Host-plant resistance

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22 Host-Plant Resistance

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Introduction

In this section, the word 'variety' will be used as an umbrella word for the many types of variation involved; varieties, cultivars, accessions, breeders' lines may all be included. The practical use of host-plant resistance (HPR) for aphid control in different crops is explored in the pest management section of this volume (Chapters 24-33).

It might be assumed that the role of symbionts in nitrogen metabolism (Chapter 6, this volume) should enable aphids to compensate for nutritional differences between crop varieties, and that the phloem-feeding habit would enable aphids to avoid many deterrent surface characters and allelochemicals in plants. However, the literature probably has more examples of HPR to aphids than to any other group of crop pests, including examples of nearly all the mechanisms of HPR known for insect pests in general. Moreover, HPR to aphids can be highly effective and dramatic; for example, the resistance of 'Avoncrisp' lettuce to *Pemphigus bursarius* (lettuce root aphid) (Fig. 22.1).

Resistance rankings between varieties can change with age and resistance to one aphid species may not give resistance to another. HPR to *Diuraphis noxia* (Russian wheat aphid) in wheat and barley seems especially specific, and has no effect on the several other species of cereal aphid (Robinson, 1992; Messina and Bloxham, 2004).

In recent years, molecular biology techniques have become routine, and much progress has been made in screening aphid populations for genetic variability. However, whether or not such genetic variability matches phenotypic variability (Thomas *et al.*, 2012), only differences in reaction to different varieties are relevant to HPR (Pompon *et al.*, 2011). Also, possibly because of the success against other pests of crops genetically engineered to express the *Bacillus* *thuringiensis* (Bt) toxin, the emphasis in HPR studies on aphids has shifted to identifying genes (e.g. Shufran and Payton, 2009). This puts emphasis on single genes coding for proteins expressing a high level of toxins, a narrow and perhaps not the most desirable HPR mechanism (Chapter 23, this volume).

Before the advent of direct gene transfer, wild relatives within the natural crossing barriers were often the source of resistance genes (e.g. Hesler, 2013). Table 22.1 lists some of the wild relatives of crops often involved in resistance breeding for aphids, usually entailing the transfer of characteristics (e.g. hairiness, toughness, high toxin levels) lost in the process of domestication (van Emden,1997).

Finally, HPR need not necessarily involve genetic change. It can sometimes be produced by some extrinsic influence on a susceptible variety ('pseudoresistance' or 'induced resistance'). Plant resistance to *Schizaphis graminum* (greenbug) in wheat after fertilization with silicon (Gomes *et al*., 2005) is one example. HPR also is manifested when the aphid pest does not synchronize with a 'susceptibility window' in the plant's phenology. Plant resistance to aphids generally tends to increase with age ('age-related resistance'); Sarwar and Sattar (2013) reported that early-sown oilseed rape was effective in reducing incidence of and damage by *Myzus persicae* (peach–potato aphid).

Associated organisms (see 'endophytes' below) may also induce HPR.

Types of Host-Plant Resistance to Aphids

The classification of Painter (1951), modified by Kogan and Ortman (1978), still has great value.

Antixenosis (close to Painter's 'non-preference')

This is resistance to colonization by aphids, and shows in the high proportion of immigrating alatae which take off from a plant after superficial probes and within a few hours of landing. At the immigration stage, aphids seem to exhibit a high degree of non-preference, even on susceptible plants. Műller (1958) showed that the eventual four-fold greater population of *Aphis fabae* (black bean aphid) on the susceptible broad bean variety Schlandstedt than on the resistant Rastatt was based on respective re-take-off rates of 95% and an only slightly higher 99%. Antixenosis is usually assessed by liberating alatae over different varieties, both in choice and no-choice situations (Adams and van Emden, 1972), although van Emden *et al*. (l99l) devised a test (involving systemic insecticide with a correction for any detection thereof by the aphids) that identifies which aphids have ingested from the plants.

Tjallingii's (1988) electrical penetration graph (EPG) technique (Chapter 9, this volume) enables the continuous monitoring of aphid penetration and probing activity (Fig. 22.2) (Mentink *et al.*, 1984).

Antibiosis

This negatively affects the multiplication of aphids that have colonized the plant, usually showing as reduced survival, growth and fecundity, and extended development time. These are measured easily on individuals confined on leaves in small clip cages, although care needs to be taken to ensure that any apparent antibiosis is no more than a first-generation expression of transfer to a novel plant. Survival, development time, and fecundity can be combined into a single statistic, the intrinsic rate of increase (r_m), and another useful single statistic is the integral of the daily weight increase of individual aphids over a few days (mean relative growth rate or MRGR) (Chapter 5, this volume). r_m can readily be converted into 'population doubling time'.

Tolerance

Tolerance of a variety shows as a better yield under the same aphid burden, both in numbers and duration. This is difficult to quantify, since any antibiosis defeats the 'equal burden' requirement, and intolerance to infestation will result in plant damage, which may cause a crash in the aphid population and defeat the 'equal duration' requirement. Havlickova (1997) has proposed a covariance model in which the main component is the slope of the relationship between the weights of infested and control seedlings. However, tolerance may perhaps be better quantified by the slopes of regressions of yield or plant biomass on initial aphid infestation.

What is the preferred type of resistance?

Antixenosis is rarely effective in a no-choice situation, and puts pressure on the population for selection of genotypes not affected by the antibiosis (see 'biotypes' later), a danger not applicable to tolerance. Burd and Puterka (2009) challenge the prioritization of tolerance over antibiosis on the grounds that crop selection was not a factor in the appearance of adapted greenbug genotypes. Moreover, a potential hazard of relying on tolerance is that farmers growing such varieties would not need to control aphids and so would breed populations to infest their neighbours' crops. Thus, there is general agreement (van Emden, 1997) that the preferred resistance is antibiosis coupled with some antixenosis, as has been found in some soybean lines (Hesler, 2013). Buschman and Ramaswamy (2012) have modelled HPR stability arising from two genes, one expressing an oviposition deterrent and the other a toxin. When the antibiosis was dominant, insect populations were managed for 150 years, but for much longer when it was recessive, presumably because the toxin was modelled as a stronger selection pressure than the deterrent. The combination of antibiosis and tolerance had also been recommended (Murugan *et al*., 2010) as delaying biotype selection in *D. noxia*.

