has been to assess a wide range of existing potato cultivars and species in the laboratory and in experimental plots in order to measure and explain aphid resistance.

Laboratory Methods

Cultivated potatoes were grown in John Innes No. 2 potting compost in pots of 15 cm diameter. Prior to experimentation they were kept in a glasshouse at 15°C with a 4°C range and with a daylength of 16 hours.

Aphid clones were obtained from the Plant Breeding Institute, Cambridge and from Rothamsted Experimental Station, Harpenden and cultured separately on potato plants (cv. Desirée) in an insect culture room (Scopes et al.; 1975) at 19°C with a range of 1°C and a daylength of 16 hours.

Cultivated potato plants were assessed for resistance to M.persicae by caging individual aphids on the abaxial surface of terminal leaflets using clip cages modified from the design of Noble (1958). The standard procedure was to cage an adult apterous aphid for 24 or 48 h until it had produced up to six nymphs. The adult was then removed, together with any surplus nymphs, the remainder being reared to maturity under the culture room conditions described above. When the nymphs reached maturity the following data were recorded: 1) time (days) to maturity, 2) teneral (<24 h. old) adult weight (mg; sensitivity of balance: 0.005 mg), 3) number of large (pigmented eyed) and immature embryos present in teneral adults, or 4) daily production of nymphs by aphids caged individually. The initial experiment involved ranking four potato cultivars (King Edward, Desirée, Pentland Crown and Majestic); three 6-week-old plants of each cultivar were used.

The performance of two aphid clones was compared. Clip cages were placed

on both sides of the midrib of each terminal leaflet under test and aphids from the two clones were randomly allocated to right or left sides. Two 6-week-old plants were used to represent each of the following 7 potato cultivars: King Edward, Desirée, Pentland Crown, Record, Pentland Dell, Majestic and Maris Piper.

Field Methods

Field cage. Eight plants from each of eight potato cultivars were randomly arranged at a 0.4 m spacing within a 3m x 3m plot. Enclosing the plot was a 3m x 3m x 2m framework covered by aphid-proof 'Tygan' mesh. Three months after planting, the plants were artificially infested with virus-free M.persicae. Four weeks later the number of aphids present on three upper, three middle and three lower leaves of each plant were counted. Leaf areas for each leaf type were measured for each potato cultivar. The following cultivars were planted: King Edward, Desirée, Pentland Crown, Majestic, Pentland Dell, Record, Maris Piper and Up to Date.

Open field plot. Five potato cultivars were planted in 25 blocks to form a Latin square design. Each block comprised 15 plants in 3 rows 0.75 m apart and with a spacing of 0.3 m between plants. Aphid population development was monitored twice weekly by examination of one plant stem from each row in each block (i.e. 15 stems per cultivar). For each aphid in each position on the plant, the aphids' developmental stage was recorded. Maximum plant height was also recorded for each cultivar. The following potato cultivars were planted in this plot: King Edward, Desirée, Pentland Crown, Maris Piper and Record.

RESULTS

Laboratory Investigation. 1. Initial ranking of potato cultivars with respect to resistance to M.persicae (Table 1). Significant differences between cultivars were found in maturation time: $F_{3,287} = 29.00$, $p < 0.001$, teneral adult weight: $F_{3,176} = 60.94$, $p < 0.001$, red-eyed-embryo number: $F_{3,176} = 43.53$, $p < 0.001$ and total embryo number: $F_{3,176} = 50.46$, $p < 0.001$. Where aphids were left to reproduce on the plants, significant differences were found between cultivars in the number of nymphs produced in the first 15 days of adult life: $F_{3,87} = 31.62$, $p < 0.001$.

Table 1. Mean maturation time (days), weight (mg), embryo complement and nymphal production by M.persicae on 5 potato cultivars.

Cultivar	Maturation time	Teneral adult wt.	Red-eyed embryos	Total embryos	No. nymphs in 10 days
King Edward	11.20a	0.452a	9.27a	28.60a	27.52a
Desirée	11.21a	0.401a	8.86a	24.63b	20.14b
Pentland Crown	12.27b	0.274b	6.87b	19.60c	13.75c
Majestic	12.62b	0.210c	5.06c	13.45d	13.14c

Means in the same column sharing a letter do not differ at the 5% significance level.

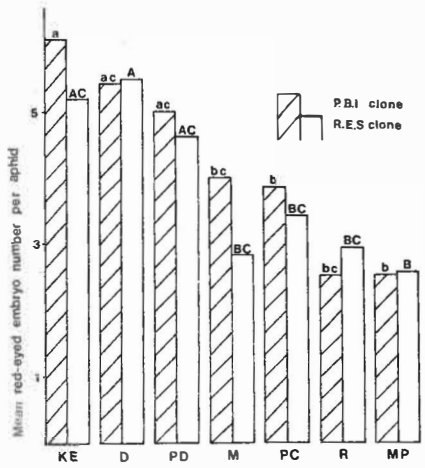

Fig. 1. Mean number of large (red eyed) embryos present in two clones of M.persicae on seven potato cultivars.

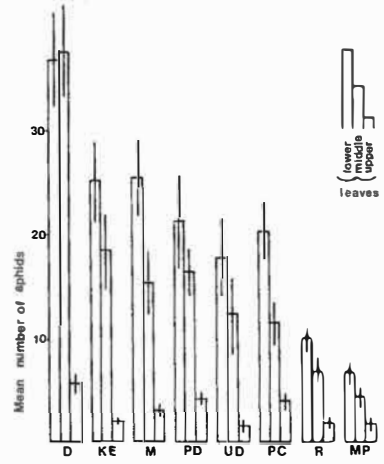

Fig. 2. Mean numbers of M.persicae on upper, middle and lower leaves of eight potato cultivars in a field cage.

Cultivar means which form sub-groups that do not differ at the 5% level are annotated a, b, c for P.B.I. clone and A, B, C for R.E.S. clone.

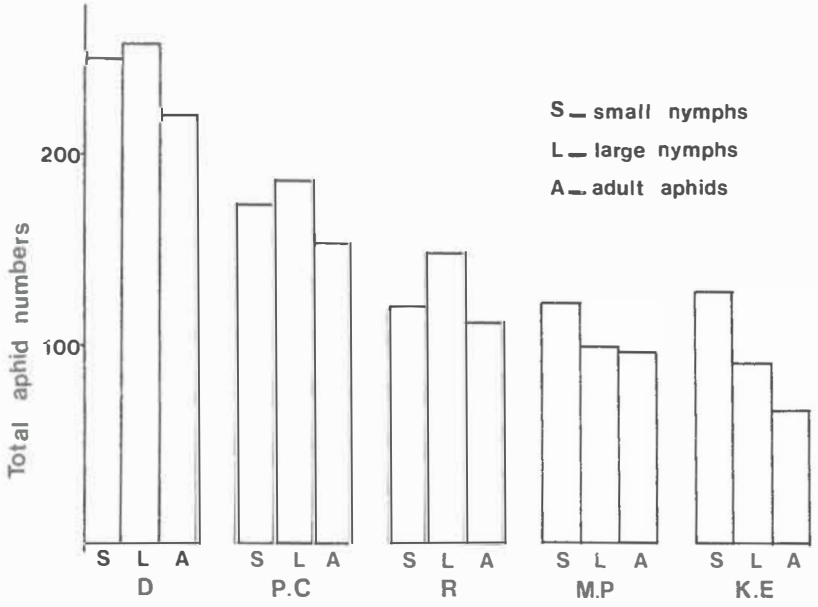

Fig. 3. Total numbers of M.persicae found on five potato cultivars on an open field plot.

2. Performance of two aphid clones on seven potato cultivars. Significant differences in maturation time were found between cultivars: $F_{6,370} = 22.53$, $p < 0.001$ but not between clones: $F_{1,370} = 1.69$, $p > 0.05$ and there was no significant interaction: $F_{6,370} = 1.05$, $p > 0.05$. Similarly, teneral adult weight was significantly different between aphids reared on the cultivars: $F_{6,370} = 68.17$, $p < 0.001$ but not between aphid clones: $F_{1,370} = p > 0.05$. There was a significant interaction: $F_{6,370} = 4.75$, $p < 0.001$. Red-eyed-embryo number was significantly different between cultivars ($F_{6,370} = 58.80$, $p < 0.001$) and clones ($F_{1,370} = 5.95$ $p < 0.05$) and there was a significant interaction: $F_{6,370} = 4.20$, $p < 0.05$. Further analysis revealed that only in the cultivar King Edward was there a significant difference in red-eyed-embryo number between aphid clones. (Fig. 1 shows the differences in red-eyed-embryo number between cultivars within clones.)

Field Investigation. 1. Field cage. Analysis has been restricted to the numbers of adult apterous aphids and the total numbers of aphids on the three leaf categories for each cultivar. (Fig. 2 shows the total numbers of aphids on the eight cultivars.) The numbers of apterous aphids were significantly different between cultivars: $F_{7,534} = 16.98$, $p < 0.001$ and between leaf types: $F_{2,534} = 69.53$, $p < 0.001$. There was a significant interaction between cultivar and leaf type: $F_{14,534} = 3.21$, $p < 0.001$. Similarly, the total number of aphids was significantly different between cultivars: $F_{7,534} = 25.34$, $p < 0.001$ and between leaf types: $F_{2,534} = 108.94$, $p < 0.001$. There was a significant interaction between cultivar and leaf type: $F_{14,534} = 5.05$, $p < 0.001$.

The mean density of aphids per cm^2 of leaf was calculated for upper, middle and lower leaves of each cultivar. There was a significant association between leaf type and aphid density: $X^2_2 = 28.21$, $p < 0.001$ leaves, with a Null Hypothesis of random distribution of aphids between the density of aphids was lower than expected on the upper leaves and higher than expected on the lower leaves.

2. Open field plot. Due to low numbers of M.persicae naturally infesting the field plot the results from all the sampling dates were pooled. This gave an estimate of the cumulative population of aphids on each cultivar over the season. There was a significant association between cultivar and total aphid numbers: $X^2_{1,4} = 286.47$, $p < 0.001$ (Fig. 3). When individual aphid age/morph classes were examined there was no significant association between the number of alates or alatiform fourth instars and the potato cultivars: $X^2_{1,4} = 6.06$, $p > 0.05$ and $X^2_{1,4} = 5.85$, $p > 0.05$, respectively. However, there was an association between cultivar and the number of apterae: $X^2_{1,4} = 105.46$, $p < 0.001$, small nymphs: $X^2_{1,4} = 76.36$, $p < 0.001$ and large nymphs: $X^2_{1,4} = 114.51$, $p < 0.001$.

Maximum plant height was measured during the season and the following results (cm) were obtained: King Edward: 53.3 ± 5.6; Maris Piper: 49.5 ± 5.8; Pentland Crown: 40.5 ± 3.8; Desirée: 39.9 ± 5.9; Record: 32.1 ± 6.1.

DISCUSSION

Commercially available potato cultivars exhibit a range of resistance to M.persicae. The resistance rankings obtained were the same for maturation time, teneral adult weight, embryo complement and nymph production for the four potato cultivars initially studied. There was approximately a 50% difference in the performance of aphids between the most susceptible and resistant cultivars for the above mentioned parameters (excluding maturation time).

One of the most significant measures of plant resistance is the reduction in the contribution that an aphid reared on the plant makes to the next generation. To assess the number of nymphs produced by an aphid is time-consuming, as aphids have to be caged individually and examined frequently throughout their life. It also gives variable results. However, embryo complement has been shown to be closely correlated with reproductive rate in several aphid species (Dixon and Wratten, 1971; Dewar, 1977; Wratten, 1977) and this measure is easily and quickly obtainable. Therefore on most occasions in this research embryo complement has been used as one of the measures of plant resistance.

In the experiments comparing two aphid clones on a larger sample of cultivars, it was apparent that although the clones varied in their performance on the potato cultivars and there were significant interactions between potato cultivar and aphid clones the overall ranking of resistance of the potato cultivars was unaffected. A similar result was obtained by Lowe (1974) using seven clones of M.persicae on seven sugar beet stocks of varying resistance. These results suggest that the variability of resistance when different aphid clones are used is less than the variability of resistance shown by crop cultivars. In fact, since the origins of alate M.persicae entering a crop are unknown it is important that resistance in potato cultivars is not confined to specific clones. Similarly, since M.persicae is polyphagous the opportunity for this species to adapt to resistant cultivars may be reduced.

The resistance rankings of potato cultivars in the field cage; which were obtained from aphid numbers per leaf, were in agreement with the rankings found in the laboratory using maturation time, teneral adult weight and embryo complement as measures of resistance. The observation that more aphids than expected from random causes were present on the lower leaves of potato plants agrees with Taylor's (1955) observation that M.persicae has a marked preference for senescing leaves.

On the open field plot the resistance ranking obtained from aphid numbers on the cultivars was similar to that found in previous experiments in the laboratory and field, with the exception of the cultivar King Edward. There were fewer aphids on this cultivar than expected from laboratory work and it is possible that this is due to the growth form of the plant. King Edward is the tallest cultivar grown in these experiments and it has small leaflets. It is possible that aphids can easily be dislodged from this cultivar by leaf brushing in wind. The only other cultivar of comparable height is Maris Piper, which would already be expected to have a low aphid population density from its position in the laboratory resistance ranking. The reason that this difference was not evident in the field cage data is that, within cages of this design, the microclimate is modified and the wind velocity is markedly reduced (Wratten, Lee and Stevens, 1979).

Certain aspects of host plant biochemistry and morphology have been investigated to determine the underlying mechanisms of resistance. Alkaloid content of potato leaves has been examined using thin layer chromatography but, to date, no correlation between aphid performance and alkaloid quantity or quality have been found.

Leaf hair density has been examined, and there are strong indications that resistance may be correlated to a certain extent with leaf hair density. It is possible that this type of resistance would operate by increasing aphid mobility on resistant cultivars, decreasing the time spent feeding and increasing mortality and development time.

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RESISTANCE A MYZUS PERSICAE SULZER CHEZ LE PECHER PRUNUS PERSICA (L) BATSCH

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I - INTRODUCTION

Des différences de sensibilité à Myzus persicae ont été signalées chez les variétés cultivées du Pêcher, mais les résistances observées sont de faible niveau. (BOGSANYI, 1966 ; MASSONIE, 1977). Or, l'amélioration de la résistance des variétés fruitières aux pucerons et aux champignons parasites a été réalisée à partir de matériels présentant une résistance élevée et à contrôle génétique simple (MASSONIE, 1978) Les caractéristiques de la reproduction sexuée du pêcher : le Pêcher est une plante autogame préférentielle et souvent homozygote pour de nombreux caractères (MONET, 1977), permettent de penser que de tels matériels existent parmi les variétés non améliorées pour la qualité du fruit. Aussi, des recherches ont été réalisées dans la collection variétale constituée par la Station d'Arboriculture fruitière de Bordeaux. Cette note fait le point des résultats obtenus de 1976 à 1979 inclus.

II - MATERIELS ET METHODES -

Matériel végétal : Les observations ont porté sur 76 variétés de P. persica (L) Batsch non améliorées pour le fruit. Chaque variété est un clone multiplié par greffage sur le pêcher porte-greffe GF 305 et conservé, à raison de trois exemplaires en verger de collection.

Certaines variétés (Tableau I) ont été également étudiées au stade semis, issus de fécondations libres, et au stade première pousse de jeunes plants greffés sur GF 305. Les semis sont cultivés dans des pots maintenus en serre chaude. Leur résistance est évaluée à partir du moment où ils présentent de 10 à 15 étages foliaires. Les plants greffés sont cultivés dans des fûts maintenus sous un abri grillagé extérieur.

Les variétés S 2678 et S 2605 ont été plus particulièrement étudiées. Pour S 2678, nous disposons de 55 arbres, issus d'autofécondation et cultivés francs de pied, ainsi que d'un hybride de première génération avec une variété cultivée. Par ailleurs, les deux variétés ont été surgreffées sur la variété cultivée, Jungermann 3197, et cette dernière a été surgreffée par les deux variétés précitées.

Pucerons : Les observations concernent les populations de la région de Bordeaux. Les contaminations artificielles ont été effectuées avec plusieurs lignées de fondatrigeniae apterae.

...

Méthodes :

* Contaminations artificielles - En verger, elles ont été effectuées de fin avril à début juin avec un nombre variable de pucerons, de dix à plusieurs centaines d'individus. Les contaminations sont effectuées en attachant un fragment de rameau d'une variété sensible, qui héberge les pucerons, sur une jeune pousse de la variété étudiée. Chaque essai comprend trois répétitions par variété et plusieurs témoins de sensibilité. Ces essais sont effectués sous manchon.

La contamination du semis est réalisée en apportant au pinceau cinq fondatrigeniae apterae . La contamination de la première pousse des plants greffés est assurée par l'une ou l'autre des méthodes précitées suivant le niveau de developpement de la pousse.

La notation du niveau des populations intervient généralement trois semaines après la contamination. L'objectif de la notation est de classer les matériels en trois catégories : résistant, intermédiaire, sensible. La première catégorie renferme les matériels non colonisés (note = 0) ou très peu colonisés (note = 1). La deuxième regroupe les matériels faiblement (note = 2) ou moyennement (note = 3) colonisés. La troisième comprend les matériels fortement (note =4) ou très fortement colonisés (note = 5). Les essais sont répétés plusieurs fois afin de confirmer la valeur du classement des variétés considérées comme résistantes ou intermédiaires.

L'observation de la réponse du feuillage, essentiellement des semis, de quelques variétés a permis de distinguer trois catégories de réaction : typique, atypique, et nécrotique. La réaction typique correspond aux déformations habituelles, ou crispations, provoquées par l'insecte. Les réactions atypiques correspondent à des déformations plus ou moins importantes mais n'ayant pas l'aspect de crispations. La réaction nécrotique est associée à l'apparition de nécroses localisées au point de piqûre ou généralisées et provoquant le desséchement des jeunes feuilles ou d'extrêmités apicales.

* Actographie. L'étude du comportement alimentaire des fondatrigeniae apterae sur semis des variétés S 2678 et GF 305 a été entreprise. Les techniques mises au point par MAC LEAN et KINSEY ont été modifiées suivant BOUCHERY (Zoologie, Colmar) et la tension du courant continu envoyé dans le pot de culture est réduite à 50 millivolts. L'enregistrement permet de distinguer plusieurs figures correspondant, par analogie avec les travaux associant actographie et histologie, (MAC LEAN et KINSEY, 1967 ; NAULT et STYER, 1972 ; KENNEDY et al, 1978) aux périodes de non activité alimentaire (zéro électrique) aux piqûres d'épreuve, aux périodes de salivation et d'ingestion. Nous ne pouvons préciser si l'ingestion intervient dans le phloème ou dans d'autres tissus car, à la vitesse d'enregistrement utilisée, un centimètre à la minute, nous n'avons pas identifié les courbes X.

L'activité alimentaire d'un puceron est étudiée d'abord sur semis de GF 305 puis de S 2678. En conséquence, les résultats sont analysés suivant le test de WILCOXSON (données appariées) établi au seuil de 2,5 % sous des hypothèses unilatérales (SOKAL et ROHLF, 1969).

III - RESULTATS

Détection des matériels résistants

Les résultats fournis par la technique de contamination artificielle sont réunis au tableau I.

La résistance des variétés, exception faite de S 2678 et S 2605, augmente avec leur vieillissement. Cette résistance est parfois associée à des réactions nécrotiques ou atypiques du feuillage aux piqûres de l'insecte. L'expression de la résistance pourrait être quelque peu modifiée par les facteurs de l'environnement.

Tableau I - Contaminations artificielles des variétés de P. persica (L) Batsch par les fondatrigeniae apterae de M. persicae Sulzer.

	Variétés (référence et provenance)	Niveau des populations de l'insecte			Réaction du feuillage des semis aux piqûres de l'insecte
		Arbre	greffon	Semis	
1	S 2678, U.S.A.	0	0	0 (115)*	nécrotique (discrète)
2	S 2605, (Rubira), USA	0	0	0 (93)	nécrotique (nette)
3	S 2811, Extrême Orient	1	2 à 3	3 (11)	atypique
4	S 2540, Corée du Sud	1	2 à 3	3 (10)	atypique
5	S 2464, Japon du Sud	1	2 à 3	3 (54)	typique
6	S 2534, Corée du Sud	1	2 à 3	-	-
7	S 2535, Corée du Sud	3	-	4 à 5 (8)	typique
8	S 2543, Japon du Nord	3	-	4 à 5 (85)	typique
9	S 2544, Japon du Nord	3	-	-	-
10	S 2508, France	3	-	-	-
11					
.					
.					
.					
76	GF 305, France	5	5	5	typique

( )* = nombre de semis examinés par variété.

Ainsi, la réaction nécrotique apparait en moins de trois jours lorsque les semis de S 2605 sont en serre chaude, en plus d'une semaine lorsqu'ils sont sous abri grillagé extérieur.

La résistance en verger des variétés classées résistantes d'après la technique des contaminations artificielles n'a été étudiée qu'avec S 2678 et, dans une moindre mesure avec S 2605. De 1976 à 1979 inclus, ces variétés n'ont pas hébergé de colonies printanières de M. persicae bien que les variétés voisines aient été très contaminées.

Transmission de la résistance

D'après les résultats du tableau I, le caractère résistance parait homozygote. Notons queles hybrides de première génération issus du croisement entre S 2678 et une variété commerciale sensible sont résistants.

Relation porte-greffe - greffon

Les variétés résistantes S 2678 et S 2605 surgreffées sur la variété sensible Jungermann 3197 demeurent résistantes. La variété sensible greffée sur les variétés résistantes demeure sensible.

Actographie

Les résultats obtenus sont résumés au tableau II

Tableau II - Comportement alimentaire de M. persicae sur semis de la variété sensible GF 305, et de la variété résistante S 2678.

	GF 305	S 2678
non activité alimentaire (sur 2 heures)	$\bar{x}$ = 21,3 ± 20 minutes (n = 20)	$\bar{x}$ = 19,7 ± 19 minutes (n = 20)
nombre de piqûres avant l'ingestion (*)	$\bar{x}$ = 7,0 ± 3,5 (n = 14)	$\bar{x}$ = 9,7 ± 7,8 (n = 14)
durée de salivation précédant la première période d'ingestion	$\bar{x}$ = 29,4 ± 9,8 minutes (n = 18)	$\bar{x}$ = 65,7 ± 26,3 minutes (n = 18)
durée de la première période d'ingestion.	$\bar{x}$ = 47,1 ± 50 minutes (n = 16)	$\bar{x}$ = 53,2 ± 50 minutes (n = 16)

Myzus persicae effectue souvent ses premières piqûres d'épreuve quelques secondes après avoir été placé sur semis de pêcher. Les nombres de piqûres effectuées pendant la phase de recherche du premier site d'ingestion ne sont pas significativement différentes suivant les variétés. Mais chez la variété résistante, le temps global de salivation est significativement supérieur à celui observé chez la variété sensible. Des facteurs de résistance modifiant le comportement de salivation interviendraient donc très rapidement lors de la pénétration des stylets dans S 2678. Cependant ces facteurs de résistance n'empêchent pas le puceron de découvrir un premier site d'ingestion et la durée de la première période d'ingestion est identique chez les deux variétés. Il faut donc admettre, si l'ingestion intervient dans la sève élaborée, que celle-ci ne renferme pas de facteur(s) de résistance ayant une influence immédiate.

IV - CONCLUSIONS

Les résultats que nous avons présentés devront être confirmés en prenant en considération la variabilité du puceron et la coévolution des cycles de l'Insecte et du Pêcher. Cependant, les observations de terrain permettent de considérer que les variétés S 2678 et S 2605 sont résistantes à M. persicae, tout au moins dans les conditions de Bordeaux. Ces variétés sont également résistantes, par contamination artificielle, à Myzus varians Davids, mais non aux autres pucerons du Pêcher (MASSONIE et MAISON, 1979). Elles sont également moins sensibles à l'inoculation du virus de la Sharka par M. persicae (MASSONIE et MAISON, 1979).

En conclusion, notons à côté des implications agronomiques des résultats présentés, l'intérêt du modèle Pêcher/Pucerons du Pêcher pour des études plus fondamentales de la relation Plante-Puceron.

(*) piqûres d'épreuve + piqûre(s) suivie(s) de salivation +.piqûre suivie de salivation et d'ingestion.

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RESISTANCE OF LETTUCE TO NASONOVIA RIBIS NIGRI: RESEARCH ON THE OCCURENCE OF DIFFERENTIAL INTERACTIONS BETWEEN HOST AND APHID GENOTYPES AND ON THE INHERITANCE OF RESISTANCE

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INTRODUCTION

Nasonovia ribisnigri is the most common aphid colonizing outdoor lettuce. Effective control of this aphid requires frequent application of insecticides because of repeated secondary infestation by winged aphids. As the aphids are mainly present on the younger leaves, inside the heads of lettuce, pesticides, especially contact ones are less effective. So the use of insecticides confronts consumers both with insecticidal residues and dead aphids. Resistant lettuce varieties could bring a solution to these problems.

APHID BEHAVIOUR AND SCREENING FOR RESISTANCE

Tests for resistance have to be adapted to aphid behaviour and characteristics of the host plant. The specific feeding behaviour and rapid disturbance of settled aphids makes artificial infestation, manipulation and aphid counting more difficult than for Myzus persicae, another lettuce-infesting aphid. N. ribisnigri is also sensitive to crowding, and winged aphids are already produced at low population densities. This phenomenon limits the duration of tests.

In certain tests, young lettuce plants (20 days old, 2 replicates and 5 plants per genotype per replicate) were inoculated with about 10 aphids at different ages and stages of development. After a few weeks, the population increase per plant varied widely between plant genotypes. As a result of a large scatter the significance of these differences for partial resistance was not always clear. However among about 300 genotypes tested, some accessions of the wild species L. virosa could be clearly distinguished from all other genotypes, because of the very high resistance to N. ribisnigri (Dieleman & Eenink, 1977) (Fig. 1).

The difference between the resistant and susceptible plant genotypes can be demonstrated in various ways. Fig. 2 shows the difference between behaviour of winged aphids on a resistant and a susceptible plant genotype.

If both resistant and susceptible plants were placed in one cage, so if the winged aphids were allowed to choose, then after about 10 hours the majority of the aphids were present on the susceptible genotype (cv. Taiwan). If the resistant and susceptible plants were placed in different cages, then after 10-16 hours almost all aphids in the cage containing the susceptible plants had landed on these plants, while in the cage with the resistant plants about 50% had landed.

Resistance was expressed quantitatively by the following test procedure. Ten first-instar larvae were put in the centre of lettuce seedlings (5 plants per genotype). These larvae were born of young alatae to avoid the production of winged aphids on the plants to be tested. After 7-10 days, larval mortality was assessed and 5-7 days later the total number of aphids per plant was counted, during the first generation of aphids born on the tested plants.

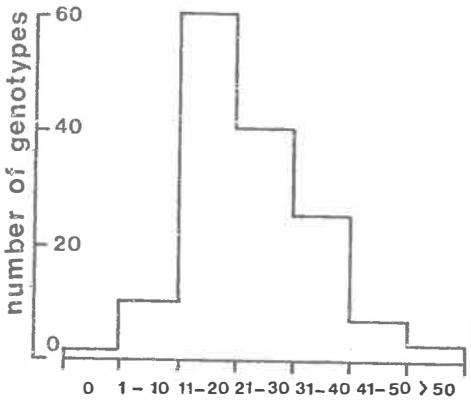

Fig.1. Distribution of numbers of plant genotypes over a scale for aphid infestation.

