ATATÜRK ÜNİVERSİTESİ YAYINLARI
ATATURK UNIVERSITY PUBLICATIONS

Review / Derleme

DOI: 10.54614/AUAF.2022.1002421

Evaluation of Interactions Among Aphids, Endosymbionts, and Host Plants: A Foresight for the Future

Afitler, Endosimbiyontlar ve Konukçu Bitkiler Arasındaki İlişkilerin Değerlendirilmesi: Gelecek için Bir Öngörü

Gülay OLCABEY ERGİN[1],
Ayten ÖZTÜRK[2],
Gazi GÖRÜR[2]

[1]Department of Therapy and Rehabilitation, Niğde Ömer Halisdemir University, Zübeyde Hanım Vocational School of Health Services, Niğde, Turkey
[2]Department of Biotechnology, Niğde Ömer Halisdemir University, Faculty of Arts and Sciences, Niğde, Turkey

Geliş Tarihi/Received: 29.09.2021
Kabul Tarihi/Accepted:12.02.2022

Sorumlu Yazar/Corresponding Author:
Gülay OLCABEY ERGİN
E-mail: gulayolcabeyergin@ohu.edu.tr

Cite this article as: Olcabey Ergin, G., Öztürk, A., & Görür, G. (2022). Evaluation of interactions among aphids, endosymbionts, and host plants: A foresight for the future. *Atatürk University Journal of Agricultural Faculty,* 53(2), 133-139.

Content of this journal is licensed under a Creative Commons Attribution-NonCommercial 4.0 International License.

ABSTRACT

Insects, the most common and most successful animals on earth, establish long-term and stable ecological relationships with bacteria. Aphids (Hemiptera: Aphididae) are an insect group of agricultural importance that can feed on many herbaceous, shrubs, and woody plants as hosts and are also in close relationship with endosymbiont bacteria. It is seen that aphid is going to further increase their current pest potential in the near future due to their high adaptability and rapid reproduction ability. In order to be effective and successful in the biological control of aphids, many features of aphids are required to be known and clarified. Therefore, determining the interactions among aphid, host plant, and endosymbiont in this relationship might make biological control of aphids more effective. In this review, what is known about the relationship among aphids, the primary endosymbiotic bacterium *Buchnera aphidicola,* and the host plant is examined, and the possibilities of using symbiont bacteria in the biological control of aphids are discussed.

Keywords: Aphid, biological control, *Buchnera aphidicola*, stress

ÖZ

Yeryüzündeki en yaygın ve en başarılı hayvanlar olan böcekler, bakterilerle uzun vadeli ve istikrarlı ekolojik ilişkiler kurarlar. Afitler (Yaprak bitleri), konak olarak birçok otsu bitki, çalı ve odunsu bitki ile beslenen, aynı zamanda endosimbiyont bakterilerle de yakın ilişki içinde olan, tarımsal öneme sahip bir böcek grubudur. Yaprak bitlerinin yüksek adaptasyon ve hızlı üreme yetenekleri nedeniyle yakın gelecekte mevcut zararlı potansiyellerini daha da artıracağı görülmektedir. Yaprak bitlerinin biyolojik mücadelesinde etkili ve başarılı olabilmek için yaprak bitlerinin birçok özelliğinin bilinmesi ve netleştirilmesi gerekmektedir. Bu nedenle, bu ilişkide yaprak biti, konak bitki ve endosimbiyont arasındaki etkileşimlerin belirlenmesi, yaprak bitleri ile biyolojik mücadeleyi daha etkin kılabilir. Bu derlemede, yaprak biti, birincil endosimbiyotik bakteri *Buchnera aphidicola* ve konak bitki arasındaki ilişki hakkında bilinenler incelenmekte ve yaprak bitlerinin bisyolojik kontrolünde simbiyotik bakterilerin kullanım olanakları tartışılmaktadır.

Anahtar Kelimeler: Afit, biyolojik mücadele, *Buchnera aphidicola*, stres

Introduction

Aphids (Hemiptera: Aphididae) are insects of agricultural importance that feed on plant sap and can choose many plants as hosts. Since 2012, the studies about Turkey aphid fauna gradually increased and the number of aphid species in Turkey aphid fauna reached 604 species (Görür et al., 2022; Kök, 2021; Kök & Özdemir, 2021). Aphids seem to have the potential to become one of the most important pests of plants in the near future, due to their rapid growth characteristics and their high adaptability to survive in any environment where environmental conditions are suitable. For this reason, in order to be effective in the biological control against aphids, the physiological characteristics of aphids should be clarified in more detail. In addition, since knowing only the characteristics of aphids may be insufficient in effective control, it is necessary to know the effect on the food chain with the change of all living relationships and ecological characteristics related to aphids on the food chain. Most aphids harbor primary and secondary symbionts in specialized cells or body cavities. It has been reported by many studies that the basis of this association is nutrition, increasing the quality of host life under stress conditions and providing protection against predators and parasites (Dale & Moran, 2006; Dunbar et al., 2007; Tsuchida et al., 2011). Recent research, which will bridge the gap between mechanical and ecological approaches, shows that herbivores and their natural enemies interact with the environment and other living things (Coppola et al., 2018; Smith & Chuang, 2014). In such interactions, human intervention and genetic changes can result in the production of certain traits (such as nutritional quality and physical structure) and defense-related products in plants, such as primary, secondary chemicals, and plant volatiles. Therefore, it is possible for pests to be affected by changes in host plants in various ways and levels.