This chapter reviews HPR to aphids by the various anatomical, physiological, and biochemical mechanisms that have been correlated with HPR phenomena and Fig. 22.3 shows these with an indication of the order in which the aphid would encounter them. However, correlations are not the same as 'cause and effect'. Kazemi and van Emden (1992) found that some proposed chemical correlations with HPR in wheats to *Rhopalosiphum padi* (bird cherry–oat aphid) broke down when a wider range of wheats was tested. Similarly, Weibull (1994) found that corre1ations of chemistry with resistance to *R. padi* in parental barley lines broke down in the F1 generation. It seems it is not difficult to correlate resistance rankings with whatever chemical group represents one's own particular interest.

Mechanisms of Host-Plant Resistance to Aphids

Mechanisms of antixenosis

Colour

Colour can influence the preference of immigrating aphids. Alatae of *Brevicoryne brassicae* (cabbage aphid) do not settle well on red cabbage varieties, even though apterae caged on such varieties have a better growth rate than those on green varieties (Radcliffe and Chapman, 1965, 1966). Similarly, in a study of 50 mustard and oilseed rape varieties in India) (Rana *et al.*, 2001), purple-leaved cultivars had fewer colonizing *Lipaphis erysimi* (mustard aphid) than dark green ones, which in turn were less infested than those that were light green. Differences in the brightness of the yellow flowers had no effect on aphid colonization.

Palatability

That so many common or Latin names of aphids reflect particular host plants (e.g. lupin aphid, *B. brassicae,* etc.) shows that aphids often accept or reject a plant on the basis of its secondary chemistry, even before reaching the phloem. Thus toxins (which would otherwise reflect antibiosis) become deterrents. Polyphagous aphids such as *M. persicae* will tolerate levels of secondary compounds such as glucosinolates in brassicas, but elevating levels still tolerable to the specialist *B. brassicae* will lead to antibiosis (van Emden, 1978; Cole, 1997b). In screening wild and cultivated brassicas for resistance to these two aphids, Cole (1997a**)** found that most of the variation in HPR was explained by four glucosinolates (2-OH-3-butenyl, 2-propenylglucosinolate, 3-methoxyindolyl and 4-pentylglucosinolate). High total phenol (especially ortho-dihydroxy phenol) content in oilseed brassicas deters infestation by *L. erysimi* (Sarwan Kumar Sangha, 2013) and the phenolic hydroxamic acids (Hx), often associated with antibiosis to aphids in cereals, are also a deterrent to *Metopolophium dirhodum* (rose–grain aphid), *Sitobion avenae* (English grain aphid) and *Schizaphis graminum*. *Rhopalosiphum maidis* (corn leaf aphid), however, is not deterred because it avoids Hx in high Hx plants by reducing puncturing of the cells by the stylets on their way to the phloem (Givovich and Niemeyer, 1995). In lucerne, other Hx compounds (the 3-amyl-4-hydroxycoumarins such as coumestrol) are deterrent to *Acyrthosiphon pisum* (pea aphid), as are saponins (Nicholas *et al.*, 2005). In tobacco, the antixenosis of some varieties to *M. persicae* is ascribed to sugar ester levels and alpha and beta monols on the leaf surface (Johnson *et al.*, 2002).

One mechanism of antixenosis in tomato to *Macrosiphum euphorbiae* (potato aphid) involves ethylene signalling. This has been shown to induce opposite effects in susceptible and resistant tomato varieties. It promotes aphid infestation on susceptible genotypes, but contributes to antixenosis in resistant ones (Wu *et al*., 2015).

Recently a trial of GM wheat with a gene (resynthesized from peppermint to eliminate inhibitory compounds) expressing the alarm pheromone of aphids was carried out (Bruce *et al.*, 2015). Although cereal aphids were deterred in laboratory tests, no substantial reductions in the population of cereal aphids were observed in the field, but the idea of using behaviour-modifying compounds in this way is novel and has potential.

Waxiness

Waxiness of the leaf surface (Fig. 22.4) has sometimes been positively linked with antixenosis to aphids, e.g. the epicuticle of some lucerne varieties resistant to *Therioaphis trifolii maculata* (spotted alfalfa aphid) had wax ester levels 50% higher than those in susceptible lucerne (Bergman *et al.,* 1991). Similarly Ren *et al*. (2014) found that the wax content on the leaf surface of the highly *Aphis gossypii*-resistant cucumber variety 'Axin' was 30 times higher than for the susceptible variety 'Pepino'. Wojcicka (2015) used the EPG technique (see earlier) to show that components in the wax of waxy genotypes of wheat completely stopped salivation and active ingestion by *R.* padi, yet it is often the less waxy (glossy) varieties that are resistant because of higher levels of deterrent chemicals in the reduced wax layer. Glossy wheats, antixenotic to *S. avenae*, contain dihydroketones as the deterrent compounds (Lowe *et al*., 1985). With *A. pisum* studied on seven pea varieties, the glossy ones again were resistant (White and Eigenbrode, 2000), and glossy brassica varieties are also antixenotic to *B. brassicae* (Thompson, 1963; Ellis *et al*., 1996), with reductions in aphid populations as high as 95% (Stoner, 1992).

Leaf surface wax components have also been implicated in the resistance of European red raspberries to *Amphorophora idaei* (large European raspberry aphid) conferred by geneA_{10} (Robertson *et al.,*1991; Shepherd *et al*., 1999a,b).

Ni *et al*. (1998) tested whether the ranking of resistance to *D. noxia* of wheat (most susceptible), oat (intermediate), and barley (most resistant) had a basis in surface wax by removing this with ethyl ether, but the resistance rankings remained as before.

Mechanical

Hardness of the plant surface is a common resistance mechanism to chewing insects but not for aphids, where a more common cause of mechanical antixenotic resistance is difficulty in reaching the phloem. Pectin in the cellular middle lamella has a role in hindering access to the phloem (Dreyer and Campbell, 1984). Resistance to *S. graminum* in some sorghum varieties is due to increased methylation of the middle lamellar pectin (Dreyer and Campbell, 1984). A variety of melon resistant to *A, gossypii* deposits callose in attacked leaf veins.

