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Host-plant resistance to insects in cucurbits—germplasm resources, genetics and breeding

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Abstract. Cucurbits are important crops for both staple and dessert foods. Past reviews have not covered insect resistance in cucurbits thoroughly, especially since much work has been done recently. Screening methods make a large difference in the efficiency of selection for resistance to insects. Resistance of cultigens should be evaluated using several biotypes of each insect being evaluated, and efficient test conditions with good control of environment. If possible, laboratory tests should be used to improve the repeatability and to reduce experimental error. Resistance to insects has been identified in cucurbits. For example, muskmelons have been identified that have resistance to melon aphid and red pumpkin beetle. On the other hand, resistance to pickleworm has not been identified after screening hundreds of cucumber cultigens. Conclusions drawn on the role of cucurbitacins in insect resistance to cucurbits are not unanimous. Studies on the genetic control of resistance in cucurbits indicate that there are at least 13 crop–insect cases where there is heritable resistance. With greater emphasis in cucurbit breeding programmes, multiple insect resistance should be obtainable in many of the cucurbit species.

1. Introduction

Members of cucurbitaceae are important to man as sources of food and fibre (Whitaker and Davis, 1962). The cultivated members of the family are used for carbohydrates (squash, pumpkin, marrow), dessert (muskmelon, watermelon) salads, and pickling (cucumber, gherkin). Out of 90 genera and 750 species belonging to cucurbitaceae, only 9 genera and 17 species are cultivated: *Citrullus* (watermelon, roundmelon), *Cucumis* (cucumber, muskmelon, longmelon, snapmelon), *Luffa* (sponge gourd, ridge gourd), *Lagenaria* (bottle gourd), *Cucurbita* (pumpkin, squash), *Sechium* (chayote), *Momordica* (bitter gourd, karhol), *Trichosanthes* (snake gourd, pointed gourd) and *Benincasa* (ash gourd).

Exclusive review on breeding for insect resistance in cucurbits appeared 20 years ago (Nath, 1971). Since then much information has been published. The objective of this paper was to review the status of insect resistance in cucurbits and to emphasize the potential for insect control in cucurbits through the use of resistant cultivars. Earlier review articles did not deal extensively with red pumpkin beetle (*Aulacophora foveicollis*), a serious insect pest of cucurbits in tropical countries, so special attention is given to it in this review.

Annual costs due to yield loss and control costs to insects on cucurbits in the southeast US in 1986 amounted to $100 000 to spotted and striped cucumber beetle and $60 000 to pickleworm (K. A. Sorensen, personal communication). Cucumber beetles are the most important insect pest on cucurbits, especially in the spring at seedling stage. The beetles also spread the bacteria that cause bacterial wilt which is especially a problem for home gardens. Pickleworm causes most damage on the autumn crop, and is a problem not only because of yield losses, but also because it can be processed along with the vegetables (for example, pickled cucumbers); it is thus a major quality control problem with the vegetable processsing industry. In tropical countries, untimely spray for the control of red pumpkin beetle and mites can lead to 100% crop failure. The list of economically important insect pests of cucurbits and the nature of damage is provided in Table 1.

2. General aspects of resistance

Plant resistance has been classified into three main categories, *viz.* non-preference, antibiosis and tolerance (Painter, 1951). The phenomenon of non-preference is not to be treated as all or none, but in most cases is a matter of degree. The extreme form of non-preference is of high value in cases where brief infestation causes severe plant damage. For example, in cucurbits, damage of seedlings at cotyledonary stage by red pumpkin beetle leads to the non-emergence of true leaves and eventual death of the seedling. Even if true leaves emerge, these are late, and bring late and non-uniform maturity of the cucurbits. Here, low intensity of non-preference or tolerance is not desirable. Colonization of aphids for a short period can transmit the virus. A similar situation occurs with spotted cucumber beetle, a vector of bacterial wilt.

The value of non-preference is also related to the ecological/agricultural context in which the resistant crop is grown. In an integrated pest management strategy, where natural enemies of the insect are also present, low damage or tolerance will permit longer exposure of the insects to the parasites and predators. Low level of resistance due to low level of non-preference is an important component of the integrated pest control programmes which permit a bare minimum application of insecticides.