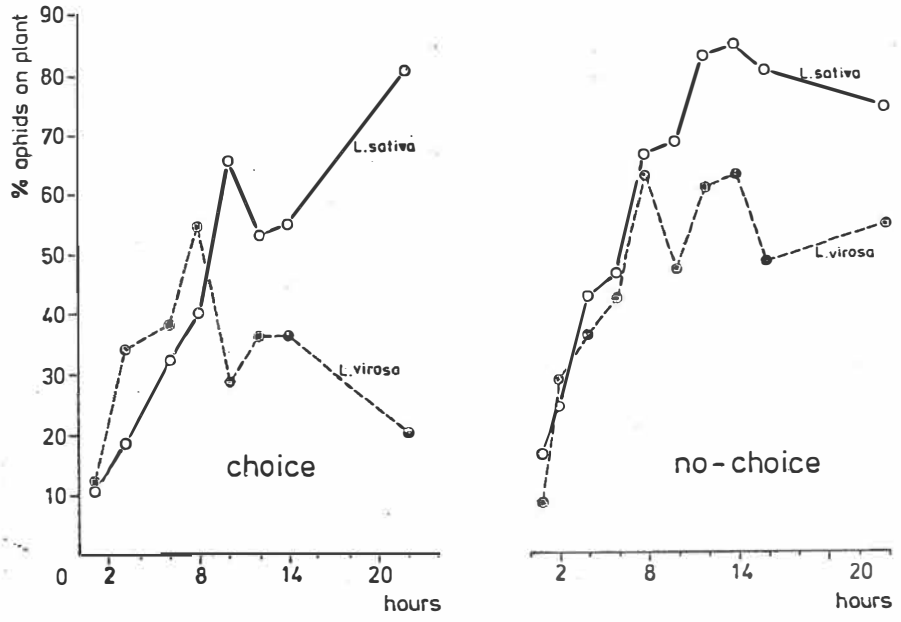

Fig.2. Differences of behaviour of winged aphids in a choice and in a no-choice situation with susceptible and resistant plants.

Table 1. Differences between a resistant and a susceptible genotype of Lactuca after artificial infestation with 10 first-instar larvae per plant (5 plants per genotype). Surviving larvae and larvae produced were counted 10 and 15 days after infestation, respectively.

L. serriola (susceptible)		L. virosa (resistant)	
number of larvae surviving	number of larvae produced	number of larvae surviving	number of larvae produced
5	70	0	0
7	78	0	0
8	70	0	0
9	70	0	0
10	140	0	0

Table 1 illustrates the difference in resistance between a susceptible genotype and the resistant L. virosa. Under natural and artificial conditions, settling of N. ribisnigri on resistant L. virosa was observed, but colonization always failed.

RESISTANCE AND SUSCEPTIBILITY WITHIN L. VIROSA

As we found various accessions of L. virosa which were almost absolutely resistant to N. ribisnigri , we were inclined to believe that resistance was closely linked to the common L. virosa character which would be very unfavourable for transfer of resistance to L. sativa. However, after screening ten different accessions of L. virosa, one genotype occurred which was almost as susceptible as the susceptible control genotypes.

Table 2. Distributions of number of plants per genotype over a scale for surviving numbers of aphids.
0 = no aphids survived on that plant.
10= 10 aphids survived.

Genotype	Number of surviving aphids 0 1 2 3 4 5 6 7 8 9 10
PIVT 726 L. virosa (resistant)	7 6 1
PIVT 793 L. virosa (susceptible)	2 1 2 2 1 3 2 2 2
L. serriola (susceptible)	0 2 0 0 3 2 4 3 4 1 1

This implies that characteristics responsible for resistance are not closely linked to the L. virosa character of the plants, as will also appear from the following paragraph.

TRANSFER OF RESISTANCE

Because resistance was present in accessions of a wild Lactuca species, which was rather distant from the cultivated species L. sativa, great barriers for transfer of the resistance to butterhead lettuce had to be taken. Another susceptible wild species, L. serriola was used as a "bridge parent" between L. virosa (resistant) and L. sativa (susceptible) The crossing scheme is outlined in Table 3.

Table 3. Crossing scheme for the transfer of resistance from L. virosa to L. sativa.

L. serriola (susceptible)	x	L. virosa (resistant)
F_1 (resistant)	x	L. serriola L. sativa
B_1	x	L. serriola L. sativa
B_2	x	L. serriola L. sativa
B_3 (susceptible or resistant)	x	L. sativa

B_3 ⊗ plants
resistant and male and female fertile

Plants of F_1 seemed to have the same resistance level as the male parent. Only a few of the F_1 plants showed some female fertility, and all plants were completely male-sterile. Many hundreds of backcrosses to L. serriola and L. sativa were made, resulting in a few B_1 seed. After further backcrossing to L. serriola and L. sativa, and cultivation of seed on nutrient medium in test tubes, some plants were eventually obtained with a moderately good male and female fertility. After testing, some of these plants seemed to have the same resistance level as the resistant parental genotype. From frequencies of susceptible and resistant plants in segregating populations it is concluded that resistance is governed by one or two dominant genes. It is not yet known if resistance in the various accessions of L. virosa is determined by the same genes.

INTERACTIONS BETWEEN PLANT AND APHID GENOTYPES

Durability of resistance is a major problem of resistance breeding. Isolates of the aphid were collected from different parts of The Netherlands to investigate whether virulence genes occurred that were able to overcome the resistance. Results of these investigations are presented in Tables 4 and 5. These Tables show that, both for a) the number of surviving larvae and b) for the number of larvae produced, no clear interactions occurred between the ten isolates of N. ribis nigri and the five plant genotypes. Significant differences were only found between the susceptible genotype (L. serriola) and the four resistant genotypes. There are some indications that the resistance level in the L. virosa accession is higher than in the derived resistant L. sativa lines.

Table 4. Mean number of surviving aphids 8 days after inoculation with 10 larvae per plant. means per plant genotype per aphid accession are based on 5 plants. ǂ means based on 1-2 plants.

Aphid accession	L. serriola (susceptible)	L. virosa ǂ (resistant)	L. sativa resistant line 1	line 2	line 3
1	5.2	0	0.6	0.6	1.4
2	7.0	0	0.2	0.2	0.8
3	4.2	0	0	0.2	0.8
4	7.6	0	0.2	0	0.8
5	6.2	0	0.4	0.2	0.6
6	4.8	0	0.0	0.4	0.2
7	8.2	0	0.2	0.2	0.2
8	5.0	0	0.2	0.8	0.2
9	6.8	0	0.0	0.2	1.4
10	5.4	0	0.4	0.2	1.0

Table 5. Mean number of aphids per plant 18 days after inoculation of each plant with 10 larvae. Means are based on 5 plants per aphid accession. ǂ means of 1-2 plants.

Aphid accession	L. serriola (susceptible)	L. virosa* (resistant)	L. sativa resistant line 1	line 2	line 3
1	71	0	0.8	0.2	1.0
2	83	0	0.8	0.2	0.6
3	69	0	0.2	1.0	3.0
4	89	0	1.0	0.6	1.2
5	100	0	0.4	1.0	0.8
6	55	0	0.2	0.8	1.0
7	82	0	0.8	0.2	1.8
8	51	0	0.8	0.2	1.4
9	10	0	0.4	0.8	0.8
10	64	0	0.4	0.8	3.2

This difference might, however, also be attributable to the small number of tested plants of L. virosa.

PROSPECTS

It is feasible to transfer the resistance from our selections to lettuce varieties. Because of high level of resistance, N. ribisnigri cannot colonize the resistant varieties. So the use of insecticides to control this aphid can be avoided. However, further investigations are needed on the inheritance and persistence of resistance.

In cooperation with the Department of Toxicology of the Agricultural University in Wageningen, investigations are carried out on the chemical background of the resistance and on the edibility. Possible toxic or carcinogenic compounds (e.g. quercitin) were investigated, so far the resistant lines have not differed from the current lettuce varieties for these feeding compounds.

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RESISTANCE TO *SITOBION AVENAE* IN WHEAT

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INTRODUCTION

The grain aphid, *Sitobion avenae* (F.) {= *Macrosiphum avenae*}, has been recognised in recent years as a considerable pest of cereals, especially wheat, in North and West Europe (Vickerman & Wratten, 1979). Lowe (1977) developed a method of testing varieties for resistance by rearing the aphids for one and a half generations on ears of wheat; but this method failed to give consistent comparisons between varieties, and experiments with adult plants in the glasshouse have been discontinued at Cambridge.

An alternative method, developed for comparative assessment of cereal varieties in the glasshouse, used immature plants (Lowe, 1980). This 'walkabout method' established that four varieties of winter wheat differed consistently in suitability for *S. avenae*. Most significantly, the greatest difference and that least affected by variation between aphid cultures was between two varieties currently used in agriculture; Maris Huntsman was susceptible and Kador was resistant. In the same experiments (Lowe, 1980), vernalised plants showed the inter-varietal differences to a much greater extent than did unvernalised plants grown to a similar size. Some further results are discussed below.

METHODS

The walkabout method, described by Lowe (1980), was used for all the glasshouse experiments. Briefly, half-grown aphids were released onto plants at the early stem extension phase, Zadoks' code 30 to 32 (Tottman & Makepeace, 1979). The plants were randomised and grouped into blocks so that the aphids could walk freely from plant to plant, and the numbers of aphids on each plant were counted after they had matured and reproduced for about 7 days.

All plants were grown in 10.5 cm diameter pots of JI No. 2 compost, and in earlier experiments they received a drench of mixed nutrient solution and about 2 weeks later a dressing of granular NH_4NO_3 on each plant. In later

experiments each dressing was replaced by a standard 50 ml dose of solution, and nutrients were supplied at two rates. At the standard rate, similar to the preceding treatment, the mixed nutrient solution contained about 0.005g N, 0.003g P and 0.009g K per plant in addition to trace nutrients, and this was followed by 0.4 g NH_4NO_3. At the low rate, the plants received the mixed solution at half strength and only 0.1 g NH_4NO_3.

In field trials, aphid numbers on 50 ears per plot were recorded on a score system with classes 0, 1-2, 3-6, 7-14, 15-30, 31-60, 61-120, 121-250 aphids per ear. Mean scores (classes valued 0, 1, 2 ... 7) were calculated for each plot and these were treated as $\log_2 (n+1)$ for analysis and calculation of estimated (geometric) mean aphids per tiller.

RESULTS AND DISCUSSION

The effects of environmental variation on the walkabout method can now be assessed from results obtained over 18 months. The earlier experiments (Lowe, 1980) were mostly carried out in winter under artificial lighting. In summer, with higher temperatures and natural lights, experiments performed in May, July and September gave results similar to those from experiments done from November to February (Table 1). Similarly, in June 1979, the differences between these varieties were greater with vernalised than unvernalised plants, as in the earlier experiments.

Table 1 Mean numbers of S. avenae on four winter wheats in the glasshouse in winter and summer

Season	Maris Huntsman	Squarehead's Master	Anna Migliori	Kador	Std. Error ±
Winter	70.7	64.4	51.9	37.5	2.4
Summer	58.0	43.0	36.7	27.9	3.0

The low level of fertilizer treatment was tested in three experiments to determine any effect of nutrient levels on the expression of resistance. (Table 2). There were significantly more aphids on plants receiving the standard dose of nutrients which, since the treatments differed mainly in respect of nitrogen, was expected. The relative ranking of the four wheat varieties was not affected by the difference in fertilizer. It is concluded that even if variation in nutrient supply may reduce discrimination between resistant and susceptible plants through increased error variability, it is unlikely to lead to erroneous classification of varieties when they are assessed by the walkabout method.

Table 2 Mean numbers of S. avenae on winter wheat grown in the glasshouse under two levels of fertilizer supply (average of 3 experiments)

Variety	Fertilizer application Standard	Low level	Standard Error ±
Maris Huntsman	135.1	116.8	5.9
Squarehead's Master	93.8	90.5	
Anna Migliori	51.5	40.7	
Kador	41.0	35.9	
Std. Error ±	6.0	6.0	
Mean	80.4	67.3	2.7

In general, the walkabout method appears relatively insensitive to environmental variation within the range commonly experienced in glasshouses; and assessments of varieties are unlikely therefore to depend closely on environmental conditions.

Table 3 Mean numbers of S. avenae on five varieties of wheat

	Variety				
	Maris Huntsman	Kador	Timmo	Highbury	Std. Error
Experiment A	103.3	68.1	91.2	73.7	10.2
B	55.8	40.9	58.7	23.2	4.6
C	52.5	19.9	59.2	39.9	6.7
D	103.1	53.2	57.2	20.3	10.6
Mean	79.5	47.0	69.0	43.0	4.9

Walkabout experiments demonstrated resistance to S. avenae in the winter wheat, Kador. In other experiments (Table 3) resistance was found in the spring wheat Highbury, another variety currently recommended for use in Britain. The level of resistance appeared comparable to that of Kador, whereas Timmo, used as a control spring variety, was nearly as susceptible as Maris Huntsman. These observations agreed with differences in numbers of S. avenae observed approximately one month after ear emergence on spring wheat field trials in 1978 (Table 4). Maris Dove, which also had relatively few aphids in these trials, was partially resistant in preliminary experiments (Lowe, 1974).

The resistance detected by the walkabout method is likely to be of value in the field by reducing the number of S. avenae present at the time of ear emergence. Experience with glasshouse tests (Lowe, 1978) and knowledge of the aphids' normal population development (Watt, 1979, Vereijken, 1979) suggest that the most important effect of host differences on the final

Table 4 Estimated geometric mean numbers of S. avenae per ear on field trials, 20 July 1978

Trial	Timmo	Maris Dove	Highbury	Std. Error x ÷
Melbourn	4.9	0.8	1.4)	
Slatehall	2.0	0.9	0.7)	0.6
Boxworth	1.8	1.6	0.5)	
Mean	2.7	1.1	0.8	0.5

levels of ear infestation will be in determining the initial number of S. avenae that reach the ear, at least with the levels of resistance known at present. It is most encouraging from the practical point of view that the greatest expression of resistance so far recognised occurs in varieties in commercial use.

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SELECTION IN RADISH FOR RESISTANCE TO CABBAGE ROOT FLY (DELIA BRASSICAE)

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Introduction

The culinary radish (Raphanus sativus L.) is rendered unmarketable if damaged by cabbage root fly larvae (Delia brassicae (Wiedemann)). Most forms of radish grown in Europe reach maturity within 50 days from sowing, and insecticides used to control the pest may leave excessive residues at the time of harvest. There are no indications that immunity to the pest occurs in radish or its relatives, but differences in susceptibility occur between varieties (Ellis et al, 1976). The most effective control may therefore be by combining reduced insecticide doses with partially-resistant varieties (Thompson et al, 1979).

Attempts to select for resistance to egg-laying under laboratory or field conditions have been largely unsuccessful because the attractiveness of different radish families changed relative to each other with age (Crisp et al, 1977; Ellis et al, 1979).

This paper describes the results of selection for resistance in the field on the basis of root damage at the time of harvest.

Experiment

The plant population used in the experiment was derived by crossing two varieties, 'Tip Top' and 'Sparkler' (Asmer Seeds). The F_2 was grown in 1976 and six plants selected as being relatively free from attack were mass-pollinated, each producing a mother plant family, all six of which were grown as the F_3 in 1977, the F_4 in 1978, and the F_5 in 1979. The F_4 and F_5 were produced without selection for resistance by mass-pollinating within each family. In each year the parental varieties were also grown.

Significant differences were found between the parent varieties and between the six families for the degree of attack, which we interpret as evidence for genetic variability. However, there was no apparent response to selection in the F_2, and there was no correlation in the differences in damage to families between subsequent generations.

Discussion

A plausible explanation for these apparently anomalous results accrues from work on oviposition preferences of the fly (Ellis et al, 1976, 1979; Crisp et al, 1977). It has been found that the attractiveness of plants increased from the time of seedling emergence until they reached a marketable stage; that genetic differences existed such that the least preferred genotype at an early stage of growth could later be the most preferred; and that the environment could change the relative attractiveness of different genotypes.

For the experiment reported here it was found that the time of peak oviposition by the flies differed widely in relation to the times of sowing of the radishes in different years. If it is assumed that the maximum damage by larvae was the result of maximum oviposition, then the damage to the plants could be an effect of their relative attractiveness at the time of peak oviposition.

Comparing the six families and their F_2 parents grown from 1976 to 1979 it was found that the relative degree of larval damage changed and in some cases reversed as families were exposed to maximum oviposition at different times from sowing.

These results require confirmation, but they suggest a hypothesis that selection by the fly is disruptive because successive plant generations are of different ages when attacked. 'Natural' radish population, because of their outbreeding nature, may therefore maintain genetic polymorphisms for age-related attractiveness which allows the population to survive. Such polymorphisms may persist in modern cultivars, which have only recently had selection pressure by the fly reduced by the advent of insecticides. Indeed, it is probable that one or both of the parental varieties used here was genetically variable in this respect. The genotype of the plant population might remain in equilibrium if selection by the fly was dependent on the relative frequencies of plant phenotypes. It is also possible that interactions between the genetic and environmental components of such a polymorphism might also result in little change in allele frequency in each generation - a hypothesis discussed by Crisp et al (1977) when explaining similar results from laboratory experiments. It is unlikely that these hypotheses can be adequately tested until inbred lines are produced from this material, a study which is now under way (Ellis et al, 1980).

Consistent differences between the 'Tip Top' and 'Sparkler' parents in this experiment were similar to those recorded in previous work (Ellis et al, 1976; Crisp et al, 1977), and support the hypothesis that radish populations may reach equilibria at different levels.

These conclusions, although provisional, support the feasibility of breeding for reduced susceptibility, with the following recommendations:

1 The similarity in results from oviposition preference and larval damage at the marketable stage suggests that the former has a major effect on the latter, that the other possible components of resistance, antibiosis and tolerance, may be of less importance, and that selection could be effected under artificial conditions where oviposition could be assessed, such as those described by Ellis & Hardman (1975).

2 Selection for early attractiveness to the pest might give genotypes which are less susceptible as the marketable stage approaches. The fly could then be controlled by applications of insecticides at an early stage of growth, allowing residues to disappear before the plants became marketable.

3 Selection based on repeated exposure to the fly (necessarily under artificial conditions) might give genotypes with an overall reduction in attractiveness. The fly could then be controlled by reduced doses of insecticides.

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SELECTION IN THE CARROT CULTIVAR 'LONG CHANTENAY' FOR RESISTANCE TO CARROT FLY (PSILA ROSAE)

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Introduction

Resistance in carrots (Daucus carota L.) to carrot fly (Psila rosae (F.)) attack had received little attention until 1969 when a search was begun at Wellesbourne for sources of resistance to this pest (Ellis, Wheatley & Hardman, 1978). In a 1971/2 steckling experiment, 'Long Chantenay' was the least damaged amongst a group of 13 carrot cultivars screened against carrot fly (Ellis, Hardman, Jackson & Dowker, 1980). Although subsequent trials did not confirm this result it was decided to continue working with 'Long Chantenay' and investigate whether it was possible to breed for resistance by repeated selection within a commercially-acceptable carrot cultivar. In this report we describe the results of three generations of selection in 'Long Chantenay' for improved resistance.

Methods

All trials were conducted at Wellesbourne in a sandy loam (mineral) soil in a field which had been set aside specifically for carrot fly studies and in which a high population of the pest had been created. The cultural details and layout of all trials was similar. Carrots were grown as a maincrop, sown in May or early June in 4.5 m rows spaced 38 cm apart and at a target density of 110 plants/m^2. Three replicates of each seed stock were used, the stocks being randomised within each of three blocks and guard rows were sown at each end of the trial. The carrots were left in the ground as late as possible in the season to maximise carrot fly attack. The carrots from each row were kept separate following harvest, the roots being washed and graded for carrot fly damage. The grading technique and derivation of % undamaged and root damage indices were as described by Ellis, Wheatley & Hardman (1978). These derived variates were compared by analysis of variance.

Initial selection within 'Long Chantenay'

The roots harvested from the three 'Long Chantenay' plots in the 1971/2 trial of 13 carrot cultivars were graded into four categories according to the severity of carrot fly damage on the roots:- $<$5% damage, 5-25%, 26-50% and $>$ 50% damage. Roots representing these four damage grades were grown on for seeding.

Trial of first-generation selections

To investigate the heritability of carrot fly damage, half-sib families from cv. 'Long Chantenay' were compared in replicated trials in 1973. These families were derived from four parental groups representing each of the four damage grades. The results showed that there was a positive correlation between the amount of damage on parent roots and corresponding offspring families indicating that there had been a response to selection. Estimates of the heritability of damage levels were derived from this trial. One hundred roots were saved from each of the least damaged progenies and seeded.

Trial of second-generation selections

The second-generation selections were tested in two similar but separate trials in the same field at Wellesbourne in 1975. Each trial included two rows of the parent 'Long Chantenay', two rows of the first-generation selection and a single row of each of the 50 second-generation selections, the seed stocks being replicated twice. An analysis of % undamaged roots and root damage indices showed that, in both trials, carrot fly damage was significantly ($P = 0.05$) less severe on selections than on the parent 'Long Chantenay'. Although the average damage on all second-generation families was similar to that on the two first-generation families, certain second-generation selections were very much less damaged than the rest of the material tested. Roots from the most promising second-generation families in each of the two trials were saved for seeding to make a further cycle of selection.

Trial of third-generation selections

A comparison was made of carrot fly attack to seed stocks representing four generations of 'Long Chantenay' in 1977. The trial included the parent 'Long Chantenay', the two least-damaged first-generation selections, the five most promising second-generation selections and 20 third-generation selections. The parent 'Long Chantenay' was the most severely damaged of the seed stocks tested, and the level of damage on the first generation selections was greater than on those of the second generation. There was no difference between the second- and third-generation selections in the overall mean damage levels but certain third-generation selections were very much less damaged than the rest of the material tested, indicating that there had been a shift towards increased resistance in the most advanced families.

Conclusions

The results of these trials were encouraging and showed that it is possible to improve the resistance to carrot fly attack of a commercially-acceptable carrot cultivar by family selection. Screening trials over five years at Wellesbourne have indicated that 'Long Chantenay' is considerably more damaged by carrot fly than several other commercial cultivars (Ellis, *et al.*, 1980). If selection within these more-promising cultivars leads to a similar response to that observed in 'Long Chantenay' then it should be possible to develop partially-resistant cultivars for use in integrated programmes of carrot fly control.

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IMPROVING THE RESISTANCE OF CARROT AND ONION TO RESPECTIVELY CARROT FLY AND ONION FLY BY RECURRENT SELECTION

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Since the large-scale introduction of synthetic pesticides, insecticides have been used routinely in the Netherlands against the carrot fly (Psila rosae) in carrot and the onion fly (Delia antiqua) in onion.
The use of these insecticides also became common practice in selection fields, so that susceptible plants were no longer eradicated or recognized. These plants will have participated in the pollination and fertilization processes of these cross-fertilized crops, which may have caused a gradual shift to a lower resistance in current carrot and onion varieties and selections (DE PONTI & FRERIKS, 1980). If old varieties are maintained under an insecticide regime, the stability of these varieties, as far as resistance to insects is concerned, is questionable.
Because of the rapid decrease in germinability of carrot and onion seed, it is not possible to compare the resistance of old varieties and selections with that of recent ones. For the same reason, old varieties and selections cannot be used as possible reservoirs of resistance. Therefore resistance was traced between and within recent varieties and selections commercially available.

WORKING METHODS

About 200 carrot (Daucus carota) varieties and selections and about 70 accessions of wild Daucus species were over many years tested for resistance to the carrot fly. About 60 onion (Allium cepa) varieties and selections and about 60 accessions of the related salad onion (A. fistulosum) were tested for resistance to the onion fly.
The material was exposed to natural infestation in areas with abundant populations of the respective insects. It was sown in 3-8 replicate rows 1.5 m long, according to the amount of seed available. Whereas the carrots are assessed for incidence of attack only at harvest, the onions are assessed three times: after emergence of the seedlings (May), at the end of the first generation attack (July) and at harvest (September). At harvest the bulbs are classified as attacked and unattacked. The first two assessments are necessery, because early attacked plants desiccate and are undetectable at harvest. From those varieties, selections and accessions that were repeatedly least attacked, about 20 unattacked plants were selected from the most heavily attacked replicates, where the selection pressure had been strongest. The next year seed was grown of each selected plant by selfing and a year later the resulting inbred (I_1) lines were tested for resistance in comparison with the parental material. From the best 1_1 lines, individual plants were again selected and selfed and the I_2 lines were screened for resistance two years later.
Although continued line selection might result in a further increase in resistance, this selection will not be continued uninterruptedly because of the

decline in fitness, quality, yield, seed yield and seed quality from repeated inbreeding. Moreover in this way one might miss a chance to increase resistance by bringing together resistance genes from different varieties. Therefore selected I_2 lines should be intercrossed and the seed harvested from each individual plant or line. The families thus obtained should again be subjected to line selection for one or two generations. This recurrent selection can be repeated as long as progress is made. Selected I_2 lines of newly discovered resistant varieties can in each case be crossed with the developed resistant population. All resistances found will eventually be combined in one population with a maximum of resistance, from which future resistant varieties can be derived.

RESULTS AND DISCUSSION

1. Resistance to the carrot fly (Psila rosae)

In 1978, the first series of I_2 lines originating from 7 varieties were tested. Tests included 35 varieties, 107 I_1 lines and 62 I_2 lines. The year 1978 was suitable for selection, because incidence of the carrot fly on susceptible varieties was up to 90%.

Two generations of line selection have resulted in an increase of resistance of the selected lines over the parental generation with about 20%. Of the I_1 lines only a few (16 of 107) met the selection criterion. This indicates that many carrots selected in the parental material were not more resistant, but just escaped attack. Of the I_2 lines, a larger proportion (16 of 62) met the selection criterion. This shows that the selected I_1 lines possessed a higher resistance than the parental material. The effectiveness of line selection for culling of wrongly selected material is thus demonstrated (DE PONTI & FRERIKS, 1980).

Figure 1 shows that within some varieties resistance varies and can be improved. Improved I_2 lines were selected from the varieties 'Nantes', 'Pioneer', 'Vertou' and 'Signal'. These I_2 lines have been intercrossed and the resulting families will be tested in 1980 together with I_1 lines selected from the varieties 'Caramba', 'Kieler Rote', 'St. Valery' and 'Brugse Zware Halflange Stomp'. In 1979 the resistance of 'Clause's Sytan', 'Touchon', 'Carentan', 'Tip Top', 'Scarla', 'Regulus Imperial' and 'Flak Record' seemed promising and selected I_1 lines will be tested in 1981.

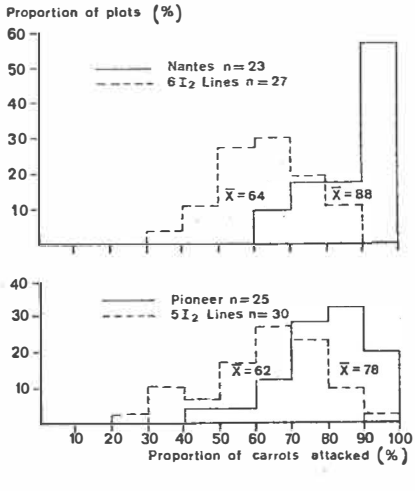

Fig. 1. Proportional frequency distributions of replicated plots of the varieties 'Nantes' and 'Pioneer' and of selected I_2 lines from them by incidence of carrot fly. n=number of plots; x=mean proportion (%) of carrots attacked (DE PONTI & FRERIKS, 1980)

MATERIAL	ORIGIN	PROPORTION OF PLANTS ATTACKED (%)
Hiberna	Czechoslovakia	54
Wolska	Poland	58
Yellow Makoi	Hungary	64
Rawska	Poland	64
Kastika	Hungary	65
Jumbo	Netherlands	90

Table 1. Proportion of attacked plants of some onion varieties as recorded in a field test in 1976. Values are averages of all plots for the whole growth season (after DE PONTI, 1980).