Aphid Endosymbiont Relationship

Almost all aphid species engage in mutualistic relationships with endosymbiotic bacteria. These symbiotic relationships may be obligatory or facultative, depending on the evolutionary process. Commonly, it has been reported that in these relationships, symbionts provide some amino acids and vitamins to their hosts, protect them against predators and parasites, and increase their host's quality of life under stress conditions. Most of the bacterial endosymbionts cannot be cultured independently and can be found in the host as obligate endosymbionts (Oliver et al., 2010). Culturing endosymbionts can be difficult due to their slow growth, lifestyle, and requirement for certain host metabolites (Pontes & Dale, 2006). Although some bacteria are parasitic and reduce their host's quality of life, most symbiotic bacteria benefit their host in different ways. In general, it is effective for the host's development, nutrition, reproduction, thermal tolerance, defense, and immune behavior (Dale & Moran, 2006; Dunbar et al., 2007; Tsuchida et al., 2011). It is stated that bacterial symbionts can increase the chance of survival of their host, as well as manipulate the reproduction of their host to benefit its own transmission (Skaljac, 2016). The most popular and known endosymbiont of the aphids is *Buchnera aphidicola*.

Aphid–*Buchnera* Relationship

Most of the aphids are in a mutualistic relationship with the primary-obligate endosymbiont bacterium *B. aphidicola* (Oliver et al., 2010). Douglas (1996), in one of their studies, expressed that endosymbionts in aphids are not related to nitrogen fixation; however, *Buchnera* contributes to the reproduction of the host by synthesizing some essential amino acids and vitamins that the aphids cannot adequately provide from the plant sap. It is thought that aphids provide a safe environment and food for endosymbiont bacteria (Güz et al., 2015). Aphids overcome amino acid deficiency with the help of the endosymbiont *Buchnera*, which can produce riboflavin with some amino acids (Nakabachi & Ishikawa 1999, Shigenobu et al., 2000). It is pointed out that *Buchnera* uses some non-essential amino acids which were taken from the sap by the aphid and converts them into essential amino acids that its host needs, and for this reason, it is of vital importance for its host (Douglas, 1996). Various studies have been conducted on what type of function endosymbionts have for their hosts. In one of these studies, when the amino acid profiles of aposymbiotic (symbiont free) *Acyrthosiphon pisum Harris,* 1776 obtained by the application of rifampicin were examined, it was stated that the concentrations of aromatic amino acids phenylalanine and tryptophan in the embryos of aposymbiotics were very low and that these amino acid amounts could limit the embryo development of aposymbiotics (Douglas, 1996). According to Douglas and Prosser (1992), aposymbiotic aphids cannot synthesize many amino acids such as tryptophan. It has also been shown that aphids fed on a diet that does not contain tryptophan are unable to sustain their growth. It has been determined that the riboflavin (vitamin B2) synthase complex of *Buchnera* works actively only when the symbiotic relationship is continuous and this relationship is well established in the young host. It has been reported that dietary riboflavin increases the performance of aposymbiotics. According to these results, it was stated that young aphids containing endosymbionts met their riboflavin needs from *Buchnera* (Güz et al., 2015; Nakabachi & Ishikawa, 1999). Machado-Assefh et al. (2015), in their study with aposymbiotic *Myzus persicae Sulzer,* 1776 individuals, tried to determine the effect of antibiotic administration on the feeding behavior of aphids and the expression of genes in salivary secretion. They reported that besides synthesizing essential amino acids and vitamins, *B. aphidicola* also contributes to plant–insect interaction. In addition, some bacterial proteins involved in the metabolism of the host plant were found in the saliva of *M. persicae*. Differences in the feeding behavior of aposymbiotic aphids, some problems during the penetration of the stylets of the aphids into the host plant, and delays in the recognition of the host plant by the aphids were observed (Machado-Assefh et al., 2015).

B. aphidicola, known to be related to *Enterobacteriaceae*, is a bacterium with a gram-negative cell wall of 2.5–4 μm in diameter. However, unlike most other gram-negative bacteria, *Buchnera* lacks the genes responsible for the production of lipopolysaccharides found in the outer membrane structure. During this symbiotic relationship dating back 160–280 million years, *Buchnera* lost some genes required for anaerobic respiration and genes responsible for the synthesis of amino sugars, fatty acids, phospholipids, and complex carbohydrates. It has also lost some regulatory factors that allow the continuous overproduction of certain amino acids, such as tryptophan (Skaljac, 2016). It has been stated that *Buchnera* has a 641 kb long genome rich in Adenin-Timin nucleotide pairs of genes responsible for the biosynthesis of many essential amino acids but lacks genes responsible for the biosynthesis of cell surface components of its genome and genes involved in cellular defense and regulatory genes (Shigenobu et al., 2000). The genome of *Buchnera*, the endosymbiont of the *A. pisum*, has been characterized as a 657 kb circular DNA molecule. In addition, when the genome map of *Buchnera* was compared with the genome map of *Escherichia coli* and *Haemophilus influenzae*, it was stated that *Buchnera* was more similar to *E. coli* (Charles & Ishikawa, 1999). The genome size varies in *Buchnera* species and even decreases to 450 kb in some species (Gill et al., 2002). Genome studies with insects indicate that during the evolutionary process, the host organism lost these genes by establishing symbiotic relationships with the bacteria responsible for arginine biosynthesis (Luan et al., 2015). It has been reported that aphids and endosymbionts evolve in parallel and endosymbionts are transferred vertically from female adult aphids to offspring (Martinez-Torres et al., 2001).