A major qualitative chemical feature of two wild brassicas resistant to *B. brassicae* was the presence of gluconapin rather than the more usual glucobrassicin, but the former had no effect on the aphid in artificial diet. Cole (1994a) proposed that the resistance mechanism was stylet blocking.

Local necrosis

Local necrosis, i.e. the death of cells with the production of deterrent polyphenols wherever the aphid tries to insert its stylets, is a valuable resistance mechanism since it also gives protection against other piercing organisms such as fungal hyphae and nematodes (van Emden, 1987). The polyphenols are produced when aphid damage brings substrate and enzyme into contact. This is a 'hypersensitive response', perhaps an unusual concept of 'resistance'. It is the mechanism of resistance of apples to *Eriosoma lanigerum* (woolly apple aphid) (Wartenberg, 1953) and *Dysaphis plantaginea* (rosy apple aphid) (Alston and Briggs, 1970). Another example is the hypersensitive cell death response of some resistant barleys to attack by *D. noxia* (Belefantmiller *et al*., 1994), though some aphid species may have reducing compounds in their saliva that counter the hypersensitive response of the plant (Miles, 1999).

Trichomes (non-glandular)

Non-glandular trichomes are mechanical barriers to many small insects, including aphids. For example, high trichome density on wheat leaves deters *Sipha flava* (yellow sugar cane aphid), but any effect on *S. graminum* is questionable (Webster *et al*., 1994). Pompon *et al*. (2010) attributed the resistance of two wild potato species to *M. euphorbiae*) and *Myzus persicae* to the trichomes on the leaf surface; high trichome density also deters *M. persicae* on crosses of tomato with wild potato (Simmons *et al*., 2005). Pubescent broccoli is as resistant to *B. brassicae* as glossy varieties (see earlier) (Stoner, 1992). However, with *A. gossypii* on cotton, it is the glabrous varieties that have fewer aphids (Weathersbee *et al.,* 1994, 1995).

Mechanisms of antibiosis

Glandular trichomes

These are of two types: long slender ones that secrete drops of fluid from the tip, and short ones bearing a spherical glandular head (Fig. 22.5). Septa in the head separate substrate and enzyme which are brought together to form polyphenols when the head is ruptured by contact with an aphid. These polyphenols are not only distasteful to the aphid (see earlier), but also harden on and disable the mouthparts and tarsi. Great interest has focused on breeding the presence of such trichomes on wild potato (especially *um berthaultii*) and tomato crossed with *Lycopersicon pennellii* (Simmons *et al.*, 2005) into varieties for resistance to aphids (Gibson, 1976), but none was ever commercialized. Any *M. euphorbiae* on the stems, however, multiply faster than on varieties without glandular trichomes (Ashouri *et al*., 2001). The wild tomatoes *Solanum habrochaites* and *S. peruvianum* have a dense pubescence with both glandular and non-glandular trichomes (Kok-Yukomi, 1978), and Dreyer and Campbell (1987) observed that the resistance attributable to the glandular trichomes decreased as the density of non-glandular trichomes increased.

Toxins

These are often the same chemicals that can also cause antixenosis, and they may only be induced following disruption of plant cell walls by aphid probing. The plant then produces signalling compounds such as jasmonic, salycilic, abscisic and gibberellic acids which lead to the mobilization of direct chemical defence responses (Smith and Boyko, 2007; Pompon *et al*., 2010; Chapter 8, this volume). The resistance to *M. euphorbiae* of tomatoes carrying the Mi-1.2 gene results from jasmonic acid triggering a proteinase inhibitor (Cooper *et al*., 2004).

Hydroxamic acids (Hx) are deterrent to many aphids (see earlier), but also decrease feeding in artificial diet of, for example, *S. avenae*. Also in diet, 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) decreases the survival of *M. dirhodum* (Cambier *et al.,* 2001), as do low concentrations of its decomposition product 6-methoxybenzoxazolin-2-one (MBOA) for *S. avenae* (Hansen, 2006). In whole plant studies, a wheat cultivar with high Hx was found to be antibiotic to *S. avenae* (Fuentes-Contreras and Niemeyer, 1998), and the growth rate of the aphid on three wheat and two oat cultivars was negatively correlated with Hx levels (Fuentes-Contreras *et al.,* 1996). Also, 26 Hungarian cultivars showed a negative correlation between Hx levels and populations of *R. padi* (Gianoli *et al.,* 1996).

Legumes are also well known to contain toxins. Ansari *et al.* (1989) discovered some varieties of cowpea (*Vigna unguiculata*) in which the leaves produced a powerful graft-transmissible but unidentified toxin that killed *Aphis craccivora* (cowpea aphid) very quickly, but did not seem to be detected by the aphid. Another example is lupin; the alkaloids in narrow-leaved lupins (*Lupinus angustifolius*) depress the fecundity of *Macrosiphum albifrons* (lupin aphid) (Berlandier, 1996). *Myzus persicae* is less affected by these alkaloids (gramine, sparteine, lupanine, lupinine, 13-hydroxylupanine, and angustifoline) than *A. craccivora*, both in plants and in artificial diet (Ridsdill-Smith *et al*., 2004).

On cotton, *A. gossypii* showed shorter longevity and lower fecundity on varieties bred to have high levels of the polyphenol gossypol than on two with lower levels (Du Li *et al*., 2004).

Unique among the role played by alkaloids in plant defence against insects, including aphids, is the production of nitrogen-rich compounds by asexual *Epichloe/Neotyphodium* spp. facultative fungal endophytes of temperate grasses (Fig. 22.6). The bioactive compounds produced by these endophytes are ergot alkaloids (particularly ergovaline), indole diterpenes (lolitrems), pyrrolopyrazines (peramine), and pyrrolizidines (lolines). Ergot and lolitrem, but not peramine and lolines, are toxic to livestock (Young *et al*., 2013).