MATERIAL		PROPORTION OF PLANTS ATTACKED (%)
I_2 Welsh Onion	78651	21
I_2 " "	78643	29
I_2 " "	78650	46
F_3 (Welsh Onion x Jumbo)	78627	47
F_3 (" " " ")	78625	49
Welsh Onion		52
Jumbo		95

Table 2. Proportion of attacked plants of I_2 lines selected from the A. fistulosum variety 'Welsh Onion' and of F_3 lines from crosses between this variety and the onion variety 'Jumbo' in comparison with the parental varieties. The results were recorded in a field test in 1979 and are averages of all plots for the whole growth season. Vertical lines indicate the significance of the differences found.

MATERIAL	PROPORTION OF PLANTS ATTACKED (%)	RANGE OF I_1 LINES
I_1 Odessa	37	15 - 53 *
I_1 Stockholm	46	41 - 51 *
I_1 Brno	50	34 - 72 *
Welsh Onion	52	
I_1 Szeged	56	40 - 66
I_1 Riga	72	40 - 82 *
I_1 Berlin	78	52 - 78 *
Jumbo	95	

Table 3. Proportion of attacked plants of some I_1 lines from A. fistulosum accessions compared with the A. fistulosum variety 'Welsh onion' and the onion variety 'Jumbo' as recorded in a field test in 1979. Vertical lines indicate significant differences between accessions. The variation within accessions is also presented; significant differences are starred.

The resistance of the wild Daucus accessions, obtained from various botanical gardens and expeditions in the Netherlands and Israel, was surprisingly low. Tested in 1979 their resistance was on an average hardly higher than that of the cultivated carrots in the same test (incidence of carrot fly in the wild carrots 46% vs. 55% in the varieties). Although 7 accessions were selected, they will not be used for the present because of the many complications involved and because of the possible progess in the cultivated carrot.

2. Resistance to the onion fly (Delia antiqua)

In 1976, the susceptible onion varieties had up to 90% attacked plants. Partial resistance to the onion fly was found in some varieties, mainly of Eastern European origin (Table 1; DE PONTI, 1980). This might be explained either by some characters inherent to this group of varieties or by a later introduction and perhaps less frequent use of insecticides in this region, especially in selection fields. This could have caused maintenance of some level of natural resistance. I_1 lines of the selected varieties were tested in 1978, when selection was hindered by a low incidence of attack (susceptible control 35%). Nevertheless incidence in the best I_1 lines was about 10% less than in the parental varieties. I_2 lines are tested in 1980.

Already in the beginning of the project the A. fistulosum variety 'Welsh onion' was found to be more resistant than any A. cepa variety. Lineselection has resulted in some I_2 lines, which in a field test in 1979 proved to be significantly more resistant than the parental variety (Table 2).
Interspecific crosses between the varieties 'Welsh onion' and 'Jumbo' have yielded some F_3 lines with a resistance equal to that of 'Welsh onion' (Table 2). These hybrid lines are, however, still non-bulbing, so that further backcrosses are needed.
Within the species A. fistulosum the resistance to the onion fly appeared to be very variable. In a first screening in 1977 some accessions seemed to be more resistant than 'Welsh onion' (DE PONTI, 1980). In 1979, I_1 lines from these selected accessions also varied markedly in resistance, but some I_1 lines were significantly more resistant than 'Welsh onion' (Table 3).
Whether these I_2 lines will exceed the resistance of the selected I_2 lines of 'Welsh onion' (Table 3), will be tested in 1981. Some I_1 lines of the accessions Odessa and Brno are promising. The most resistant A. fistulosum lines will then be crossed with the most resistant A. cepa lines to obtain a maximal accumulation of resistance genes originating from the two species.
Until now the A. cepa and A. fistulosum material has been bred in alternate years, because the resistance of A. fistulosum seemed to be underestimated, when that species grew mixed with A. cepa. It seems that the onion flies attracted by A. cepa will readily attack A. fistulosum. This suggest that ovipositional non-preference or antixenosis during the orientation of the onion fly to the crop is a main cause of the resistance. This was also found by ELLIS et al. (1979) in greenhouse studies with A. cepa and A. fistulosum.

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CARROT RESISTANCE TO THE CARROT FLY - CONTRIBUTING FACTORS

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A number of workers have observed marked differences between carrot cultivars, *Daucus carota* (L.), in their ability to withstand attack by the carrot fly, *Psila rosae* (F.) (see Ellis et al., 1978). In an experiment where the levels of attack on eight carrot cultivars were observed in five European countries for two consecutive years, the cultivar "Clause's Original Sytan" was least attacked at most sites and cv. "Danvers Half Long 126" was generally most attacked. While the proportion of carrots attacked may be high in all material it is possible to discriminate for resistance between cultivars on the basis of a damage index based on the percentage surface area of root damaged (Ellis et al., 1978). Selecting material in this manner helps to identify potential sources of resistance, however, the underlying causes remain obscure. Causative factors which must be considered include those outlined in Painter's (1951) definition of resistance: 1) nonpreference behaviour of females during host selection and oviposition (factors associated with carrot foliage); 2) nonpreference behaviour of the larvae during orientation to the roots as affected by the availability of suitable attractants (Ryan and Guerin, in press), and 3) antibiosis which may affect initial biting and maintenance of feeding on the roots by the larvae. Factor 2 is probably the least interesting since in the field situation there is no choice between cultivars and the ability of first instar larvae to move through the soil is rather limited. Here we present evidence for antibiosis.

MATERIALS and METHODS

In 1977 eight cultivars (table) were hand-sawn in early May at approximately 40 seeds/metre row in 5 m rows spaced 40 cm apart. There were three replicates of each cultivar and these were fully randomized within three blocks. Two guard rows were sown at each end of the trial. On September 15 each carrot row was artificially infested by applying carrot fly eggs suspended in a 16% sugar solution at a rate of 170 eggs/metre row. A similar trial of these eight cultivars in 1978 was exposed to natural infestation only. In May 1979 four cultivars were sown in separate blocks consisting of three rows 5 m long (40 cm between rows). Each cultivar was screened off to prevent natural infestation. The cultivars observed were "Clause's Original Sytan" and "Danvers Half Long 126", representing the extremes of resistance and susceptibility, respectively, in 1977 and 1978, together with cvs.

"Tip-Top" and "Regulus Imperial" for comparative purposes. On July 18 each cultivar was thinned to an equal density of 13 plants/metre row. Carrot fly eggs (in 16% sugar solution) were applied to individual roots at mean of 27/plant. Carrots were harvested in December.

RESULTS and DISCUSSION

In 1977 the mean percentage unattacked carrots was 82 in the guard rows and 21 in the artificially infested rows. The major proportion of the attack in the latter can therefore be ascribed to the inoculation with eggs. The resultant percentage unattacked roots ranged from 37.6 on "Clause's Original Sytan" to 5.6 on "Danvers Half Long 126"; "Clause's Original Sytan" and "Glebe Rheinische" being significantly less damaged than "Danvers Half Long 126" ($P < 0.005$) (table). Similarly in 1979 when individual roots of four cultivars were infested artificially, the high percentage unattacked roots on "Tip-Top" (42.5) and "Clause's Original Sytan" (40.7) contrasted with "Danvers Half Long 126" (24.8) and "Regulus Imperial" (18.0). In 1978 the attack due to natural infestation ranged from 41.5% unattacked roots on "Vertou LD" to 19.4% on "St. Valéry". "Clause's Sytan Original and "Danvers Half Long 126" were again at the extremes of the scale (39.6% and 21.2% unattacked roots, respectively) but these differences were not significant.

TABLE Percentage undamaged roots on eight carrot cultivars following artificial and natural infestation by the carrot fly.

	Infestation		
	1977 - Artificial	1978 - Natural	1979 - Artificial
Glebe Rheinische	38.0	25.5	-
Clause's Original Sytan	37.6	39.6	40.7
Clause's Jaune Obtuse du Doubs	20.4	22.6	-
Long Chantenay	19.2	27.0	-
Vertou LD	15.4	41.5	-
Royal Chantenay Elite	14.9	25.7	-
St. Valéry	14.6	19.4	-
Danvers Half Long 126	5.6	21.2	24.8
L.S.D. (P 0.05)	17.37	N.S.	

As the criterion used was unattacked roots, the large and consistent differences observed between "Clause's Original Sytan" and "Danvers Half Long 126" suggest that early instar larvae establish themselves more easily on "Danvers Half Long 126". Differences between the cultivars could include the availability of side roots for first instar feeding or the presence of suitable host cues affecting preference/nonpreference behaviour. Larval establishment on the roots could also be affected by antibiotic factors such as tissue texture, the presence in the roots of toxins or feeding deterrents or the

production of defensive compounds at the site of invasion, or a combination of these factors. Such mechanisms have been shown to affect the susceptibility of members of other plant families to insect attack (Howe, 1949; Sutherland et al., 1975; Russell et al., 1978; Picman et al., 1978; Woodhead and Bernays, 1978). The contrasting results obtained for "Vertou LD", 15.4% unattacked roots when artificially infested in 1977 and 41.5% under conditions of natural infestation in 1978, suggests nonpreference for this cultivar by the female in the field.

We conclude that the use of the percentage root surface damaged may be a useful index in screening for resistance between large numbers of cultivars. However, it would be advantageous to discriminate between nonpreference resistance and antibiosis for breeding programmes. In this manner it may be possible to select for a number of effective factors which would bestow a broader and thereby more persistent basis to the resistance developed. Antibiotic mechanisms would appear to be of more value in the long term as nonpreference may not be adequate in monocultures exposed to large populations of the pest.

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CONSIDERATIONS SUR LA RESISTANCE PAR HYPERSENSIBILITE AU PUCERON CENDRE DU POMMIER DYSAPHIS PLANTAGINEA PASS.

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I - INTRODUCTION

La Station d'Arboriculture fruitière d'Angers a entrepris un programme d'amélioration de la résistance du pommier au Puceron cendré du pommier D. plantaginea. Ce programme utilise le matériel résistant découvert à East Malling : Malus robusta MAL 59 (BRIGGS, 1967). Cette résistance est contrôlée par un gène majeur dominant, le gène Smh (ALSTON et BRIGGS, 1970). Elle s'exerce à l'encontre des fondatrices et fondatrigeniae qui ne parviennent pas à édifier de colonies mais non à l'encontre des sexupares et des sexués. Elle est décelable dès le stade semis car les tissus des matériels résistants réagissent par nécrose, réaction assimilée à l'hypersensibilité, aux piqûres des fondatrices et des fondatrigeniae.

La valeur de la sélection engagée demeure à préciser, notamment en ce qui concerne la stabilité de la résistance qui n'a été étudiée que par rapport aux populations présentes à East Malling (ALSTON et al, 1974). Or, la virulence*(GILIOMME et al., 1968 ; SEN GUPTA et MILES, 1975 ; KEEP, 1977) et l'agressivité * (LOWE, 1974) ou la combinaison de ces deux caractères peuvent varier suivant les lignées d'une même espèce aphidienne. Il était donc indispensable d'élargir l'étude de la résistance conférée par le gène Smh à d'autres populations de D. plantaginea.

Le travail que nous présentons fait état des observations que nous avons effectuées, suivant deux techniques de contamination, avec diverses lignées de l'insecte. Par lignée, nous entendons la descendance parthénogénétique d'une fondatrice.

II - METHODOLOGIE

Matériel végétal - Les hybrides sont issus du croisement BOUET X (JONATHAN X Malus robusta 59/1), BOUET étant le parent femelle. La détection des semis résistants a été effectuée à Angers en mai 1976, puis 30 hybrides résistants et autant de sensibles ont été transférés à Bordeaux. Depuis lors, ces hybrides ont été maintenus en abri grillagé extérieur et cultivés d'abord en pots puis en fûts.

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* la signification accordée à ces termes est celle définie par VAN DER PLANCK, 1968.

Puceron - Fondatrigeniae apterae : Elles proviennent des populations d'Angers (une lignée) ou de Bordeaux (cinquante lignées). Elles ont été prélevées dans des élevages maintenus sur des semis de porte-greffe ou sur les hybrides sensibles et en voie de croissance active.

Oeufs d'hiver. En 1977, une femelle virginopare ailée a été isolée sur plantain Plantago lanceolata L. cultivé dans l'abri grillagé hébergeant les hybrides. Des sexués sont apparus dans la descendance de cette femelle et des oeufs d'hiver ont été déposés sur les hybrides sensibles ou résistants, librement colonisés par les femelles gynopares.

En 1978, les oeufs d'hiver proviennent des populations mises en place en 1977 et qui ont pratiqué l'alternance d'hôte.

Réalisation des essais.- Les essais réalisés à Bordeaux ont été effectués sous abri grillagé extérieur, dans des conditions très proches des conditions naturelles. Les essais réalisés à Angers ont été effectués en serre. Ces essais appartiennent à deux types : contaminations artificielles par des fondatrigeniae apterae et contaminations naturelles par les fondatrices nées des oeufs d'hiver déposés sur les hybrides cultivés dans l'abri grillagé.

* Contaminations artificielles

Tri initial du matériel. Il a été effectué suivant la méthodologie mise au point à East Malling : dépôt d'une larve sur une feuille apicale de chacun des jeunes semis puis, à 24 heures d'intervalle, contrôle de la présence des pucerons et éventuellement remplacement de ceux qui sont partis ; enfin notation des nécroses (ALSTON et BRIGGS, 1970).

Etude de la stabilité de la réponse des hybrides aux fondatrigeniae apterae . Ces essais ont été réalisés de mai à aout 1976. Tous les quinze jours, 5 pucerons ont été déposés sur une feuille apicale de trois hybrides différents, considérés, d'après le tri initial, comme résistants ou sensibles. Nous avons observé à 24 heures d'intervalle, la présence des insectes et la réaction nécrotique du végétal.

Etude de l'apparition des nécroses en fonction de la durée de séjour des pucerons sur les hybrides résistants. Pour ces essais réalisés de mai à juillet 1977, 10 pucerons étaient déposés sur une feuille apicale puis retirés après 1, 2, 4, 8, 24 ou 48 heures de séjour..

* Contaminations naturelles.

Au printemps 1978, nous avons noté l'évolution phénologique des hybrides, la présence de fondatrices et l'évolution de leur descendance, la nature et l'importance des dégâts subis par les hybrides. Ces observations ont été arrêtées le 25 mai en raison des risques de contamination secondaire, par les fondatrigeniae apterae pullulant sur les hybrides sensibles. Des observations identiques ont été effectuées au printemps 1979 mais elles ne concernent pas les matériels indiqués au tableau I, qui à cette époque n'étaient plus dans un abri grillagé.

III - RESULTATS

Contaminations artificielles

D'après l'ensemble des observations, les fondatrigeniae apterae ne parviennent pas à fonder de colonies sur les matériels porteurs du gène Smh. Elles quittent ces matériels après des séjours de durée très variable mais inférieurs à une semaine. Les organes végétatifs réagissent aux piqûres de l'insecte par des nécroses qui apparaissent de 24 à 96 heures après la contamination. Les nécroses peuvent n'être visibles qu'après le départ des pucerons. Ainsi, en 4 heures de séjour, les pucerons induisent parfois le processus nécrotique.

Contaminations naturelles (Tableau I)

Au début du printemps 1978, 13 hybrides porteurs du gène Smh et 5 hybrides dépourvus de ce gène hébergeaient de une à cinq larves de fondatrices. L'élimination des pucerons colonisant 9 hybrides porteurs du gène Smh est intervenue, à une exception près, pendant le développement larvaire des fondatrices. Par contre, les 4 hybrides restants ont été colonisés pendant tout le printemps. Quatre des cinq hybrides dépourvus du gène Smh ont également été colonisés pendant tout le printemps.

Il est apparu que 5 fondatrices sur 31 ont fondé des colonies permanentes sur les hybrides porteurs du gène Smh, 7 sur 13 sur les hybrides sensibles, dépourvus du gène Smh.

Les hybrides porteurs du gène Smh et ayant hébergé des colonies permanentes ont eu une croissance très perturbée car les pucerons se déplacent des organes colonisés vers les organes non colonisés. Leurs piqûres provoquent la nécrose et le dessèchement des feuilles, le ralentissement de la croissance des rameaux. Ces hybrides exercent une influence très défavorable sur l'insecte qui est de petite taille et peu fécond. Ainsi, le 25 mai, l'effectif des pucerons colonisant les hybrides porteurs du gène Smh variait de 10 à 30 individus alors que sur les hybrides dépourvus de ce gène, il était de plusieurs centaines d'individus.

Des résultats analogues ont été observés en 1979 avec les deux hybrides porteurs du gène Smh, qui ont été colonisés pendant tout le printemps.

Les hybrides présentent des différences importantes en ce qui concerne leur précocité de débourrement et la croissance de leur feuillage. Les larves de fondatrices ont été éliminées d'autant plus rapidement que ces caractères sont tardifs.

IV - DISCUSSION ET CONCLUSION -

Lors des essais réalisés suivant la technique de contamination naturelle, certaines lignées de D. plantaginea se sont maintenues sur certains hybrides porteurs du gène Smh. Ces observations vont à l'encontre des données publiées (ALSTON et al., 1974). Ces hybrides présentent, bien que colonisés, une résistance de haut niveau car l'insecte ne prolifère pas. Malheureusement, les organes végétatifs subissent, par suite de la réaction nécrotique associée à la présence du gène Smh, des dégats importants. La signification de ces observations ne peut être actuellement précisée car trois hypothèses peuvent être formulées : 1 - Variabilité des hybrides. Dans cette hypothèse, un ou plusieurs gènes mineurs compléteraient l'action du gène Smh et la transmission héréditaire des gènes serait indépendante. Ainsi sur 13 hybrides présentant le gène Smh; 4 seraient dépourvus de gène (s) mineur(s). 2 - Variabilité de l'insecte. Dans cette hypothèse, la fréquence de(s) gène(s) permettant au puceron de coloniser les hybrides porteurs du gène Smh serait plus importante dans les populations de Bordeaux que dans celles d'East Malling. 3 - Influence des conditions expérimentales. L'on peut supposer, par analogie avec l'influence des blessures sur la résistance du pommier au puceron lanigère (SEN GUPTA et MILES, 1975) que nos conditions de culture ont modifié la physiologie de certains hybrides vers une plus grande sensibilité.

La technique de contamination naturelle pourrait être plus discriminante que celle par les fondatrigeniae apterae. Cependant, l'hypothèse n'est pas vérifiée puisque les observations concernent des lignées différentes de D. plantaginea.

TABLEAU I - CONTAMINATIONS NATURELLES SOUS ABRI GRILLAGE
Evolution des lignées de D. plantaginea Pass.

Date des observations	Hybrides porteurs du gène Smh														Hybrides dépourvus du gène Smh				
	* a			b	c									d	a	c			d
	** 1	26	30	29	2	10	12	14	18	21	23	27		6	15	5	7	19	12
10.4.78	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+
18.4.78	-	-	-	+	+	+	+	+	-	+	+	+		+	-	+	+	+	+
3.5.78				-	-	+	+	+		-	-	-		+		+	+	+	+
25.5.78						+	+	+						+		+	+	+	+

* La phénologie est appréciée par la notation du 18.4 1978, avec
a - stade bourgeon fermé
b - stade bourgeon ouvert
c - les premières feuilles sont apparues
d - les premiers rameaux feuillés sont apparus.

** numéro de référence des hybrides

\+ présence de fondatrice(s) et, ou, des fondatrigeniae apterae
\- absence de fondatrice et, ou, des fondatrigeniae apterae

L'apparition de nécroses après le départ des fondatrigeniae apterae des hybrides porteurs du gène Smh indique que le puceron est indispensable à l'induction du processus nécrotique mais non à son développement ultérieur. Des observations identiques ont été effectuées avec une variété de pêcher résistante à Myzus persicae Sulz. (MASSONIE et MAISON, 1979)

Nous confirmons l'intérêt du caractère tardif de l'apparition du feuillage (BRIGGS et ALSTON, 1967) car les hybrides présentant ce caractère ont éliminé le puceron pendant le premier ou le second stade larvaire de la fondatrice.

En conclusion, les observations attirent l'attention sur les inconvénients éventuels d'une résistance associée à une réaction nécrotique lorsque le niveau de cette résistance ne permet pas l'élimination de tous les pucerons dès le stade fondatrice. Néanmoins, la signification des observations et l'importance réelle des dégâts commis par les insectes qui ne seraient pas éliminés demeurent à préciser, en particulier au niveau de l'ovaire de la fleur car les piqûres effectuées au niveau de cet organe provoquent des déformations du fruit qui constituent l'essentiel du dégât de D. plantaginea (LECLANT, 1974).

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SOME TECHNIQUES FOR DETERMINING RESISTANCE TO ERIOSOMA LANIGERUM AND DYSAPHIS PLANTAGINEA IN APPLE

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Host resistance to Eriosoma lanigerum

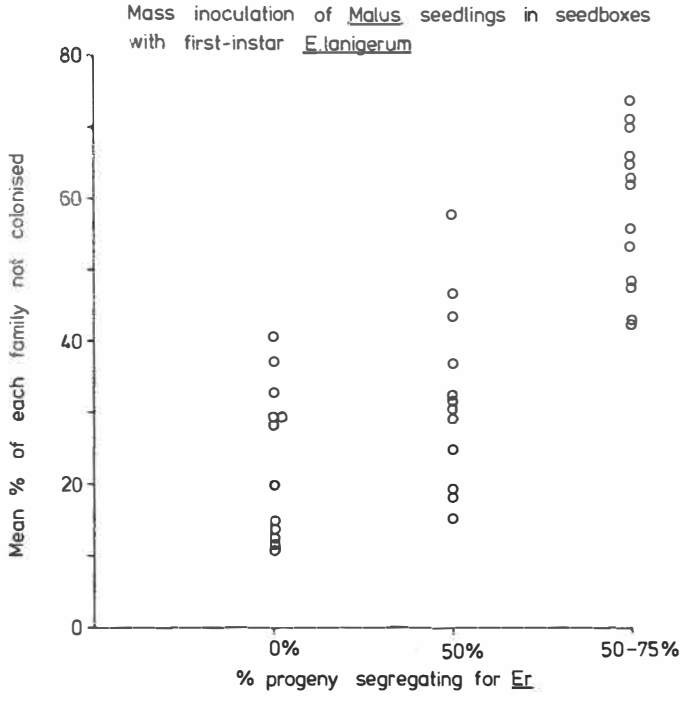
The woolly aphid, Eriosoma lanigerum (Hsmnn.) is a widespread pest colonising both roots and aerial parts of apple. Characteristic galls may be produced which can subsequently rupture and provide entry for diseases such as Gloeosporium spp. In Britain the aphid occurs sporadically in orchards and does not breed on roots although it may occasionally attack the collar or exposed roots. Infestations above ground can be controlled by spraying and in some areas of the world, by the parasite Aphelinus mali (Hald.) but root colonies are protected by their cryptic habitat and are a source of reinfestation. The highly resistant Northern Spy is extensively used as a donor of resistance. This was thought to be controlled by a single major gene Er (Knight, Briggs, Massee & Tydeman, 1962) but modifier genes are now thought to contribute (Cummins & Aldwinckle, 1974) and vary the expression of Er-conferred resistance. Although a few instances of resistance breakdown in Northern Spy derivatives have been reported, the resistance remains important (Knight & Alston, 1972).

For some years at East Malling apples were screened by mass-inoculating young seedlings in seedboxes, each holding about fifty plants, using first-instar larvae. This was a convenient method of processing large numbers of seedlings in relatively little glasshouse space. Cox x Worcester stock plants bearing aphid cultures were gently tapped while being passed horizontally over the seedboxes; first-instar larvae (the mobile, dispersive stage of the aphid) were readily detached. This was done on each of three consecutive days to obtain complete coverage and constituted a 'single' inoculation. Susceptible seedlings were identified about three weeks later, by the wool produced by active colonies.

Although convenient, the method was inefficient since many individuals in fully susceptible control families escaped colonisation; and also inconsistent since the proportions of such individuals differed among

families. Susceptible and resistant families were sometimes not clearly differentiated (Fig. 1).

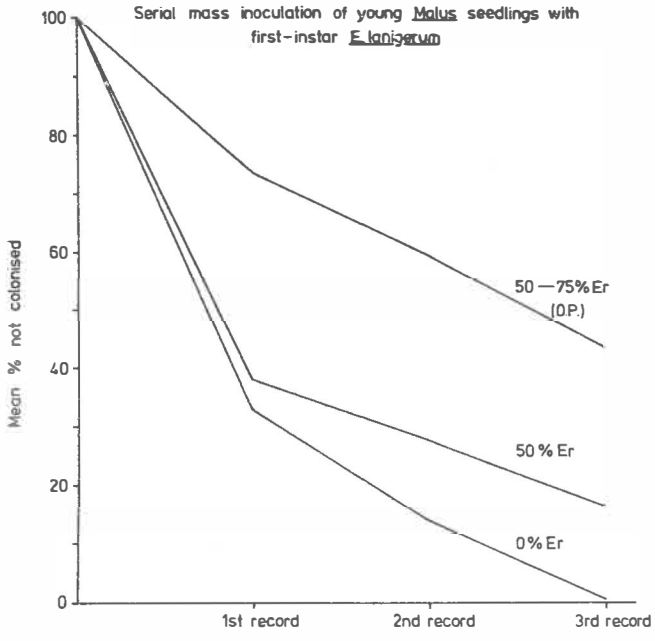
Fig. 1.



To approximate maximum efficiency (100% of susceptible controls colonised) it was necessary to apply a 'single' mass inoculation three times. Colonised seedlings were removed each time and plants were transferred to 7.5 cm pots before the second inoculation. However, many seedlings expected to carry the Er gene were also colonised leaving seedlings with presumably higher levels of resistance free from aphids (Fig. 2).

Mass inoculating young seedlings was destructive, since heavily-colonised plants sometimes died or became less suitable for the further tests often required in breeding programmes. To prevent this premature loss of genetic information, rooted hardwood cuttings from selections grown in the field for several years were used as subject material. Each plant was inoculated in the glasshouse with ten first-instar larvae placed on young leaves at the growing tip. This clonally

Fig. 2.



propagated material allowed replication of genotypes and ten plants per stock plus fifteeen of each of the rootstocks M.16 (susceptible) and MM.106 (resistant) were compared at each screening.

Aphid numbers can be estimated by a number of methods but for regular screening an easily-obtained index of colonisation is desirable. A convenient measure was found to be the mean colony-length per genotype. Where colonies did not encircle the shoot, rough corrections were applied to the nominal colony-length but no account was taken of possible variations in colony cross-section or aphid density. However, although only an approximate index, rootstocks could be quickly ranked according to the degree of infestation, and this order was identical to that achieved by estimating aphid numbers volumetrically.