The primary symbiont *Buchnera* is typically found in specialized cell groups called mycetocytes or bacteriocytes in the body cavity of its host (Sasaki & Ishikawa, 1995). An adult aphid may carry an estimated 5.6×10^6 *Buchnera* cells (Baumann & Baumann, 1994). However, the number of endosymbiont bacteria can be affected by many factors such as the performance of the host, seasonal changes, temperature changes, and the quality of the host plant on which the aphid feeds (Yao, 2019). Numerous studies have been conducted to determine the effect of temperature on this symbiotic relationship. For example, it was determined that the bacterial density of aphids increased from 1.3×10^7 to 2.0×10^7 at temperatures between 15°C and 25°C, and the endosymbiotic relationship was disrupted at 37°C and −10°C. It has also been stated that the density of endosymbiotic bacteria in aphids may vary according to the developmental stage of the insect (Humphreys & Douglas, 1997). There are many studies on the role of endosymbionts in the nutrition of aphids. These studies have been facilitated by the development of synthetic media, the use of antibiotics, and the application of heat shock to produce aposymbiotic aphids (Dixon, 1998). In order to study the effect of bacteria on the aphid-endosymbiont relationship, it is tried to make aphids aposymbiotic by applying antibiotics at different doses and in different ways. It is known that antibiotic application has different effects on the amount and structure of honeydew in aphids. It was concluded that the honeydew particle size of aposymbiotic *A. pisum* is smaller than that of symbionts (Wilkinson & Douglas, 1995).

There are also many studies investigating the effects of *Buchnera* presence on aphid morphology. It has been observed that there are limitations in the growth and development of aphids treated with chlortetracycline, and their fertility decreased. In addition, it was observed that *A. pisum* and *Megoura viciae* Buckton, 1876, had similar effects on their size and fertility but did not affect wing development (Hardie & Leckstein, 2007). In the study examining the effects of starvation and symbiont *Buchnera* on the wing dimorphism of the *Sitobion avenae Fabricius,* 1775 aphid species, it was determined that the fertility, body weight, and the number of winged individuals decreased in the aposymbiotics and that starvation also reduced the winged individual percentage and the survival rate (Zhang et al., 2015). They discussed the potential importance of reduced winged formation in integrated management of aphids.

Besides primary symbionts, aphids can also contain facultative symbionts known as secondary symbionts (Guo et al., 2022; Sharma et al., 2021). As facultative symbionts may be non-essential for aphid species survival, aphids obtain some ecological benefits, such as host plant use, defense against natural enemies, body color modifications, temperature tolerance, and manipulation of their reproduction (Guo et al., 2017). Particular attention should be given to facultative symbionts' effect on natural enemies in aphid management applications. Secondary symbiotic bacteria associated with aphids are *Hamiltonella defensa*, *Regiella insecticola*, *Erwinia aphidicola*, *Serratia symbiotica*, *Pseudomonas aeruginosa*, *Wolbachia pipientis*, *Rickettsiella* sp., *Rickettsia* sp., *Spiroplasma* sp., *Arsenophonus* sp., *Photorhabdus* sp., *Xenorhabdus* sp., and X-type (Oliver et al., 2010, Zepeda-Paulo & Lavandero, 2021). Jousselin et al. (2016) stated that *S. symbiotica* is the most common endosymbiont bacteria after *B. aphidicola* in *Cinara* aphid species. They reported that *H. defensa* contains a lysogenic bacteriophage that protects its host against parasitic *Aphidius ervi*, while *R. insecticola* provides resistance against the fungal pathogen (Jousselin et al., 2016). Secondary symbionts are not found in specialized cell groups like primary symbionts. Instead, they are usually localized in secondary bacteriocyte cells, sheath cells, which are small flat cells found around primary bacteriocyte cells and hemolymph (Moran et al., 2005). For example, while *H. defensa*, *S. symbiotica*, *R. insecticola,* and *Rickettsiella* are located in the cytoplasm of secondary bacteriocytes and sheath cells, they are also found in the hemolymph of *A. pisum* (Fukatsu et al., 2000; Moran et al., 2005; Tsuchida et al., 2005). Secondary symbionts can be transmitted vertically between individuals and between species, as well as horizontally (Guo et al., 2022; Russell et al., 2003, Sharma et al., 2021). Facultative symbionts are not obligatory, but they are reported to take on very important tasks. It is stated that secondary symbionts have important roles such as protecting their host against predators, improving host resistance against biotic and abiotic factors, nutrition, and differentiation of body color (Brinza et al., 2009; Koga et al., 2003; Sharma et al., 2021; Zepeda-Paulo & Lavandero, 2021; Zhang et al., 2015). It is also reported that some secondary symbionts provide the necessary cofactors for the synthesis of some amino acids (Gosalbes et al., 2008). Koga et al. (2003) studied the interactions of *Buchnera* and pea aphid secondary symbiont (PASS) with each other and their effect on aphid reproduction–development in members of *A. pisum*. As a result of the elimination of *Buchnera*, it was determined that PASS replaced *Buchnera*, allowing its host to survive and reproduce. On the other hand, it has been reported that PASS suppresses *Buchnera* and adversely affects the performance of aphid. In the symbiotic relationship of *Regiella insecticola* and *A. pisum*, it is stated that *Regiella* reduces the amount of spores produced by entomopathogenic fungi such as *Pandora neoaphidis* and *Zoophthora occidentalis* (Parker et al., 2013; Scarborough et al., 2005). Some secondary symbionts such as X-type bacterium (Heyworth & Ferrari, 2015) protected aphids against the fungal pathogens (e.g., *Pandora neoaphidis),* increased the resistance to the parasitoids (e.g., *Aphidius ervi* (Haliday, 1834), and also affected the response of aphid to heat stress (Guo et al., 2022; Heyworth & Ferrari, 2015). In general, phylogenetic analyses in *S. symbiotica* show that there are some differences in the distribution, morphology, and functions of symbionts, which potentially play a role in aphid feeding (Burke et al., 2009), and such secondary symbionts provide benefits by supporting their host under different conditions such as heat stress (Koga et al., 2003, Montllor et al., 2002; Zepeda-Paulo & Lavandero, 2021). It was stated that the number of PASS in aphids increased in hot weather, aphids without PASS could not reproduce under heat stress, and 80%–100% of aphids containing PASS gave offspring. It has been reported that temperature changes affect some vital parameters of aphids such as survival rate, offspring development, development time, and age-related fertility rate (Morgan et al., 2001).

