

Review

The Known and Unknowns of Aphid Biotypes, and Their Role in Mediating Host Plant Defenses

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Abstract: Insect species are subjected to disparate selection pressure due to various biotic and abiotic stresses. Management practices including the heavy use of chemical insecticides and introduction of insect-resistant plant cultivars have been found to accelerate these processes. Clearly, natural selection coupled with human intervention have led to insect adaptations that alter phenotypes and genetic structure over time, producing distinct individuals with specialized traits, within the populations, commonly defined as biotypes. Biotypes are commonly found to have better fitness in the new environment and, in the case of aphids, the most commonly studied system for biotypes, have the ability to successfully infest previously resistant host plants and new species of host plants. Although a large number of studies have explored biotypes, the concept for defining biotypes varies among scientists, as we lack a consistency in estimating biotype behavior and their variation within and between biotypes. The concept of biotypes is even more complicated in aphid species (Aphidoidea), as they undergo parthenogenetic reproduction, making it difficult to understand the source of variation or quantify gene flow. In this review, we aim to illuminate the concept of biotype and how it has been used in the study of aphids. We intend to further elaborate and document the existence of aphid biotypes using sugarcane aphid (*Melanaphis sacchari*) as a model to understand their differences, level of variation, evolution, and significance in pest management.

Keywords: biotype; host; aphid; resistance; sugarcane aphid



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1. Background

Insects are the most diverse group of organisms and have broad genetic variability that allows them to adapt to a wide array of less-than-ideal conditions, including their host plants, host animals and habitats [1]. Insect species feeding on different host plants experience different microclimatic conditions, presence of predators and natural enemies, variation in nutrient compositions, primary and secondary host plant metabolites, and different forms of plant defenses that consequently expose them to divergent selection [2–6]. In addition, insect species are also vulnerable to abiotic stresses, such as sudden fluctuation in temperature and humidity, compounded by the scarcity of food sources. Management strategies such as the development of insect-resistant plant varieties and application of various insecticides and pesticides in agroecosystems may add to the intensity of selection pressure [7]. Consequently, these selection pressures and divergent selection in insects lead to ecological adaptations [3,8,9], leading to phenotypic and genotypic differences among populations [9]. Although these differences have been observed and studied in many insect species, this is predominantly observed within and among different species of aphids.

2. Aphids

About 5000 species of aphids (class Insecta, order Hemiptera) have been described, and they form one of the largest, most geographically widespread, and economically important insects around the globe [10,11]. Aphids are plant sap feeders, and they suck sap

from the phloem by inserting their stylets on plant parts such as stems, leaves, panicles, and roots. During the process, they also inject toxic saliva into the plants, which causes leaf discoloration and leads to tissue death [12]. Aphids also secrete a sticky substance called honeydew that favors the growth of black sooty mold that impairs photosynthesis, plant growth, and may ultimately kill plants [13,14]. Besides direct damage through feeding, aphids also transmit a suite of viral diseases. Some of the common aphid-vector diseases include maize dwarf mosaic virus, cucumber mosaic virus, potato leaf roll virus, barley yellow dwarf virus, potato virus Y, banana bunchy top virus, carrot mottle virus, lettuce necrotic yellow virus and sugarcane mosaic virus [15–17]. All these traits have contributed to aphids, considered one of the most devastating pest groups of the major agricultural crops all over the world. Aphids have the dynamic ability to change into different forms (morphs) throughout their lifetime, which may specialize in feeding, reproduction, dispersal, and survival [18]. The reproductive methods of aphids may vary even within the same species. They can reproduce asexually and form clones or reproduce sexually and produce eggs. They can combine these two methods of reproduction and may alternate between cyclical and obligate parthenogenesis [18,19]. Under certain conditions, such as extreme weather, scarcity of food and attack by natural enemies, aphids can produce winged or wingless males, which leads to sexual reproduction [20]. Cyclical parthenogenesis, where they can alternate between asexual and sexual reproduction, is the most common mode of reproduction among many aphid species [19,20]. Aphids also have a unique and interesting reproductive phenomenon referred to as telescoping of generations, where a female viviparous aphid has a daughter developing inside her, and that daughter has a parthenogenetic daughter developing inside her [19,21]. These varied methods of reproduction highlight the great reproductive potential that aphids have in comparison to other than animals [10,22].

