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Host plant resistance to aphids in cultivated crops: Genetic and molecular bases, and interactions with aphid populations

La résistance des plantes cultivées aux pucerons : bases génétiques et moléculaires et interaction avec les populations de pucerons

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ABSTRACT

Host plant resistance is an efficient and environmentally friendly means of controlling insects, including aphids, but resistant-breaking biotypes have occurred in several plant–aphid systems. Our review of the genetic and molecular bases of aphid resistance in crop species emphasizes the limited number of aphid resistance genes and alleles. Inheritance of aphid resistance may be monogenic (dominant or recessive genes) or polygenic. Two dominant, aphid resistance genes have been isolated to date. They both encode NBS-LRR proteins involved in the specific recognition of aphids. Strategies to ensure aphid resistance effectiveness and durability are discussed. Innovative research activities are proposed.

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R É S U M É

La résistance génétiquement déterminée des plantes est un moyen efficace et respectueux de l'environnement de lutter contre les pucerons. Cependant, des biotypes de pucerons, capables de contourner les résistances, sont apparus dans plusieurs systèmes plantes–pucerons. Dans cet article, sur les bases génétiques et moléculaires des résistances aux pucerons chez les espèces cultivées, nous insistons sur le nombre de gènes de résistance aux pucerons disponibles est limité. Les résistances aux pucerons sont contrôlées par des gènes majeurs (dominants ou récessifs) aussi bien que par des facteurs génétiques quantitatifs. Deux gènes de résistance aux pucerons ont été clonés jusqu'à présent, chez la tomate et le melon. Ils codent pour des protéines NBS-LRR, qui sont impliquées dans la reconnaissance spécifique des pucerons. Les stratégies de gestion durable des résistances aux pucerons sont discutées. De nouvelles voies de recherches sont proposées.

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1. Introduction

Aphids are major insect pests of plants. They feed specifically from the sieve element and cause damage by draining plant nutrients. They also are major vectors of plant viruses [1]. Management of aphids is challenging

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because of their short life cycles and extremely high reproductive rates. As a result, large quantities of insecticides are currently used. These are expensive to apply, damage ecosystems and the environment, and destroy non-targeted beneficial insects (predators, parasitoids, and pollinators). Moreover, this management practice has led to high levels of resistance to insecticides in several aphid species, which further complicates aphid control. Host plant resistance is an environmentally safe mean of controlling aphids that promotes the production of healthy products, free of pesticide residues. It has to be considered as an essential component of an integrated crop management system to control aphid pests [2 this issue].

Hereafter, host plant resistance will be understood as a heritable trait within a plant species that reduces aphid populations in the crops. Host plant resistance to aphids has been described in several crops. However, to be incorporated into a commercial cultivar using more or less complex breeding programs, the genetic basis of the resistance has to be understood and molecular genetic markers are required to assist the breeding process. The spectrum of action of the resistance towards the variability of aphids is also a crucial point. This information is available for a few aphids/crops interactions; consequently aphid genetic resistance was still scarcely used. Moreover, our understanding of the molecular mechanisms underlying plant resistance against aphids is limited compared with plant resistance against pathogens, such as fungi, oomycetes, bacteria, and viruses. The rapid development of plant and aphid genomic technologies will greatly facilitate a better knowledge of aphid/plant interaction and should lead to a larger use of crops resistant to aphids in the perspective of a sustainable production system.

This article reviews the literature on aphid resistance in crop species with a major emphasis on the genetic and molecular bases of the resistance. We first provide a brief review of the genetic basis of aphid resistance in various crop species, highlighting the diversity of the reported plant/aphid resistances and the diversity of their genetic control. Next, we summarize the rapid advances which have been made in understanding the molecular bases of aphid resistance. We then speculate how these data should be taken into consideration to develop more durable aphid resistant crops. We conclude by describing key areas that are now becoming active and exiting research directions, such as the fine characterization of the molecular interaction between resistant plants and aphids.