Aphid–Host Plant Relationship

Insect–plant interaction is a complex relationship influenced by biotic and abiotic factors. Plants produce a range of chemical compounds to cope with insect infestations (Sharma et al., 2021). Structural chemicals are produced even when the plant is under no stress (Wittstock & Gershenzon, 2002). Herbivorous insects use these chemicals as a cue to recognize host plants (Ali & Agrawal, 2012; Karban et al., 2014). Most herbivorous insects have developed various mechanisms to overcome these changes in the host plant. Thus, both parties develop different mechanisms to overcome the defense response of the other and enter the process of co-evolution (Sharma et al., 2021). However, both insects and plants are associated with many organisms and determine the outcome of insect feeding on a plant. Microbiome studies associated with plants and insects provide a new perspective on this issue and show that these interactions are more complex than they seem (Bultman & Bell, 2003; Frago et al., 2012; Sharma et al., 2021).

Aphids are insects with different adaptation mechanisms that can adapt to changing environmental conditions in a short time. Some factors such as crowding, host plant quality, and temperature may cause stress in aphids. The nutritional quality of the host plant is a very important factor in determining the size, distribution, survival, and reproduction rate of aphids. Some factors, such as the aging of the plant, can lower the plant's nutrient content. These changes in host plant quality trigger the formation of winged individuals in aphids. In addition, they can increase the number of winged individuals very quickly in a short time on the host plant they live on. The increase in the number of individuals causes the aphids to not benefit enough from the host plant. For example, while *A. pisum* reacts to crowding during the feeding process from mature leaves, *Dysaphis devecta* (Walker, 1849) only increases the number of winged individuals in response to changes in host plant quality (Dixon, 1998). Not only endosymbionts activate the resistance and adaptation of aphids to the environment but also aphids activate the resistance mechanisms of their host plant against stress conditions. A wide variety of biotic and abiotic environmental factors in nature cause stress in plants. Plants have many defense mechanisms to protect themselves from pathogen attacks. Although these defense mechanisms play a deterrent role for some pathogens, they are ineffective for some pathogens (Koç & Üstün, 2008).

Plants, which are food sources for many organisms, cannot be isolated from pathogens, but they have evolved appropriate defense strategies to detect and counter the inevitable pathogen attacks. In order to prevent pathogen invasion, plants use inducible defense responses activated by pathogen attack as well as physical and chemical barriers existing in their structures (Koç & Üstün, 2008). In some studies, it has been determined that aphid infestation increases the insect resistance of the plant and creates a vaccine effect on the plant (Coppola et al., 2018; Smith & Chuang, 2014). Plants can either cope with stress or move away from that stress factor. Various studies have shown that some aphids can stimulate plant resistance, as well as plants resistant to aphid attack. It has been determined that aphid infestation increases the plant's defense against secondary invasions by creating various metabolic changes such as triggering the synthesis of stress hormones salicylic acid and jasmonic acid in plants (Coppola et al., 2018; Jaouannet et al., 2014; Smith & Chuang, 2014). It has been stated that insect and pathogen invasion increases the production of various secondary metabolites in plants as well as stress hormones and these secondary metabolites are associated with the plant's defense system. On the other hand, it has been demonstrated in different studies that aphids try to attenuate the defense responses of plants with various chemicals and enzymes found in their salivary glands (Cheynier et al., 2013; Mugford et al., 2016; Thorpe et al., 2016; Wang et al., 2016).

Aphid Endosymbiont–Host Plant Tritrophic Interaction

The relationship between aphid endosymbiont–host plants is quite complex. Insects choose hosts according to the nutrient biosynthesis capacity of their endosymbionts. Endosymbiont bacteria synthesize essential amino acids and vitamins to their host by using some non-essential amino acids found in the plant sap of their host. Endosymbiont bacteria have a very important role in the synthesis of these compounds and in choosing the right host for aphids. However, some endosymbionts have lost the ability to produce different compounds in the evolutionary process. For example, it has been reported in various studies that *B. aphidicola* lost genes responsible for tryptophan and riboflavin synthesis in *Cinara cedri* Mimeur,1936 biotin biosynthesis in *A. pisum* and arginine biosynthesis in *Baizongia pistaceae Linnaeus,* 1767 (Pérez-Brocal et al., 2006; Shigenobu et al., 2000; van Ham et al., 2003). Such loss of biosynthetic capacity may put pressure on the selection of the right host that can provide the insect with the food it needs (Clark et al., 2010; Sharma et al., 2021). In addition, there is information that some symbionts change the behavior of their hosts for their own evolutionary benefit (Giordanengo et al., 2010; Thomas et al., 2005).