Integrated pest management (IPM) has been considered the most sustainable way for combining and integrating various aspects of plant protection against aphids. IPM prioritizes physical, cultural, and biological control methods, with chemical control methods as the last resort [23,24]. Under IPM for aphids, host plant resistance has been established as the most practical solution. However, the colossal diversity, adaptable body structure, high fecundity, short generation time and innate plasticity of aphid species gradually overwhelm the resistance in cultivars by evolving new forms with increased ability to severely infest and damage previously known resistant host cultivars [1,25,26]. These new and distinct forms of insects isolated by host preferences, not yet considered a new species, are commonly referred to as biotypes [27–29].

3. The Concept of Biotype

Benjamin Walsh (1864) [30] was the first entomologist who incorporated evolutionary concepts in his studies and recognized insect populations that are morphologically similar but having different biological traits and named them “phytophagic varieties.” He found that 15 similar species of gall wasps differed primarily in their preference for varied species of willow plants. Chlodkovsky (1908) [31] used the term “biological species” for populations of adelgids who differed from each other in their biological activity. In 1951, Painter published a book [32], *Insect Resistance in Crop Plants*, where he freely interchanged biotype with biological strains and races. Since then, entomologists and applied biologists have recognized different races and strains among insects, and many definitions on biotypes have been discussed. Some of the major ones are identified in Table 1.

Table 1. Commonly used definitions of biotypes.

S.N.	Biotype Concept	Reference
1.	Biotypes are the populations that can reproduce and survive on cultivars developed for resistance to a particular insect or can resist insecticides.	[33]
2.	Biotype is a taxonomic concept mostly used by non-taxonomists and has been defined as consisting of all individuals of equal genotype. Biotypes are recognized by a biological function rather than by morphological characters. In practice, a biotype contains those individuals performing whatever biological feat interests the observer and thus may contain one or more races or strains.	[34]
3.	Biotype is an individual or a population whose phenotype is determined by the interaction between plants having different genes for resistance and the larva's ability or inability to survive on and stunt the plant.	[35]
4.	Biotype of insects are individuals or populations that are distinguished from the rest of its species by criteria other than morphology, for example, a difference in parasite ability.	[36]
5.	Diverse biological differences have been used to designate populations as biotypes. They are (a) nongenetic polyphenisms, (b) polymorphic or polygenic variation within populations, (c) geographic races, (d) host races, and (e) species.	[37]
6.	Biotype is an intraspecific category referring to insect populations of similar genetic composition for a biological attribute. The biotype populations may be partially and temporarily sympatric, allopatric, or parapatric with other compatible populations, but differ in one or more biological attributes.	[1]
7.	The concept of biotypes, strain, and host race: "strain designates a population arising from a single collection or clonal individual; biotype is a category designating shared phenotypic traits; host race is a biotype that is better adapted to a specific host than are other biotypes."	[38]
8.	Biotypes are populations within an arthropod species that differ in their ability to utilize a particular trait in a particular plant genotype.	[39]

Clearly, these definitions designate biotypes based on their biological characteristics and differential performance on their host plants. However, Downie (2010) [40] criticized the previous definitions listed in Table 1, emphasizing that the definitions are too basic and confusing. He further stated that race and species terms denote meaningful meaning of biotype and would be more appropriate to use and understand. Variations in views about biotype among scientists cannot be ignored, as the definitions are not unified and the meaning itself is not consistent either within or between biotypes. This confusion might have come up since a greater number of biotypes are seen in aphid species, which reproduce almost exclusively by parthenogenesis, and do not obey the gene for gene relationship/principle that many scientists have used as a basic explanation for evolution of insect biotypes [7,37]. Though complex and complicated in nature, the existence of variation in factors that influence host choice within an insect population for various parameters cannot be ignored, and different populations with varied factors that influence host choice cannot just simply be labeled as races, clones, or species. Hence, the term biotype has served the purpose of defining the variations among different populations of arthropod species and that differentially affect their life history traits and host plant response.

Some parameters used in identifying biotypes are host preference, virulence, genetic composition, reproductive behavior, physiological response to biotic and abiotic conditions, disease vector capabilities, migration patterns, pheromone differences and insecticide resistance [34,41,42], and in a few cases morphological variations [1,43–45]. However, insect virulence on a particular host plant is a common parameter implicated in identifying insect biotypes [46]. This biotype concept has been universally used to describe the differences among populations of insect species, mainly aphids. As discussed above, other factors include the continuous use of insect-resistant plant varieties, the change in morphological behavior and phenotype of insects, which may be due to various genetic

and/environmental factors, or both might have led to the evolution of biotypes. Failure to recognize an existing biotype of an insect may also lead to the evolution of a more virulent biotype. Furthermore, to complicate the evolution of biotypes, the parasitic or mutualistic relationship of an insect pest with its endosymbiont has been found to spawn the variation and interdependence between and within species [47–50]. Natural enemies of herbivores, especially predators, may also be a causal factor in generating variation and change of host plant range. Thus, multitrophic interlinkages between host plant, herbivore, endosymbiont, predator, and other environmental factors and interference of various natural processes by human beings also contribute to initiate variation, and thus formation of biotypes.