Lolines alone protect infected tall fescue and perennial rye grass (*Lolium pratense*) from *R. padi* (Siegel *et al*., 1990; Eichenseer *et al.*, 1991; Wilkinson *et al.*, 2000; Schardl *et al*., 2007). Additionally, lolines alone in meadow fescue (Wilkinson *et al*., 2000) and peramine only in other infected grasses (Siegel *et al*., 1990) have been associated with resistance to *S. graminum.* Compared to endophyte-free plants, infected perennial ryegrass (Clement *et al*., 1992), tall fescue (Clement *et al.*, 1996), and some wild perennial barley (*Hordeum* spp.) (Clement *et al*., 1997), are strongly resistant to *D. noxia*. Endophyte infection of another wild temperate grass, *Phleum alpinum*, confers resistance to *R. padi* (Clement *et al*., 201l). The expression of insect resistance (antixenosis, antibiosis) is affected by the host grass species/genotype, endophyte strain (including associated alkaloid profile) and insect species/biotype involved in a given interaction (Clement *et al.*, 1994; Popay, 2009; Crawford *et al*., 2010) and soil nutrition (Lehtonen *et al*., 2005).

Perennial ryegrass cultivars harbouring a specific endophyte strain (AR37) are used for protection against the root aphid *Aploneura lentisci*, and other pasture pests on farms in New Zealand (Hume *et al.*, 2007; Popay and Hume, 2013) and Australia (Moate *et al*., 2012).

Although endophytic fungi are also frequently found in dicotyledenous plants (Saikkonen *et al*., 1998), any role they may have in HPR to aphids (or indeed any other insect) has yet to be established.

Bacillus thuringiensis (Bt) toxins used for GM Lepidoptera resistance are not regarded as aphicides, but a GM potato cultivar with Bt against *Leptinotarsa decemlineata* (Colorado potato beetle) also depressed the growth and fecundity of *M. euphorbiae* (Ashouri *et al*., 2001).

Other toxins studied specifically for their potential in GM crops against aphids include lectins, but these usually give only partial resistance to aphids. When 30 were tested in artificial diet against *A. pisum* (Rahbe *et al.*, 1995), most caused only low toxicity. However, those from jack-pine (*Pinus banksiana*), love-lies-bleeding (*Amaranthus caudatus*), lentil (*Lens culinaris*), snowdrop (*Galanthus nivalis*) induced worthwhile mortality. Concanavilin A (the jack-pine lectin) was then tested on five other aphid species, but with very variable results. A chitin-binding lectin in two wild brassicas shows some insecticidal activity against *B. brassicae* (Cole, 1994b). There have also been studies with proteinase inhibitors. Oryzacystatin 1, effective against leaf-chewing insects in transgenic oilseed rape, inhibited growth of *A. gossypii, A. pisum,* and *M. persicae* (Rahbe *et al*., 2003), and (in transgenic eggplant) of *M. persicae* and *Macrosiphum euphorbiae* (Ribeiro *et al.,* 2006). Tobacco genetically engineered to accumulate two ketosteroids (cholestan-3-one and cholest-4-en-3-one) in the phloem caused high mortality of *M. persicae* (Bouvaine *et al.*, 2014).

Nutritional factors

Given the limiting levels of nitrogen dietary requirements for aphids in the phloem (Chapter 6, this volume), one might expect nutrition to be a valuable source of HPR. AucIair *et al.* (1957) studied several pea varieties and found a negative correlation between their resistance to *A. pisum* and the soluble and total amino nitrogen content of the leaves. Kazemi and van Emden (1992) analysed a wide provenance range of wheats (European, Iranian and the 'ancient' diploid wheat Einkorn (*Triticum monococcum*) and found that the leaf concentration of three amino acids (alanine, histidine and threonine) was an excellent predictor for the performance of *R padi*, accounting for over 95% of the variation in the fecundity of the aphid. By contrast, Weibull (1994) analysed EDTA (ethylenediaminetetraacetic acid) leaf exudates as a better reflection of phloem content than whole leaf analyses, but found a negative correlation between several amino acids and the performance of *R. padi* on common barley (*Hordeum spontaneum*). However, since the segregating offspring of crosses showed no such relationship, no cause and effect was attached to the correlation.

Although nutritional factors are a mechanism of HPR to aphids, such resistance is particularly likely to fail under different environmental conditions such as different soils and fertilizer regimes.

Extrinsic factors

Factors extrinsic to the plant may be responsible for greater mortality on the apparently 'resistant' than on the 'susceptible' variety. In the absence of such factors, true HPR may be much less, or even absent. Thus, Gowling and van Emden (1994) showed that the number of *M. dirhodum* falling from wheat plants was doubled when parasitoids were added, and doubled again if the wheat variety was partially aphid-resistant. The partially resistant variety 'Rapier' was only 25% resistant compared with the susceptible 'Armada', yet the increased falling of aphids in the presence of searching parasitoids caused it to appear 86% resistant.

Another example of extrinsic resistance is that of the 'leafless' pea varieties bred for low leaf area to be resistant to powdery mildew (*Erysiphe polygoni*) and, instead of leaves, it has a profusion of photosynthesizing tendrils (Fig. 22.7) (Kareiva and Sahakian, l990). The apparent resistance to *A. pisum* in the field was considerably greater than the true intrinsic resistance of only some 8%, because the ladybirds *Coccinella septempunctata* and *Hippodamia convergens* could grip the tendrils, whereas a high proportion fell off the shiny leaves of normal peas. The proportion falling was from 47 to 26% for *C. septempunctata* and from 32 to 9% for *H. convergens.*

Mechanisms of tolerance

Rather little is known about the mechanisms of tolerance of plants to aphids. Tolerance is often coupled with antibiosis, and the latter may explain the increased yield sufficiently for tolerance not to be identified. The examples of tolerance reported in the literature therefore tend to be dramatic, with crop growth and yield little affected despite high aphid infestation. For example, Hesler (2005) found that three triticale (x *Triticosecale* spp.) accessions showed difference in shoot length whether infested or uninfested with *R. padi*.

Compensation

Some lines of wheat show much enhanced growth with increased tillering when attacked by *S. graminum* or *D. noxia* (Castro *et al.*, 2001). Such compensatory growth as a response to aphid attack may, however, lead to a delay in harvest.