Understanding how and why the host plant–aphid-endosymbiont relationship is affected by the environment and other factors are important not only for effective biological control against aphids but also for the continuity of plant productivity. Therefore, examining the relationship between aphid-*Buchnera* and aphid-host plant alone will not be sufficient to clarify these relations from all aspects. At the same time, all the parameters of the tritrophic relationship should be examined without overlooking as there are contrast findings (McLean et al., 2010). Such interactions also raise the following questions. Why are the plant species used as hosts by aphid species different? What are the effective parameters on the host plant and feeding preferences in aphids? What is the importance of *Buchnera* in the aphid–host relationship? In order to answer these and similar questions, the internal (characteristics of the living thing) and external (such as the temperature, water, humidity, and CO_2 ratio of the living thing's environment) variables in the food chain and their interactions with each other should be investigated in more detail. In terrestrial environments, strong trophic interactions are modified by the chemistry, morphology, and behavior of the organisms in question. It has been observed that plants attract the natural enemies of herbivores by using volatile substances (Agrawal, 2000; Birch et al., 1999). Examining such tri-trophic interactions is important to understand the interactions of natural species and to be able to use these interactions in pest control. It is seen that the common denominator in the plant–*Buchnera*–aphid relationship is nitrogen compounds and nutritional needs. Therefore, the host plant is very important in the evolution and ecology of phytophages such as aphids. As it is known, nitrogen is a limiting element for living things. It has been determined that changes in nitrogen availability affect the nutritional and defense properties of the plant (Mattson, 1980), the quality of host plant components (such as C, N, and defense metabolites), herbivore productivity and reproductive strategies (Awmack & Leather, 2002). Since host selection also causes various mating preferences, it has been argued that the mechanisms underlying these preferences will contribute directly to the understanding of speciation, and the functions of chemosensory genes that have an effect on smell and taste in speciation and host selection are sought to be investigated (Eyres et al., 2017). Many herbivorous insects change the quality of the host plant by affecting its internal and external relations. It has been observed that the quality of the host plant affects the higher trophic relationships of predators and parasites and that it affects insect productivity at both individual and population scales (Awmack & Leather, 2002). In addition, the salivary secretion of aphids has a key role in aphid–plant relationship. Saliva content is affected by the environment the stylet tip encounters. Enzymes and proteins such as various pectinases and cellulases in saliva break plant defenses and increase the availability of organic nitrogenous compounds. It has been suggested that some enzymes detoxify plant phenols and that some salivary proteins may act as effectors, suppressing or promoting plant defense (Giordanengo et al., 2010). It has also been pointed out that some salivary proteins such as GroEL are produced from *Buchnera* origin and that this protein is an excretory product that induces defense reactions of the plant. It has also been suggested that chitin fragments in saliva may trigger the plant's defense reactions (van Bel & Will, 2016). In various studies in which endosymbionts were removed from aphids, it was clearly determined that the growth of aphids decreased. It is stated that the associations formed by microorganisms living in common with plants and insects affect plant and insect relationship. It has been shown that insect–microorganism associations suppress the plant's defenses and support the development of insects in the plant by detoxifying protective phytochemicals. Phytopathogens can change the effectiveness and behavior of insects by changing plant quality and defense. The plant–beneficial microorganism relationship can promote plant growth by affecting the plant nutrient and phytochemical composition and may positively or negatively affect the effectiveness of insects. From the results obtained, it was stated that the protein contents of the aphids were affected by the host plant and the symbionts contributed to the adaptation of the aphids (Francis et al., 2006, 2010).

Conclusion and Recommendations

Since it is predicted that insects such as aphids, which are plant pests, will feel their negative effects more with the increase in global warming, some unknowns need to be revealed in the biological control of these pests. In order to carry out an effective biological control, it is necessary to determine exactly what the functions of the obligate endosymbiont bacteria *Buchnera* will play a very important role in the metabolism of aphids and other facultative endosymbionts. In the studies carried out so far, different parameters have been studied in aposymbiont aphids. However, in these studies, the aphid–*Buchnera* relationship was generally considered, while the host plant effect was ignored. For this reason, in order to be more effective in the biological control of aphids, it is necessary to consider not only the aphid–*Buchnera* relationship but also the aphid–*Buchnera*–host plant relationship together. In many studies, it is stated that the presence of plant pest herbivores such as aphids causes stress in the plant and triggers the production of some special chemicals in the plant. It was concluded that aphids fed with plant sap may also undergo some morphological and physiological changes by being affected by the plant composition, and therefore, differences may be observed in *Buchnera* function. Based on this, it was emphasized in the aphid–*Buchnera* relationship that host plant can cause various changes in the metabolism of both aphids and endosymbionts and host plant metabolism should not be ignored in these relationships. It is thought that revealing the aphid–*Buchnera*–host plant relationship will lead to significant progress in the biological control of aphids in the long term. It has also been observed that there are important trends in this field recently. In this review, it was emphasized that aphids can be controlled more effectively by considering the aphid–*Buchnera*–host plant tritrophic interaction together, and it was revealed that more studies should be done on this subject. In this context, researchers should focus on finding out the answers to the following questions which are: How did aphid obtain *Buchnera*? Why was *Buchnera* compelled into the aphid? How *Buchnera* became an endosymbiont?