4. Importance of Studying Insect Biotypes

Studying biotypes is of prime importance for insect pest management involving resistance management and manipulating host attraction traits. It has been found critical to incorporate the biotype concept in designing integrated pest management strategies involving host-plant resistance and biological control [1,51]. Insect populations with avirulent-dominant genes can be strategically released in populations with virulent-recessive genes, which might result in insect control by the production of biotypes with dominant genes for avirulence after a few generations [52–54]. For example; Foster and Gallun (1973) [52] studied two biotypes of Hessian flies (*Mayetiola destructor*)—Great Plains (GP) biotype and biotype B—which were released on a wheat cultivar susceptible to biotype B, but resistant to the GP biotype. The results from both greenhouse and field studies suggesting that the population of biotype B was completely suppressed. Thus, biotypes can be considered when deploying a strategy for genetic control of insects. Boller and Prokopy (1976) [55] proposed the possibility of biological control of the European cherry fruit fly (*Rhagoletis cerasi*) by using and releasing their incompatible biotypes into the population of compatible ones. Knowledge of biotypes helps entomologists and plant breeders study diverse genetic and phenotypic plasticity in insects, quantify the effects of gene flow, and develop new insect-resistant crop varieties [56]. For example, new resistant cultivars of wheat against the Hessian fly (*Mayetiola destructor*) have been developed by using this analysis, as Hessian fly biotypes can differentiate resistant genes in different wheat varieties [52]. Further, two biotypes of brown plant hopper (*Nilaparvata lugens*) have been selected for by rearing them on resistant rice varieties, and are deployed in identifying brown plant hopper-resistant varieties of rice [1]. Multiple studies have been conducted on aphid biotypes, and subsequently that information has become handy in breeding programs and used to generate aphid-resistant plant cultivars. Comprehending aphid biotypes and considering their response to insecticides can also guide the use, formulation, and production of insecticides [42]. Clearly, the study of biotypes enhances our knowledge on evolution, evolutionary divergence in organism and speciation [1,37].

Biotypes have been identified and studied in several insect orders [7,27,32,37,43,57]. Initially, biotypes were listed into 36 arthropod species belonging to 17 families of 6 orders, with aphids contributing almost half to this list [1]. This biotype list was later updated and about 50 arthropod species belonging to 20 families from 7 orders have been documented to exist as biotypes [7,57]. Even with this update, about 50% of described biotypes are of aphids [7,11,39], making it the most important and interesting group to explore biotypes in detail.

5. Aphid Biotypes

The concept of biotype apropos of aphids was first reviewed by [34], and he suggested that the term biotype in the case of aphids was synonymous with clone, as they are the individuals of same/similar genotypes. Aphids are mostly host specialized and are specific to one or two related plant species [58]. It is for this reason that aphids are referred to as ecological specialists [3,59]. For example, Ferrari et al. (2006) [60], found that pea aphid (*Acyrtosiphon pisum*) populations collected from alfalfa and red clover differed genetically and showed preference for the plant from which they were collected.

Nibouche et al. (2015) [61] showed that different populations of sugarcane aphids had their genetic structure linked to their respective host plants. For example, the study compared four main isofemale lineages of sugarcane aphids, where Ms11 lineage was found mainly on sugarcane, Ms15 lineage was exclusively found on sorghum and Ms16 lineage were found on both sorghum (Ms16_{sorghum}) and sugarcane (Ms16_{sugarcane}). Furthermore, host transfer experiments showed both Ms16_{sorghum} and Ms16_{sugarcane} had fitness tradeoffs on alternate host plants. Aphids have characteristic features that may vary, resulting in different morphs. Aphids have alate and apterous forms, oviparous and viviparous forms, and different combinations of these forms where each form or morph has its own ecological function and are distinct in their response to various environmental factors [62]. In cotton aphid (*Aphis gossypii*), it has been found that a single individual can produce offspring with four different and distinct phenotypes—normal light green apterous aphid, normal dark green apterous aphid, dwarf yellow apterous aphid and alate aphid—as a response to the change in its environment and type and quality of host plants [63–67]. Thus, the inherent phenotypic plasticity, host-associated genetic divergence, underlying plasticity in gene expression [68], and the ability to thrive in diverse environmental and geographic locations promotes the faster development of biotypes in aphids than any other insect groups [10,19,69–72].