Symptom expression

The plant reaction to aphid saliva can vary with the particular genotypes of both aphid and plant involved. Thus, some genotypes of wheat are specifically tolerant to the E biotype of *S. graminum* with a lack of symptoms (Morgham *et al.*, 1994). A mechanism for such tolerance to *S. graminum* was proposed by Maxwell and Painter (1962), who compared two wheats, 'Dickson' (tolerant) and 'Pawnee' (intolerant). These two varieties differed as to the timing of the cessation of further expansion of the flag leaf, on the photosynthesis of which much of the grain yield depends. Since the aphids tend to feed in an aggregation on the underside of the leaf, growth there is inhibited, while the upper leaf surface continues growing. The leaf therefore curls strongly, reducing the effective leaf area exposed to solar radiation. In 'Dickson', the growth of the flag leaf stops earlier than with 'Pawnee’, and feeding by the aphids on the underside of the leaf does therefore does not induce curling.

Further Considerations

Yield drag or other fitness costs

The majority of HPR mechanisms involve the production by the plant of more chemical compound or additional plant tissue, yet fitness costs of pest-resistance have rarely been reported. Thus, Assad *et al.* (2004) found no negative correlations between the height, grains per spike or total biomass of 14 wheat genotypes and their antixenosis to *D. noxia,* and in two Rag genes for resistance to *Aphis glycines* (soybean aphid), even when pyramided (i.e. combined on the same variety), incurred no yield penalty (Hesler *et al.,* 2013). Data of Gershenzon (l994) suggest that different secondary compounds can account for between 0.01 and 30% of the glucose in leaf tissue, but such static concentrations are negligible in comparison with the glucose production by photosynthesis over a period of time. Foyer *et al.* (2007) calculated that 30-40 min of photosynthesis (4-6 % of the total photosynthetic output over a 12 h day) would suffice to synthesize the DIMBOA in wheat and maize. Moreover photosynthesis is more often sink- than source-limited, and so any fitness costs would reveal themselves only under conditions of extreme stress.

Negative effects on natural enemies

Crop varieties developed for resistance to aphids can have deleterious effects on natural enemies, especially where the resistance is based on toxins (see above). DIMBOA, a hydroxamic acid studied extensively in relation to HPR to cereal aphids (see earlier), is toxic to the ladybird *Eriopis connexa*. Paradoxically, maize varieties with high DIMBOA cause less mortality of this predator than varieties with intermediate levels, since it can detect the compound in the aphids and avoid ingesting a toxic dose (Martos *et al*., 1992). In contrast, the ladybird *Propylaea japonica* showed increased weight and faster development on a high gossypol aphid-resistant cotton variety (Du Li *et al.*, 2004).

The parasitoid *Aphidius rhopalosiphi*, reared on the smaller individuals of *M. dirhodum* on the partially aphid-resistant wheat 'Rapier', showed progressively smaller size and reduced egg load on emergence in consecutive generations. After ten generations on ‘Rapier’, size and egg load had decreased by 15 and over 50%, respectively. However, parasitoids returned to an aphid-susceptible variety (‘Huntsman’) regained their fitness in one generation (Salim Jan and H. F. van Emden, unpublished but summary data given by van Emden, 1995). Reductions in size and fecundity of *Aphidius nigripes* emerging from *M. euphorbiae* reared on Bt potato have also been attributed to the poorer quality of the host aphids (Ashouri *et al.*, 2001; Ashouri, 2004). *Aphis glycines* showed such reduced longevity on aphid-resistant soybeans that fewer *Binodoxys communis* could develop to the mummification stage (Ballman *et al*., 2012).

Problem trading

There is therefore always the possibility that the plant modification made in developing HPR to aphids will make the plant more susceptible to another damaging organism. An early example is found in the hairy South African cottons, resistant to leafhoppers but especially susceptible to *A. gossypii* (Dunnam and Clark, 1938). When lucerne varieties resistant to lucerne wilt (*Verticillium albo-atrum*) were released in California, they proved especially susceptible to *T. trifolii* (van den Bosch and Messenger, 1973).

Glossy brassica varieties resistant to *B. brassicae* suffer from increased *Phyllotreta cruciferae* (flea beetle) damage compared with waxy ones (Stoner, 1992; Eigenbrode *et al.*, 2000), and glossy peas resistant to *A. pisum* are more heavily attacked by *Sitona lineatus* (pea and bean weevil) (White and Eigenbrode, 2000).

Surprisingly, problem trading has also been reported in tall fescue plants resistant to *R. padi* because of alkaloids produced by the fungal endophyte *Neotyphodium coenophialum*. The noctuid armyworm *Spodoptera frugiperda* showed enhanced performance on the endophyte-infected plants (Bultman and Bell, 2003).

In breeding F2 hybrid willows as biomass fuels, resistance to a *Chaitophorus* sp. aphid and the eriophyid mite *Aculus tetanothrix* were found to be inversely related (Czesak *et al*., 2001).

Biotypes

Species of aphid often show genotypic variation expressed through different behavioural traits, including sensitivity or tolerance to varieties bred for HPR. Tolerant variants are often referred to as 'resistance-breaking biotypes', but Blackman and Eastop (Chapter 1, this volume) express doubts about the use of the word because such genotypes may be just a single clone subject to recombination by sexual reproduction. However, the word 'biotype' is so well embedded in the literature of HPR that it would probably be misleading to the reader to use an alternative terminology here.

Some cowpea varieties producing a toxin strongly aphicidal to *A. craccivora* collected at the International Institute for Tropical Agriculture (IITA) in Nigeria proved susceptible to the first aphids collected from another location (Ansari, 1984), and the 'biotype problem' with pests indeed seems particularly common with aphids; 8% of 423 references between 1972 and 2015 concerning HPR and aphids are about this aspect, though many identify resistance-breaking biotypes in the glasshouse rather than reporting a problem in the field.