Peer-review: Externally peer-reviewed.

Author Contributions: Concept – G.O.E., A.Ö.; Design – G.O.E.; Supervision: A.Ö., G.G.; Resources – G.O.E., A.Ö., G.G.; Data Collection and/or Processing – G.O.E.; Analysis and/or Interpretation – G.O.E., A.Ö., G.G.; Literature Search – G.O.E., A.Ö., G.G.; Writing Manuscript – G.O.E.; Critical Review – A.Ö., G.G.

Declaration of Interests: The authors declare that they have no conflicts of interest.

Funding: The authors declared that this study has received no financial support.

Hakem Değerlendirmesi: Dış bağımsız.

Yazar Katkıları: Fikir – G.O.E., A.Ö.; Tasarım – G.O.E.; Denetleme: A.Ö., G.G.; Kaynaklar – G.O.E., A.Ö., G.G.; Veri Toplanması ve/veya İşlemesi – G.O.E.; Analiz ve/veya Yorum – G.O.E., A.Ö., G.G.; Literatür Taraması – G.O.E., A.Ö., G.G.; Yazıyı Yazan – G.O.E.; Eleştirel İnceleme – A.Ö., G.G.

Çıkar Çatışması: Yazarlar, çıkar çatışması olmadığını beyan etmişlerdir.

Finansal Destek: Yazarlar, bu çalışma için finansal destek almadıklarını beyan etmişlerdir.

References

Agrawal, A. A. (2000). Mechanisms, ecological consequences and agricultural implications of tri-trophic interactions. *Current Opinion in Plant Biology*, *3*(4), 329–335. [CrossRef]

Ali, J. G., & Agrawal, A. A. (2012). Specialist versus generalist insect herbivores and plant defense. *Trends in Plant Science*, *17*(5), 293–302. [CrossRef]

Awmack, C. S., & Leather, S. R. (2002). Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology*, *47*, 817–844. [CrossRef]

Baumann, L., & Baumann, P. (1994). Growth kinetics of the endosymbiont, *Buchnera aphidicola*, in the aphid *Schizaphis graminum*. *Applied and Environmental Microbiology*, *60*(9), 3440–3443. [CrossRef]

Birch, A. N. E., Geoghegan, I. E., Majerus, M. E. N., McNicol, J. W., Hackett, C. A., Gatehouse, A. M. R., & Gatehouse, J. A. (1999). Tri-trophic interactions involving pest aphids, predatory 2-spot ladybirds and transgenic potatoes expressing snowdrop lectin for aphid resistance. *Molecular Breeding*, *5*(1), 75–83. [CrossRef]

Brinza, L., Viñuelas, J., Cottret, L., Calevro, F., Rahbé, Y., Febvay, G., Duport, G., Colella, S., Rabatel, A., Gautier, C., Fayard, J. M., Sagot, M. F., & Charles, H. (2009). Systemic analysis of the symbiotic function of *Buchnera aphidicola*, the primary endosymbiont of the pea aphid *Acyrthosiphon pisum*. *Comptes Rendus Biologies*, *332*(11), 1034–1049. [CrossRef]

Bultman, T. L., & Bell, G. D. (2003). Interaction between fungal endophytes and environmental stressors influences plant resistance to insects. *OIKOS*, *103*(1), 182–190. [CrossRef]

Burke, G. R., Normark, B. B., Favret, C., & Moran, N. A. (2009). Evolution and diversity of facultative symbionts from the aphid subfamily Lachninae. *Applied and Environmental Microbiology*, *75*(16), 5328–5335. [CrossRef]

Charles, H., & Ishikawa, H. (1999). Physical and genetic map of the genome of *Buchnera*, primary endosymbiont of the pea aphid *Acyrthosiphon pisum*. *Journal of Molecular Evolution*, *48*(2), 142–150. [CrossRef]

Cheynier, V., Comte, G., Davies, K. M., Lattanzio, V., & Martens, S. (2013). Plant phenolics: Recent advances on their biosynthesis, genetics, and ecophysiology. *Plant Physiology and Biochemistry* , *72*, 1–20. [CrossRef]

Clark, E. L., Karley, A. J., & Hubbard, S. F. (2010). Insect endosymbionts: Manipulators of insect herbivore trophic interactions? *Protoplasma*, *244*(1–4), 25–51. [CrossRef]

Coppola, M., Manco, E., Vitiello, A., Di Lelio, I., Giorgini, M., Rao, R., Pennacchio, F., & Digilio, M. C. (2018). Plant response to feeding aphids promotes aphid dispersal. *Entomologia Experimentalis et Applicata*, *166*(5), 386–394. [CrossRef]

Dale, C., & Moran, N. A. (2006). Molecular interactions between bacterial symbionts and their hosts. *Cell*, *126*(3), 453–465. [CrossRef]

Dixon, A. F. G. (1998). *Aphid ecology - An optimization approach* (2nd ed). Chapman& Hall.