2. Sources of resistance to aphids

Screening germplasm for aphid resistance led to the discovery of resistant accessions in several crop species against various aphid species (Table 1). However, sources of aphid resistance are limited and usually scarce. More often, aphid resistance was identified in unimproved landraces, in wild accessions or even in related species, thus requiring a long breeding process to introduce the resistance into cultivated varieties. In soybean, eleven aphid-resistant accessions were identified after screening more than 3500 soybean germplasm accessions [3,4]. In lettuce, the screening of 1200 accessions of *Lactuca sativa*

and related species allowed the identification of two *L. serriola* and *L. virosa* aphid-resistant accessions; the genetic relationship with the previously known resistance conferred by *Nr* is yet unknown [5]. In wheat, over 40 000 accessions have been evaluated for seedling reaction to the Russian wheat aphid *Diuraphis noxia* and 300 have shown resistant or moderately resistant reactions. Very few of them, mostly identified in relatives of wheat, are currently being used in breeding programs and incorporated into the elite germplasm [6]. More recently, a screening effort was performed to find new resistance sources to the now predominant, virulent biotype 2 of the Russian wheat aphid; about 8% of accessions were resistant and belonged to distinct phylogenetic subgroups, suggesting that new genes or alleles may be identified [7,8].

The relative high number of resistant accessions discovered in certain species should not mask the fact that aphid resistance usually relies on a small number of genes with limited numbers of resistance alleles. In most cases, the genetic studies have still to be made to determine if the selected accessions are sources of novel resistance genes. In melon, about 50 accessions out the 500 tested were found resistant to the melon-cotton aphid *Aphis gossypii*. Among them, a large majority carries the same resistance *Vat* allele, whatever their geographical origins and only very few accessions carry a distinct allele [9]. Thus, aphid resistance in crop species is a valuable resource and our first rule should be to manage this natural biodiversity in a sustainable perspective.

3. Resistance phenotypes

Aphid resistance is manifested by different phenotypes depending on host plant and aphid genotypes. Entomologists have distinguished two mechanisms of resistance that affect insects: antixenosis (also known as non-preference), which affects the behaviour of insects and deters primary infestation of the crop, and antibiosis, which affects their biotic potential, e.g. growth, development, and reproduction [10]. Antixenosis was described in melon toward the melon-cotton aphid *A. gossypii* [11] and in barrel medic (*Medicago truncatula*) towards the blue-green aphid, *Acyrtosiphon kondoi* [12]. Antibiosis affects aphids primarily by reducing fecundity or increasing mortality. For example, *Vat*-mediated resistance in melon reduces fecundity by 80 to 90% within three days [13], and the *Mi-1*-mediated resistance in tomato causes 100% mortality of the potato aphid *Macrosiphum euphorbiae* within 10 days [14]. However, in several cases, the reduction of the aphid biotic potential (antibiosis) results from a modification of the aphid feeding behaviour (antixenosis). Thus, in melon, barrel medic and tomato, the resistance is mainly due to a drastic reduction of the phloem sap ingestion by the aphids, *A. gossypii*, *A. kondoi*, and *M. euphorbiae*, respectively [15,16,12].

Aphid resistance in certain plant genotypes is associated with localized cell death at the aphid-feeding site, analogous to a hypersensitive response and associated with production of reactive oxygen species (ROS) like hydrogen peroxide (H₂O₂). Necrotic lesions were reported in some wheat resistant varieties after *D. noxia* feeding.

Table 1
Major genes and QTLs for aphid resistance in cultivated crops.