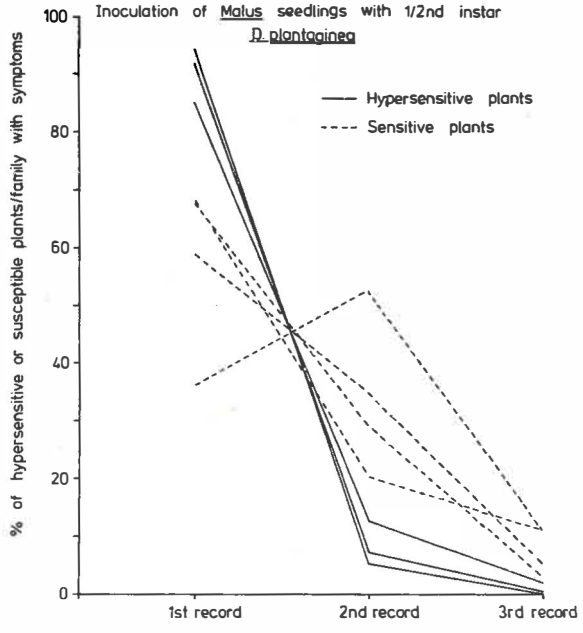
Host resistance to Dysaphis plantaginea

Dysaphis plantaginea (Pass.), the rosy apple aphid, is the most serious aphid pest on apple in this country. Infested leaves become severely curled and may turn yellow, shoots remain short and twisted, and fruits on infested trusses are small, distorted and ripen prematurely.

Feeding can induce pronounced stem curvature and leaf rolling within twenty-four hours of infestation (Forrest & Dixon, 1975). In hypersensitive plants necrotic areas are rapidly produced on the leaves in response to feeding by this aphid. Hypersensitivity in the Malus robusta derivative MAL59/9 is controlled by a single dominant gene, Sm_h (Alston & Briggs, 1970). The effectiveness of this gene in conferring host resistance was demonstrated at East Malling in 1974 during a heavy field infestation of the aphid. On an unsprayed plot, one out of 470 seedlings preselected in the glasshouse for hypersensitivity showed slight attack while 79 out of 156 seedlings without Sm_h were severely affected.

Seedlings were screened in 7.5 cm pots in the glasshouse by inoculating each plant with a first-or second-instar larva placed on a young, expanded leaf. Plants were recorded several days or a week later. Identification was efficient for hypersensitive, less so for susceptible, plants but most were identified within two inoculations (Fig. 3). An average of 31% (mainly susceptible) required a second inoculation, 5% a third inoculation and only 0.1% a fourth. The hypersensitive response in young seedlings was often sufficient to deform or kill the growing point but plants generally recovered.

Fig.3.



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BREEDING FOR RESISTANCE TO PESTS OF RUBUS AND RIBES CROPS AT EAST MALLING

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Various stratagems are being used at East Malling to enable a team of four, with occasional help from colleagues in other departments and from students, to cope with breeding for resistance to the major pests and diseases of three crop plants - raspberries (some ten organisms) and black currants and gooseberries (six organisms each). The overall strategy has been gradually to introduce into the breeding pool one or, preferably, more donors of resistance to all the pests and diseases of interest. Some donors already in use for other characteristics were found to carry useful resistances. Plants were deliberately selected as resistance donors only if they could provide additional useful attributes. It was accepted that the rate of progress in transferring the various resistances was likely to vary considerably, with maximum effort being devoted to the organisms that were the most damaging or the most difficult to control. To some extent, resistances to the less important pests and diseases would be left to 'float' in the population, being picked up and worked on as opportunity offered.

BREEDING STRATAGEMS

Use of strong resistance

As far as possible donors of really strong resistances are selected. Such resistances often prove to be under major gene control and this means that selection techniques either in the glasshouse or in the field can be relatively quick and simple. It also means progeny sizes can be kept low since a high proportion of the seedlings will be resistant. This saves screening time and also avoids the need for huge progenies when combining resistances to several different organisms.

The large raspberry aphid Amphorophora idaei (Börn.) (formerly A. rubi (Kalt.)) is in many ways an ideal pest to deal with, as there are numerous sources of dominant, monogenic resistance (Keep et al., 1970) and it is a very active creature which rapidly removes itself from resistant plants. Some 6000 young seedlings a year are screened for resistance in the glasshouse (Parker, 1977). Most of our raspberry material now carries one or more genes for resistance to A. idaei and since 1970 four resistant varieties have been introduced; Malling Delight and Malling Orion are both heterozygous for the gene A_1 and are therefore resistant to the most common British biotype, strain 1, and also to the rare strain 3, while 'Malling' Leo and 'Malling' Joy are heterozygous for both A_{10} and A_1 and are resistant to all four British strains of the aphid.

Dominant monogenic resistance is also being employed against the black currant gall mite, Cecidophyopsis ribis (Westw.). All

black currant varieties commonly grown in Britain are susceptible to the mite which is very prevalent, and its control involves the use of a rather toxic pesticide, Endosulfan. The gene Ce from the gooseberry provides very strong resistance to this pest and has been transferred by backcrossing into black currants (Knight et al., 1974), three of which are now on trial at the National Fruit Trials, Brogdale, Kent. These three selections are third or fourth backcrosses from gooseberry. Planting into an infection plot is an effective and labour saving method of screening for resistance. One inspection per year in late winter for four years, to note and discard galled seedlings is all that is needed (Knight, 1977).

Virus avoidance through vector resistance

The raspberry aphid and the gall mite are both virus vectors. The aphid of itself does little harm and colonies can build up without obvious symptoms. It is, however, the vector of four viruses, raspberry leaf spot, raspberry leaf mottle, black raspberry necrosis and rubus yellow net, which alone or in combination can be very damaging to sensitive varieties. By breeding for resistance to a single vector, we can impart avoidance of four viruses, so saving time, labour and land.

The black currant gall mite is highly damaging both of itself and as the sole vector of reversion virus, to which all our present day black currants are more or less susceptible. Resistance to the vector has proved highly effective in preventing or delaying virus infection (Knight, 1980).

'Pantechnicon' donors

In both Rubus and Ribes breeding, several donors are providing resistances to a combination of pests and diseases. The Asiatic Rubus coreanus Miq. is being used primarily as donor of strong resistance to four fungal diseases of the cane and to mildew (Keep et al., 1977), but it is also supplying the gene A_{cor1} for resistance to all four British races of A. idaei (Keep et al., 1970) and it is fairly resistant to the raspberry beetle, Byturus tomentosus (Deg.) (Briggs, 1972). In the F_1 and BC_1 it was possible to select aphid resistant plants that were highly resistant to all four cane diseases and to mildew. In BC_2, resistant plants with fairly good fruit quality were selected for further backcrossing.

Potentially even more versatile as donors in Ribes breeding are the North American flowering currant, Ribes sanguineum Pursh., and the very similar R. glutinosum Benth. R. sanguineum is being used primarily as donor of spinelessness in gooseberry breeding, and R. glutinosum as donor of a good erect plant habit, many-flowered inflorescences and disease resistance in black currant breeding. Accessions of both species are highly resistant to at least seven pests of black currant and gooseberry, including the currant-sowthistle aphid Hyperomyzus lactucae (L.), and three aphid pests of gooseberry - H. pallidus (H.R.L.), Nasonovia ribisnigri (Mosley), and Aphis grossulariae (Kltb.). Resistance to all four aphids is recessive and as forecast in 1976 (Keep, 1977) transference of resistance has been hindered by difficulties in selection within inbred progenies lacking vigour.

In attempting to transfer into black currants resistance to the currant-sowthistle aphid from R. glutinosum, inbred backcross progenies were raised. These showed marked inbreeding depression and apparent field resistance to the aphid could have been due to the abnormally slow growth and generally poor condition of the seedlings rather than to inherent resistance. Many of the plants that were not infested or only slightly infested in the field died before flowering. Those that survived and flowered were mostly male sterile. A decision to abandon active work on R. glutinosum derivatives, at least temporarily, was reinforced by the discovery of resistance in vigorous trispecific hybrids which included both the Siberian R. dikuscha Fisch. and the N. American R. bracteosum Dougl. in their ancestry. Progenies of this origin appeared to segregate for field resistance to H. lactucae, some plants remaining completely free from symptoms of infection for three years in succession. Replicated tests on clonal material in the insectary (Lyth, unpublished) confirmed that plants showing field resistance were poor hosts under insectary conditions.

Although work on aphid resistance in early backcross derivatives of R. glutinosum and R. sanguineum has not been very successful, it is possible that when later backcross generations are intercrossed, the recessive resistances carried by these species will prove to have been maintained in the population, will surface in vigorous progenies, and will be picked up during routine field selection.

Field screening for resistance

Although preselection for resistance in young seedlings in the insectary has many advantages, for some pests field selection may be more appropriate. In breeding for resistance to the raspberry beetle, after initial tests by a trained entomologist to identify resistance donors, subsequent work has been based mainly on field screening by non-specialist temporary workers.

The raspberry beetle is an important pest of raspberry but because it is easily controlled by sprays, we do not give it top priority in resistance breeding. The Japanese wineberry, R. phoenicolasius, Maxim. and another Far Eastern raspberry species, R. kuntzeanus Hemsl. were reported as highly resistant to the beetle by Rietsema (1936). To determine if other Asiatic species already in use in the raspberry breeding programme might also serve as donors of resistance, sleeving tests on field plants were made by Briggs (1971, 1972). These tests showed that both species, R. crataegifolius Bge. and R. coreanus, their F_1's with raspberry, and some BC_1 and BC_2 derivatives carried useful levels of resistance. Subsequent work has been based mainly on boosting field populations of beetles by introducing adults collected elsewhere, and recording natural damage caused by beetle larvae to the receptacles and fruits. In this way, resistant individuals have been indentified in BC_3 and these have been used as parents in further backcrossing.

In sum, by taking a sometimes opportunist and slightly empirical approach, a small team is able to carry forward resistance breeding against a wide range of pests and diseases. By working

on all the major pests and diseases of the crop plant, the potential for producing varieties needing far fewer sprays or even none at all has been established.

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PEST RESISTANCE IN APPLE BREEDING

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INTRODUCTION

Pest and disease control in apple depends on a complex spray programme. Most insecticidal spray regimes combat two or more pests; therefore breeding for resistance to one pest is not likely alone to result in the removal of a particular spray application. Other factors must be considered in breeding for resistance:- the apple is clonally propagated and highly heterozygous, and has in addition a long juvenile phase prior to cropping (4-7 years on M.27 rootstock at East Malling). Such factors emphasise the use of strong, simply inherited types of resistance. Attempts to incorporate low levels of 'difficult-to-handle-polygenic-resistance' could drastically handicap breeding progress since pest resistance is only one of many important factors in a complex breeding programme.
The incorporation of resistance to all pests is not essential since some can be effectively controlled by predators and other components of integrated control schemes.

SOURCES OF RESISTANCE

Extensive surveys for pest resistance among Malus species at East Malling and in over 2,000 cultivars at the National Fruit Trials (Briggs, 1967; Briggs and Alston, 1967; 1969) together with a literature survey (Knight, 1963) revealed sources of resistance or avoidance to the principal English apple pests.

Woolly aphid, Eriosoma lanigerum

The 170-year-old N. American cultivar Northern Spy has long been acknowledged as very resistant. Resistant rootstocks derived from Northern Spy were selected at East Malling (Crane et al., 1936) and distributed throughout the world as the MM series (Preston, 1966). This resistance is controlled by a single dominant gene, Er (Knight et al., 1962). Selection for resistance can be effectively carried out in the greenhouse (Knight et al., 1962; Lyth, 1980).
There are three reports of E. lanigerum biotypes infesting MM rootstocks, in S. Africa (Giliomee et al., 1968), North Carolina (Rock and Zeiger, 1974) and S. Australia (Sen Gupta and Miles, 1975). So far the MM rootstocks have remained free from attack in the important apple growing regions of W. Europe and N. America. Alternative sources of resistance are known (Knight et al., 1962; Briggs, 1973; Cummins et al., 1980) one of which, Robusta 5, has also been found to be resistant to the N. Carolina biotype (Cummins et al., 1980). But despite the susceptibility of its resistance gene to some biotypes, Northern Spy remains the most useful woolly aphid resistant parent for English conditions, since it also carries genes for resistance to Dysaphis devecta (Alston and Briggs, 1977) and Phytophthora cactorum (Alston, 1970) and transmits good fruit size, good quality and late maturity to its derivatives.

Rosy leaf-curling aphid, Dysaphis devecta

Several cultivars are resistant to the common biotype (Alston and Briggs, 1968). Greenhouse selection on 2-month seedlings is rapid; susceptible seedlings can be discarded five days after inoculation.

Three biotypes have been delineated (Alston and Briggs, 1977), two are rare, but resistance to all three can be provided by combining the gene Sd_1 from Cox's Orange Pippin with Sd_3 from M. robusta MAL59/9. Cox is the principal English commercial cultivar and MAL59/9 one of the most promising sources of high resistance to mildew, Podosphaera leucotricha (Alston, 1977).

Rosy apple aphid, Dysaphis plantaginea

This is the most serious pest in English apple orchards. Severe infestations prevent growth of both fruit and shoots. Several Malus species are resistant (Briggs, 1967). The most useful source, hypersensitivity determined by a single dominant gene, Sm_h comes from M. robusta MAL59/9 (Alston and Briggs, 1970). Pre-selection of 2-month-old seedlings is practised in the greenhouse; hypersensitive seedlings are selected five days after inoculation. The success of greenhouse screening was well demonstrated in the field following a severe natural infestation of the pest (Alston and Lyth, 1975).

Sawfly, Hoplocampa testudinea

Briggs (1967) found a high level of resistance in a clone of the small-fruited species M. zumi, MAL68/5 which is another promising source of high resistance to mildew, P. leucotricha (Alston, 1977). At present resistance selection cannot be carried out until fruiting occurs.

Fruit tree red spider mite, Panonychus ulmi

Indications of high resistance were found in M. prattii (Briggs, 1973). In greenhouse tests this species transmitted resistance to leaf bronzing although most bronze resistant plants supported moderate mite populations (Alston and Briggs, unpublished).

Codling moth, Laspeyresia pomonella

Varying levels of resistance have been reported (Cutright and Morrison, 1935; Goonewardene et al., 1975). Laboratory selection has been tried but so far selection in established plantations appears most effective (Sarasola, 1976). Such selection is essentially long term depending not only on establishing fruiting plantations but also on the build-up of a sufficiently large population of the pest to ensure its even dispersal in the plantation.

Late flowering

Late flowering varieties avoid damage from apple-grass aphid, Rhopalosiphum insertum, apple sucker, Psylla mali, rosy apple aphid, Dysaphis plantaginea and various caterpillars (Briggs and Alston, 1967). The incorporation of late flowering should provide a more effective means of controlling spring pests than searching for and transferring direct genetic resistance to individual pests. Early selection for late flowering is possible in the nursery one year after germination since leafing out in juvenile seedlings is correlated with flowering time in mature trees (Tydeman, 1964).

Mildew resistance

Most mildew fungicides are toxic to the natural predators of the fruit tree red spider mite, Panonychus ulmi. Although new fungicides are available which are not toxic to predators there is some doubt about their effect on fruit skin finish. For these reasons it seems reasonable to consider mildew, Podosphaera leucotricha resistance as a component of all round pest control, particularly since the prospects of breeding specifically for red spider mite resistance are not promising. At East Malling strong resistance to mildew is being transferred from the small fruited species M. robusta MAL59/9 and M. zumi MAL68/1 (Alston, 1977). After two backcrosses to cultivated apples, selections with commercial fruit size and yield have been produced. Some of the M. robusta derivatives are also resistant to the rosy apple aphid, D. plantaginea. Greenhouse selection is possible one month after germination (Alston and Bates, 1979). After 14 years this resistance is still effective on unsprayed plots.

BREEDING PRIORITIES

It is not practicable to combine all the available resistances in one or even two crosses since due attention has to be given to the main aims of the apple breeding programme, the production of high yielding quality apple cultivars with good fruit size, appearance and flavour. Previously decisions were made in the context of the recommended spray programme with the elimination of all sprays as the prime aim (Alston, 1971; Knight and Alston, 1974). Such an aim is essentially long-term. Present priorities have been chosen after considering eight principles:-

1. Economic importance of the pest
2. Type of resistance available (strong simply inherited resistance preferred)
3. Selection efficiency (seedling stage selection preferred)
4. Ease of transference from donor to commercial type
5. The role of plant resistance in integrated pest control
6. Alternative methods of pest control (predators, etc.)
7. Effectiveness of current spray programme
8. Cost of sprays

Woolly aphid, E. lanigerum and rosy leaf curling aphid, D. devecta are not economically important pests of scion cultivars.
Fruit tree red spider mite, P. ulmi can be controlled by predators.
Some control of codling moth, L. pomonella can be achieved through predators and improved orchard hygiene directed towards the elimination of over wintering sites. Any necessary spray applications can be kept to a minimum by using pheromone traps to monitor populations.
Late-flowering can provide a means of controlling the spring pests of the apple (although only one such pest, rosy apple aphid, D. plantaginea is of serious economic importance). The avoidance of pest damage provided by late-flowering could be sufficient to eliminate the spring insecticide application. The absence of spring insecticides would allow a build-up of the natural population of predators of the fruit tree red spider mite.

However, there are two possible drawbacks in connection with late flowering. Firstly, there is an increased chance of fireblight, Erwinia amylovora infection in the flowers of late-flowering cultivars. Secondly, most late-flowering cultivars are late-flowering by virtue of an inherently long winter chilling requirement, which can result in prolonged and sporadic blossom periods following mild winters.

Rosy apple aphid can be most effectively controlled by hypersensitivity from M. robusta MAL59/9 (also a donor of strong mildew P. leucotricha resistance which can permit improved predator control of fruit tree red spider mite by the elimination of mildew fungicides).

Only breeding for sawfly, H. testudinea resistance remains somewhat of a problem since the prolonged nature of the resistance selection procedure precludes this from becoming a major breeding objective.

BREEDING POLICY

As a result of the foregoing considerations the East Malling breeding programme emphasises the incorporation of strong mildew resistance and hypersensitivity to rosy apple aphid into commercial apples. Parental selections have been produced at East Malling which carry both these characteristics, together with commercial fruit size and yield; some also incorporate late-flowering.

Where possible, major resistance genes are combined with polygenes for resistance - as for example with mildew resistance (Alston, 1977). In this way the crop will have some safeguard against a new gene specific race of a pathogen, and will retain at least a moderate level of resistance. The real value of the pest and disease resistance which is being introduced into commercial apples cannot be fully assessed until resistant cultivars are widely grown. At present resistance should be regarded as a very valuable bonus in cultivars bred primarily for improved horticultural, market and consumer factors. It is highly desirable in a long-term crop like the apple, that new cultivars should not be vulnerable to new races of pathogens. However, new apple cultivars should possess improved features for which they will be maintained in cultivation whatever their response to pathogens. In the event of a breakdown of resistance it is intended that although the pathogen would have to be controlled by other methods growers and consumers could still benefit from a commercially improved variety.

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SCREENING BLACK CURRANTS FOR RESISTANCE TO THE GALL MITE *CECIDOPHYOPSIS RIBIS* (WESTW.)

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INTRODUCTION

The gall mite is a serious pest to black currants (*Ribes nigrum* L.) in causing direct reduction in crop and as the only known vector of reversion virus. Resistance originating in gooseberry (*R. grossularia* L.), due to a single, dominant gene, *Ce*, is being used in the black currant breeding programme at East Malling Research Station (Knight *et al.*, 1974). The black currant progenies in this paper segregated for this gene.

FIELD SCREENING FOR RESISTANCE

Gall mite response is assessed by exposing test seedlings to large numbers of mites in an infestation plot. Every fourth row is planted in advance with black currants heavily infested with mites. Later, three rows of seedlings are planted between these infector rows. The seedling rows are planted 2 m apart but the plants are only 0.25 m apart within the row. The breeding programme generates up to 4,000 seedlings per year to be screened for gall mite response and at this close spacing not more than a quarter of a hectare is required per year.
Mites emerge from galled buds from early April until late June, with the peak emergence in May (Smith, 1960). They migrate to developing axillary buds and penetrate by crawling inwards towards the bud centre. Mites are very vulnerable to desiccation during their free living phase but once inside a bud they are protected from predators and contact acaricides such as sulphur and lime sulphur.
By mid-winter multiplication within an infested bud has resulted in a typically swollen and round 'big bud'. On dormant plants these galled buds are easily recorded and seedlings with one or more galled buds are generally culled. It takes 4 years to reliably select the gall mite resistant seedlings but time spent recording is short and during the less busy dormant season.

GLASSHOUSE INOCULATION

A glasshouse test that enabled the mite susceptible seedlings to be identified and discarded prior to planting would be extremely valuable.
In 1972 and 1973 seedlings segregating for gall mite resistance were germinated in the autumn and inoculated with mites when young seedlings were still in the seed tray (Knight, 1977). In 1972 and 1973 5% and 10% respectively developed abnormal leaves which resembled leaf symptoms induced by mite feeding (Thresh, 1963).

Seed from four crosses made in 1975 was divided into two lots per cross. One lot was germinated in autumn 1975 and the second lot in spring 1976. At both times the seedlings were inoculated soon after germination. Ten percent displayed leaf symptoms following the autumn inoculation, compared with 70% following the spring inoculation. In 1977 all seedlings segregating for Ce were inoculated in the spring and 28% displayed leaf symptoms. However leaf symptoms in young seedlings in the glasshouse are not a reliable guide to gall mite susceptibility in the field because seedlings showing leaf symptoms do not invariably develop galled buds in the field (Table 1).

Table 1

Percentage of plants developing galled buds in the field after 2 mite dispersals, following seedling inoculation in the glasshouse

Date inoculated	Year planted	No. of seedlings planted	% galled seedlings in the field: Leaf symptoms in the Glasshouse	% galled seedlings in the field: Normal in the Glasshouse
Autumn 1972	1973	265	46	46
Autumn 1973	1974	2790	50	41
Autumn 1975 and Spring 1976	1976	721	45	36
Spring 1977	1977	694	73	37
	Total	3470	Mean 57	40

Taking the results of the planting from 1973 to 1977 together 57% of plants which had previously displayed leaf symptoms were galled compared with 40% for the symptomless plants, after two natural mite dispersals. However 43% of seedlings which previously displayed leaf symptoms were free from galls in the field.

Seedling inoculation is a fairly quick method of exposing seedlings to additional mites and can be done early in the spring in the glasshouse, before general field records take precedence.

Seedlings planted in 1977 and 1978 have not had their full four years' exposure in the field but the figures to date suggest that the rate of galling in the field is not increased following glasshouse inoculation (Table 2).

Table 2

Cumulative percentage galled seedlings following field exposure to mites; with or without prior inoculation as young seedlings in the glasshouse

Year planted	No. of seedlings	No. of mite dispersal periods after planting			
		1	2	3	4
	Inoculated in glasshouse before planting				
1973	244	38	45	47	47
1974	344	8	36	42	46
1976	561	-	40	54	57
1977	922	-	42	46	*
1978	2015	11	47	*	*
	No glasshouse inoculation				
1970	1295	-	20	50	58
1973	145	37	49	50	50

* Results available after 1980, 1981 mite dispersals

EFFECT OF MITE RESISTANCE ON TRANSMISSION OF REVERSION VIRUS

Since 1976 seedlings in infestation plots and material propagated from infestation plot for agronomic selection in mite-free plots have been recorded for flower bud and leaf symptoms of reversion (Thresh, 1966).
The majority of mite susceptible seedlings are culled immediately galls are seen but two groups of mite susceptible seedlings have been retained and recorded for reversion symptoms. In the first group 24 out of a sample of 27 mite susceptible plants (89%) retained in 1976 displayed reversion symptoms within 18 months. The second group consisted of several progenies planted in 1978. These progenies are segregating for mite resistance but whole progenies were retained for genetic investigations. In spring 1980 593 mite susceptible and 718 mite resistant seedlings were examined for reverted inflorescences; 62% of the mite susceptible plants were reverted compared with 6% of the mite resistant

plants. These progenies have not had their full exposure to mites and it is probable that a proportion of the non-galled plants will become galled. Also it is likely that some mite susceptible plants colonised recently will develop reversion symptoms. The results from these two groups of seedlings show that a high proportion of mite susceptible (ce) seedlings become reverted and suggest that the gene Ce prevents or delays infection with reversion virus.

In winter 1974-75, after 4 years exposure to mites, 478 mite resistant seedlings were propagated from an infestation plot to a plot where mites are controlled by spraying. These seedlings have been recorded for reversion symptoms for 5 years and only 2% were confirmed as reverted.

Seedlings planted in 1973 and 1974 segregated for mite response and the mite resistant seedlings were recorded for reversion symptoms prior to propagation in winter 1976-77 and 1977-78. Thirteen and 2% of the mite resistant seedlings showed reversion symptoms in the 1973 and 1974 plantings respectively. However 10 plants in the 1973 planting were only partly reverted and healthy plants were propagated from unaffected shoots. A further 10% of the original seedlings planted in the infestation plot in 1973 displayed reversion symptoms in spring 1977, a further 2% of seedlings planted in 1974 were reverted in spring 1978. By spring 1980 18 of the 299 propagated mite resistant seedlings displayed reversion symptoms. Table 3 shows that, overall, 61 out of 314 (19%) mite resistant seedlings were reverted.

Table 3

Incidence of reversion symptoms in gall mite resistant seedlings after 4 years exposure to mites and after propagtion to a mite-free plot

Planted in infestation plot	Propagated	No. of seedlings Healthy	Reverted	% Healthy
1973	1976-77	113	49	70
1974	1977-78	140	12	92

DISCUSSION

Higher transmissions of mites in spring and summer during the dispersal phase than in the autumn were reported by Smith (1962) and seedlings inoculated in the spring displayed a higher

percentage of abnormal leaves than seedlings inoculated in the autumn. However, although these leaf symptoms are indicative of mite activity, they do not directly relate to mite susceptibility. Seedlings with leaf symptoms in the glasshouse cannot be discarded as susceptible, nor can lack of leaf symptoms be equated with resistance (Table 1).

Glasshouse inoculation at best is supplementary to the bombardment of mites the seedlings experience in a well established infestation plot. In the event of a very warm, dry dispersal period the preliminary inoculation may be important, but under normal conditions the additional mites do not appear to increase the rate of galling (Table 2).

A much higher proportion of mite susceptible seedlings became infected with reversion virus than mite resistant seedlings carrying the gene Ce. Single mites can transmit the virus (Smith, 1962) and the infection pressure in an infestation plot is enormous. The much reduced incidence of reversion in mite resistant plants demonstrates the efficacy of strong resistance to the vector. Under commercial conditions mite resistance derived from gooseberry is likely to be very effective in preventing both the spread of mites and transmission of reversion virus.

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CHEMICAL MECHANISMS OF POTATO RESISTANCE TO THE POTATO LEAFHOPPER

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Insect stress causes enormous losses in potato yield. At present, the only available means of combatting insect stress involves large-scale applications of insecticides. In 1971, 2,889,000 lbs. of insecticides were applied to potatoes in the United States (Andrilenas, 1974). The high costs and environmental hazards associated with such large-scale insecticide application need to be reduced by the development of genetic resistance to insects. The potato leafhopper, Empoasca fabae (Harris) is a serious pest of potato. In North America, leafhoppers have been known to reduce potato yield by 80% and more (Linn et al., 1948). Although numerous sources of resistance to the potato leafhopper have been identified, resistance, in general, has been greatest in wild, diploid potato species. Consequently, much effort at Cornell and elsewhere is currently being devoted to the transfer of resistance genes from these wild species to commercially important lines.