The main effects of antibiosis are to retard the growth and rate of reproduction of individual insect pest. This phenomenon has been exploited for the development of pickleworm, aphid and two-spotted spider mite-resistant cultivars of cucumber and muskmelon. While evaluating breeding material for antibiosis to one insect pest, its consequences on the host parasite relationship with respect

Table 1. Important insect pests of cultivated cucurbits

Common name	Scientific name	Plant part affected
Spotted cucumber beetle	*Diabrotica undecimpunctata*	All plant parts
Southern corn rootworm	*D. u.* howardi	
Banded cucumber beetle	*D. baltrata*	
Western corn rootworm	*D. virgifera*	
Northern corn rootworm	*D. longicornis*	
Striped cucumber beetle	*Acalymma vittatum*	
Western striped cucumber beetle	*A. trivittata*	
Red pumpkin beetle	*Aulacophora foveicollis*	Roots, cotyledons, 1st, 2nd true leaf stage
Aphids	*Aphis gossypi*	Underside of leaves
	Myzus persicae	Spread of virus only
Leaf hoppers	*Empoasca abrupta* *E. filamenta* *E. arida* *E. solana*	Leaves
Leafminer	*Liriomyza pictella*	Leaves
Squash bug	*Anasa tristis*	Leaves
Melon fly	*Dacus cucurbitae*	Fruits
Squash vine borer	*Melittia cucurbitae*	Stem
Pickleworm	*Diaphania nitidalis* *D. hyalinata*	Floral parts Fruits
Spidermites	*Tetranychus urticae* *T. pacificus* *T. atlanticus* *T. desertorum*	Leaves
Epilachna beetles	*Epilachna chrysomelina* *E. similis* *E. fulvosignata* *E. sparsa*	Leaves
Cutworms	*Agrotis* spp. *Euxoa* spp.	Young plants

to the second type of pest must not be ignored. For example, in muskmelon and cucumber, resistance to oviposition by the adult female is due to the lack of plant hairs; but glabrous plants are less vigorous and are susceptible to feeding by pickleworm larvae (Elsey and Wann, 1982).

Tolerant plants are less damaged by pests. Desirability of tolerance at a specific plant growth stage should be decided in advance in cucurbit breeding programmes. Tolerance to red pumpkin beetle in cucurbits is more important up to second leaf stage.

3. Screening techniques

In cucurbits the measure of host damage by cucumber beetle, aphids, fruit fly, spider mite, red pumpkin beetle, squash borer, pickleworm and leafminer provides a reliable key for identifying resistant (tolerant) plants.

For screening, the use of both natural and artificial tests helps to resolve a complex resistance into its various components, and to enhance the level of resistance through accumulation of genes for resistance. In developing laboratory tests, high correlation with field tests is important (de Ponti, 1977). Low temperature during planting time of cucurbits in the North Indian plains prevents the active movement of red pumpkin beetles producing a variable amount of damage in experimental plots. Here, evaluation in cages would be preferable to field screening. Good agreement ($r = 0{\cdot}76$) between reactions of summer squash cultigens following feeding in cages and reaction under the conditions of natural infestation of the beetle in experimental areas was reported by Dhillon and Sharma (1989).

In laboratory studies of two-spotted spider mites on cucumber, acceptance and reproduction traits appeared to be positively correlated (de Ponti, 1978). Oviposition was preferred to acceptance because the former is based on more independent observations. Here, relation between oviposition and damage index was not established. Until conclusive results appear, screening on the basis of damage index can also be done as the unfavourable linkage between bitter gene and damage index has been verified (de Ponti, 1980). Selection should be practised for these components in segregating generation with higher estimate of heritability.

Efficient field methods for evaluating spider mites on cucurbits are lacking. For a rapid evaluation of resistance to mites in cucurbits an effective intraplant sampling strategy should be developed. Recently, in muskmelon, Perring *et al.* (1987) reported that a primary branch was optimal for use in sampling. They developed a three-leaf (consecutive) sampling plan based on the average number of primary branch leaves. However, research on sampling procedures for mites on cucumber, watermelon, summer squash, bitter gourd and round melon has not attracted much attention from breeders and entomologists.