Crop species	Aphid		Inheritance of aphid resistance and genes
	Genus and species	Common name(s)	
Legumes			
Alfalfa, <i>Medicago sativa</i>	<i>Acyrtosiphon pisum</i> Harris	Pea aphid	Polygenic [84,85]
Barrel medic, <i>Medicago truncatula</i> .	<i>Acyrtosiphon kondoi</i> Shinji	Bluegreen aphid	AKR [12,41,84]
	<i>Acyrtosiphon pisum</i>	Pea aphid	RAP1 [18]
	<i>Therioaphis trifolii</i> Monell f. <i>maculata</i>	Spotted alfalfa aphid	TTR [41,84]
Cowpea, <i>Vigna unguiculata</i>	<i>Aphis craccivora</i> Koch	Cowpea aphid	Rac1, Rac2 [86]
Peanut, <i>Arachis hypogea</i>	<i>Aphis craccivora</i> Koch	Groundnut aphid	One recessive gene [31]
Soybean, <i>Glycine max</i>	<i>Aphis glycines</i> Matsumura	Soybean aphid	Rag1, Rag2, Rag3, two recessive genes, two QTLs + 1 epistatic interaction between these two QTLs [4,28,29,33, 37,87,58]
Fruit trees			
Apple, <i>Malus domestica</i> and spp.	<i>Aphis pomi</i> De Geer	Green apple aphid	Polygenic, one QTL mapped [38]
	<i>Dysaphis devectora</i> Walker	Rosy leaf curling aphid	Sd-1 and Sd-2 closely linked or alleles, Sd3 from <i>M. Robusta</i> [26,38,88]
	<i>Dysaphis plantaginea</i> Passerini	Rosy apple aphid	Sm from <i>M. robusta</i> [89]
	<i>Eriosoma lanigerum</i> Hausmann	Woolly apple aphid	Er1, Er2, Er3 (Er1 and Er3 closely linked or alleles) [42]
Pear, <i>Pyrus</i> spp.	<i>Dysaphis pyri</i> Boyer de Fonscolombe	Pear bedstraw aphid	Dp-1 from <i>P. nivalis</i> [27]
Peach, <i>Prunus persicae</i> and spp.	<i>Myzus persicae</i> Sulzer	Green peach aphid	Rm1, Rm2, polygenic in <i>P. davidiana</i> , 8 QTLs [21,22]
Raspberry, <i>Rubus idaeus</i>	<i>Amphorophora agathonica</i> Hottes	Larger raspberry aphid	Ag1, two complementary dominant genes Ag2 and Ag3 [69]
	<i>Amphorophora idaei</i> Börn	European raspberry aphid	13 dominant genes A1-A10, AK4a, Acor1, Acor2 (only A1 mapped) [65,69]
Vegetables			
Lettuce, <i>Lactuca sativa</i> and spp.	<i>Nasonovia ribisnigri</i> Mosely	Lettuce aphid	Nr from <i>L. virosa</i> , mapped in <i>L. seriola</i> [5]
	<i>Pemphigus bursarius</i> L.	Lettuce root aphid	Ra or Lra mapped [59]
Melon, <i>Cucumis melo</i>	<i>Aphis gossypii</i> Glover	Melon-cotton aphid	Vat cloned, polygenic, four QTLs + two pairs of epistatic QTLs mapped [40,51,52]
Tomato, <i>Solanum lycopersicum</i>	<i>Macrosiphum euphorbiae</i> Thomas	Potato aphid	Mi-1 (or Meu) cloned [44,45,46]
Cereales			
Barley, <i>Hordeum vulgare</i>	<i>Diuraphis noxia</i> Mordvilko	Russian wheat aphid	Polygenic, three QTLs mapped [32,36]
Maize, <i>Zea mays</i>	<i>Rhopalosiphum maidis</i> Fitch	Corn leaf aphid	Two recessive genes <i>aph</i> and <i>aph2</i> , polygenic (<i>aph2</i> mapped) [32]
Sorghum, <i>Sorghum bicolor</i>	<i>Schizaphis graminum</i> Rondani	Greenbug	Polygenic, from three to nine QTLs mapped [34,35]
Wheat, <i>Triticum aestivum</i> and related species	<i>Diuraphis noxia</i> Mordvilko	Russian wheat aphid	Dn1, Dn2, dn3 from <i>T. tauschii</i> , Dn4, Dn5, Dn6, Dn7 from rye, Dn8, Dn9, Dnx, Dn2414 (all mapped except dn3) [6,24,72]
	<i>Schizaphis graminum</i> Rondani	Greenbug	gb1 from <i>T. durum</i> , Gb2 from rye, Gb3 and Gb4 from <i>Aegilops tauschii</i> , Gb5 from <i>A. speltoides</i> , Gb6 from rye, Gby (Gb2, Gb3, Gb5, Gb6 mapped) [6,25,90]

Interestingly, the hypersensitive-like response was observed after infestation with one biotype but not another, while the resistance was effective towards both biotypes [17]. The *RAP1* gene confers resistance to the pea aphid *Acyrtosiphon pisum* in barrel medic, independent of the hypersensitive reaction [18]. These data clearly indicate that the hypersensitive response is not required for aphid resistance. Furthermore, in several cases, no signs of localized cell death were reported, such as in *A. kondoi* resistant barrel medic plants (while susceptible plants develop necrotic patches and reddening on aphid feeding sites) [12] or in *Mi-1* *M. euphorbiae*-resistant tomato plants [19]. In melon, although aphid resistant plants exhibit no visible necrotic symptoms after *A. gossypii* infestation, a microscopic hypersensitive response was reported [20].