Harrington (1943) [73] was the first to document the occurrence of biotype in aphid species. His study indicated the occurrence of four biotypes (referred to as physiological races) of pea aphid, which differed from one another significantly in size and virulence in the United States. Later, biotypes of the pea aphid were described, showing differences in morphology [74,75], life cycle [76,77], host plant preferences [77–79], growth rates [77,80] and nutrition [77]. Cartier and Painter (1956) [81] worked on corn leaf aphid (*Rhopalosiphum maidis*) and documented the differential reaction of two biotypes of corn leaf aphid to resistant and susceptible varieties of sorghum. Later, Painter and Pathak (1962) [82] proposed four biotypes of corn leaf aphid based on their reproduction on different plants and plant reaction to aphid feeding. This was revised again by Wilde and Feese (1973) [83], who documented a fifth biotype of corn leaf aphid that differed significantly from those previously observed based on its ability to attack a plant species that had been considered resistant and its ability to reproduce well at higher temperatures. Nielson and Don (1974) [84] studied four biotypes of spotted alfalfa aphid (*Therioaphis maculata*) on different varieties of alfalfa with varying resistance to different biotypes. In the case of greenbugs or wheat aphids (*Schizaphis graminum*), more than 10 biotypes have been reported, four of which are highly damaging [85–87].

Many aphid biotypes have been discovered and studied based on their behavior and characteristics on new or previously resistant host plant species or varieties, suggesting that a change in feeding preference and/or behavior will produce a new biotype. Saxena and Chada (1971) [86] studied two greenbug biotypes and found that they have differences in their ability to penetrate the plant tissue. They found that biotype A could penetrate its stylet up to the phloem, while biotype B ended its stylet penetration in the mesophyll parenchyma and could not reach the phloem tissue. Campbell et al. (1982) [88] suggested that the differential feeding behavior of greenbug biotypes on different resistant and susceptible varieties of sorghum might be because of the difference in chemical constituents of phloem between them. It has also been suggested that resistant host plants produce defensive chemical substances in response to the aphid stylet penetration [84,89,90]. Another, similar, study conducted by Montllor et al. (1983) [91] on two greenbug biotypes found that they differed in time spent on phloem feeding, fecundity, longevity, post reproductive life, development time and larger size when monitored on a sorghum variety that was previously known for having resistance against greenbug [88,92–94]. Kim et al. (2008) [94] confirmed two distinct soyabean aphid biotypes for the first time based on their unique virulence patterns on soybean genotypes.

In most cases, aphid biotypes have been known to evolve to break the host plant resistance and changing or expanding their host range. It is estimated that there are 26 aphid species known to have biotypes now. Aphid species with their respective host plants, number of known biotypes and the basis of classification are documented in Table 2.

Table 2. Detailed documentation of aphid biotypes across various host plants.