4. Factors affecting the assessment of resistance

4.1. *Light, temperature and humidity*

Cloudy (dark) and cold days prevent the active and random movement of red pumpkin beetles and result in non-uniform dispersal of the insect over the experimental area. Under these circumstances screening of cucurbits should be carried out in laboratory where light, temperature and humidity can be controlled. De Ponti (1977) reported that, for measuring differences in resistance to two-spotted spider mite in cucumber, laboratory rooms should be conditioned for temperature (26°C), relative humidity (50–70%), day length (1 h) and light intensity (1200 mwm).

4.2. *Nutrition and moisture*

Adequate nutrition and moisture level should be maintained in test plants, whether in pots or field plots. This will ensure that the plants are in normal unstressed physiological state.

Seedlings of summer squash grown in nitrogen-deficient culture are less preferred by squash bug than healthy plants (Benepal and Hall, 1967). The differing reaction to nutrients of muskmelon plants in segregating populations affected the amount of melon aphid damage. Reliable information on the genetics of antibiosis to the aphid could be obtained only after the nutritional needs of the parents (resistant and susceptible) had been stabilized through further breeding (Kishaba *et al.*, 1976). Water stress influenced the level of resistance of two cucumber cultivars, Marketmore 70 and Hawaiian, to two-spotted spider mite (Gould, 1978).

4.3. *Growth stage of the host-plant*

Expression of resistance to a specific insect may vary at different stages of development of a host. Tests at one stage of growth may give results that do not apply to others. Maximum infestation of red pumpkin beetle on cucurbits is recorded at cotyledonary to second true leaf stage (Grewal, 1981).

4.4. *Insect population pressure*

The optimum insect density to use in a test is not necessarily at the point of maximum plant damage, but that which provides the maximum discrimination between resistant and susceptible plants. A uniform density of two red pumpkin beetles per plant for 48, 72 and 76 h on cotyledonary, first and second true leaf stage, respectively, of cucurbits is sufficient to distinguish between resistant and susceptible plants (Grewal, 1981).

4.5. *Choice of the test insect*

The reproductive capacity of the two-spotted spider mite varies enormously among its many host species (Van De Vrie *et al.*, 1972). When the mites are moved from one species to another, their reproduction on new species may be affected significantly (Brauenboer, 1959; Dosse, 1952). Therefore, in studies of mite resistance in cucumber, mites should first be reared on a susceptible cucumber cultigen and then moved to the cucumber cultigens to be tested. Definitive results may require rearing the mites for several generations on cultigens thought to be resistant. Similarly, red pumpkin beetle has many alternative hosts other than cucurbits (Grewal, 1981). It needs to be determined whether the behaviour (preference/non-preference) of beetles changes when they are collected from alternative hosts and placed on cucurbits, and whether the resistance of the cultigens tested is maintained.

4.6. *Horticultural practices*

Field practices (plot size, planting density) can also affect the insect test. For screening cucumber for resistance to cucumber beetles maximum differences could be realized by using six replications of single-hill plots with 15 seed per hill (Quisumbing and Lower, 1975).

4.7. *Screening methodology*

Screening methods affect the results of screening study. For example, line 15–2–6 of summer squash was reported to be resistant to the red pumpkin beetle by Grewal (1981) but susceptible by others (Dhillon and Sharma, 1987). That discrepancy may be due to the use of difference rating scales, those of the latter researchers being more stringent and discriminatory.

5. Evaluation of the bitter (Bi) locus in relation to the resistance

Cucurbitacins are highly oxidized tetracyclic triterpenoids which are common in plants of the cucurbitaceae (Peterson and Schalk, 1985). Bitterness as researched in cucumber is governed by the major gene Bi, whose action is influenced by one or more additively inherited modifying intensifier genes which are active only in the presence of the allele Bi (de Ponti, 1980). Earlier research reports that bitterness causes resistance to two-spotted spider mite (Dacosta and Jones, 1971; Gould, 1978; Kooistra, 1971). But de Ponti and Garretsen (1980) found no relationship between the bitter gene (Bi) and resistance factors acceptance and oviposition, and high linkage between the degree of bitterness intensifiers and resistance genes. This kind of linkage should not pose difficulties because these intensifier genes are inactive in non-bitter (bibi) genotypes, which will be the aim of breeders. While breeding non-bitter cucumbers, at the end of each selection cycle, despite using tests such as acceptance and oviposition, practical test (damage index) must be applied to trace, if any, the undesirable linkage between the gene Bi, its intensifier genes and resistance genes. Breakage of this linkage will help in isolating non-bitter and resistant genotypes.