Aphid resistance in some crops is enhanced by prior aphid infestation. This is the case in peach, where the resistance to the green peach aphid, *Myzus persicae*, conferred by the dominant gene *Rm2* is enhanced by prior infestation [21,22], and in barrel medic against *A. kondoi* [12].

4. Genetic basis of aphid resistance in crop plants

Inheritance of aphid resistance may be monogenic or polygenic across plant and aphid species. Single, dominant R genes control aphid resistance in cereals, forages, fruits and vegetables (Table 1). In wheat, twelve genes are involved in resistance to the Russian wheat aphid *D. noxia*. Eleven of the genes are dominant, each conferring resistance in a different resistance source; most of them are located on group 1 and 7 chromosomes of Triticeae, and may be allelic or closely linked to the same cluster [23,24]. In wheat, barley and rye, resistance to the greenbug, *Shizaphis graminum*, is conferred by single dominant genes [25]. Dominant genes provide resistance to different biotypes of the rosy leaf-curling aphid, *Dysaphis devectora* (*Sd1*, *Sd2* and *Sd3*), and of the woolly apple aphid, *Eriosoma lanigerum* (*Er1*, *Er2* and *Er3*), in apple and related species (*Malus domestica* and *Malus* spp.) [26]. A dominant gene (*Dp-1*) provides resistance to *Dysaphis pyri* in pear (*Pyrus* spp.) [27]. In soybean, three dominant genes, *Rag1*, *Rag2* and *Rag3*, for resistance to the soybean aphid, *Aphis glycines*, were mapped to independent soybean linkage groups [28,29].

Several aphid resistances were reported with a recessive inheritance but researches on these resistances are scarce. Recessive gene *dn3* confers resistance to the Russian wheat aphid, *D. noxia*, in *Triticum tauschii* [30] and *gb1* from *Triticum durum* confers resistance to the greenbug, *S. graminum* (cited in [6]). Monogenic recessive resistances to the cowpea aphid, *Aphis craccivora*, and to the corn aphid, *Rhopalosiphum maidis*, were also reported in peanut and in maize, respectively [31,32]. Resistance to the soybean aphid, *A. glycines*, is conferred by two recessive genes with duplicate, dominant epistasis (ratio 15S:1R in F₂ populations) in soybean accessions PI 567541B and PI 567598B [33].

In several cases, aphid resistance is quantitative and polygenic. Genome locations of the genetic factors or QTL (Quantitative Trait loci) involved in aphid resistance have thus far been reported in very few instances. Aphid

resistance was measured as intensity of infestation in field conditions or after controlled infestation in most cases. QTL analysis performed in sorghum for resistance to the greenbug, *S. graminum*, using different resistance sources and different aphid biotypes revealed three to nine genomic regions involved in the resistance that are likely distinct in the different resistance sources [34,35]. Two QTL in barley with large effects and a third QTL with minor effect confer resistance to the Russian wheat aphid, *D. noxia*; these three QTL are not located in syntenic regions with the monogenic dominant *Dn* genes of wheat [36]. Two QTL in cowpea control soybean aphid abundance; they have additive and epistatic effects [37]. A first study of quantitative abundance of aphids in field conditions in a segregating population of apple localized a putative QTL (detected only once) of resistance to the rosy apple aphid, *Dysaphis plantaginea*, and a QTL of resistance to the green apple aphid, *Aphis pomi*, which both explained from 8 to 20% of the variation, depending on sites and years [38]. Quantitative resistance was measured in two instances using parameters that affect behavioural and life history traits of aphids. In peach, two QTL for resistance to the green peach aphid, *M. persicae*, were identified, that together affect the infestation rate, the leaf curling of infested plants and, interestingly, the aphid feeding behaviour as determined by the electronic penetration graph technique [39]. In melon, four additive QTL and two couples of epistatic QTL affect the melon-cotton aphid *A. gossypii*. Among them, a major QTL affects both the behaviour and the biotic potential of *A. gossypii*; it co-localizes with and likely corresponds to the *Vat* cloned gene [40].