S.N.	Aphid Species	Common Name	Crop	# of Biotypes	Biotypes Based on	References
1	<i>Acyrtosiphon kondoi</i> (Shinji)	Blue alfalfa aphid	Lucerne (<i>Medicago sativa</i>)	2	Virulence	[7,95]
2	<i>Acyrtosiphon pisum</i> (Harris)	Pea aphid	Lucerne (<i>Medicago sativa</i>), dyer's whin (<i>Genista inctoria</i>), winged broom (<i>G. sagittalis</i>), common sainfoin (<i>Onobrychis viciifolia</i>), white clover (<i>Trifolium repens</i>), broad beans (<i>Vicia faba</i>) and horseshoe vetch (<i>Hippocrepis comosa</i>)	15	Genetic divergence and differential association with endosymbionts, virulence, body size, body color, differential survival rate, reproduction, mortality, virus transmission	[7,73,76,79,80,96,97]
3	<i>Amphorophora agathonica</i> (Hottes)	Large raspberry Aphid	Red raspberry (<i>Rubus idaeus</i>)	6	Colonizing ability on host plant and virulence	[98,99]
4	<i>Amphorophora idaei</i> (Born)	Large raspberry aphid	Red raspberry (<i>Rubus idaeus</i>)	5	Genetic variation and virulence	[100,101]
5	<i>Amphorophora rubi</i> (Kalt.)	Raspberry aphid	Red raspberry (<i>Rubus idaeus</i>)	4	Virulence and difference in reproductive rate	[1,102–106]
6	<i>Aphis craccivora</i> (Koch)	Cowpea aphid	Cowpea (<i>Vigna unguiculata</i>)	2	Host plant preference, virulence	[1,7,107–110]
			Groundnut (<i>Arachis hypogaea</i>)	2	Differential ability to transmit viral strain	
			Bush sitao (<i>Vigna unguiculata sesquipedalis</i>)	5	Host preference, virulence	
7	<i>Aphis fabae</i> (Scopoli)	Bean aphid	Broad bean (<i>Vicia faba</i>)	2	Host preference, phenotypic plasticity	[7,111,112]
8	<i>Aphis glycine</i> (Matsumura)	Soybean aphid	Soybean (<i>Glycine max</i>)	4	Virulence (ability to colonize on resistant plants)	[94,113–115]
9	<i>Aphis gossypii</i> (Glover)	Cotton or melon aphid	Cotton (<i>Gossypium spp.</i>)cucumber (<i>Cucumis sativus</i>) and melon (<i>Cucumis melo</i>)	2	Host plant based genetic differentiation, host preference	[71,116–118]
10	<i>Aphis nasturtii</i> (Kaltenbach)	Buckthorn aphid	Potato (<i>Solanum tuberosum</i>)	2		[1,7]
11	<i>Aulacorthum solani</i> (Kaltenbach)	Foxglove aphid	Potato (<i>Solanum tuberosum</i>)	2	Difference in host use	[1,7,119]
12	<i>Brevicoryne brassicae</i> (Linnaeus)	Cabbage aphid	Vegetables	2	Virulence	[120,121]
13	<i>Chaetosiphon fragaefolii</i> (Cockerell)	Strawberry aphid	Strawberry (<i>Fragaria ananassa</i>)	2	Host plant preference and aphid probing behavior	[1,7,122]
14	<i>Diuraphis noxia</i> (Kurdjumov)	Russian wheat aphid	Wheat (<i>Triticum spp.</i>)	10	Virulence	[123–129]
15	<i>Dysaphis devectora</i>	Rosy leaf-curling apple aphid	Apple (<i>Malus spp.</i>)	3	Virulence	[130]

Table 2. Cont.

S.N.	Aphid Species	Common Name	Crop	# of Biotypes	Biotypes Based on	References
16	<i>Dysaphis plantaginea</i> (Passerini)	Rosy apple aphid	Apple (<i>Malus spp.</i>)	3	Virulence	[131]
17	<i>Eriosoma lanigerum</i> (Hausmann)	Woolly apple aphid	Apple (<i>Malus spp.</i>)	3	Virulence and Life history traits	[132–135]
18	<i>Macrosiphum euphorbiae</i> (Thomas)	Potato aphid	Tomato (<i>Solanum lycopersicum</i>) and Hairy nightshade (<i>Solanum sarrachoides</i>)	2	Virulence and host preference	[136,137]
19	<i>Melanaphis sacchari</i>	Sugarcane Aphid	Sugarcane (<i>Saccharum officinarum</i>), sorghum (<i>Sorghum bicolor</i>), Johnsongrass (<i>Sorghum halepense</i>), Columbus grass (<i>Sorghum alnum</i>)	6	Micro-locus lineages and host preference	[61,138,139]
20	<i>Myzus persicae</i> (Sulzer)	Green peach aphid	Tobacco (<i>Nicotiana tabacum</i>), cabbage (<i>Brassica oleracea var. capitata</i>), peach (<i>Prunus persica</i>), potato (<i>Solanum tuberosum</i>) and sugar beet (<i>Beta vulgaris</i>)	3	Body color, life history traits, host plant preference and insecticide resistance,	[1,140]
21	<i>Nasonovia ribisnigri</i> (Mosley)	Lettuce leaf aphid	Lettuce (<i>Lactuca sativa</i>)	2	Virulence	[7,141–143]
22	<i>Rhopalosiphum maidis</i> (Fitch)	Corn leaf aphid	Barley (<i>Hordeum vulgare</i>), corn (<i>Zea mays</i>), sorghum (<i>Sorghum bicolor</i>)	5	Differential reproduction, host plant response and virulence	[81–83,144]
23	<i>Schizaphis graminum</i> (Rondani)	Greenbug or wheat aphid	Barley (<i>Hordeum vulgare</i>), wheat (<i>Triticum spp.</i>), oats (<i>Avena sativa</i>), sorghum (<i>Sorghum bicolor</i>)	11	Virulence, a few morphological differences	[7,85,87,145–152]
24	<i>Sitobion avenae</i> (Fabricius)	English grain aphid	Wheat (<i>Triticum spp.</i>)	6	Virulence, life history traits, body color	[72,153]
25	<i>Therioaphis maculata</i> (Buckton)	Spotted alfalfa aphid	Lucerne (<i>Medicago sativa</i>)	6	Biological activity and response to organophosphate insecticides.	[33,154,155]
26	<i>Therioaphis trifolii</i> F. <i>maculata</i> (Buckton)	Spotted alfalfa aphid	Alfalfa (<i>Medicago sativa</i>), clover (<i>Trifolium spp.</i>)	2	Host plant based genetic differentiation, host preference	[1,7,156–159]