Surprisingly, the non-bitter resistant lines of cucumber selected in The Netherlands showed low resistance to two-spotted spider mite in the United States and the resistance of bitter lines was consistent, independent of location (de Ponti *et al.*, 1983). It is yet to be ascertained whether this is due to differences in environment or in the mite population or both; but these data support the earlier-mentioned hypothesis of causal relation between resistance and bitterness. Here, speculation of existence of different types of mite resistance in cucumber needs to be probed.

Spotted, striped and banded cucumber beetles, western and southern corn rootworm are attracted by cucurbitacin (Benepal and Hall, 1967; Chambliss and Jones, 1966; Dacosta and Jones, 1971; Howe and Rhodes, 1976; Metcalf *et al.*, 1982). On the contrary, Lower (1972) and Quisumbing (1975) found non-bitter cucumber varieties susceptible to the striped cucumber beetles and southern corn rootworm. We should always be careful in relating resistance to the specific compound. The possibility of other biochemical factors in relation to resistance, and of independent identity of resistant genes, needs to be investigated.

Recently, Mehta (1985) reported that selecting for cucurbitacin-free cucurbitaceous plants could achieve resistance by non-preference, and may reduce damage to seedlings of cucurbits by red pumpkin beetle. But on testing three pairs of isogenic bitter (Bi) and non-bitter (bi) lines of cucumber, no relationship was found to exist between the bitter gene (Bi) and degree of damage of this beetle (Dhillon, 1990). Even in summer squash, resistant and susceptible lines contained cucurbitacin at susceptible plant growth stage (cotyledonary). Resistance to red pumpkin beetle in summer squash is conditioned by polygenes with additive gene effects (Dhillon and Sharma, 1987). But cucurbitacin synthesis in this crop is regulated by a single dominant gene Bi (Robinson *et al.*, 1976). Based on the existence of bitter + resistant genotypes of summer squash and bitter gourd, it is speculated that major gene Bi or some other genes governing the degree of bitterness might be linked with red pumpkin beetle resistance genes.

The preceding discussion leads to the conclusion that the role of cucurbitacin in insect resistance of cucurbits is complex.

6. Breeding for resistance

Cultigens of cucurbits differing in levels of resistance to most of the insect pests have been identified. A high level of resistance has been reported in cucumber to two-spotted spider mite (Gould, 1978; Knipping *et al.*, 1975; de Ponti, 1978; de Ponti *et al.*, 1983; Soans *et al.*, 1973) and striped and spotted cucumber beetle (Nath, 1965; Wiseman *et al.*, 1961). Resistance has been reported in muskmelon to melon aphid (Bohn *et al.*, 1972; Ivanoff, 1944, 1957), striped, spotted and banded cucumber beetle (Chambliss, 1978; Nath and Hall, 1965; Wiseman *et al.* 1961), fruit fly (Khandewal and Nath, 1978), melon aphid (MacCarter and Habeck, 1973), leafminer and red spider mite (Dhooria and Sukhija, 1986). In watermelon there is resistance to spotted, banded cucumber beetle (Chambliss, 1978), fruit fly (Khandewal and Nath, 1978), melon aphid (MacCarter and Habeck, 1973) and red spider mite (Dhooria *et al.*, 1987). Resistance has been reported in summer squash to striped, spotted, and banded cucumber beetle (Brett *et al.*, 1961; Chambliss, 1978; Hall and Painter, 1968; Nath and Hall, 1963), squash vine borer (Painter, 1958) and squash bug (Novero *et al.*, 1962). In pumpkin (*Cucurbita maxima*) there is resistance to fruit fly (Dutta and Nath, 1970) and in *C. moschata* to squash borer (Howe, 1949). Round melon (*Citrullus vulgaris* var. *fistulosus*) is resistant to fruit fly (Nath, 1964).