5. Clusters of resistance genes

Aphid resistance genes are often located within clusters of resistance genes in the same chromosomal region, as is the case for many pathogen resistance genes. These 'hot spots' of resistance genes combine genes that confer resistance to aphids and other insects and pathogens. The barrel medic, *M. truncatula*, *AKR*, *TTR* and *RAP1* genes, each of which confers the resistance to a distinct aphid species (the bluegreen aphid, *A. kondoi*, to the spotted alfalfa aphid, *Therioaphis trifolii* f. *maculata*, to the pea aphid *A. pisum*) are located within about 40 cM [41,18]. The apple genes, *Er1* and *Er3*, for resistance to the woolly apple aphid, *E. lanigerum*, map to the same genomic region with a major gene for powdery resistance and with resistance gene analogues [42]. The *Mi-1* gene was located on the short arm of tomato chromosome 6, which carries an impressive collection of resistance genes effective against fungi, oomycetes and nematodes [43]. These clusters of resistance genes targeting taxonomically distinct pests and pathogens suggest that genes with a similar nature confer resistance to different organisms; duplication, recombination and multiple rearrangements events during evolution may have contributed to the development of new resistance specificities.

6. Molecular basis of aphid resistance

More than 40 genes conferring resistance to diverse pathogens, such as bacteria, fungi, nematodes and viruses

have been cloned during the last 20 years. In contrast, very little was known until recently about molecular mechanisms underlying aphid resistance. Two aphid resistance genes have been isolated and results to date suggest that plant aphid resistance is mediated by the specific recognition of aphid-effector proteins that triggers signalling cascades that rapidly activate plant defences against aphids in a similar scheme that was widely described for most plant-pathogen interactions.

The *Mi-1* gene, which confers resistance to three species of the root knot nematodes *Meloidogyne*, was isolated in tomato. The same gene/allele was shown to confer resistance to a biotype of the potato aphid *M. euphorbiae* as well as other insects, whiteflies and the psyllids [44,45,46,47,48,49]. The melon *Vat* gene confers resistance to the melon-cotton aphid *A. gossypii*. It has also the unique feature of conferring resistance to non-persistent viruses when vectored by *A. gossypii* [50]. We isolated the *Vat* gene by a map-based cloning strategy [51,52]. Both isolated aphid resistance genes, *Vat* and *Mi-1*, are members of the nucleotide-binding-site and leucine-rich repeat region (NBS-LRR) family of resistance genes, to which belong the majority of the genes, isolated to date, conferring resistance to bacteria, viruses, fungi and nematodes [53]. Genes *Vat* and *Mi-1* share structural similarities. Their encoded proteins belong to the coiled-coil (CC)-NBS-LRR, subfamily resistance proteins, which possess a coiled coil domain in N-terminal extremity of the NBS region. They differ, however, in several specific features. The gene *Mi-1* possesses a long N-terminal leucine-rich extension of about 200 amino acids, which was shown to play a role in regulating signal transduction and cell death [54]. In contrast, the N-terminal region of the *Vat* gene is short. The C-terminal region of the *Vat* gene comprises four near-perfect repeats of 65 amino acids flanked by highly imperfect copies of a LRR motif, absent in *Mi-1*. Both genes are constitutively expressed at low levels and encode proteins predicted to be located in the cytoplasm.

The identification of signalling cascades activated by aphid resistance genes is still at its infancy, but the data available to date indicate they partially overlap with those activated by pathogens [55]. Moreover, there is evidence that different aphid resistance genes activate distinct signalling pathways. *Mi-1*-mediated resistance is dependent upon the salicylic acid (SA) signalling pathway, while the jasmonic acid-responsive gene pathway is predominantly or exclusively induced in bluegreen aphid-resistant *M. truncatula* [56,57].