Our research on chemical mechanisms of leafhopper resistance in wild species is designed to streamline the aggregation of resistance factors into commercial lines through the development of rapid methodology for the identification of leafhopper-resistant clones. We have focused upon two defensive mechanisms, namely resistance mediated by (1) glycoalkaloids and (2) glandular trichomes. In this paper we will review our present knowledge of these mechanisms and then discuss the relevance of such mechanistic considerations to breeding strategies for improved pest resistance.

Nature of Resistance

A. Glycoalkaloid-mediated resistance.

Glycoalkaloids are a class of toxic nitrogen-containing steroidal glycosides found in foliage and tubers of potatoes. The first glycoalkaloid to be found in potatoes was α-solanine (Baup, 1826). This was considered to be the only one present until the discovery of α-chaconine over a century and a quarter later (Kuhn and Low, 1954). Although α-solanine and α-chaconine are, historically, the predominant potato glycoalkaloids, Schreiber (1968) has reported a wide range of individual glycoalkaloid contents in Solanum species and there are indications that more remain to be characterized. Only recently a new glycoalkaloid, commersonine, was discovered in two Solanum species (Osman et al., 1976). Glycoalkaloids, which have no clear-cut metabolic role in solanaceous plants, have long been considered fungitoxic compounds (Sinden et al., 1973), and have also been associ-

ated with gastrointestinal disturbances, nervous depression and death following ingestion by humans (Willimot, 1933).

Potato glycoalkaloids have been implicated as resistance factors against 2 insect pests of potato, the Colorado potato beetle, Leptinotarsa decemlineata (Say) (Kuhn and Low, 1955; Pierzchalski and Werner, 1958), and the potato leafhopper, Empoasca fabae (Harris) (Dahlman and Hibbs, 1967). More recently, we have demonstrated that foliar concentration of total glycoalkaloids in wild Solanum species is highly correlated ($r = -0.75$, $p = 0.01$) with field infestations of potato leafhopper nymphs (Tingey et al., 1978), suggesting a defensive role for these compounds. Subsequently (Raman et al., 1979), we performed feeding studies with total glycoalkaloid fractions isolated from the same accessions studied by Tingey et al. (1978). The effects of the total glycoalkaloid preparations on nymphal survival and on feeding behavior were assessed, and specific components of the feeding process thus affected were identified by use of an electronic recording system. We found that nymphal survival, and duration of settling, salivation-ingestion, and non-feeding were significantly correlated with total glycoalkaloid concentration ($r = -0.86$, -0.79, -0.93 and 0.82 respectively), thus providing further evidence of a causal role for potato glycoalkaloids in leafhopper resistance.

B. Glandular trichome-mediated resistance.

The glandular trichomes of wild, tuber-bearing Solanum species defend against many potato-infesting pests (Gibson and Turner, 1977), and offer exceptional opportunity for exploitation in breeding resistant potato cultivars. Gibson (1971) was among the first to associate glandular pubescence with insect resistance of the wild potato species S. berthaultii, S. polyadenium, and S. tarijense. These 3 species have high densities of 4-lobe (Type A) and/or simple glandular trichomes (Type B) on leaves, stems, and petioles (Gibson, 1974); upon contact by an arthropod, a viscous exudate is discharged, and accumulates on the arthropod's body, severely impeding the insect's movement (Gibson and Turner, 1977). Tingey and Gibson (1978) have demonstrated such entrapment of Empoasca fabae by glandular trichomes of S. polyadenium and S. berthaultii, and have also shown that trichome exudates accumulate on leafhopper mouthparts, preventing feeding and resulting in significant mortality.

A browning reaction is associated with entrapment of insects by glandular trichome exudates of S. berthaultii, S. polyadenium and S. tarijense. Soon after rupture of the trichomes, the viscous exudate darkens and hardens as it accumulates on the insect's legs and mouthparts. Gibson (1971) suggested that the browning reaction might involve production of a polymeric phenol by action of polyphenol oxidase (PPO). The conclusion was tentative because it was based entirely upon in vivo studies and not on direct biochemical evidence. Recently, studies in our laboratory indicated the presence in vitro of at least two separate enzymic systems, in glandular trichomes of S. berthaultii, capable of oxidizing simple phenols, namely PPO and peroxidase (PO) (Ryan, unpublished). To the best of our knowledge, this is the first report demonstrating the localization of oxidative enzyme systems in plant hairs.

The analysis of glandular trichome secretions presented a major problem associated with the collection of these miniscule droplets (average diam. 30-65 μ) from the leaf surface. However, a simple technique of wiping the epidermis with a buffer-dampened cotton swab proved satisfactory. Micro-

scopic examination of the epidermis following wiping, revealed that three light passes of the swab over the leaf discharged most of the Type A (four-lobed) hairs, removed most of the droplets from the longer Type B hairs, and caused little damage to the leaf cuticle. After washing the trichome secretions from the swabs in phosphate buffer, assays for PPO and PO (Hori, 1973) were conducted in a Varian/Cary 219 double-beam spectrophotometer. The assays indicated that the trichome extract had high levels of activity for both putative enzyme systems. Non-enzymic oxidation was ruled out when boiled extract showed no activity. Curves for pH optima in both systems were broad with activity in both cases dropping off rapidly below pH 3 or above pH 9; optimum PPO and PO activity was observed at pH 6.2 and 6.8 respectively.

Both systems were analyzed for substrate specificity using a variety of simple phenols. The PPO assay was highly specific for catechol and, while other substrates were oxidized to some degree by the extract, none had more than half the activity obtained with catechol. The PO assay, on the other hand, was much less specific when assayed with the same substrates. The peroxide-dependent system readily oxidized most substrates with which it was interfaced. Owing to the similarity of the assay conditions used, this was the first evidence of two separate oxidative systems in the trichome secretions.

The differential enzymic activity of the extract was further elucidated by use of diethyldithiocarbamate (DEDTC) and 1-phenyl-2-thiourea (PTU). Both inhibitors irreversibly complex the copper prosthetic group of PPO and the heme group of peroxidase is also complexed by these compounds (Dawson and Tarpley, 1951). Increased inhibitor concentration from 0.1 to 0.5 mM in both cases resulted in stepwise reduction in activity with 90% loss in activity at the highest concentration. Another inhibitor, 2,3-dimercapto-propanol [British Anti-Lewisite (BAL)] provided the second major distinction between the enzymic systems. BAL chelates heavy metals, is specific for heme, and in early stages of incubation with peroxidase, inhibition is reversible (Gibson and Liu, 1978). BAL produced the same stepwise inhibition in the PPO assay as DEDTC and PTU. The action of BAL on the PO assay was quite different, however, and led to a significant delay in the onset of the PO reaction. In addition, the reaction rate was retarded.

This evidence provides a strong case for the localization of at least 2 enzymic systems capable of oxidizing phenolic compounds in glandular trichome secretions of S. berthaultii.

Besides finding the 2 enzymic systems, we have recently demonstrated by a combination of TLC and HPLC, the presence of several phenolics in trichome secretions of S. berthaultii. In addition to caffeic acid and protocatechuic acid, trichome exudates contain several other phenolic compounds and work on their identification is continuing (Hannigan, unpublished).

According to Beckman et al. (1972), glandular trichomes of tomato, which are morphologically similar to the Type A hairs of S. berthaultii, contain compartmentalized phenols. The fragile membrane which surrounds the head of the Type A trichome may serve to compartmentalize phenolic substrates from oxidative enzymes, until the membrane is ruptured by insect contact. Histochemical studies are needed to confirm the location of both the oxidative enzymes and phenolic substrates within the Type A hairs. The role of the longer Type B hair in insect-induced browning is unclear. Whe-

her its sticky droplet contains precursors for phenolic polymerization or whether it mechanically impairs the insect's movement as suggested by Gibson (1971) is yet to be determined. Results of field studies, however, indicate that the combination of both types of trichomes is more effective in defense against insects than either type alone (Tingey, unpublished). More research into this aspect of the resistance mechanism is obviously needed.

One component of the browning reaction not yet found is the peroxide necessary for the peroxidative oxidation of phenols. Peroxide is frequently a product resulting from injury to plant cells, however, and might result from mechanical rupture of the membrane surrounding the head of the Type A trichomes.

Resistance Mechanisms and Breeding Strategies

Our data suggesting a causal role for foliar glycoalkaloids in potato resistance to the potato leafhopper raise the possibility of manipulating foliar glycoalkaloid content by breeding to provide improved protection against this pest. Unfortunately, levels of these broadly-toxic steroidal glycosides in foliage and tubers are highly correlated (Schwarze, 1963). While it may be possible to find clones segregating for pest-active levels in foliage and safe levels in tubers (Schwarze, 1962), such an approach would be feasible only with the availability of a rapid, inexpensive, and reliable screening method. Despite considerable research effort, screening for glycoalkaloid content is currently too problematical for routine adoption in potato breeding programs, and there appears to be no simple solution in sight (Mackenzie and Gregory, 1979). Until there are economical and streamlined analytical methods adaptable for use in screening large populations, breeding for glycoalkaloid-based resistance is not feasible. In addition, resistance conferred by glycoalkaloids is analogous, in part, to the protection provided by exogenous application of chemical insecticides, and may be subject to similar failure following appearance of host-specific biotypes.

Exploitation of glandular pubescence appears to have fewer serious limitations as a pest management tool. The glandular species, S. berthaultii, has already been hybridized with S. tuberosum and many clones of the former species are relatively free of undesirably high levels of glycoalkaloids (Raman et al., 1979; Tingey et al., 1978). However, the methodology for selection of progeny segregating for resistance needs further refinements. Clones with superior densities of trichomes can be identified by simple microscopy, but recently, we have found that high trichome density per se is not always associated with high levels of resistance, presumably because glandular trichomes are chemical as well as physical barriers to the insect. Specifically, we have been evaluating the usefulness of PPO and PO activities as indicators of leafhopper resistance in S. tuberosum x S. berthaultii hybrids. Preliminary data suggest that these assays, which are extremely simple, rapid and inexpensive, may play an important role in our breeding program (Ryan, unpublished).

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BREEDING FOR RESISTANCE TO LEPIDOPTEROUS PESTS IN CABBAGE AND CAULIFLOWER

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Damage from the cabbage looper, Trichoplusia ni (Hubner), the imported cabbageworm, Pieris rapae (L.), and the diamondback moth, Plutella xylostella (L.) larva is a worldwide problem. Tolerance in cole crops to insects is well documented.

Earlier we had reported that PI 234599, a dark green glossy leaved cauliflower, was highly resistant to T. ni and P. rapae. Later we observed that in Australia it was also resistant to Plutella xylostella.

In this report we compare the merits of 2 sources of resistance for future use in breeding programs and inheritance studies on them and the effect of plant maturity on selection for resistance.

Effect of Plant Maturity

Earlier we observed some lines that were heavily injured when young, but became relatively resistant as maturity approached. Experiment I was designed to study the effect of plant maturity on resistance to worms. Two plantings involving 9 lines were made. Seed was sown in 1977 on May 13 and June 2. The 9 lines included King Cole and Round Up, Snowball Y, PI 234599, BM15, 1228, 3270, and 3243. Previous observation indicated that the latter 4 cabbage lines possessed moderate to high levels of resistance at maturity while being susceptible at earlier stages.

Damage ratings for the studies reported were on a basis of 1 equal to no damage and 5 equal to more than 50% of the leaf tissue destroyed.

Table 1. Ratings for damage due to caterpillar feeding on selected cabbage and cauliflower lines as influenced by plant maturity.

Lines	Damage Ratings: Days from Transplanting 33	63	Mean	Maturity effect (33-63)
Storage Green	4.43	3.20	3.94	1.23
Snowball A	3.57	2.80	3.26	.77
Round Up	4.00	2.80	3.52	1.20
King Cole	3.90	2.75	3.44	1.15
BM15	3.40	1.60	2.68	1.80
1228	3.77	1.50	2.86	1.77
3270	2.77	1.90	2.42	.87
3243	1.70	1.90	1.78	.20
PI 234599	1.07	1.00	1.04	.07
LSD 0.05	.89	1.04	.75	.94

PI 234599 and the related line 3243 were less injured that the 4 susceptible commercial cultivars (Table 1). Low ratings were recorded on these resistant lines even when the plants were immature. On the other hand, lines BM15, 1228, and 3270 exhibited only reduced injury when they were mature, suggesting that this moderate resistance was associated with increasing plant maturity.

Diallel Inheritance Study

The purpose of Experiment II was to study the inheritance of worm resistance in cabbage using sources of resistance other than PI 234599. Inbred #1 (G364) was susceptible to worms; #2 (BM15), #3 (1228), #4 (3220), and #5 (3222) were selections which exhibited reduced levels of feeding at maturity. A diallel population derived from these 5 cabbage lines was tested for resistance in 1978 and 1979.

Evaluation of resistance was based on 1) a total larval count on 4 random plants removed from each plot in each replicate; and 2) a damage rating of whole plants.

To increase the chances of obtaining as uniform a population of pests as possible, all plots included a susceptible cultivar in every third row. 'Snowball A' or Y were used in the cauliflower plots and 'Round Up' in the cabbage plots.

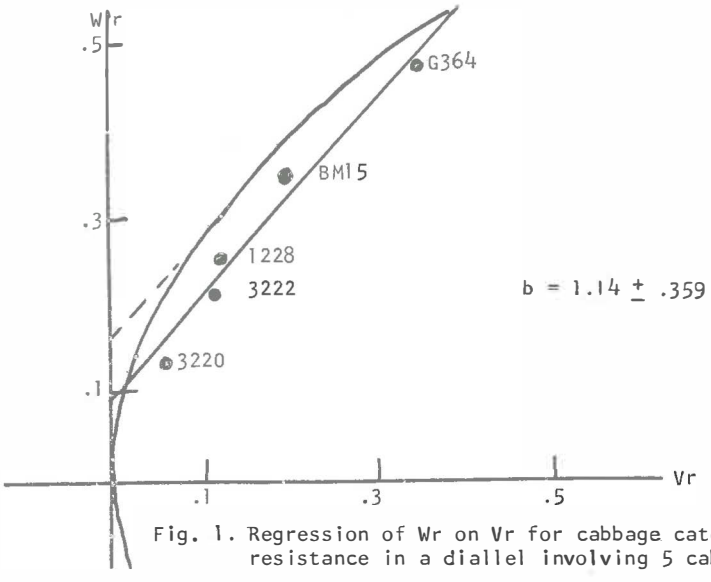

Fig. 1. Regression of Wr on Vr for cabbage caterpillar resistance in a diallel involving 5 cabbage lines.

The Wr Vr regression (Fig. 1), based on damage ratings in the diallel, indicated there was no genetic interaction since the regression line is not significantly different from 1, indicating simple additive dominance. Wr-Vr was constant over arrays. The susceptible parent 1 was clearly at the upper end of the regression line, indicating more recessive than dominant genes for resistance. Parents 3, 4, and 5 exhibited partial dominance for resistance (68%), while parent 2 was intermediate.

The hybrid 2 x 3 and inbred 5 had low damage scores for much of the season, but by the end of the season (after the ratings) considerable injury was noted on these individuals. It appeared that when nearby plants were severely injured the pests began to oviposit on the undamaged plants in these 2 lines. Correlation between actual pest counts and damage ratings were poor except when repeat pest counts were taken at weekly intervals.

Inheritance of Resistance from PI 234599

The inheritance of the resistance exhibited by the PI 234599 was studied. Populations involving the parents, F_2, and reciprocal backcrosses of the cross Snowball A x PI 234599 were grown in the field in 1979.

Table 2. Number of plants in different damage score classes in population from crosses of Snowball A and PI 234599

Pedigree	Leaf type	Damage Score Classes 1	2	3	4	5	$\bar{x}$	s^2
Snowball A	N[z]	-	-	3	21	19	4.4	.382
PI 234599	G	46	3	-	-	-	1.1	.059
PI 234599 x Snowball A F_2	N	1	5	16	12	20	3.8	1.20
"	G	7	4	6	-	-	1.9	.81
F_1 x PI	N	-	3	10	12	9	3.8	1.20
"	G	24	5	8	-	-	1.6	.70
F_1 x Snowball A	N	-	6	8	22	17	3.9	.94
NSH G+N = 28% BSH G+N = 87%								
N = 22%				N = 82%				

[z]N=Normal leaf with bloom; G=Glossy leaf

Table 2 presents the damage ratings on August 15 of a population of plants from the cross Snowball A x PI 234599. The narrow sense heritability of 22% indicated a workable heritability for transferring resistance to superior horticultural type plants.

Discussion

Maturity had no influence on the strong resistance exhibited by late-maturing PI 234599 or by its offspring. In contrast, under severe infestation pressure the relatively resistant inbreds such as #5 in the diallel or some of the more resistant hybrids eventually were damaged. A large planting of moderately resistant individuals, however, might be less damaged than was noted in our plots.

The results of the diallel (Fig. 1) agree with the data in the inheritance study (Table 2), where the mean of the F_2 approaches the parental mean. These studies indicate: resistance to the 3 cabbage caterpillars is quantitative with additive dominance for resistance to the pests; moderately-resistant plant lines or individuals can best be assessed by visual damage ratings rather than insect counts; and narrow sense heritability is low (22-28%) indicating selection in later generations will be preferable to selection in early generations. The resistance of PI 234599 is unrelated to plant maturity, and it is a higher level of resistance than other sources.

High-level resistance has been transferred from PI 234599 but non-glossy acceptable lines with the same levels of resistance have not yet been obtained. Glossy leaf is a relative term and some cauliflower lines such as 4160 and 4166 have the level of resistance equal to PI 234599 but the leaves are less glossy than the PI. However lines which have a slight bloom and a mat rather than a glossy appearance with quite good horticultural type have resistance to the PI 234599. We feel that with continued breeding and selection acceptable lines with bloom and high levels of resistance will be obtained.

FIRST OBSERVATIONS UPON THE PREFERENCE FOR OVIPOSITION OF THE EUROPEAN CORN BORER AND THEIR SIGNIFICANCE IN BREEDING FOR RESISTANCE

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The distribution of the European Corn Borer (*Ostrinia nubilalis* Hbn) egg masses has been studied in several experimental plots used for the evaluation of new hybrids.

In 1977, the experimental design of the Levesville trial, in the Beauce area, included more than forty hybrids of the same group of earliness with 3 replications of 2 rows of 25 plants for every variety. On 14 hybrids taken at random, the egg masses of the European Corn Borer were numbered four times at intervals of 10 days during the oviposition period on 10 plants per replication.

The data obtained, after a transformation to log $x + 1$ were put through a variance analysis. The F test F 13/26 = 2,91 is highly significant for the varieties. Their mean number of egg masses varies from 37 to 143 egg masses for 100 plants.

Furthermore, among the observed varieties, 6 of them were in addition observed in two other experimental plots of the same type, in the same area but with lower rates of egg masses deposited : Poinville 39/100 plants, Selommes 23/100 pl, against Levesville 75 egg masses for 100 plants. We can observe very good correlations between the ranks of these varieties in the different localities (for instance the correlation coefficient of Spearman is r_s = 0.90 between Poinville et Levesville.) (table I)

Table I - Numbers of egg masses of the European Corn Borer observed on the leaves of 100 plants of different varieties on experimental plots at different localities of Beauce area for the 2 years 1977 and 1978 and ranking of these varieties

Maize varieties	LOCALITIES AND YEARS											
	Selom.77		Poinv.77		Leves.77		Poinv.78		Lev.1 78		Lev.2 78	
W 182E x W 117	13	*1*	13	*1*	37	*1*	13	*2*	195	*2*	217	*2*
Royal 255	13	*1*	33	*3*	37	*1*	7	*1*	60	*1*	-	-
INRA 302	13	*1*	30	*2*	63	*3*	-	-	-	-	-	-
Monclair INRA 290	-	-	40	*4*	70	*4*	20	*3*	255	*3*	190	*1*
HD 234	17	*4*	47	*5*	97	*5*	40	*4*	330	*4*	313	*3*
HTV (TxFPB 329)	57	*5*	70	*6*	143	*6*	77	*5*	405	*5*	590	*4*

So the differences of numbers of egg masses are observed among the 6 varieties whatever the conditions of environment, of mean density of oviposition and of multiple choice with surrounding varieties may be.

In 1978, similar countings of egg masses have been done in the same localities, on similar experimental designs. The ranks of the same 6 varieties for the 6 trials and the two years are very highly correlated although the rates of oviposition at Levesville 1978 are very higher than those already observed, varying from 60 egg masses for 100 plants for Royal 255 to 590/100 plants for the experimental three-ways hybrid HTV(TxFPB 329).

So, the 1978 data confirm those previously obtained. The differences among varieties for the level of egg masses seem to be independant of the variations of years, localities, mean rate of oviposition, hybrids in competition, experimental design.

On the same year 1978, 10 hybrids were sown especially for test of oviposition with a different experimental design : one row of 20 plants instead of 2 rows of 25 plants per hybrid. The egg masses were numbered four times from the 10th July to the 10 th of August on 10 plants per replication.

At the first counting, the mean level of oviposition is only 9 for 100 plants and none significant difference can be observed between varieties. On the 20th July, the mean level of oviposition reaches 78/100 plants and a non parametric analysis using Friedman and Kramer tests gives 3 groups with significant differences. The same results may be observed with the two other countings on the beginning of August (table 2).

Table II - Number of egg masses of the E.C.B. observed on the leaves of 100 plants of different varieties on experimental plots at Levesville in 1978 at different dates during the whole oviposition period with the groups of varieties according to the results of a statistic analysis.

	VARIETIES	OBSERVATIONS				TOTAL
		VII/10	VII /20	VII/30	VIII/10	
Gr. 1	Royal 255	7	23	35	37	102
Gr. 2	W 182E x W 117	3	43	135	57	238
	Monclair INRA 290	5	48	165	32	250
	(F7.F2) W 182 E	5	58	170	40	273
	HTV (T x F 1444)	3	80	165	50	298
	HTV (T x EA 2087)	5	40	200	77	322
	HTV (T x F 1417)	10	83	165	65	323
	HD 234	12	73	190	72	347
Gr 3	HTV (T x FPB 329)	17	165	215	90	487
	F 186 x F 478	12	123	320	113	568

Once again, very high differences in the level of egg masses appear between hybrids cultivated in the experimental plots with multiple choice offered to the females. The results obtained seem to give evidence of a preference or non-preference mechanism for oviposition.

In 1979, the two varieties Royal 255 (group 1 in 1978) and the single cross F 186 x F478 (group 3 in 1978) were sown in a special experimental design including 6 replicates of 16 rows of 25m in view to know if the differences in the level of egg masses are always observed with simple choice between two hybrids cultivated in larger plots.

The observations were made on the four border lines and on two lines in the middle of the plot, four times during the oviposition period from the 8th of July to the 9th of August. A sequential sampling method was used for estimating the level of egg masses for 100 plants.

The data show a very highly significant difference between the two varieties Royal 255 14.8 egg masses for 100 plants ; FF : 39.6 e.m/100 plants. That difference is observed for every counting, but the ratio FF/R is more and more high along the oviposition period as if one variety was more and more preferred.

Observations dates	VII/9	VII/18	VIII/1	VIII/9
N° of egg masses on R	33	169	58	6
" on FF	72	415	195	29
Ratio FF/R	2.2	2.5	3.4	4.8

Turning now to the separate data for the different lines, the analysis shows a non significative (P 0.2-0.1) trend for observing more egg masses on the first border lines 49/100 pl., then on the second border lines, 37/100 pl than on the middle lines, 34/100 pl., on the preferred variety FF only. The difference between the two hybrids seem for a part to be due to a phenomena of choice when the two varieties are available side by side for the ovipositing females, although a large difference on oviposition exists also in the middle of the experimental plot.

	ROYAL				FF			
Varieties and lines	8+9	.....	2	1	1	2	.....	8+9
N° of egg masses	16	.....	16	12	49	37	.....	34

Furthermore, in 1979, the egg masses numbered by the usual procedure on a diallel experimental test at Levesville. The 91 single hybrids resulting from diallel crossing among 14 inbred lines were examined four times at ten days intervals. The data vary from 7 egg masses/100 plants to 117/100 plants for the hybrids and from 17.9 to 52.3 for the means of the parents. The variance analysis gives a very highly significant F ratio, so that we can assu-

me that genotypic differences exist. General and specific combining ability effects for oviposition evaluation are highly significant so that true differences among these effects do occur. Two parents have good gca value for increase of oviposition. The differences in the rate of oviposition seem to be independant of the differences in earliness of the hybrids.

Another set of 10 hybrid lines resulting from diallel crossing among 4 inbred lines suspected to induce large differences in oviposition will be observed in 1980.

In conclusion, the 77-79 observations of the European Corn Borer egg masses in plots of experimental hybrids of maize cultivated in the Beauce area reveal an interesting pattern of egg masses distribution in a such experimental design. The distribution is not at random and in the cases of multiple choice the phenomena of preference or non preference for oviposition may be put forward.

On a practical point of view, this fact makes more difficult the testing of new varieties for resistance or tolerance to the European Corn Borer based upon the susceptibility of the plants under such a heterogeneous natural infestation.

The differences observed among varieties are very high, and it is interesting to see that new genotypes seem to receive more egg masses than the commercial varieties already grown in the area since several years. The charm of novelty is it a component of the oviposition behaviour of the females of the E.C.B. ?

We dont know the mechanisms involved in the existence of such differences in the number of egg masses among hybrids.

It would be the choice at distance controlled by a balance of hypothetic attractive or repulsive volatil substances emitted by the plants and acting on olfactive receptors.

It would be also some arrestant or incitant/deterrent effects for oviposition exerted on the female after its landing on the plant or may be only the ability of the egg mass to remain sticked to the leaves.

This second type of factors would be able to have direct influence, independant of the possibility of choice and it would be use in breeding for non preference

Further investigations are necessary for a better knowledge of the mechanisms involved.

RESISTANCE AND GLABROUSNESS: DIFFERENT APPROACHES TO DEVELOP BIOLOGICAL CONTROL OF TWO CUCUMBER PESTS, TETRANYCHUS URTICAE AND TRIALEURODES VAPORARIORUM

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Glasshouse cucumbers are threatened by several pests of which the two-spotted spider mite, Tetranychus urticae and the glasshouse whitefly, Trialeurodes vaporariorum are the most serious ones. In the Netherlands the biological control of the two-spotted spider mite using the predatory mite Phytoseiulus persimilis has expanded to 50% of the acreage, whereas biological control of the glasshouse whitefly with the parasitic wasp Encarsia formosa hardly occurs (VAN LENTEREN et al,. 1980). The incorporation of two essentially different characteristics, viz. resistance and glabrousness, in future cucumber varieties aims at (1) promoting the biological control of T. urticae, (2) enabling that of T. vaporariorum and (3) reducing the need of chemical control.