Much research on host-plant resistance to red pumpkin beetle has been done in India. Useful resistance to that beetle has been found in muskmelon (Nath *et al.*, 1968; Nath and Rajgopal, 1969; Vashistha and Choudhury, 1974), watermelon (Vashistha and Choudhury, 1974), summer squash (Dhillon and Sharma, 1987; Grewal, 1981; Nath, 1964; Sandhu *et al.*, 1979), bottlegourd (Nath, 1964, 1966; Nath and Thakur, 1965; Vashistha and Choudhury, 1974) and ridge gourd (Nath, 1964; Nath and Thakur, 1965). Research on host-plant resistance to this beetle in cucumber is yet to be initiated. Most of these reports lack information on heritability of resistance, the knowledge of which can speed the breeding process.

After examining extensive cucumber collections, genetic differences for leaf antibiosis of cucumber to pickleworm larvae were not found (Wehner *et al.*, 1985). It may be possible to find useful levels of resistance with additional germplasm from diverse areas of the world (especially India), perhaps using improved screening methods. In India there is no reported problem of pickleworm to cucumber, but a different species of pickleworm, *Diaphania indica* (Saundars) has been observed on ridge gourd (A. S. Sohi, personal communication). Here, previous research findings offer hope for success in breeding for resistance. For example, genetic differences accumulate in isolated plant populations, and presence of the insect species of interest is not necessary to the development of resistance in a host population (Painter, 1951). Resistance to hessian fly (*Mayetiole destructor*) was obtained from wheat from the Iberian Peninsula, which was not considered a place of origin for the fly (Painter, 1951).

Tetranychus cinnabarinus is a serious pest on cucurbits in India and is closely related to *T. urticae* (Boudreaux, 1956) an economic pest of cucurbits in Europe and North America. We suggest that germplasm of cucurbits resistant to either of the two species be evaluated for resistance to the other.

Various patterns of inheritance of resistance to insects have been reported in cucurbits (Table 2). In order to be useful in a breeding programme, insect resistance must be heritable, relatively permanent during the susceptible stage of the host plant and compatible with other horticultural characteristics. Because cucurbits generally are cross-pollinated species, open-pollinated population would be expected to differ from plant to plant for insect resistance. Therefore, progress might be made by selecting within populations of old cultivars for improved resistance. Recurrent selections of populations developed by crossing insect-resistant selections with elite cultivars provides a solution in those cases where insect resistance has a low heritability. Inbred lines from the above population can be developed with no loss of vigour, since cucurbits generally do not express inbreeding depression (Allard, 1960).

If the resistance to an insect pest is controlled by non-additive or dominance gene effects, then recurrent selection for specific combining ability should be used with the objective of developing hybrid cultivars. Hybrid seed production is not a problem in cucurbits and provides the additional advantage of combining dominant gene traits from both parents into the hybrid. One system that capitalizes on dominant genes includes summer squash resistance to red pumpkin beetle (Dhillon and Sharma, 1986), and early maturity and fruit yield (Dhillon and Sharma, 1987).

The small plots of breeding material should be grown at different sites having different variants of the insect. That will help to avoid race-specific resistance, as in the case of melon aphid from California, which was able to colonize muskmelon cultigens reportedly resistant to the aphid population tested in the southeastern USA (Kishaba *et al.*, 1971).

While breeding for resistance to one insect species, it is wise to ensure that gene(s) for susceptibility to other economic pests are not being transferred. When resistance and susceptibility are under separate genetic control (no linkage), then enhanced susceptibility can be eliminated through breeding. Muskmelon cultigen LJ 90234 provided the