Several other aphid resistance genes may encode NBS-LRR proteins. Resistance to the bluegreen aphid *A. kondoi* in *M. truncatula* were mapped in a cluster of CC-NBS-LRR sequences and may be encoded by one of them [12]. Resistance to the soybean aphid *A. glycines* in soybean was mapped in a 115 kb region including two candidate TIR-NBS-LRR genes [58]. The lettuce *Ra* gene, which confers resistance to the lettuce root aphid, *Pemphigus bursarius* L., was shown to belong to the large RGC2 NBS-LRR gene cluster in lettuce, which comprises several downy mildew (*Bremia lactucae*) resistance genes [59]. Several NBS-LRR analog sequences have been mapped in the vicinity of loci associated with resistance to the rosy leaf curling aphid in

apple [26] and resistance to aphids in barley and wheat [60]. As knowledge of crop plant genomes develops, the cloning and sequencing of new aphid resistance genes from different crop plants will provide valuable information on the identity of resistance genes and the specific features of the molecular basis of the interaction between plants and aphids.

The molecular bases of recessive resistances to aphids have yet to be elucidated. Recessive resistances to viruses and fungi showed that resistance alleles correspond to mutations or deletions in a gene required for the infection cycle of the pathogen or in a resistance repressor [61,62,63,64]. Recessive resistance to aphids may result from the interruption of mechanisms used by the aphid for efficient feeding. The isolation of such recessive genes will be of great interest and is an exiting new avenue of research.

7. Specific interactions between plants and aphids

Several crops are hosts of different aphid species e.g., apple, wheat, raspberry, lettuce, barrel medic, whereas plant resistance to aphids is specific to an aphid species or even to a biotype within the species. A biotype is a clone able to survive, reproduce on, and/or cause injury to a cultivated plant that is resistant to other clones of the same species. Thus, most aphid resistances were shown biotype-specific, such as resistance to the greenbug, *S. graminum*, (*Gb* genes) to the European raspberry aphid, *Amphorophora idaei*, (*Ag* genes), to the soybean aphid, *A. glycines*, (*Rag* genes), and to the woolly apple aphid (*Er* genes) [6,42,65,66]. Some accessions are resistant to several biotypes, such as the barley 'Post' cultivar, resistant to 7 of the 11 known biotypes of greenbug [6]. The gene *Dn7* from rye and the two genes present in the wheat introduction Ctr2401 confer resistance to all the biotypes of the Russian wheat aphid known to date [67]. Some genes such as *Rag2* in soybean are known to confer resistance to different biotypes [28]. In melon, an allele of the *Vat* gene confers resistance to only a biotype of *A. gossypii*, while another allele confers resistance to two biotypes which are genetically distant [9].

8. Durability of resistance genes

Evidence of biotypes in some aphid species suggests potential for breakdown of major genes of resistance to aphids. Breakdown of resistance conferred by the *Nr* gene in lettuce to the lettuce aphid, *P. bursarius*, occurred in Europe ca. 10 years after the initial release [68] and subsequent wide deployment of this resistance. The resistance gene, *Ag1*, to the larger raspberry aphid, *Amphorophora agathonica*, was extensively used in raspberry from the 1930s to the 1980s, when a resistance-breaking biotype appeared [69]. Nevertheless, since the 1990s, the *Vat* resistance allele has been used extensively, incorporated into over 30 cultivars and representing over 40% of the area of melon cultivation in France (ca. 15 000 ha in total). Even if a few adapted biotypes were reported [70], we did not observe any extension of resistance-breaking biotypes.

Occurrence of sexual reproduction in pathogen species significantly increases the risk of resistance-breaking

biotypes or races [71]. The relevant data for aphids are far less numerous than for pathogens. The melon-cotton aphid, *A. gossypii*, is anholocyclic (only asexual reproduction occurs) in southern France where the resistance has been deployed without breaking down for 20 years. The Russian wheat aphid, *D. noxia*, is holocyclic (sexual and asexual reproduction occur) in its native range of Central Asia, but is anholocyclic in the Americas and South Africa; since 2003, new biotypes were found in the United States capable to overcome the resistance gene *Dn4*, which has been used since 1994 [72]. The greenbug, *S. graminum*, is considered holocyclic only beyond the 35th parallel; resistance-breaking biotypes have been discovered within 2 to 5 years of the release of every greenbug-resistant sorghum cultivar [73]. Virulent biotypes of greenbug were observed prior to deployment of some resistances [74], which suggests existence of genetic diversity in greenbug populations on non-cultivated grasses including future biotypes able to overcome newly deployed resistances.