6. Molecular Advances in Aphid Biotype Studies

Molecular methods have been well employed to study the biotypes in aphids. Aphids mainly undergo a parthenogenetic form of reproduction, due to which their gene flow is restricted, and are usually observed to have low genetic diversity. Most research findings show that the genetic divergence of aphid biotypes is linked to their host plants. This has also been studied as host-associated genetic makeup among aphid biotypes and host-associated genetic divergence between aphid biotypes. Microsatellite analyses, DNA markers, transcriptome profiling and analyses, and different mitochondrial sequences are commonly used to identify different biotypes of different aphids. Sunnucks et al. (1997) [157] studied different populations of the spotted alfalfa aphid (*Therioaphis trifolii* F. *maculata*) collected from lucerne and subclover using RAPD-PCR techniques and mitochondrial DNA genetic markers. The result showed that there were significant differences in the genetic makeup of the spotted alfalfa aphid, where aphids collected from lucerne and subclover had different genetic makeup. The study concluded that these aphids are different host-associated biotypes of spotted alfalfa aphid and thus had host plant-based

genetic differentiation. Similarly, using mitochondrial DNA sequences, host-adapted races of wheat aphid or greenbug (*Schizaphis graminum*) were confirmed and three different clades noted in a study conducted by Anstead et al. (2002) [160]. Wang et al. (2016) [71] found different mitochondrial sequences in two biotypes of cotton aphid (*Aphis gossypii*) where cotton aphids collected from cotton plant had a different five single-nucleotide polymorphisms when compared to the cotton aphids collected from cucumber plant, and further, they named the same aphid species cotton biotype and cucumber biotype based on their host plant specialization. Similarly, five genetic lineages, named *Burk*, *C*, *Ivo*, *Auber* and *PsP4* of cotton aphids were observed using microsatellite markers and the lineages found to be host-specialized [161]. Simon et al. (2003) [162] studied the genetic differentiation of different populations of pea aphid (*Acyrtosiphon pisum*) collected from pea, clover, and alfalfa plants by using allozyme and microsatellite markers and found that the aphid populations collected from different host plants were genetically divergent. Frantz et al. (2006) [163] conducted population genetic analyses on pea aphids collected from different pea, faba bean, red clover, and alfalfa where they observed three genetic clusters of pea aphid, and one from pea and faba bean, another from red clover and the third one from alfalfa. These results clearly indicate host-associated genetic difference in pea aphid biotypes. Genetic analysis of different biotypes of large raspberry aphid (*Amphorophora idaei*) has shown high genetic variability within and between its five biotypes [101]. Furthermore, Wang et al. (2019) [72] studied genetic differentiation of different populations of English grain aphid (*Sitobion avenae*) collected from different wheat and barley plants using microsatellite markers. The study found that the populations collected from barley had higher genetic diversity than the populations collected from wheat. The results also showed low genetic differentiation among the populations from different geographic locations and hence provided an important insight to consider plant factors to be of relatively higher importance than geographical factors for stimulating genetic differentiation in aphid biotypes. In addition, the populations in different geographical locations having few or no phenotypic variations and some genetic variations are sometimes referred to as ecotypes [37].