Table 2. Inheritance and gene action of insect resistance in cucurbits

Crop/insect	Insect resistance†	Number of genes involved	Gene action	Reference
Cucumber (*Cucumis satisvus*)				
Two-spotted spider mite	—	Polygenes	Additive and transgression	De Ponti, 1979
Spotted, banded cucumber beetle	Rc	Single recessive gene	—	Chambliss, 1978
Muskmelon (*Cucumis melo*)				
Melon aphid	Dom	Single gene with additional minor genes	—	Kishaba *et al.*, 1976
	Dom	Single gene	Complex	Bohn *et al.*, 1973
	Dom	Small number of genes	—	MacCarter and Habeck, 1973
Red pumpkin beetle	Dom	Single gene	—	Vashistha and Choudhury, 1974
Fruit fly	Dom	Two complementary	—	Challiah and Sambanolam, 1973
Leafminer	Rc	More than one factor	—	Kennedy *et al.*, 1978
	Prt	More than one factor	—	Kennedy *et al.*, 1978
Watermelon (*Citrullus lanatus*)				
Spotted, banded cucumber beetle	Rc	Single recessive gene	—	Chambliss, 1978
Fruit fly	Dom	Single gene	—	Khandewal and Nath, 1978
Summer squash (*Cucurbita pepo*)				
Striped cucumber beetle	Prt	More than one factor	Additive	Nath and Hall, 1963
Cucumber beetle	Prt	Polygenes	Additive	Nath and Hall, 1965
Squash bug	Prt	Three pairs	Additive	Benepal and Hall, 1967
Red pumpkin beetle	Dom	Polygenes	Additive and non-additive No epistasis	Dhillon and Sharma, 1986, 1987
Pumpkin (*Cucurbita maxima*)				
Fruit fly	Dom	Single gene	—	Nath *et al.*, 1976

† Resistance was either dominant (Dom), recessive (Rc), or partially dominant (Prt).

genes for resistance to melon aphid, but was susceptible to western flow thrips (*Frankliniella occidentalis* Pergud.) and the western potato leaf hopper (Bohn *et al.*, 1972; Kishaba *et al.*, 1971). This was eliminated by a backcross breeding programme which involved selection only for aphid resistance.

7. Discussion

Insect resistance in cucurbits has not received high priority in research as has been the case of major field crops such as wheat, maize and cotton. A possible explanation is that no single insect is a limiting factor in the production of any cucurbit species, except for squash bug. However, a major factor is the small number of cucurbit researchers available to solve the many problems of production, and the firm belief in many instances that breeding for insect resistance should not be an objective where efficient chemical control is available.

In India, the senior author has observed breeders using insecticides to save their progeny plots, and the lines are tested for resistance at the end of the breeding programme. This breeding under a pesticide umbrella, discussed in detail by de Ponti (1982), results in the erosion of useful resistant genes in early generations of testing using insecticides.

Control of insects with general insecticides can cause epidemics of other insects to break out. Use of insecticides for thrips control on watermelon may increase the number of *Liriomyza* leafminer as a result of the decimation of its natural enemies (Johnson and Oatman, 1982). In this situation breeding for resistance should be evaluated as a more effective alternative to the use of insecticides.

Movement of insects from one region of the world to another can produce new problems for cucurbit breeders. For example a newly introduced thrip species, *Thrips palmi* Karny, has become a serious problem on cucurbits in Hawaii (Nakahara *et al.*, 1984). A diverse germplasm background (if available) in the new cultivars being released may prevent new pests from spreading rapidly through whole regions planted to a particular crop. To maximize the chances of success, cucurbit breeders should identify resistant cultigens having a different pedigree and originating from different geographic areas than the elite cultivars used in crosses as sources of yield and quality. Intercrossing and progeny testing programmes involving that kind of breeding material would increase the chances of identifying new genes for resistance.

Search for sources of resistance should also be initiated at places where the insect in question is absent. For example, in the USA genetic resistance to leafminer in muskmelon has been found in introductions from Africa and India (Kennedy *et al.*, 1978). This phenomenon is an allopatric resistance which is due to the pleiotropic effects of genes which are present as a result of selective forces unrelated to the insect pest (Harris, 1975). Allopatric resistance (may be polygenic) is more useful than sympatric resistance (likely to be monogenic). It can affect insect biology in many ways.

In short, a tremendous amount of effort has resulted in the identification of many sources of heritable resistance to insects in cucurbits, and the challenge is to utilize this resistance in the development of insect-resistant cucurbits. This is the only way left to fulfil the promises of host-plant resistance.

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