Three strategies for deployment of resistance genes have been suggested. First, continual identification and introduction of new resistance genes in order to stay ahead of aphid populations that adapt to host resistance genes [6]. The number of genes and alleles of resistance are limited, as reported above, and it is feared that adapted biotypes spread into or develop *de novo* in areas, where biotype-specific resistance genes are deployed. This is a short-sighted strategy, especially for aphid species predicted to adapt quickly (holocyclic species). Second, combine (pyramid) as many resistance genes as possible in order to reduce the probability of new resistance-breaking biotypes. This pyramiding strategy requires the use of resistance genes, which are not already overcome individually. Three, identify and introduce resistance controlled by multiple, quantitative loci or by recessive loci demonstrated to be more durable. The combination of a major, recessive gene with a resistance QTL increased the durability of a major gene for virus resistance in pepper [75]. These different strategies have yet to be supported by experimental studies on aphids.

Thus it is critical that entomologists and plant breeders collaborate in development of aphid-resistant germplasm and cultivars. They need to better know the mode of reproduction and the genetic structure of the aphid populations that affects breeding crops. They have to investigate whether aphid biotypes, able to defeat resistance genes, pre-exist before the deployment of new resistant varieties. Such efforts will more likely challenge putative sources of aphid-resistance with different aphid populations, perhaps by testing in different environments (locations), and reveal occurrence or emergence of resistance-breaking biotypes. When controlled infestations are done, aphid colonies, collected in different production areas and genetically well characterized, have to be monitored for resistance bioassays.

9. Elucidation of possible virulence factors in aphid saliva

The development of genomic resources and the first sequencing of an aphid genome, that of the pea aphid

A. pisum, have begun to provide new insights into the structure and function of aphid genes [76,77]. In order to gain understanding of the basis of resistance durability, one of the most important developments likely to occur in the coming years is the elucidation of mechanisms involved in the break-down of plant resistance by aphids. The molecular basis of aphid avirulence is presently unknown, but will be revealed using the new developed genomic tools, and an aphid elicitor has yet to be identified. Aphid salivary secretions have a central role in aphid feeding activities and in the interaction between aphids and plants [78]. Thus it is highly likely that aphid saliva contains effector proteins that interact with plant proteins of resistant plants. Aphids secrete two kinds of saliva: gelling, which solidifies to form the stylet sheath, and non-gelling or watery. Aphids continuously inject watery saliva during their feeding activity. They penetrate and salivate into epidermal and mesophyll tissues during their probing activity, into parenchyma cells during their intercellular pathway before they reach the phloem, and they salivate into sieve tubes before and during sustained ingestion of phloem sap. Elicitors present in saliva may recognize plant cellular factors and trigger plant defence responses. Watery saliva contains enzymes, such as phenoloxidases, peroxidases, and pectinases, and other factors, which promote colonization of the host [79] and prevent the occlusion of sieve elements during aphid feeding [80]. Proteomic approaches initiated in several labs have identified some major proteins in the saliva of the pea aphid and green peach aphid [81,82]. The pattern of aphid salivary proteins strikingly differs among the aphid species and several minor and highly variable proteins still need to be identified [83].

10. Conclusions

Host plant resistance offers a very effective and promising way to control aphids in cultivated crops, and effective sources of resistance are available for a number of crops. Resistant cultivars must be developed and deployed with an awareness of the potential for emergence of resistance-breaking biotypes. In order to increase our understanding of aphid resistance, new resistance genes should be isolated, exploiting the genomic resources, which are available (or will be in a near future) for an increasing number of crop species. A particular effort should be dedicated to elucidate the molecular basis of recessive resistance genes, none of which have been isolated to date; this will likely provide new research avenues on aphid and plant interactions. Molecular characterization of aphid avirulence factors may enable evaluation and prediction of the potential durability of specific host plant resistance genes.

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