1. RESISTANCE TO TETRANYCHUS URTICAE

1.1. The development of highly resistant breeding lines

Of 800 varieties tested in laboratory and practical tests, only nine were significantly different from the susceptible control for acceptance, reproduction and damage index (DE PONTI, 1978a), as was already reported at the first meeting of this Working Group.
After moving mites from a susceptible to other (resistant) varieties the reduction in reproduction might, however, only be temporary. If so, the resistance of the selected varieties would not be genuine. To investigate this, both resistance tests were repeated after the mites had been reared on the selected varieties for 10-20 generations. The degree of acceptance and reproduction and the damage decreased rather than increased, providing evidence for the genuineness of the resistance (DE PONTI, 1978b).
In an attempt to increase the level of resistance the partially resistant varieties were intercrossed and the successive generations subjected to selection in laboratory and practical tests (DE PONTI, 1979).
Table 1 and Figure 1 demonstrate clearly that this breeding procedure was successful. Some F_5 lines were selected with a significantly lower reproduction and damage index than those of the parental varieties. The 15 most resistant lines were released to private breeding firms in the Netherlands.
The implications of the resistance of these lines for development and control of the two-spotted spider mite are best shown in the practical test (Fig. 1). On the most resistant F_5 lines the economic injury level will be reached several weeks later than on the susceptible control, causing a significant reduction in the frequency of acaricide applications.

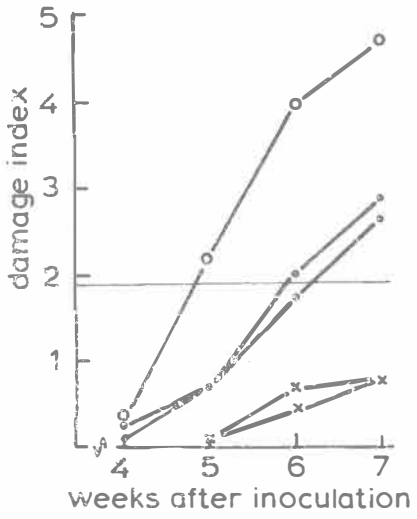

Fig. 1. Increase of damage on the susceptible line G6 (O), on the two partially resistant varieties HLGP and Robin 50 (●) and on two F_5 lines derived from crosses between the varieties (x) The economic injury level (eil) lies at 1.9.

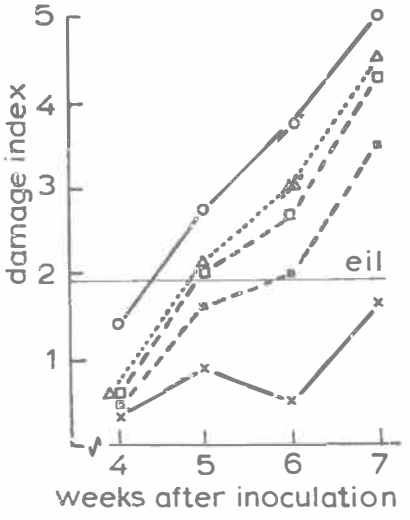

Fig. 2. Increase of damage of bitter (■) and non-bitter (□) plants of B_{11} and F_3 lines segregating for the gene Bi, compared with the parental lines G6 (O) and F_5 (HLGP x Robin 50) (X). Homogeneous non-bitter lines (Δ) are also represented.

1.2. The inheritance of the resistance (and bitterness).

In laboratory tests the inheritance of the resistance has been studied in three sets of P_1, P_2, F_1, F_2, B_{11} and B_{12} of crosses between three of the most resistant F_5 lines and one susceptible line, G_6. As measured by acceptance and reproduction resistance to the two-spotted spider mite appeared to be governed by many genes, which are mainly inherited in additive fashion.
Bitterness is basically governed by the gene Bi, which, contrary to earlier reports is inherited in an intermediary way, while the expression of Bi is influenced by additively inherited intensifier genes.(DE PONTI & GARRETSEN, 1980).

1.3. The development of non-bitter resistant lines

Because in the inheritance studies the resistant lines were bitter and the susceptible line non-bitter, it was possible to investigate the intriguing question, whether bitterness is responsible for the resistance. In these studies no relation was found between the gene Bi, its intensifiers and the resistance factors acceptance and reproduction in F_2, B_{11} and B_{12}. This was also true for selected B_{11} and F_3 lines. Therefore we were able to select non-bitter lines, whose resistance, as measured by reproduction, is equal to that of the bitter resistant parent (Table 2).
B_{11} and F_3 lines segregating for Bi and some non-bitter lines were also tested in practical tests. Figure 2 shows that on an average the non-bitter plants are significantly ($P \leq 0.01$) more damaged than the bitter plants.

Variety or line	Acceptance (%)	Number of eggs per female in 3 days
Hybrid LGP	36	14.1
Robin 50	45	15.1
F_5 (HLGPxRobin 50)	45	8.4
F_5 (HLGPxRobin 50)	34	9.4
Susceptible control	72	21.0

Table 1. Degree of acceptance and fecundity of the two-spotted spider mite on a susceptible control, on 2 partially resistant cucumber varieties and on 2 lines derived from crosses between these varieties.

Material	Bitterness	Number of eggs per female in 3 days
P_1	-	16.2
P_2	+	12.4
B_{11}	-	12.0
F_4	-	11.6
F_4	-	10.3

Table 2. Bitterness and degree of fecundity of the two-spotted spider mite on 3 non-bitter lines from the cross $G_6 \times F_5$ (HLGPxRobin 50), compared with these parental lines.

Moreover the non-bitter lines are, relatively, also more damaged. Of some lines, however, the non-bitter plants were equally or even less damaged than the bitter plants, indicating a non-absolute relation. These practical tests clearly demonstrate a significant relation between the gene Bi and the damage index, reflecting the resultant of all aspects of resistance and tolerance (DE PONTI, 1978a). This relation could be caused by identity or linkage of the genes concerned.

The only known non-bitter mutant was found at our institute in the variety Improved Long Green, and we were fortunate that germinable seed of the original sample of this variety and of the first progeny of the mutant was still available. This material and other pairs of near isogenic varieties were tested for resistance in laboratory and practical tests. Because no differences were found between the near isogenic varieties for acceptance, reproduction or damage index, any causal relation based on pleiotropy of Bi between bitterness and resistance is denied (DE PONTI, 1980). Therefore linkage of the gene Bi with some resistance or tolerance genes, only expressed in practical tests, remains the only plausible explanation for the relation found. The occurrence of such unfavourable linkages, only traceable in practical tests, emphasizes the importance of this method of testing for resistance and tolerance to the two-spotted spider mite. In 1980 many non-bitter lines from F_2 and backcross generations will be selected in practical tests.

2. BIOLOGICAL CONTROL OF TRIALEURODES VAPORARIORUM

2.1. The benefit of glabrous leaves

On glasshouse tomatoes in the Netherlands the biological control of the glasshouse whitefly (Trialeurodes vaporariorum) with the parasitic wasp Encarsia formosa is successfully applied on an ever increasing scale (VAN LENTEREN et al., 1980). On glasshouse cucumbers sufficient control is rarely achieved, even when more wasps are released than in a tomato crop. VAN LENTEREN et al. (1980) ascribed this difference in control result to a difference in leaf structure of the two crops. Wasps, once landed on a leaf, search for their hosts mainly by walking and drumming on the leaf with their antennae. Contrary to tomato, cucumber leaves have many large hairs, which reduce the mobility of the wasps. Further, honeydew easily attaches to such hairs and wasps that walk into a honeydew droplet may preen for hours and die. It was hypothized the low mobility and high probability to encounter honeydew droplets might reduce the parasitization activity of the wasp. If the hypothesis is true the parasitization frequency would be higher on hairless (glabrous) leaves.
Based on a publication of STRELNIKOVA and MASHTAKOVA (1973) seeds of a spontaneous glabrous mutant were requested from the N.I. Vavilov All-Union Institute of Plant Industry in Leningrad. After receipt of this material the mobility of the wasp was studied. It appeared that on the glabrous leaves the wasp was no longer hampered by hairs and walked 3.5 times as fast on this mutant as on a hairy variety (HULSPAS-JORDAAN & VAN LENTEREN, 1978). A glasshouse experiment showed that the parasitization efficiency was about 20% higher on that mutant. Anticipating these results the breeding of glabrous cucumber varieties was already started. Because of the simple inheritance (1 recessive gene) and selectability of the character rapid progress has been made. In 1978 advanced breeding lines (non-bitter, gynoecious, parthenocarpic) were released to private breeding firms in the Netherlands.

The only unfavourable character found in the material is a physiologically determined pin-point necrosis, but in recently selected lines this disorder is less prominent. It is expected that growers will welcome glabous varieties, because they also cause less fruit damage and skin irritation.

2.2. The need of resistance to T. vaporariorum

Further glasshouse tests are needed to obtain certainty that glabrous leaves alone can increase the parasitization efficiency on cucumber sufficiently for reliable biological control. If not, it would be necessary to find or develop varieties that are partially resistant to the glasshouse whitefly. This is only possible with suitable screening methods. At the moment such methods are developed in a project on resistance of tomato to the glasshouse whitefly (BERLINGER & DE PONTI, 1980), which can later be adapted to cucumber.

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METHODS FOR TESTING RESISTANCE TO WHITEFLIES IN TOMATO AND RELATED SPECIES*

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The glasshouse whitefly, Trialeurodes vaporariorum Westw., causes economic damage to glasshouse tomatoes in the temperate zones of the world. Its control by chemicals is expensive, dangerous and not always sufficiently effective.

Biological control, with the parasitic wasp Encarsia formosa Gahan, is generally successful and in western Europe relatively widespread. Nevertheless, there are still some obstacles to its use; 1) Because of the seasonality of the crop the parasites must be released every year anew, which makes the procedure somewhat of a nuisance, expensive, and dependent on a reliable supply of parasites. 2) The proper timing of parasite introduction into the glasshouse is crucial. 3) Most important of all, relatively high temperatures are needed for effective bio-control (Burnett, 1949). Lowering the temperature, in order to conserve energy, will destroy the desired level of parasite activity and result in an insufficient level of control.

Breeding tomatoes resistant to the whiteflies might provide a solution to these problems. Even partial resistance would be of great help if it were complementary to biological control (De Ponti, 1978). Attempts to breed resistance to the glasshouse whitefly in tomato have been made by Hussey & Gurney (1959). Gentile et al.(1968), Curry & Pimentel (1971), O'Reilly (1974), Plage (1975) and Georgiev & Sotirova (1978).

At the IVT, De Ponti and his colleagues started a breeding program in 1972 by screening 85 accessions of Lycopersicon esculentum and related species. He found (De Ponti et al., 1975) high levels of resistance in L. hirsutum, L. hirsutum glabratum and Solanum pennellii. His tests in cheese-cloth cages yielded reliable results but the cages were not convenient to handle. Potted plant tests were less time - and space - consuming, but the results were unacceptable because of their inconsistency. The breeding program was therefore continued in tests in a glasshouse, where the tested accessions and lines were planted separately in isolated chambers. One day after planting, each of the plants was inoculated by 20 or 30 whitefly females of unknown age. The degree of resistance was then evaluated 2, 3 and 4 months later by rating the plants (on a scale of 0 = clean or resistant, to 9 = contaminated or susceptible), according to the estimated number of adult whiteflies and their damage: the amounts of honey-dew produced by them and of sooty-mold developed on it. The above mentioned methods were either not reliable enough or too time-consuming and therefore expensive.

Our aim was to improve the testing method in order to evaluate the resistance of the plants in a more quantitative manner and as quickly and conveniently as possible to enable mass-screening. Since the glasshouse test

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is considered to be the most reliable one, we compared the results of our experimental methods always with those of a glasshouse test. With these ideas in mind, our work proceeded along two directions: 1) to improve the evaluation methods of the glasshouse test by quantifying the results thus making it more objective than the rating method is; and 2) to shorten the time required by using leaf cages.

The following experiments were compared with the rating method:

A. Glasshouse test under practical conditions:

1) Counting the number of leaves infested by no, a few, an intermediate number or many scales (big larvae and pupae) at a height between 0.5and 1.5 m.

2) Counting the number of eggs, larvae and pupae on ten samples of leaf discs (14 mm in diameter), sampled at heights of 20, 60, 100, 140, 180 cm and on the top leaves.

3) Yellow sticky traps (Berlinger, 1980) were used to estimate the population levels.

B. Leaf cages were used both under controlled conditions (27°C) and in the glasshouse:

4) Survival and oviposition rates: 1-day-old females (1 or 6) were confined on a leaf by means of a clip-on leaf-cage. Every 4 days the surviving females were counted and transferred to a new leaf. The leaf was detached and the number of eggs was counted.

5) The rate and duration of development, as well as the sex ratio among the progenies, were determined by confining a large number of females of unknown age on a leaf by means of a leaf-cage. After 24 hours the whiteflies were removed, their eggs were counted and allowed to develop. The duration of development was found by daily countings of the emerging progenies, and their sex ratio was simultaneously determined. The number of progeny per egg laid gives the rate of development. The whiteflies were reared on a susceptible tomato cultivar.

RESULTS

In the glasshouse test (Fig. 1), three testing methods (1-3) were compared with the rating method (De Ponti et al.,1975). All of them showed the same trend; A (Allround) and the FS line(F_7 hybrid H 1370 x L. hirsutum glabratum which was expected to be susceptible) were indeed susceptible, while G (L. hirsutum glabratum) and the FR line (an F_7 hybrid of H 1370 x L. hirsutum glabratum which was expected to be resistant) seemed to be resistant, at least as compared with A and FS.

Various parameters of population build-up were tested using leaf-cages (methods 4 and 5). The results are shown in Fig. 2. Under glasshouse conditions, in March, the FR line seemed to be resistant, like G, but in January or under constant temperatures (27°C) it was as susceptible as FS and A, although G was resistant in comparison with A.

DISCUSSION

1) In the leaf-cage tests the whiteflies were confined onto the plants, whereas in the glasshouse tests they could move freely and even leave the plants.

2) In the glasshouse test (Fig. 1), two parameters of resistance 'Non-acceptance' and 'antibiosis' may be involved, whereas in the leaf-cage test (Fig. 2) only antibiosis is measured.

3) With the glasshouse test (Fig. 1), the whitefly population is correlated with a plant unit, while with the second group of methods (Fig. 2) the whitefly population build-up per female is shown.

4) Based on our present experiments, routine glasshouse and leaf-cage tests are now developed.

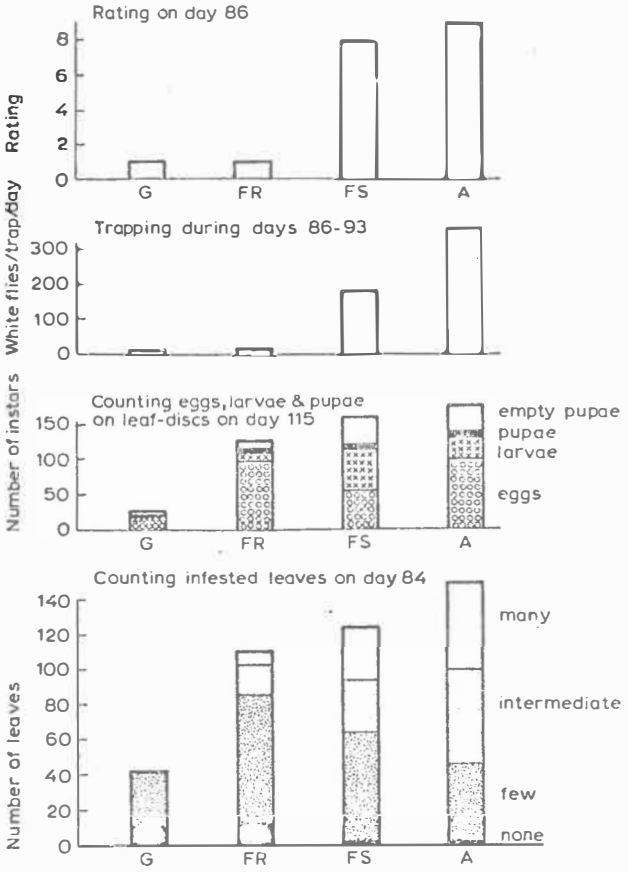

Fig.1 Evaluating the resistance of Lycopersicon hirsutum glabratum (G), L. esculentum cv "Alround" (A) and of two of their hybrid lines (FR and FS) by rating the plants, trapping whiteflies, counting developmental instars and infested leaves, under glasshouse conditions (September-December, 1978)

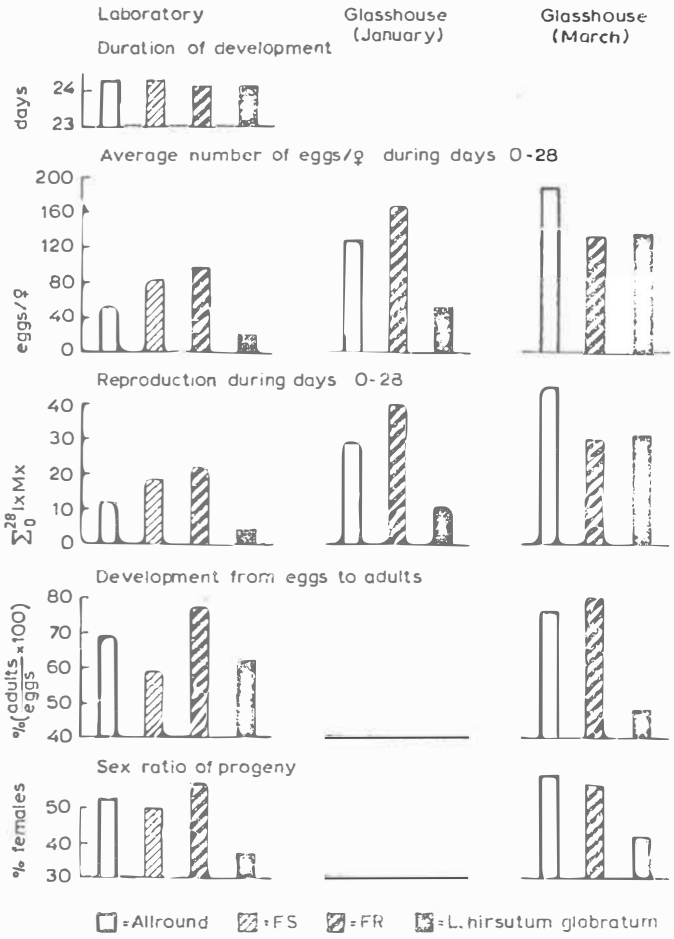

Fig.2 Evaluating the resistance of Lycopersicon hirsutum glabratum (G), L. esculentum cv "Alround" (A) and of two of their hybrid lines (FR and FS) by parameters of population build-up, in a laboratory test (27°) and on two glasshouse tests (January, March, 1979)

5) The advantages of the leaf-cage test are twofold: it saves time and provides the necessary base for a simulation model which may be an aid of invaluable importance.
6) The evaluation of resistance in the glasshouse by rating the plants 2, 3, or 4 months after planting, can be improved by quantifying the results as described by methods 1-3 (Fig. 1). This procedure is necessary for the verification of simulation models.
7) The methods applied are of great importance for the progress of a breeding program. As demonstrated by the partial disagreement between the leaf-cage and the glasshouse tests (e.g. line FR). Therefore, the final test must be carried out under practical conditions.

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SCREENING BEANS (PHASEOLUS VULGARIS L.) FOR RESISTANCE TO MEXICAN BEAN BEETLE (EPILACHNA VARIVESTIS MULSANT)

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The Mexican bean beetle (Epilachna varivestis Mulsant) is a very serious pest of beans (Phaseolus vulgaris L.) and is also becoming a pest of economic importance of soybeans. The adults are 0.6 - 0.8 cm long and 0.4 - 0.6 cm wide. The adult and larvae feed on underside of leaves. The larvae are very active feeders and cause more damage than adults. During heavy infestations when the foliage has been consumed, the insects move to feed on stems and pods, and total defoliation of plants occurs in a very short time. Each female lays more than 1,000 orange-yellow elipticle eggs on the underside of leaves in clusters of 40-50 during a period of 4-5 weeks. The eggs hatch in about a week. There are 4 larval stages and the larval period lasts 2-3 weeks before pupae emerge. The pupal stage lasts for about a week. The adults start to lay eggs within 1 week of their emergence. The total period from egg to egg is 5-6 weeks. There are 3-4 generations of Mexican bean beetle in the Southern states of the United States. Thus, the host plants are repeatedly subjected to heavy infestations of the Mexican bean beetle during their entire growing period.

The resistant varieties are an ideal solution of the problem. However, the chance of locating resistant germplasm is in proportion to the number of accessions that can be screened. Rapid screening methods for field as well as phytotron conditions are urgently needed. A rapid screening method for Mexican bean beetle is also very essential in mutation breeding when a vast number of lines are to be screened for resistance in a short time. The time consuming screening process can be considerably hastened if rapid and reliable methods of screening are available. The insect feeding response has been reported to be affected by its age, sex, conditioning process and rearing conditions, and various plant and environmental factors (Abernathy and Thurston 1969, Smith 1978, Greene and Morrill 1970, Roberts and Tyrell 1961, and Roth and Willis 1963). An effort was, therefore, made to develop a fast and reliable method of screening beans to Mexican bean beetle under phytotron and field conditions keeping in view some of the important insect-host plant factors.

Materials and Methods

A randomized block design experiment with 4 factors as follows was conducted: Location (experiments were conducted under phytotron and field conditions); insect rearing (fifth generation laboratory reared, and natural populations of Mexican bean beetle); sex and number of insects (1 female, 1 male, 1 female and 1 male, and 2 females/leaflet); and insect feeding time (2,4,8, and 24 hours). Thus, a total of 64 treatment combinations were used. The experiment was repeated 3 times. Two-week-old Mexican bean beetles conditioned on deionized water for 24 hours were used. The female and male Mexican bean beetles were identified based on the terminal abdominal segment. There is a small identation of this segment in males only. The experiments were conducted in Phytotron, North Carolina State University at Raleigh, and under field conditions at Randolph Farm, Virginia State University at Petersburg. The bean variety Blue Bush Lake-290 was used in

Table 1. Effect of location (phytotron and field), insect rearing (fifth generation laboratory reared and natural populations), sex and number of insects (1 female, 1 male, 1 female and 1 male, and 2 females/leaflet), and time of feeding (2,4,8 and 24 hours) on Mexican bean beetle feeding damage (cm2/leaflet).[1]

Location	Insect Damage	Insect Rearing	Insect Damage	Sex & No. of insects	Insect Damage	Insect Feeding	Insect Damage
Phytotron	3.68a	Laboratory	2.93b	1 Female	3.16b	2 Hrs.	2.36d
Field	2.31b	Natural Population	3.06a	1 Male	2.01c	4 Hrs.	2.55c
				1 Female & 1 Male	3.21b	8 Hrs.	2.97b
				2 Females	3.36a	24 Hrs.	4.11a

[1]Means with the same letter are not significantly different according to Duncan's multiple range test, 5% level.

all experiments.

The phytotron conditions were as follows: The plants were grown under a combination of cool white fluorescent and incandescent lamps which provided an energy illuminance equivalent of 430-480 hlx. A 9 hour photoperiod was used. Day/night temperatures were maintained at 26/22 C+ 0.25C. Relative humidity varied from 55-65 during day and 75-85 at night. Carbon dioxide concentration was controlled at 300-400 ppm by injecting commercial grade CO2. Bean seeds selected for size uniformity were planted in 15.2 cm plastic pots containing 900 ml of 2/3 gravel and 1/3 RediEarth substrate. Plants were irrigated twice each day with deionized water till germination and then once each day with deionized water and once with NCSU phytotron nutrient solutions (Downs and Bonaminio 1976) Plants were thinned to 1/pot seven days after planting. In the field, plants were grown following common cultural practices. The experiments were initiated in the first week of June on 3-week-old plants. Two-week-old Mexican bean beetles conditioned on deionized water for 24 hours were caged on the primary leaflets of the first trifoliate leaves. After 2,4,8, and 24 hours of feeding, leaflets were excised and feeding damage determined by an electronic area meter. Data were analyzed by analysis of variance and the means were separated by Duncan's multiple range test.

Results and Discussion

The effect of location, insect rearing, sex and number of insects, and insect feeding time is shown in Table 1.

Location: The insect feeding damage was significantly higher (1.6X) in phytotron as compared with in field (Table 1). This may be due to the optimum environmental conditions in phytotron as compared with fluctuations in environmental factors in the field. A difference in texture of leaves of plants grown under two locations was also observed.

Table 2. Interaction between rearing (laboratory and natural populations of insects) and location (field and phytotron). Mean Mexican bean beetle feeding damage in cm2/leaflet.[1]

Insect rearing	Location	
	Phytotron	Field
Laboratory	3.59 b	2.27 c
Natural Populations	3.78a	2.34 c

[1]Means with the same letter are not significantly different according to Duncan's multiple range test, 5% level.

Table 3. Interaction between location (phytotron and field) and sex and number of insects (1 female, 1 male, 1 female and 1 male, and 2 females). Mean Mexican bean beetle feeding damage in cm2/leaflet.[1]

Sex and number of insects	Location	
	Phytotron	Field
1 Female	3.88 b	2.43 d
1 Male	2.52 d	1.50 e
1 Female and 1 Male	3.96 b	2.45 d
2 Females	4.35a	2.85 c

[1]Means with the same letters are not significantly different according to Duncan's multiple range test, 5% level.

The leaves of plants grown in phytotron were very succulent as compared with the leaves of field grown plants. Screening in phytotron provided an underestimate of resistance. Therefore, plants observed to be resistant in phytotron are expected to be far more resistant in field. Benepal (unpublished) also studied the economics of screening bean germplasm in phytotron and in the field. Screening in phytotron proved to be 3X more economical than in field. It is extremely difficult to screen 10,000 accessions in one year under field conditions with one research scientist, one technician, 10 full-time workers, a graduate student, and two undergraduate students. In a phytotron 30,000 accessions can be accurately screened using 600 sq. feet of space, one scientist, one technician, one graduate student, and two undergraduate students.

Insect rearing: There was a significant difference in feeding between the fifth generation laboratory reared and natural populations of insects. The natural population of Mexican bean beetles showed significantly higher feeding damage as compared with the laboratory reared insects (Table 1). This may be due to some loss in vigor due to inbreeding of insects. This

Table 4. Interaction between location (phytotron, and field), and insect feeding time (2,4,8, and 24 hours). Mean Mexican bean beetle damage in cm2/leaflet.[1]

Insect feeding time	Location	
	Phytotron	Field
2 Hours	2.77 cd	1.94 g
4 Hours	2.96 c	2.15 f
8 Hours	3.48 b	2.44 e
24 Hours	5.51a	2.71 d

[1]Means with the same letter are not significantly different according to Duncan's multiple range test, 5% level.

Table 5. Interaction between insect feeding time (2,4,8 and 24 hours) and sex and number of insects (1 female, 1 male, 1 female and 1 male, and 2 females). Mean Mexican bean beetle feeding damage in cm2/leaflet.[1]

Insect feeding time	Sex and number of insects			
	1 Female	1 Male	1 Female & 1 Male	2 Females
2 Hours	2.48 f	1.69g	2.49 f	2.75 ef
4 Hours	2.66 f	1.79g	2.74ef	3.02 de
8 Hours	3.10 d	1.99g	3.16 d	3.61 c
24 Hours	4.39 b	2.58 f	4.43 b	5.02 a

[1]Means with the same letter are not significantly different according to Duncan's multiple range test, 5% level.

implication may be kept in view while using laboratory reared insects.

Sex and number of insects: There was significant difference in feeding damage except between 1 female, and 1 female and 1 male (Table 1). The lowest feeding damage was observed when 1 male, and the highest when 2 females were used. The feeding did not increase proportionately as expected when two Mexican bean beetles were used. One female showed the same feeding damage as 1 female and 1 male (which is approximately the ratio between females and males in natural populations). The feeding damage by a female was observed to 1.6X as compared with a male Mexican bean beetle. It has been reported that female Colorado potato beetles and Mexican bean beetles fed significantly more as compared with males both on resistant and susceptible plants of tomato and soybean, respectively (Schalk and Stoner 1976).