Biotypes in relation to HPR have proved particularly important with *S. graminum* on cereals, with the biotypes distinguished according to their responses to a clearly defined set of plant varieties. The resistance-breaking biotypes have proved a major headache in the field. For example, biotype E breaks the resistance incorporated in some sorghum varieties (Eisenbach and Mittler, 1987). No single resistance gene in either sorghum or wheat is effective against all biotypes of *S. graminum*. Anstead *et al*. (2003) located several biotypes of *S. graminum* on wild grasses, including one new biotype, and proposed that new biotypes are formed on wild grasses rather than on cereal crops.

The use of HPR against *A. glycines* in soybean has similarly identified at least three biotypes, though it is still possible to find soybean accessions resistant to all (Bansal *et al.*, 2013).

Attempts in the USA to manage *D. noxia* on cereals ran into biotype problems only five years after the appearance of the pest in Texas in 1986. Five biotypes have been distinguished (Shufran and Payton, 2009). The emergence of biotype 2 in Colorado made all resistance genes, other than one in rye, ineffective (Murugan *et al*., 2010). However, even the resistance-breaking biotypes vary in the chlorosis and stunting they cause (Shufran *et al*., 2007). Some of the resistance genes no longer effective in the USA are still effective in South Africa (Tolmay *et al*., 2013). Merrill *et al*. (2014) released two biotypes of *D. noxia* differing in their tolerance to resistant wheat in a known proportion at three sites along a gradient from northern Colorado to Florida, and found that the resistance-breaking biotype rapidly displaced the other, with an apparent more than 10-fold advantage.

Since the late 19th century, grapes in most parts of the world have been grafted on to rootstocks of old communion wine varieties resistant to *Daktulosphaira vitifoliae* (grape phylloxera) and brought from Europe to North America by the early settlers. This resistance lasted for a long time, but was finally broken by a biotype appearing in Germany in 1994 (Anonymous, 1994). Thus, in spite of the potential for ‘biotypic breakdown' of resistance, HPR to aphids may be quite durable. Di Pietro and Caillaud (1998) reared *S. avenae* on resistant wheat (including highly resistant 'Einkorn ') for two years and could find no selection for breaking the HPR.

As can be seen from the above, the occurrence of biotypes is variable both between and within species (in relation to geographical distribution). Puterka *et al.* (1992) recorded seven biotypes of *D. noxia* worldwide, but as yet only a few are found m the USA. A detailed study of *Elatobium abietinum* (spruce aphid) compared 40 populations each from the UK and New Zealand (Nicol *et al.,* 1998). There were 28 genotypes (but of course not necessarily 28 biotypes) in the UK collections, but only one in New Zealand.

There is little information as to the mechanisms whereby aphid biotypes break HPR. It is, however, known that resistance to *S. graminum* in sorghums, based on increased methylation of the middle lamellar pectin, is defeated in resistance-breaking biotypes of the aphid by their saliva possessing enhanced pectin methylesterase activity (Dreyer and Campbell, 1984). Biotypes of *Nasonovia ribisnigri* (currant–lettuce aphid) not affected by the Nr gene in resistant lettuce suppress the wound response of the sieve elements (ten Broeke, 2013). There is also the intriguing hypothesis that it is the symbionts that enable biotypes of *T. t. maculata* to break the resistance of some lucerne varieties (Rugg1e and Gutierrez, 1995) and of some *M. euphorbiae*-resistant tomato varieties (Francis *et al.,* 2010).

Coping with the biotype problem involves the continual development of varieties with new resistance genes available if control begins to fail, as has been the history with *S. graminum* (Puterka and Peters, 1990). The breakdown of plant resistance is usually far more serious with fungal diseases, and plant pathologists have developed strategies for deploying resistance genes so as to delay such breakdown. These strategies are equally applicable to HPR against aphids.

One such strategy is combining more than one resistance gene in a variety (‘pyramiding'). Porter *et al*. (2000) used a model for *S. graminum* to test whether pyramiding or sequential release of genes would maintain HPR for longer. The model predicted that pyramiding was the longer-lasting strategy, but Porter *et al.* claimed that experimental evidence actually pointed to the opposite conclusion. Bush *et al.* (1991) studied the value of variety mixtures against greenbug biotypes C and E. They used three varieties of wheat, one susceptible to the aphid (S) and one resistant to each of the biotypes C and E (CR and ER). The mixtures 3R:1S in separate experiments for each biotype, or 1CR:1ER:1S with both biotypes, managed the biotypes successfully, and the two-variety mix worked as well as the three-variety one.

Spread of viruses (see also Chapter 15, this volume)

Some workers have argued that, because aphids on resistant varieties are more restless, the spread of virus in such varieties is likely to be accelerated, particularly with non-persistent virus diseases. Atiri *et al*. (1984) reported such greater spread of *Cowpea mosaic virus* in small cage experiments with *A. craccivora* on cowpeas. Other work in Africa (Roberts *et al*., 1993) appears to confirm this in field experiments on chemical control of the same aphid with pyrethroids (which increase restlessness of aphids – van Emden and Service, 2004). In these experiments, the secondary spread of virus was greater on an aphid-resistant than on a susceptible cowpea variety. It is also possible that the phenomenon may occur with aphids in watermelon (Webb and Linda, (1993) – but see Kishaba *et al.* (1992) below) and with *M. persicae* in sugar beet, on which this aphid shows high mortality, especially as the plants get older. However, survival is improved on plants infected with either *Beet yellows virus* or *Beet mild yellowing virus* (Kift *et al.,* 1996). However, such reports are in the minority, perhaps partly because much of the spread of non-persistent viruses is by alatae of species for which the crop is not a host, and therefore totally resistant regardless of its resistance status to other aphid species. Even in respect of pest species, the overwhelming evidence is that HPR to aphids leads to less virus spread (van Emden, 1987). Thus Kishaba *et al.* (l992) compared *Watermelon mosaic virus 2* transmission by *A. gossypii* in one aphid-susceptible and three resistant water melon lines that were all equally good virus sources, and yet transmission by the aphid on the three resistant lines was reduced by 31, 71, and 74%. The number of aphids needed to give 59% infection was only 20 per plant on the susceptible line, but varied from 60-400 on the three aphid-resistant lines. Chen *et al*. (1997) also found that, for the water melon/*A. gossypii* combination, levels of non-persistent virus were negatively correlated with resistance to the aphid.