7. Ecotypes and their Differences from Biotypes

Ecotypes are individuals or group of individuals of the same species that live in similar habitats, but different geographical regions or localities. They are also referred to as ecological races. Ecotypes may share similar morphology and behavior, but still consist of distinct populations [37]. While they have some genetic variation, they can breed among themselves, but do not do so because of geographical barriers. For example, sugarcane aphid biotypes are categorized as having different multiloci lineages (MLLs). Biotype MLL-A is found in East and West Africa, MLL-B in Australia, MLL-C in a wide region covering South America, the Caribbean, East Africa and the Indian Ocean, and other biotypes in another region [138]. Here, MLL-A, MLL-B and MLL-C represent different SCA biotypes. However, MLL-C found in South America and West Africa are the same biotype but can be called ecotypes as they are in different environmental conditions prevalent in the different continents. Diverse environmental components can be held accountable for determining ecotypes from among the biotypes of a species [164]. Over a prolonged period of evolution, the phenotypic differences among the biotypes may get genetically fixed and may also give rise to ecotypes. Some parameters useful in differentiating biotypes and ecotypes of insect species are described in Table 3.

Table 3. Commonly used parameters to differentiate biotypes and ecotypes.

Parameters	Biotypes	Ecotypes
Found in	Same or different geographical locations	Different geographical locations
Breeding	Cannot breed among themselves	Can breed among themselves
Genetic variation	High (except for insects who reproduce mainly by parthenogenesis like aphids)	Low
Morphological variation	May or may not be present	Present
Variations due to	Mostly plant factors and to some extent environmental factors	Exclusively by environmental factors

Sugarcane Aphid (Melanaphis sacchari) and Sorghum (Sorghum bicolor)

Sorghum (*Sorghum bicolor* (L.) Moench) is a multipurpose crop grown for its food, fodder and fuel production and is rich in nutrients and bioactive phenolic compounds. Sorghum is also a nutrient-use efficient crop with high water and nitrogen use efficiencies and can further tolerate drought and elevated temperatures [5,90,165,166]. However, sorghum is also susceptible to various insect pests, and are a major target of aphids [167–170]. The most common aphid species feeding on sorghum are *Schizaphis graminum* (the previously mentioned greenbug), *Rhopalosiphum maidis* (corn leaf aphid), *Sipha flava* (yellow sugarcane aphid), and *Melanaphis sacchari* (sugarcane aphid) [90].

Melanaphis sacchari, the sugarcane aphid is tiny, soft-bodied, with a gray, tan, or yellow body color. It belongs to the order Hemiptera, suborder Sternorrhyncha, superfamily Aphidoidea, and family Aphididae. They are globally distributed, and its host plant includes members of Poaceae family, including sugarcane, sorghum, rice, millet, corn, and wild grasses [171]. The sugarcane aphid has distinct dark-black cornicles, tarsi, and antennae, which distinguish it from other aphids. However, the feeding injury on sorghum appears similar to corn leaf aphid [172]. In the United States, *M. sacchari* was first reported in 1877 in Florida [173,174] and in 1999 in Louisiana on sugarcane (*Saccharum officinarum* L.) [175,176]. An outbreak of *M. sacchari* in sorghum was first reported near Beaumont, Texas in 2013 [172,177–179]. By the end of 2013, it was reported from 38 counties from four states—Texas, Louisiana, Mississippi, and Oklahoma [172] and has subsequently expanded its geographic range to 20 states [138]. Among aphids, *M. sacchari* sucks copious amounts of sap from plant tissue and produces enormous amounts of honeydew, which favors growth of sooty mold on plants [171,172,179]. The black sooty mold coats the leaf surface, due to which the leaves cannot receive adequate sunlight, and this impairs photosynthesis. The reduced photosynthetic capacity can lead to stunting in plants and can ultimately cause significant yield losses [180,181]. In addition, it also vectors diseases including sugarcane yellow leaf virus [182]. Since 2014, sorghum fields in Louisiana and Mississippi have been reported to be 100% infested with *M. sacchari*, costing approximately \$10 million for aphid control alone [178] and yield loss on susceptible sorghum hybrids can reach up to 60% [183]. During 2014 and 2015, *M. sacchari* caused an estimated loss of \$64.53/ac primarily by increased production costs as well as reduced sorghum yields in the Rio Grande Valley, Texas [179].