Insect feeding time: The feeding significantly increased with each increment of time (Table 1). The feeding increased 1.7X when Mexican bean beetles were allowed to feed 24 hours as compared with 2 hours.

Interactions: Significant interactions were observed between location and insect rearing (Table 2), location and sex and number of insects (Table 3),

location and insect feeding time (Table 4), and insect feeding time and sex and number of insects (Table 5).

There was no significant feeding difference under field conditions whether laboratory reared or natural populations of insects were used. However, natural populations as compared with laboratory reared insects fed significantly more in phytotron (Table 2).

The interaction between location and sex and number of insects showed somewhat same trend in phytotron as in field but the magnitude of feeding difference was significantly greater in phytotron than in field (Table 3). The interaction between location and feeding time was highly signficant (Table 4). There was no significant difference in Mexican bean beetle feeding between 2 hours in phytotron and 24 hours in field. Two hours of feeding time can be safely used for screening beans in phytotron.

There was a significant interaction between insect feeding time, and sex and number of insects (Table 5). A significant progressive increase, in feeding, except for 1 male, was observed after 4 hours. Two females in 4 hours fed the same as 1 female, and 1 female and 1 male after 8 hours. Significantly higher feeding as compared with any of the other treatments was observed in case of 2 females after 24 hours.

On the basis of this study 1 female Mexican bean beetle from natural populations can be used for 2 hours for screening beans in phytotron; whereas 2 female beetles from natural populations need to be used for 24 hours in field studies. Screening beans for resistance to Mexican bean beetle in phytotron is a reliable and rapid method.

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BREEDING SNAP BEANS (*PHASEOLUS VULGARIS* L.) FOR RESISTANCE TO THE MEXICAN BEAN BEETLE (*EPILACHNA VARIVESTIS* MULSANT.)

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The Mexican bean beetle (MBB) entered the U. S. from Mexico before 1850 (Pepper, 1945) and has spread throughout the southeastern states to the Atlantic coast. Both the adult and larval stages of the life cycle feed on foliage of several *Phaseolus* species (Wolfenbarger and Sleesman, 1961), as well as the cowpea (*Vigna unguiculata* (L.) Walp.) and the soybean (*Glycine max* (L.) Merr.). *P. vulgaris* L. is the preferred host species.

Adult beetles hibernate through the winter in dry sheltered areas near fields planted in beans the previous year. They emerge in early spring and begin to feed on young bean plants. They then mate, and after several days, lay eggs. Moderate numbers of over-wintered adults are not a serious threat to vigorously growing bean plants which can tolerate substantial defoliation without economic loss. The larval stage is more destructive and it is not uncommon to experience complete defoliation of a bean field if larvae are not controlled (Raina, 1978). Insecticides are recommended for control if large populations of over-wintered adults are present in bean fields in early spring. Insecticides give adequate control of both adults and larvae but genetic resistance would be more desirable due to economic and environmental factors.

Plant Introduction (PI) 169903 has an intermediate level of resistance to MBB larval feeding (Wolfenbarger and Sleesman, 1961) when compared with several other *Phaseolus* species and *P. vulgaris* cultivars. We have tested about 400 lines each year for 3 years and have confirmed that PI 169903 sustained less feeding damage than other lines in adjacent plots. Adults and larvae will feed on PI 169903 but initiation of feeding is delayed and foliage is retained longer than on other lines.

PI 169903 has an indeterminate growth habit, short fibrous pods, late maturity and is not acceptable as a commercial cultivar. Our objective was to incorporate MBB resistance into a horticulturally acceptable type using a breeding system based on testing genetically stable lines.

We crossed PI 169903 with the commercially accepted cultivar 'Bush Blue Lake Supreme' and grew the F_1 in the greenhouse. Field selections were made in F_2 for determinate habit and in F_3 for round, stringless pods and acceptable yield. Seeds from 70 single F_3 selections were increased as F_4 progeny rows to produce F_5 families for screening in 1979.

The F_5 lines were tested at 3 locations in randomized complete blocks with 6 replications. The number of lines at each location was dependent on F_5 seed supply; 70 lines were tested at the U. S. Vegetable Laboratory (VL), 47 lines were tested at Virginia State University (VS), and 22 lines were tested at the Edisto Experiment Station (ES). Plots consisted of 25 seeds planted in 1-meter rows. Feeding damage estimates were begun when the 2nd trifoliate leaf was expanding and adult beetles were actively feeding. Damage estimates were made at VL 2 times, at ES 4 times and at VS 1 time. Plots were rated on a scale of 1 to 5 with 1 = slight feeding damage and 5 = severe feeding damage. Data were analyzed after damage estimates were transformed to $\sqrt{n + 1}$. Significant differences between means were based on $LSD_{.05}$.

We found that several lines at all locations and at all evaluation dates had resistance equal to or greater than that of PI 169903 (Table 1). The resistant breeding lines responded in a manner similar to PI 169903; a small amount of early-season damage was seen on resistant lines compared to susceptibles but as the season progressed, susceptible lines were defoliated while resistant lines retained some foliage. As larval populations increased and larvae became larger, lines with resistance finally were consumed. We have not observed antibiosis on resistant lines; resistance is probably due to non-preference factors.

Table 1. F_5 snap bean breeding lines with resistance equal to or greater than PI 169903 at three locations, 1979.

	VL[1]		VS[2]	ES[3]			
	Evaluation date		Evaluation date	Evaluation date			
	5-17	5-29	6-26	5-23	5-30	6-13	6-21
No. of F_5 lines tested	70	70	47	22	22	22	22
No. of lines with resistance PI 169903[4]	15	39	14	18	1	13	1
Mean damage score of resistant lines	2.34	2.53	1.95	2.83	1.70	2.46	2.00
Mean damage score of susceptible lines	2.88	2.93	2.50	3.88	3.05	3.59	3.83
Mean damage score of PI 169903	2.10	1.60	1.33	2.50	2.70	1.83	1.17
% of lines with resistance PI 169903	21.4	55.7	29.8	81.8	4.5	59.1	4.5

[1]U. S. Vegetable Laboratory, Charleston, SC.
[2]Virginia State University, Petersburg, VA.
[3]Edisto Experiment Station, Blackville, SC.
[4]Breeding line means compared to PI 169903 mean by $LSD_{.05}$.

Several lines were resistant at multiple locations and evaluation dates (Table 2). This gives some indication of the effectiveness of this resistance in diverse environments.

Table 2. Selected F_5 snap bean lines with resistance to the Mexican bean beetle at multiple locations and evaluation dates.

Line number	Location and date with resistance PI 169903[1]	Mean damage score[2] Resistant line	PI 169903
49	1, 2, 3	1.79 ns[3]	1.68
53	1, 2, 4, 6	1.96 ns	2.01
61	1, 2, 4, 5, 6	2.03 ns	2.15
64	2, 3, 6	2.03 ns	1.59
65	2, 4, 6, 7	2.10 ns	1.78

[1] 1 = VL, 5-17-79, U. S. Vegetable Lab., Charleston, SC.
2 = VL, 5-29-79, U. S. Vegetable Lab., Charleston, SC.
3 = VS, 6-26-79, Virginia State University, Petersburg, VA.
4 = ES, 5-23-79, Edisto Experiment Station, Blackville, SC.
5 = ES, 5-30-79, Edisto Experiment Station, Blackville, SC.
6 = ES, 6-13-79, Edisto Experiment Station, Blackville, SC.
7 = ES, 6-21-79, Edisto Experiment Station, Blackville, SC.

[2] 1 = slight feeding damage, 5 = severe feeding damage.

[3] ns = not significantly different from PI 169903 mean at each location and evaluation date. Means compared by $LSD_{.05}$.

The advantage of snap bean cultivars with MBB resistance is that insecticidal applications may be delayed or deleted. This will result in reduced chemical residues in the environment, a more favorable balance of predators and parasites in bean fields, and a lower cost of applying insecticides.

Several factors may be involved which result in higher levels of MBB resistance. These may include chemical attractants or repellents produced by the plants, decreased ovipositional preference by the insect or interference with adult and larval development. The resistant lines developed as a result of this study will be useful in further research on the nature of MBB resistance.

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VARIABILITY OF THE NET REPRODUCTIVE RATE OF CLONES OF THE PEA APHID ON LUCERNE

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The demonstration of genetic causes in plant resistance to insects leads to the question of the stability of the resistance. This stability is dependant on the variability of insect species. In our study of the Lucerne (Medicago sativa L.) resistance to the pea aphid (Acyrthosiphon pisum HARR.) we have observed, on different occasions that the varietal aptitude of cultivars selected in North America are not always maintained in our tests. Although we have not done a systematic screening of numerous varieties, we have noted variations in the classment, either under controled conditions or in the field. These constatations have led us to estimate the variability of the pea aphid on three levels : between populations, in a single population and in the descendance of one virginoparous female.

METHODS

All the experiments stated in this note were conducted in a growth chamber at a temperature of 20° ± 2 and a photophasis of 16 hours. We have previously described the methods of assessing resistance. This is done by an "antibiosis test" which evaluates the net reproductive rate of 4th stage larvae bred during two weeks (BOURNOVILLE et COMTE, 1977). The variability between populations was studied on aphids sampled in Lucerne fields from Normandy, Center West and South West of France. Twenty-one clones were randomly obtained by breeding one virginoparous female of each origin. The variability within a population was tested on twenty seven clones originating from one local population of the pea aphid, found in Lucerne fields of Centre de Recherches de Lusignan (near Poitiers). The variability in the descendance of a single clone was tested on the nineteen descendants of one 4th stage larva isolated from this population.

One of the main difficulties when studying variability in aphids is to prevent variations caused by environment. We bred aphids on a plant as constant as possible. It was too fastidious to obtain a suffisant number of plants by cloning a single plant so we used a multiplied hybrid of Lucerne called "Milfeuil" which has a narrow genetic basis. Each 4th stage larvae was placed in an aerated plastic box of 720 cubic centimeters at the top of a stem of Lucerne which was at least at budding stage. Mortality and fecundity were controled at the end of the first and second week of breeding. As we evaluated the reproductive rate of aphids we had to prevent the variations related to the condition of the parents of the aphids tested. MURDIE in two publications (1969 a, 1969 b) demonstrated that temperature and overcrowding are the main causes of reduction in fecundity. This author noticed that recovery from size decrease caused by overcrowding is accom-

plished in about one generation but recovery from undesize caused by high temperatures requires two generations. We have already mentionned the controled conditions of the growth chamber. Overcrowding was avoided by keeping aphids alone with their own descendance born each week of experiment. We tried to eliminate the possible deleterious effects induced by the parents and grand-parents of the aphids tested by breeding three successive generations of aphids according to the general protocol, before testing the different strains. The larvae begining each of these generations of homogeneization were taken at random and weighted one by one to estimate the condition of the clone. The Lucerne variety used during this phasis was "Europe", which is a variety of reference in our tests for resistance evaluation.

RESULTS AND DISCUSSION

The mean net reproductive rate (N.R.R.) of pea aphids are presented in table 1.

Table 1

Mean net reproductive rates (N.R.R.) of 4th stage pea aphid larvae bred during two weeks on the lucerne hybrid "Milfeuil"

	N. R. R.	
STUDY ON VARIABILITY	MEANS ± CONF. LIMITS	VARIANCE
IN A CLONE	71,1 ± 3,7	53,8
INTRA - POPULATION	48,0 ± 9,5	576,0
INTER - POPULATIONS	42,9 ± 11,9	675,0

The variability of N.R.R. among clones isolated from different origins is very important as expressed by large variance. The same constatation must be made about the variability of N.R.R. in a local population. The comparison of these two variances is not significant ($F = 1,17$). The N.R.R. of the descendants of a single parthenogenetic female is as expected much more homogeneous as the variance is ten times less. The weights of the larvae during the phasis of homogeneization are presented in table 2. For the descendants of our local population the weights of which were increased threefolds, it is very clear that the care taken in breeding the aphids allowed improvment in the physiological conditions of the clones. The mean initial weights of the clones coming from different populations were rather high for "natural" populations, but it decreased a little during the phase of homogeneization.

Table 2

Mean weights ± conf. limits (mg) of

4th stage larvae during the successive generations

EXPERIMENTS ON VARIABILITY :	GENERATION TESTED (N)	GENERATIONS OF HOMOGENEIZATION N-1	N-2	N-3
IN A CLONE	2,55 ± 0,31	Already homogeneized		
INTRA-POPULATION	1,67 ± 0,16		1,20 ± 0,10	0,58 ± 0,09
INTER-POPULATIONS	1,27 ± 0,23	1,80 ± 0,41	1,39 ± 0,16	1,53 ± 0,29

The clone tested in "intra-clonal" experiments had been bred for several generations in good conditions as shown by the high initial weight. The weight is not always in correlation with N.R.R., because N.R.R. is the result not only of fecundity but also of mortality of aphids. DEWAR (1977) has shown in cereal aphids that their weight is correlated with embryo number.

These results prove once more the great heterogeneity of populations of aphids. They prove also that variability is expressed as well in clones coming from only one local population as in clones coming from several populations. In fact, the west part of France has no main geographical separations and the populations gathered on different part are similar as far as reproductive capacity is concerned. The implication of the similarity in the variability between intra-population and inter-population strains is that the estimation of the risk of resistance overstepping can be estimated, at the level of the geographic region already mentionned, for example, by using a local population (but not a clone). We must also insist about methodology, in other words on the necessity of using stocks of aphids which can express totally their performances.

Biotypes of the pea aphid are not a problem in Lucerne production in the United States (SORENSEN & al., 1972), although CARTIER & al. (1965) tested ten Lucerne clones for resistance with different strains of pea aphids originating from KANSAS and QUEBEC which showed sometimes biological differences. More numerous are the studies about the biological variations in pea aphid populations in host-plant preference that is at the plant species level.

Our results do not explain the changes observed in France in the classification of varieties labelled "resistant" or susceptible by North

American authors. In fact, pea aphid was introduced on America and recorded in KANSAS in 1877 and it could be as for the ulterior case of Therioaphis maculata BUCK, that only a genetically limited stock of aphids was introduced. Recently, AUCLAIR (1978) has bred several clones of the pea aphid coming from four regions of North America (from New Mexico to Quebec) and two from our laboratory. On Pea plant (variety Lincoln)but not on artificial diets, the French clone of green form of the pea aphid was rather comparable to a clone originating from Quebec but different in all cases from clones coming from Kansas and New Mexico.

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APHID RESISTANCE IN VICIA IN RELATION TO NON-PROTEIN AMINO ACIDS

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INTRODUCTION

Resistance to major pests is found in some cultivars of most crop plants. The extent and nature of this resistance is less well known. The potential of resistant cultivars as components of integrated pest control can be more readily assessed with a knowledge of the causes of resistance and their effect upon pest species. Further, knowledge of aphid resistance in wild plant species has potential in the use of such plants as germ plasm in plant breeding programmes.

In this paper, the extent of resistance in the genus Vicia (the vetches) including cultivars of V. faba to two major aphid pests, Acyrthosiphon pisum Harris (pea aphid) and Aphis fabae Scop. (black bean aphid) is described. Antibiotic resistance has been measured largely in terms of the aphids' development time, reproduction and survival.

Investigation of the plant attributes making a possible contribution to resistance in Vicia has so far concerned amino compounds. A range of rare non-protein amino acids has been found in Vicia seeds (Bell and Tirimana, 1965) and several of these amino acids have been found to be toxic to insects (Janzen et al., 1977). In addition, protein amino acids are well known for their role in aphid feeding (van Emden and Bashford, 1974). The establishment of links between resistance to insects and the physical or chemical properties of the host is valuable, both in understanding the nature of the resistance process and as a means of detecting resistant host plants other than by laborious bioassay techniques, which can produce variable results.

From the points of view of both integrated pest control and plant breeding, the taxonomic distribution of resistance and of implicated chemicals is of interest.

The genus Vicia, comprising approximately 140 spp., is divided in the most recent classification (Kupicha, 1976) into two subgenera, each with a number of sections. So far there has been no success in efforts to cross V. faba with other members of the section Faba. V. narbonensis, a member of the section Faba is reported as resistant to Aphis fabae (Bond and Lowe, 1975), and to contain three rare amino acids in its seeds (Bell and Tirimana, 1965).

In the project described here, leaf extracts of 10 Vicia spp. and 6 V. faba cultivars have so far been examined, both for protein and non-protein

amino acids. A possible link between patterns of aphid resistance and host plant amino acids is being examined.

METHODS

1. Bioassay experiments

a) Laboratory. All experiments were carried out in controlled environment culture boxes (Scopes et al., 1975) with a mean temperature of 20°C ranging from 19°C to 21°C. Wherever possible, comparative aphid performance between Vicia spp. was measured on plants of similar age, growth stage and condition. Performance data was obtained for clonal, virus-free Aphis fabae and Acyrthosiphon pisum reared on Vicia faba cv. The Sutton. Individual aphid adults were confined to middle-aged leaves in clip-cages (Noble, 1958). The number of progeny produced was monitored for 25 days on test host plants. Published work indicates that adult 'teneral' (up to 24 hour old) weight and embryo complement (total and pigmented-eyed, i.e. largest) can be used to predict aphid fecundity on test cultivars. (Dewar, 1977; Wratten, 1977). However more recent work (Kempton, Lowe and Bintcliffe, in press) has shown that the relationships between weight and embryo complement, and between weight and fecundity, differ between cultivars i.e. an aphid weighing 1 mg may not be equally fecund on all cultivars within a species. Wherever possible in this work, therefore, nymphal survival and development time, adult reproductive delay, survival and daily reproduction were recorded on each replicated host. These data were used to calculate daily intrinsic rates of increase, r_m (Birch, 1948).

b) Field. Individual adult Aphis fabae (P.B.I. 'Cogs' clone reared on cv. The Sutton) were caged on eight replicated cultivars of Vicia faba arranged in a randomized block design. Nymphal production was then monitored over a 3-day period to assess field fecundity.

2. Chemical methods

a) Amino acid extraction. Leaves of age and condition similar to those used in bioassay experiments were selected for extraction of amino compounds, using a 3 stage ethanolic extraction method (Przybylska and Rymowicz, 1965). Prior to separation, extracts were desalted using Dowex 50W-X8 resin (Smith, 1969).

b) High voltage electrophoresis. Charged amino compounds were separated using a pyridine: acetic acid: water buffer of pH 3.6 run at 4 400 v. for 30 minutes (Bell and Tirimanna, 1965).

c) Two-dimensional paper chromatography. Neutral amino acids were separated using butan-1-ol: acetic acid: water as the first solvent and phenol: ammonia as the second (Smith, 1969).

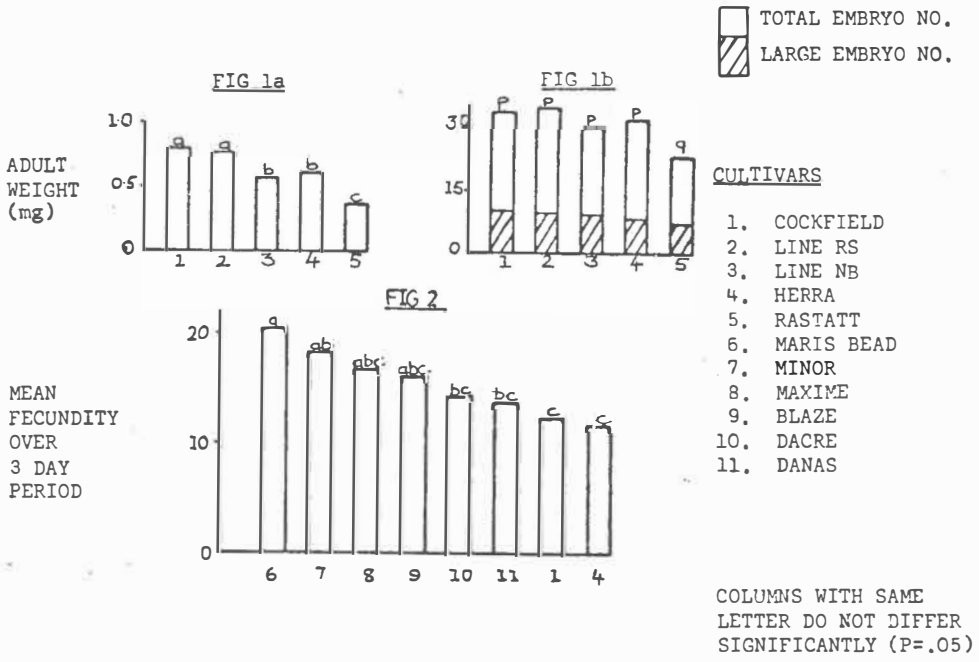
d) Identification of chemicals. Substances separated were identified, where possible, by comparison of Rf values with standards, by colour reactions with general amino acid reagents (Ninhydrin, Erlich reagent, Sakaguchi reagent, fluorescence under U.V.) and with specific reagents such as P.C.A.F. (Smith, 1969). Standards of protein amino acids and some non-protein amino acids were obtained commercially, whilst 7 rare non-protein amino acids of

the Vicieae were kindly supplied by Professor E. A. Bell.

RESULTS

1. Aphid bioassay. A screen of 5 Vicia faba cultivars using Aphis fabae produced similar trends when using either mean teneral weight or embryo complement as a measure of aphid performance. The range of mean teneral weight was from 0.75 mg (cv.Cockfield) to 0.45 mg (cv.Rastatt). The range in total embryo complement was from 33 (cv.Cockfield) to 23 (cv.Rastatt). Analyses of variance of these results are shown in Fig. 1.

FIGS 1 & 2 WEIGHTS, EMBRYO COMPLEMENTS, AND FECUNDITIES OF APHIS FABAE ON VICIA FABA CULTIVARS

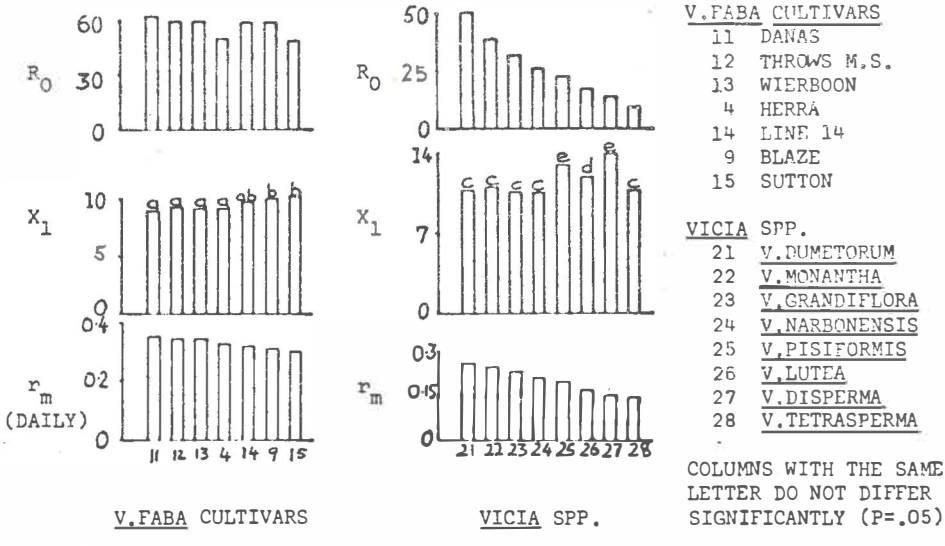


In the field there was a 1.8-fold difference between 3-day nymphal production on the most susceptible (cv Maris Bead) and moderately susceptible (cv.Herra) Vicia faba cultivars. Results for the analysis of variance for 8 cultivars examined in the field are shown in Fig. 2.

A more complete assessment of aphid performance was obtained by measuring additional parameters of population growth. These experiments produced a range of mean progeny number (R_o), mean pre-reproductive period (X_1) and intrinsic rate of natural increase (r_m) for Acyrthosiphon pisum on

7 Vicia faba cultivars and 8 Vicia spp. (Fig. 3). Estimates of r_m were based on 10 days' nymphal production by adults reared on the test species. Increases in r_m obtained by incorporating fecundity after this period were found to be less than 2%.

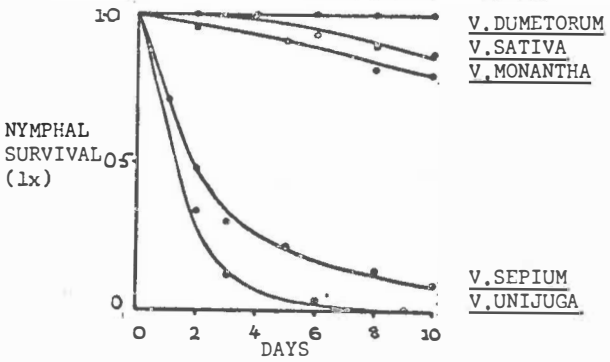
FIG 3 RATES OF INCREASE FOR ACYRTHOSIPHON PISUM ON VICIA FABA CULTIVARS AND OTHER VICIA SPP.



Analysis of variance of the results for X_1 are also shown in Fig. 3. A greater range of r_m values was found between wild Vicia spp. (0.26 to <0) than between Vicia faba cultivars (0.35 to 0.30). The highest r_m on the most susceptible wild Vicia species (V. dumentorum L., r_m = 0.268) was markedly lower than the r_m value on the least susceptible cultivar (cv. The Sutton, r_m = 0.30). The complete range of resistance in wild Vicia spp. is not shown in Fig. 3. because very high (80% - 100%) nymphal mortality in the highly resistant species (V. sepium L., V. unijuga A. Braun, V. cassubica L., V. articulata Hornein) prevented calculation of r_m values.

Survival rates from birth(l_x) of A. pisum nymphs on moderately susceptible and resistant wild Vicia spp. are shown in Fig. 4. Values of l_x (for 10 day old nymphs) range from 1.00 to 0.80 for moderately susceptible wild species to 0.20 to 0.0 for the highly resistant wild species previously mentioned. This compares with a range of 1.00 to 0.65 for V. faba cultivars.

FIG 4 NYMPHAL SURVIVAL RATES FOR ACYRTHOSIPHON PISUM ON VICIA HOSTS



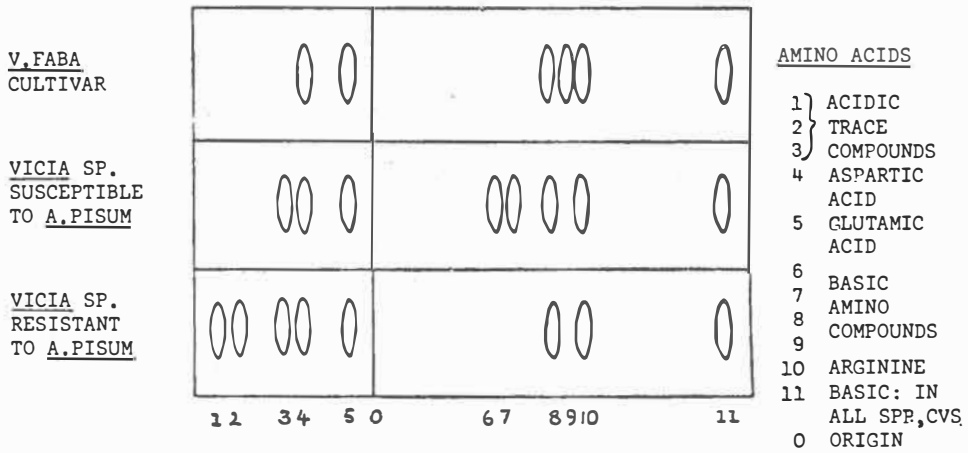
2. Amino acids in leaves. Leaves of 10 wild Vicia spp. and 6 V. faba cultivars have been screened for amino compounds using high voltage electrophoresis. The results (of which Fig. 5 is a typical example) show:

a) that a small number of protein amino acids are present in high concentration in all the leaves (glutaimic and aspartic acids and arginine)

b) that the wild Vicia spp. show variations in the presence or absence of several amino acids not found in V. faba cultivars. However, it is also clear that the full range of non-protein amino acids recorded for Vicia spp. seeds (Bell and Tirimanna, 1965) have not been detected in the leaves.