Interactions with other control measures

The aphid literature provides many examples of HPR having a positive effect on the impact of natural enemies. HPR also affects the susceptibility of aphids to insecticides. Such interactions are not discussed here, but are reviewed in Chapter 23, this volume.

Conclusions

Host-plant resistance has far greater potential for reducing populations of aphids than has as yet been exploited. This is partly because plant breeders have sought to use HPR as a single-component control measure, and have therefore screened for high resistance to aphids. Such levels of resistance are most likely to be based on toxic allelochemicals, often the expression of a single gene. This has certainly been the approach with the industrial production of insect-resistant transgenic crops, although as yet no transgenic event effective against aphids has been commercialized.

It will be evident from this account of HPR that such monogenetic resistance/ high expression of allelochemicals is likely to accentuate the potential disadvantages of HPR as a control method, including damaging side-effects on natural enemies and biotypic breakdown. The increased tolerance to insecticides that such HPR may cause is discussed on Chapter 23, this volume).

It is more broadly based, partial HPR to aphids that needs to be given greater research emphasis, especially given the worldwide move towards the integration of several control methods represented by IPM.

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Table 22.1. Some examples of wild relatives as sources of genes in traditional breeding for host plant resistance to aphids.

‘Wild’ relative	**Crop**	**Resistance character (if known)**	**Sample reference(s)**
Avena macrostachya and *Avena barbata*	Oats		Weibull (1987)
Solanum habrochaites and *Lycopersicon pennellii*	Tomato		Simmons *et al*. (2005)

Solanum peruvianum	Tomato	Glandular hairs and high tomatine	Kok-Yukom (1978)
Solanum tuberosum	Potato		Novy *et al*. (2002)
Brassica fruticolosa and *Brassica spinescens*	Cabbage	Bluconapin; lectin	Cole (1994a,b)
Triticum monococcum	Wheat		Sotherton and van Emden (1982); Deol *et al*. (1995); Di Pietro *et al*. (1998) Migui and Lamb (2004)
Triticum monococcum subsp. *aegilopoides* *Triticum urartu*	Wheat		Di Pietro *et al*. (1998)
Solanum berthaultii	Potato	Glandular trichomes	Gibson (1976)

Note: The same source of resistance may influence several aphid species attacking the same crop; hence, names of aphids affected are not included in the table. However, aphid names are usually given in the reference titles.

Legends for figures

Fig. 22.1. Junction of experimental lettuce plant testing for host plant resistance to *Pemphigus bursarius*. The impact of variety as an aphid control measure is seen clearly in the contrast between the susceptible variety 'Mildura' in the foreground and the resistant 'Avoncrisp' behind (courtesy of J.A. Dunn).

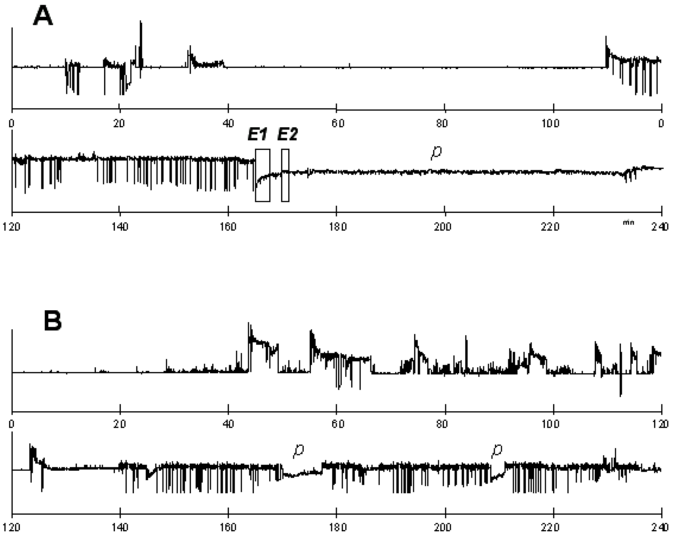

Fig 22.2. Electrical penetration graph (EPG) recordings for *Nasonovia ribisnigri* (currant–lettuce aphid) on susceptible (a) and nearly isogenic resistant (b) lettuce varieties. On susceptible lettuce, beginning at about 170 min, one long continuous phloem phase (*p*) is shown. This starts with sieve element (watery) salivation (waveform *E1*) and continues for the rest of the 4 h recording (only the first 2 h are shown) with sieve element ingestion (waveform *E2*). In contrast, the graph from the resistant lettuce shows only two short phloem-feeding periods (*p*), mainly of E1 waveform with some very brief switches to E2. The average start of the first phloem phase does not differ between the graphs from the two varieties; a phloem factor prevents sieve element ingestion (courtesy of W.F. Tjallingii).