Douglas, A.ss E. (1996). Reproductive failure and the free amino acid pools in pea aphids (*Acyrthosiphon pisum*) lacking symbiotic bacteria. *Journal of Insect Physiology*, *42*(3), 247–255. [CrossRef]

Douglas, A. E., & Prosser, W. A. (1992). Synthesis of the essential amino acid tryptophan in the pea aphid (*Acyrthosiphon pisum*) symbiosis. *Journal of Insect Physiology*, *38*(8), 565–568. [CrossRef]

Dunbar, H. E., Wilson, A. C. C., Ferguson, N. R., & Moran, N. A. (2007). Aphid thermal tolerance is governed by a point mutation in bacterial symbionts. *PLoS Biology*, *5*(5), 1006–1015. [CrossRef]

Eyres, I., Duvaux, L., Gharbi,K., Tucker, R., Hopkins, D., Simon, J. C., Ferrari, J., Smadja, C. M., & Butlin, R. K. (2017). Targeted re-sequencing confirms the importance of chemosensory genes in aphid host race differentiation. *Molecular Ecology*, *26*(1), 43–58. [CrossRef]

Frago, E., Dicke, M., & Godfray, H. C. J. (2012). Insect symbionts as hidden players in insect–plant interactions. *Trends in Ecology and Evolution*, *27*(12), 705–711. [CrossRef]

Francis, F., Gerkens, P., Harmel, N., De Pauw, E., & Haubruge, E. (2006). Proteome variations of the *Myzus persicae* aphid according to host plant change. *Insect Biochemistry and Molecular Physiology*, *36*, 219–227.

Francis, F., Guillonneau, F., Leprince, P., De Pauw, E., Haubruge, E., Jia, L., & Goggin, F. L. (2010). Tritrophic interactions among *Macrosiphum euphorbiae* aphids, their host plants and endosymbionts: Investigation by a proteomic approach. *Journal of Insect Physiology*, *56*(6), 575–585. [CrossRef]

Fukatsu, T., Nikoh, N., Kawai, R., & Koga, R. (2000). The secondary endosymbiotic bacterium of the pea aphid *Acyrthosiphon pisum* (Insecta: Homoptera). *Applied and Environmental Microbiology*, *66*(7), 2748–2758. [CrossRef]

Gil, R., Sabater-Munoz, B., Latorre, A., Silva, F. J., & Moya, A. (2002). Extreme genome reduction in *Buchnera* spp: Toward the minimal genome needed for symbiotic life. *Proceedings of the National Academy of Sciences. Proceedings of the Natural Academy of Sciences*, *99*(7), 4454–4458. [CrossRef]

Giordanengo, P., Brunissen, L., Rusterucci, C., Vincent, C., van Bel, A., Dinant, S., Girousse, C., Faucher, M., & Bonnemain, J. L. (2010). Compatible plant-aphid interactions: How aphids manipulate plant responses. *Comptes Rendus Biologies*, *333*(6–7), 516–523. [CrossRef]

Görür, G., Şenol, Ö., Akyıldırım Beğen, H., & Akyürek, B. (2022). Turkish aphid. Retrieved from https://www.turkishaphid.com/.

Gosalbes, M. J., Lamelas, A., Moya, A., & Latorre, A. (2008). The striking case of tryptophan provision in the cedar aphid *Cinara cedri*. *Journal of Bacteriology*, *190*(17), 6026–6029. [CrossRef]

Guo, J., Hao, G., Hatt, S., Wang, Z., & Francis, F. (2022). Host plant adaptability and proteomic differences of diverse *Rhopalosiphum maidis* (*Fitch*) lineages. Archieves of insect. *Biochemistry and Physiology*, *109*(1), e21853.

Guo, J., Hatt, S., He, K., Chen, J., Francis, F., & Wang, Z. (2017). Nine facultative endosymbionts in aphids. A review. *Journal of Asia-Pacific Entomology*, *20*(3), 794–801. [CrossRef]

Güz, N., Dağeri, A., & Aksoy, S. (2015). The impacts of endosymbiotic bacteria on insects. *Türkiye Entomoloji Bülteni* (Turkish with abstract in English). *5*(2), pp. 101–113.

Hardie, J., & Leckstein, P. (2007). Antibiotics, primary symbionts and wing polyphenism in three aphid species. *Insect Biochemistry and Molecular Biology*, *37*(8), 886–890. [CrossRef]

Heyworth, E. R., & Ferrari, J. (2015). A facultative endosymbiont in aphids can provide diverse ecological benefits. *Journal of Evolutionary Biology*, *28*(10), 1753–1760. [CrossRef]

Humphreys, N. J., & Douglas, A. E. (1997). Partitioning of symbiotic bacteria between generations of an insect: A quantitative study of a *Buchnera* sp. in the Pea Aphid (*Acyrthosiphon pisum*) reared at different temperatures. *Applied and Environmental Microbiology*, *63*(8), 3294–3296. [CrossRef]

Jaouannet, M., Rodriguez, P. A., Thorpe, P., Lenoir, C. J. G., MacLeod, R., Escudero-Martinez, C., & Bos, J. I. B. (2014). Plant immunity in plant–aphid interactions. *Frontiers in Plant Science*, *5*, 663. [CrossRef]

Jousselin, E., Clamens, A. L., Galan, M., Bernard, M., & Maman, S., Gschloessl, B., Duport, G., Meseguer, A. S., Calevro, F., Coueurdacier, A., (2016). Assessment of a 16S rRNA amplicon Illumina sequencing procedure for studying the microbiome of a symbiont-rich aphid genus. *Molecular Ecology Resources*, *16*(3), 628–640.