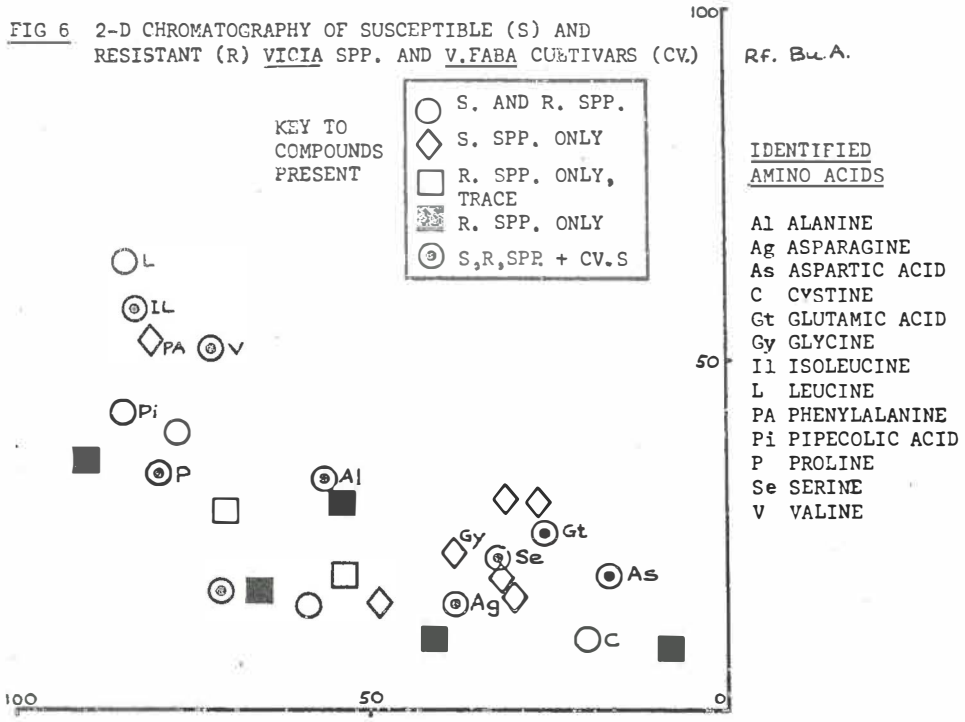
c) that a small number of as yet unidentified amino compounds are present in low concentration in the highly resistant wild species.

FIG 5 H.V.E.P. AMINO ACID ANALYSIS OF VICIA SPP. LEAF EXTRACTS. SUMMARY DIAGRAM.



Work is now in progress to complete the identification of all the substances isolated by HVEP and to discriminate between the neutral amino acids (omitted from Fig. 5) by two-dimensional paper chromatography Amino compounds of 2 V. faba cultivars, two moderately susceptible wild Vicia spp, and two resistant wild Vicia spp, are shown in Fig. 6. Unidentified amino compounds have been given a number.

FIG 6 2-D CHROMATOGRAPHY OF SUSCEPTIBLE (S) AND RESISTANT (R) VICIA SPP. AND V.FABA CULTIVARS (CV.)



CONCLUSIONS

Measurements of aphid fecundity, development time and survival reveal that consideration of any one of these alone is misleading in predicting population growth on the host. Differences in fecundity are not always paralleled by differences in development time. For aphids reared on V. faba cv. Herra, low fecundity is compensated for by short development time so that the rate of population increase (measured by r_m) is not as low as would be expected from fecundity measurements alone (Fig. 3). The contributions made by fecundity, survival and development time differ with the degree of

resistance of the host. Differences in r_m for aphids on different cultivars of V. faba are paralleled closely by development time. In contrast, differences in r_m between more resistance Vicia spp. show more relation with survival and fecundity data (Ro; Fig. 3).

Although the link between host protein and non-protein amino acids and aphid resistance is so far circumstantial, it is hoped that a clear pattern will emerge as the study proceeds and multivariate analyses of the data can be carried out.

We are grateful to Professor E. A. Bell for advice and for supplying some rare amino acids and to Dr. D. A. Bond for advice and for supplying some V. fabae cultivars.

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NONACCEPTANCE OF MELON TO APHIS GOSSYPII, ITS INHERITANCE AND RELATION TO ANTIBIOSIS, TOLERANCE AND RESISTANCE TO VIRUS TRANSMISSION

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Resistance of melon (*Cucumis melo* L.) to *Aphis gossypii* Glov. has been intensively investigated for ten years by G.W. Bohn, A.N. Kishaba and coworkers (Bohn et al., 1972 and 1973 ; Kishaba et al., 1971 and 1976). Nonpreference, antibiosis and plant tolerance have been reported and inheritance of antibiosis and tolerance has been studied. We become interested in this aspect of insect resistance after the discovery of resistance to cucumber mosaic virus (= CMV) transmission by *A. gossypii* (Lecoq et al., 1979).

In this communication we report some data on the inheritance of nonacceptance and on the relation between nonacceptance and resistance to virus transmission. We prefer to use the word "nonacceptance" instead of "nonpreference" because "preference" suggests a choice between two plants. In our trials this form of resistance is effective even with no alternative source of food.

This study includes two independent experiments : in the first one, plants were tested for nonacceptance and 1 to 3 hr later for resistance to CMV transmission ; in the second one plants were tested for nonacceptance and aphids allowed to develop for 1 wk to evaluate tolerance (freedom from leaf curling). Plants were then fumigated with an aphicide and 1-2 months later they were tested for antibiosis.

Nonacceptance was appreciated on plantlets (15-20 days after sowing) by the number of adults remaining 24 hr after the deposit of 10 young adult apterae per plant. Virus transmission was achieved by two inoculations with 4 viruliferous adult apterae each per plant. Antibiosis was measured by the number of larvae produced for 3 days by 4 young adults placed in a leaf cage (2 cages per plant).

Inheritance of nonacceptance and relation with resistance to CMV transmission

On PI 161375 (= Songwhan charmi = SC), aphids present a strong tendancy to leave the plants soon after their deposit whereas on Doublon almost all the aphids remain on the plants (Fig. 1). We have analysed F_1 (SC x Doublon), F_2 and BC_1 (F_1 x Doublon) generations for this character. Plants with 8 or more adults per plant are rated as susceptible for nonacceptance and plants with 7 or less adults per plant as resistant. The F_1 generation is resistant, the F_2

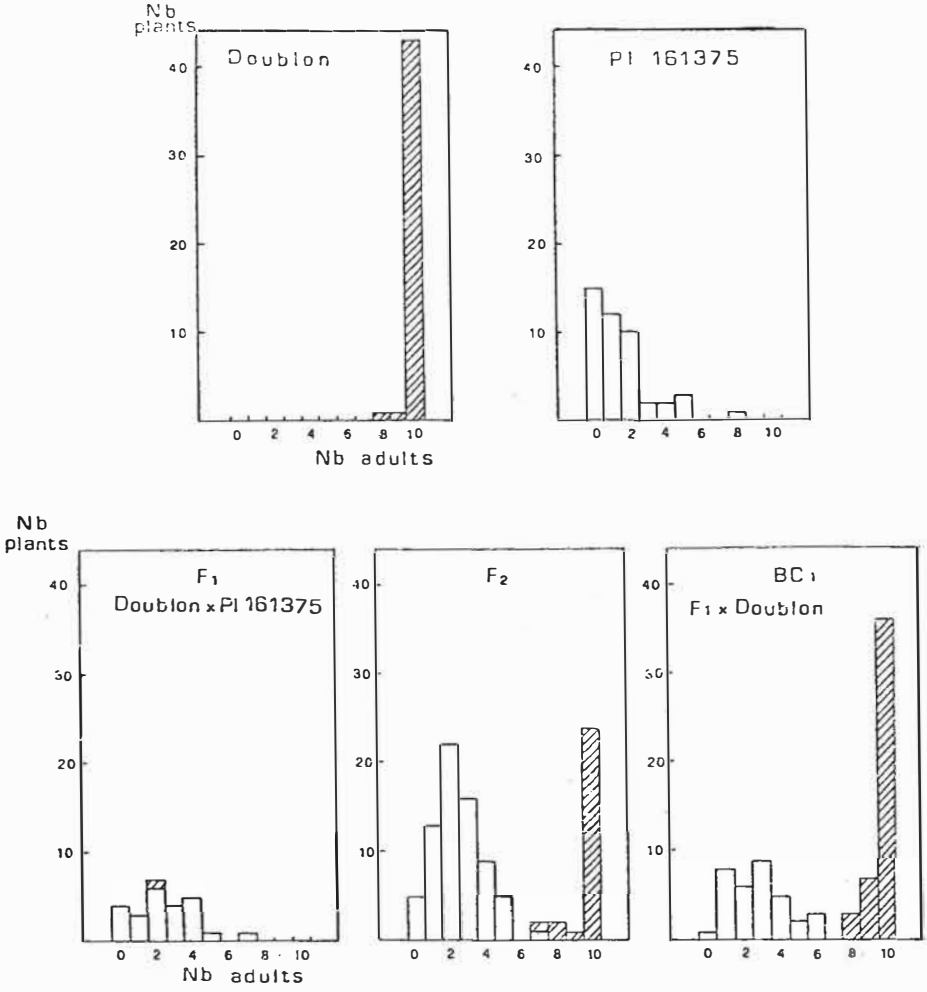

Figure 1. Relationship between nonacceptance (number of adults remaining 24 hr after the deposit of 10 adults per plant) and resistance ☐ or susceptibility ▨ to CMV transmission by *Aphis gossypii*.

segregates 3 resistant : 1 susceptible (χ^2 = 0.853 ; 0.30 < Prob. < 0.50) and the BC_1 generation segregates 1 resistant : 1 susceptible (χ^2 = 1.800 ; 0.10 < Prob. < 0.20) (Fig. 1). It can be concluded that nonacceptance is controlled by one dominant gene.

SC is resistant to CMV transmission by A. *gossypii* (Lecoq et al., 1979) and Doublon is susceptible. In the F_1 generation all plants but one are resistant to CMV transmission. In the F_2 and BC_1 progenies all the plants which are susceptible for nonacceptance are susceptible for CMV transmission and all the plants but one which are resistant for nonacceptance are resistant to CMV transmission. These two plants may represent cases where resistance to CMV transmission is broken. Therefore the gene controlling nonacceptance appears to also control resistance to CMV transmission.

Genetic relation between nonacceptance, antibiosis and tolerance

On Doublon the mean number of larvae produced in test for antibiosis is 100.7. On PI 414723 this mean number is 4.5. This line resistant by antibiosis is also resistant by nonacceptance (Fig. 2). In the segregating F_2 and BC_1 progenies, very few plants can be considered as recombinants ie susceptible for nonacceptance and resistant for antibiosis or resistant for nonacceptance and susceptible for antibiosis. It cannot be excluded that these plants represent cases of escapes to infection. These "recombinant" plants have been kept and will be selfed to check this hypothesis.

Kishaba et al. (1976) demonstrated that in line 90234 (= PI 414723), antibiosis is controlled by a major dominant gene but minor additional genes have a slight effect on the antibiosis level. According to our first results it seems that the gene governing nonacceptance and the major gene for antibiosis are the same gene or are very closely linked.

Bohn et al. (1973) reported that tolerance (freedom from leaf curling following mass infestation) is under the control of a single dominant gene (symbol Ag). Breeding line 90386 is susceptible for nonacceptance and antibiosis but leaves remain flat following aphid infestation. The gene for nonacceptance is therefore not the Ag gene for melon aphid tolerance.

Our program was initiated to search different mechanisms of resistance to CMV. In this study we demonstrated that resistance to CMV transmission by A. *gossypii* and nonacceptance to this aphid are controlled by a single dominant gene. The first results reported here suggest that this gene is also effective for antibiosis but is different from the gene for tolerance.

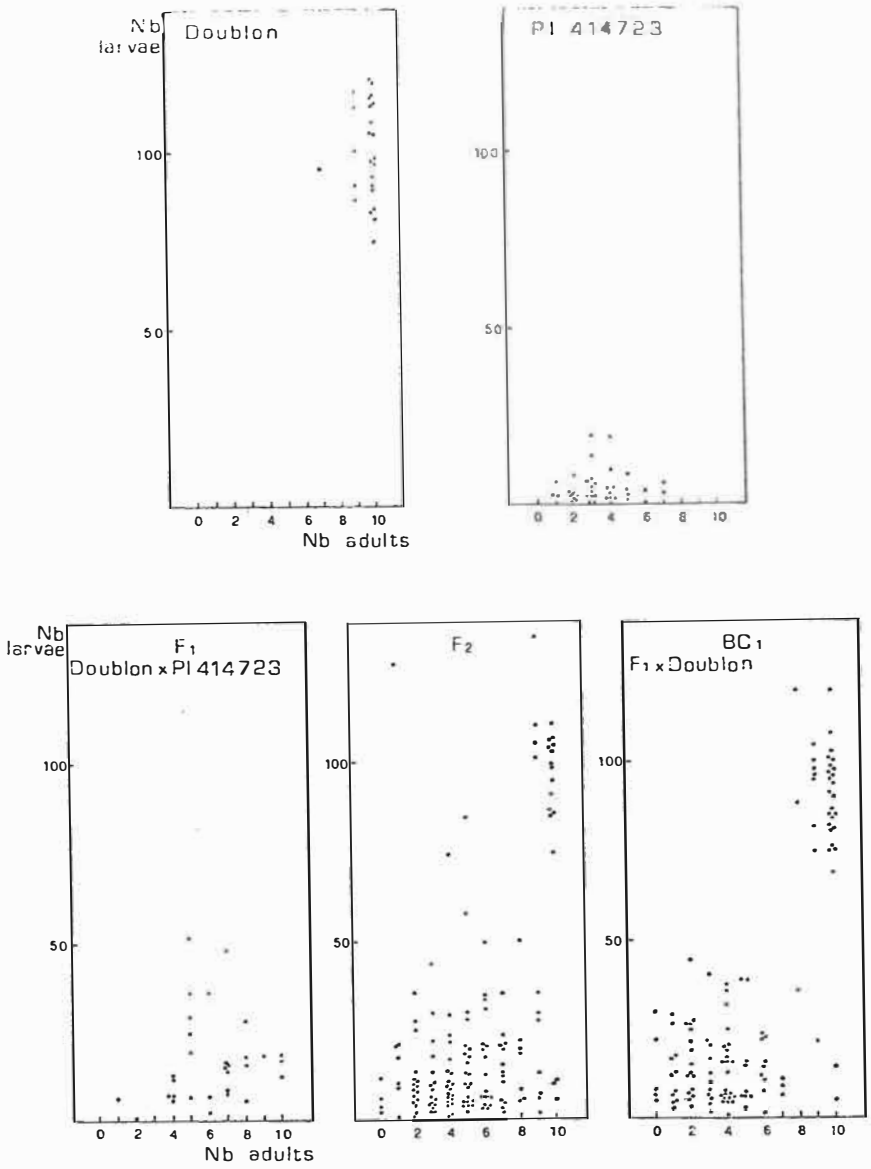

Figure 2. Relationship between nonacceptance (number of adults remaining 24 hr after the deposit of 10 adults per plant) and antibiosis (number of larvae produced for 3 days by 4 adults).

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RESISTANCE TO VIRUS TRANSMISSION BY APHIDS IN A CUCUMIS MELO LINE PRESENTING NONACCEPTANCE TO APHIS GOSSYPII

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INTRODUCTION.

Aphid stylet borne viruses cause every year important damages to the muskmelon (*Cucumis melo* L.) crops in southeastern France. Among them cucumber mosaic virus (CMV) is the most widely spread, and field muskmelons often may show a 100 % CMV contamination rate by the middle of June (Messiaen et al., 1963 ; Quiot et al., 1979).

Watermelon mosaic virus II (WMV II) is also frequently encountered in muskmelons (Luis Arteaga et al., 1976), and it may severely reduce the fruit yield in the case of early infections.

In order to reduce the incidence of CMV in muskmelon, Risser et al. (1977) have started a breeding program to introduce into the Charentais type muskmelons the oligogenic recessive resistance to CMV "Common" strains found in P.I.161375 (= Songwhan Charmi = SC). However CMV strains able to infect systemically SC have been isolated from naturally infected weeds and vegetables. Indeed, 35 % of 1124 CMV isolates tested were observed to produce in SC symptoms ranging from light mottle to severe mosaic. These strains have been grouped in the "Song" pathotype (Leroux et al., 1979).

In the course of search for other mechanisms of resistance to CMV, a resistance to the transmission of CMV by *Aphis gossypii* Glov., a major CMV vector, has been observed in SC (Lecoq et al., 1979). This variety was also found to present nonpreference or nonacceptance to *A.gossypii* (Pitrat and Lecoq, 1980). In contrast, Cantaloup Charentais (= CH), as the other varieties commercially grown in France,was susceptible to CMV transmission by *A.gossypii*.

TESTING PROCEDURE.

After a 2 to 4 hours starvation period groups of 10-15 apterous adult aphids were placed in small leaf cages, which were then affixed for 3.5 minutes to young infected CH leaves. CMV-14, a strain belonging to the "Song" pathotype, was inoculated to the CH plants serving as virus sources for the aphids 6-9 days before the transmission experiments, while for the WMV, a 14-18 days incubation period was allowed. After the acquisition period, the cages were removed, and the aphids found in probing position were carefully picked up and transferred with a camel hair paint brush to the test plants. Unless otherwise stated, three viruliferous aphids were deposited per test plant and plants were inoculated at the first leaf stage. In order to randomize the experimental conditions, aphids were alternatively deposited on CH and SC plants. At least 3 hours after the exposure to

viruliferous aphids plants were fumigated with an aphicide. Then, plants were maintained in an insect proof greenhouse at 18-25°C and were periodically fumigated with aphicides.

Results were analyzed by the Wilcoxson test. For a detailed description of the aphid productions and of the virus strains used in this study see Lecoq et al., 1979, 1980.

RESULTS.

1 - Resistance to CMV-14 transmission by *Aphis gossypii*.

CMV-14 when inoculated mechanically induces severe mosaic symptoms in SC and CH. When the same virus strain is inoculated to the same varieties by *A.gossypii*, only CH plants become infected (Table 1). Indeed, in conditions where almost all the CH plants are virus infected (3 viruliferous aphids per test plant) no SC plant shows mosaic symptoms. However when large amount of viruliferous aphids (10) are deposited on young SC test plants, a limited number of them may become infected (10 %).

Table 1 : Comparison of the susceptibility of Songwhan Charmi (= SC) and Cantaloup Charentais (= CH) melons to CMV-14 transmission by *A.gossypii*.

Number of viruliferous aphids per test plant	Number of plants inoculated	Transmission rate to CH	Transmission rate to SC	Probability of equality
1	100	64 %	0 %	P < 0.005
3	50	96 %	0 %	P < 0.005
10	30	100 %	10 %	P = 0.025

This resistance which is expressed at the first leaf stage is also efficient when test plants are older : when 5 viruliferous aphids were deposited on the youngest leaves of plants at the 4 to 5 leaves stage respectively 56 CH and 0 SC plants of 60 inoculated developped mosaic symptoms.

When alate *A.gossypii*, instead of apterous adults are used for the transmission experiments, SC maintains its resistance ; in experiments where 30 CH and 30 SC plants were each inoculated with 3 viruliferous alate *A.gossypii*, respectively 24 CH and 0 SC became virus infected.

In order to determine whether the resistance to CMV-14 transmission by *A.gossypii* is independent or not from the oligogenic recessive resistance to CMV "Common" strains previously described in SC by Risser et al. (1977), several varieties were tested for these two characters. Table 2 indicates that 4 groups of varieties were found (1) those, as CH, possessing none of the resistance characters (2) those, as SC, possessing both of them (3) those, as L.J.90436, possessing only the resistance to CMV "Common" strains and (4) those, as P.I.414723, possessing only the resistance to CMV transmission by *A.gossypii*. These results suggesting the independence of the two resistance characters have been further confirmed by the study of the inheritance of the resistance to CMV transmission by *A.gossypii* (Pitrat and Lecoq, 1980).

Table 2 : Response of *C.melo* varieties to mechanical inoculation of CMV "Common" and "Song" strains and to CMV "Song" strains transmission by *A.gossypii*.

Variety	Mechanical inoculation of : CMV "Common" strains	CMV "Song" strains	Transmission of CMV "Song" strains by *A.gossypii*
Cantaloup Charentais (= CH)	S°	S	S
P.I.161375 (= SC)	R°°	S	R
L.J.90436	R	S	S
P.I.414723	S	S	R

° S = susceptible °° R = resistant

2 - Specificity of the resistance to virus transmission.

CMV is transmitted by over 60 aphid species (Kennedy et al., 1963). In our conditions *A.gossypii* prevails and may be regarded as one the most efficient and most frequent CMV vectors (Laboune unpublished). However other aphids are involved in the epidemiology of cucumber mosaic virus. Therefore it was of particular interest to determine whether SC was also resistant to CMV-14 transmission by other aphids. Table 3 indicates that although SC was still resistant to CMV-14 transmission when a clone of *A.gossypii* from Guadeloupe (French west Indies) was used as vector, *Myzus persicae* Sulz., *A.citricola* V.D.Goot, *A.craccivora* Koch. and *A.fabae* Scop were able to transmit CMV-14 to SC.

Table 3 : Comparison of the susceptibility of Songwhan Charmi (=SC) and Cantaloup charentais (=CH) melons to CMV-14 transmission by different aphid species.

Aphid species	Number of plants inoculated	Transmission rate to CH	SC	Probability of equality
Aphis gossypii	50	96 %	0 %	$P < 0.005$
A.gossypii (Guadeloupe)	60	68 %	2 %	$P < 0.005$
Myzus persicae	75	67 %	45 %	$P < 0.025$
A.fabae	30	13 %	7 %	$P > 0.05$
A.craccivora	60	18 %	12 %	$P > 0.05$
A.citricola	60	7 %	7 %	$P > 0.05$

Resistance to virus transmission by *A.gossypii* was observed by testing the transmission of CMV-14 by this aphid to SC. It was necessary to check whether this resistance mechanism would also be efficient to prevent (i) the transmission of other strains of CMV (ii) the transmission of other viruses infecting muskmelon and transmitted by *A.gossypii*. Therefore transmission tests were carried out using CMV-MG 18 and CMV-TEZ strains (both belonging to the "Song" pathotype) two strains of watermelon mosaic virus I (WMV I) and one strain of watermelon mosaic virus II (WMV II).

Table 4 indicates that SC was resistant to the transmission of all these virus strains by *A.gossypii*, although all of them were able to infect systemically SC following mechanical inoculation.

Table 4 : Comparison of the susceptibility of Songwhan Charmi (= SC) and Cantaloup Charentais (= CH) melons to the transmission of various viruses by *A.gossypii*.

Virus strain °	Number of plants incculated	Transmission rate to CH	SC	Probability of equality
CMV-14	30	90 %	0 %	P = 0.025
CMV-MG 18	15	100 %	0 %	-
CMV-TEZ	15	100 %	0 %	-
WMV I-FR	30	67 %	0 %	P = 0.025
WMV I-FWI	30	67 %	0 %	P = 0.025
WMV II-MAR	30	83 %	0 %	P = 0.025

° all virus strains were isolated in southeastern France, except WMV I-FWI, which was isolated in Guadeloupe (French West Indies). All of them induces mosaic symptoms in SC and CH after mechanical inoculation.

DISCUSSION.

Resistance to virus transmission in SC appears to be specific as far as the vector is concerned (i.e. it is efficient only when the vector is *A.gossypii)*, and to be not specific as far as the virus transmitted is concerned, providing that the vector is *A.gossypii* (i.e. it protects SC against CMV as well as against WMV I and WMV II when they are transmitted by *A.gossypii*). When *M.persicae*, *A.craccivora* or *A.fabae* are used as vectors they transmit CMV-14 with a better efficiency to CH than to SC (although the differences observed are not always significant at the 0.05 level). It is not yet known whether this is the result of a partial expression of the resistance to virus transmission by *A.gossypii* or of a partial expression of the resistance to CMV "Common" strains. The comparison of the behaviour of varieties possessing only one of these two resistance mechanisms will permit to clarify this point.

The efficiency of such a resistance in the field will obviously depend on a great variety of factors and *inter alia* :

- it will depend on the nature of the aphid population and particularly on the relative importance of *A.gossypii* among the whole vector population. It is likely to be of no pratical interest when *A.gossypii* is of limited importance as a virus vector (as it is the case in Southern California, Dickson et al., 1949), providing that the partial resistance observed with *M.persicae* is independent from the resistance to virus transmission by *A.gossypii*.

- it will depend on the effect of the resistance to *A.gossypii* by nonacceptance which is associated to the resistance to virus transmission (Pitrat and Lecoq, 1980) on the built up of *A.gossypii* populations and on the interplant movements of alate melon aphids. Indeed Kennedy and Kishaba (1976, 1977) observed that *A.gossypii* produced much smaller number of alates on plants resistant to this aphid (by nonpreference or nonacceptance, antibiosis and tolerance) than on susceptible melon varieties. Also they observed in greenhouse tests that interplant movements were more frequent on resistant than on susceptible melon plants.

- it will also depend on the frequency of the virus sources in the vicinity of the resistant plant field. When a large proportion of *A.gossypii* are viruliferous it is to be expected that the pression of the virus inoculum may be such that it will lead to resistance breaks as it has been observed when 10 viruli-

ferous aphids are deposited on young SC plants (table 1).

From this it appears that only field experiments done in various locations will lead to a proper evaluation of the agronomical interest of the resistance to virus transmission by *A.gossypii*. Although this type of resistance is partial, it may contribute to some extent to the protection of the crops and strenghten other forms of partial resistance such as the resistance to CMV "Common" strains.

The mechanisms which prevents *A.gossypii* to transmit CMV, WMV I and WMV II to SC is not yet known. However it should interfere with the first stages of the virus infection process. Indeed these viruses may readily infect SC following either mechanical inoculation or inoculation by an other aphid : eg.*M.persicae*. Observations of the behaviour of *A.gossypii* on SC show that this aphid starts quickly to probe when deposited on these plants : an additional proof of this is that *A.gossypii* is able to acquire CMV-14 from infected SC plants after a short acquisition period (Lecoq et al., 1979). Therefore when a viruliferous *A.gossypii* probes on SC, virus particles carried on the aphid stylet either do not reach some sites necessary to start the infection process (may be because of a particular probing behaviour) or cannot spread from such sites (may be because of a barrier such as the death of cells along the stylet path). Further studies will try to elucidate this point of major importance in the understanding of resistance to virus transmission.

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