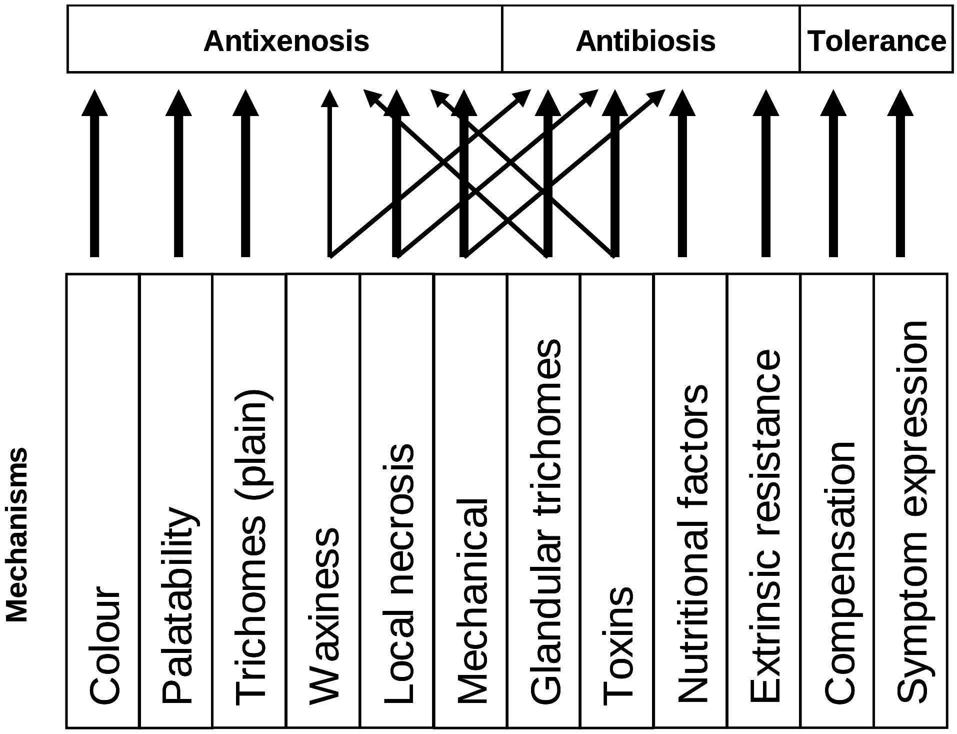

Fig.22.3. Mechanisms of host plant resistance to aphids, from left to right approximately in the sequence in which they will affect colonizing aphids. Thickness of arrows indicates the likely outcome of the interaction between mechanism and aphid in terms of plant antixenosis, antibiosis, or tolerance.

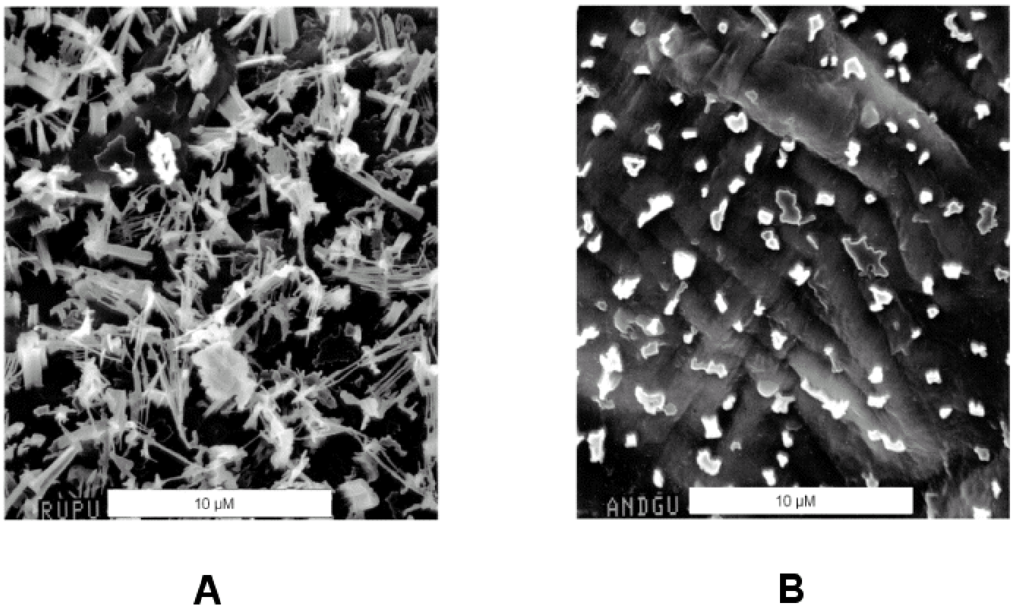

Fig. 22.4. Electronmicrographs of wax quantity and its distribution on normal (a) and glossy (b) cabbage leaf surfaces (courtesy of S.G. Eigenbrode).

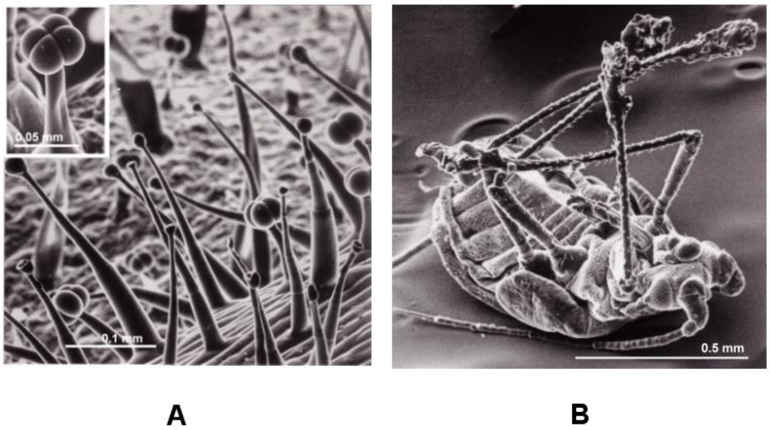

Fig. 22.5. Glandular trichomes. (a) Scanning electron micrograph of the leaf surface of *Solanum berthaultii* showing both trichomes with the four-celled head (magnified on insert) and those surmounted by a glandular vesicle. (b) Scanning electron micrograph of an aphid that was on *Solanum polyadenium*, showing the material from the glandular trichomes hardened on the feet (courtesy of R.W. Gibson).

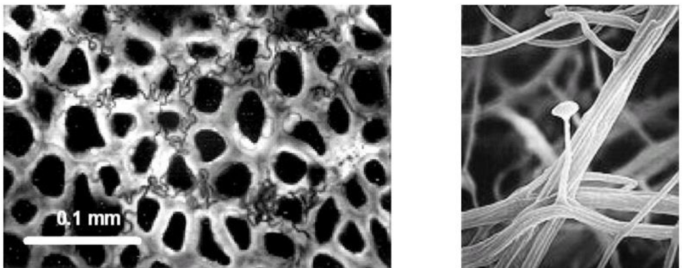

Fig. 22.6. The endophytic fungus *Neotyphodium.* (a) Section through a tall fescue (*Lolium arundinaceum*) seed showing mycelium between the aleurone cells. (b) Electronmicrograph of hyphae, conidiophore and conidium (4 µm long) in culture. Host is wild barley (*Hordeum* sp.) (courtesy of S.L. Clement).

Fig. 22.7. (a) Normal and (b) ‘leafless’ cultivars of peas ((b) courtesy of C. Coyne).