For a very long time, *M. sacchari* had contrasting feeding behavior and host choice in different continents. *M. sacchari* was not considered a pest of sugarcane and was a serious pest of sorghum in Africa and Asia over a long period of time [184], which is opposite to what we observed in North America. In recent times, *M. sacchari* seems to have extended its host choice and feeding behavior within the same geographical region. The question, therefore, lies in whether this change in feeding behavior is due to the emergence of a new biotype of *M. sacchari* or the introduction of new genotypes of sorghum from Asia or Africa [138] or a combination of both. Genetic diversity has been examined worldwide for *M. sacchari*, and several multiloci lineages (MLL), including MLL-A, MLL-

B, MLL-C, MLL-D, MLL-E, and MLL-F, have been identified [185]. Genotypic analysis using microsatellite markers suggested that MLL-F has been the lineage associated with the widespread outbreak of *M. sacchari* in the United States since 2013 [61,138,186]. In Brazil, Lopes da Silva et al. (2014) [187] showed that an aphid clonal lineage collected from sugarcane exhibited higher demographic parameters in terms of longer reproductive period, higher fecundity, and greater longevity of the aphid on sorghum than on sugarcane. In 2019, host plant specialization studies among *M. sacchari* by Paudyal et al. [188] found that in the US, there exist two different host-specific biotypes where *M. sacchari* collected on sugarcane belonged to the multilocus lineage MLL-D, and *M. sacchari* collected from sorghum and Columbus grass belonged to MLL-F. Collectively, data from these studies indicate that there are host-associated genotypes of *M. sacchari* in the US, and should be explored further.

8. Conclusions and Future Directions

Collectively, studies on biotype and their emergence point out that the principle of biotype evolution relies on natural selection and human-mediated interference by manipulating the genome of host plants. They are coevolved with host plants, herbivores, parasitoids, and their endosymbionts over time. Biotypes are derived from the survivors of resistant cultivars and other various biotic and abiotic stresses. A plant's resistance to pests is made vulnerable and threatened by the emergence of a new biotype. Based on our literature survey and synthesis, another consideration for a biotype definition could be: "Biotypes are the individuals and/or populations of insect species that demonstrate distinct characteristics and behavior influenced by the spatial and temporal variation of host plant species, biotic and abiotic factors, and human interventions." As new biotypes emerge, research about their similarities and differences inform the use of improved methods to produce healthy plants and ensure their sustainability. To progress the study of biotypes and their evolution ultimately leads to the question on how to disentangle the role of host plant among other biotic and abiotic factors that influence biotypes. Ultimately, as new biotypes emerge, the affected plants also adapt and evolve as a countermeasure, as observed in various crop species. The continuous use of resistant cultivars and heterogeneous methods applied to control pests also leads to the rise in biotypes and should be the basis and the subject of more research on them.

Insect management programs that incorporate host plant resistance are imperative and strategic in future pest control. To implement and make these strategies effective, there is a need to understand plant–insect interactions at both ecological and mechanistic levels. An effective surveillance program can also be developed to assess the gene mutation or population migration in pests/aphids that would provide results that could be used to improve strategies in growing stronger and resilient plants. An important feature of this surveillance program would include more time spent gathering data on insects from (PCR) techniques and DNA probes [1]. These efforts can be used as a springboard for further investigation of biotypes in the future. The electrical penetration graph (EPG) technique (which assesses the feeding behavior of sap-sucking insects), PCR techniques (which can discriminate trivial differences in DNA between individual insects) and the development of molecular markers can better enable biotype identification and differentiation. This differentiation is important to implement biological control approaches to correctly match the right pest control agent with the right host biotype. For example., Wang et al. (2020) [189] studied defense-related genes of two biotypes of cereal aphid (*Sitobion avenae*), which indicated that the expression of these genes was plastic and related to the original and alternative host plants. Thus, study of host plant association and associated defensive genes of aphids might provide important insight into the adaptive evolution and differentiation mechanism of different biotypes on different host plants.

To decrease the potential development and/or outbreak of new insect biotype on new or previously resistant host plants, there is a need for the development of various short and long-term strategies. Plant breeding for insect-resistant cultivars should focus on broadening the genetic makeup for resistance in plants and thus diversifying the genetic base in terms of both major and minor genes. Gene pyramiding for resistance can be brought into effective use if thoroughly tested and evaluated for its efficacy. Also, horizontal resistance can be more effective and durable than single-gene resistance [39]. These abovementioned mechanisms of plant resistance might lower the probability of development of new biotype that is more virulent and robust than a previously existing biotype.

To conclude, the continuous use of resistant plant varieties along with the incremental use of chemical pesticides has caused the emergence of more virulent aphid biotypes. We should continue to study and quantify the phenotypic changes through life-history traits and correlate these with genetic diversity among aphid populations, which can contribute to a better understanding of aphid population dynamics and pest status and thus will be useful in implementing various pest management strategies, even with the emergence of more biotypes in future.

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