Karban, R., Yang, L. H., & Edwards, K. F. (2014). Volatile communication between plants that affects herbivory: A meta-analysis. *Ecology Letters*, *17*(1), 44–52. [CrossRef]

Koç, E., & Üstün, A. S. (2008). Defence against pathogen in plants and antioxidants. *Erciyes Üniversitesi Fen Bilimleri Enstitüsü Dergisi*, *24*(1–2), 82–100.

Koga, R., Tsuchida, T., & Fukatsu, T. (2003). Changing partners in an obligate symbiosis: A facultative endosymbiont can compensate for loss of the essential endosymbiont *Buchnera* in an aphid. *Proceedings Biological Sciences*, *270*(1533), 2543–2550. [CrossRef]

Kök, Ş. (2021). Diversity and plant interactions of aphids (Hemiptera: Aphidomorpha) adjacent to Çardak Lagoon with new aphid and host records for Turkey. *Turkish Journal of Entomology*, *45*(4), 425–439. [CrossRef]

Kök, Ş., & Özdemir, I. (2021). Annotated systematic checklist of the aphids (Hemiptera: Aphidomorpha) of Turkey. *Zootaxa*, *4925*(1), zootaxa. 4925.1.1. [CrossRef]

Luan, J. B., Chen, W., Hasegawa, D. K., Simmons, A. M., Wintermantel, W. M., Ling, K. S., Fei, Z., Liu, S. S., & Douglas, A. E. (2015). Metabolic coevolution in the bacterial symbiosis of whiteflies and related plant sap-feeding insects. *Genome Biology and Evolution*, *7*(9), 2635–2647. [CrossRef]

Machado-Assefh, C. R., Lopez-Isasmendi, G., Tjallingii, W. F., Jander, G., & Alvarez, A. E. (2015). Distrupting *Buchnera aphidicola*, the endosymbiotic bacteria of *Myzus persicae*, delays host plant acceptance. *Arthropod-Plant Interactions*, *9*(5), 529–541. [CrossRef]

Martinez-Torres, D., Buades, C., Latorre, A., & Moya, A. (2001). Molecular systematics of aphids and their primary endosymbionts. *Molecular Phylogenetics and Evolution*, *20*(3), 437–449. [CrossRef]

Mattson, W. J. (1980). Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics*, *11*(1), 119–161. [CrossRef]

McLean, A. H. C., van Asch, M., Ferrari, J., & Godfray, H. C. J. (2010). Effects of bacterial secondary symbionts on host plant use in pea aphids. *Proceedings of the Royal Society, Series B*, *278*(1706), 760–766.

Montllor, C. B., Maxmen, A., & Purcell, A. H. (2002). Facultative bacterial endosymbionts benefit pea aphids *Acyrthosiphon pisum* under heat stress. *Ecological Entomology*, *27*(2), 189–195. [CrossRef]

Moran, N. A., Degnan, P. H., Santos, S. R., Dunbar, H. E., & Ochman, H. (2005). The players in a mutualistic symbiosis: Insects, bacteria, viruses, and virulence genes. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(47), 16919–16926. [CrossRef]

Morgan, D., Walters, K. F. A., & Aegerter, J. N. (2001). Effect of temperature and cultivar on pea aphid, *Acyrthosiphon pisum* (Hemiptera: Aphididae) life history. *Bulletin of Entomological Research*, *91*(1), 47–52.

Mugford, S. T., Barclay, E., Drurey, C., Findlay, K. C., & Hogenhout, S. A. (2016). An immuno-suppressive aphid saliva protein is delivered into the cytosol of plant mesophyll cells during feeding. *Molecular Plant-Microbe Interactions* , *29*(11), 854–861. [CrossRef]

Nakabachi, A., & Ishikawa, H. (1999). Provision of riboflavin to the host aphid, *Acyrthosiphon pisum*, by endosymbiotic bacteria, *Buchnera*. *Journal of Insect Physiology*, *45*(1), 1–6. [CrossRef]

Oliver, K. M., Degnan, P. H., Burke, G. R., & Moran, N. A. (2010). Facultative symbionts in aphids and the horizontal transfer of ecologically important traits. *Annual Review of Entomology*, *55*, 247–266. [CrossRef]

Parker, B. J., Spragg, C. J., Altincicek, B., & Gerardo, N. M. (2013). Symbiont-mediated protection against fungal pathogens in pea aphids: A role for pathogen specificity? *Applied and Environmental Microbiology*, *79*(7), 2455–2458. [CrossRef]

Pérez-Brocal, V., Gil, R., Ramos, S., Lamelas, A., Postigo, M., Michelena, J. M., Silva, F. J., Moya, A., & Latorre, A. (2006). A small microbial genome: The end of a long symbiotic relationship? *Science*, *314*(5797), 312–313. [CrossRef]

Pontes, M. H., & Dale, C. (2006). Culture and manipulation of insect facultative symbionts. *Trends in Microbiology*, *14*(9), 406–412. [CrossRef]

Russell, J. A., Latorre, A., Sabater-Muñoz, B., Moya, A., & Moran, N. A. (2003). Side-stepping secondary symbionts: Widespread horizontal transfer across and beyond the Aphidoidea. *Molecular Ecology*, *12*(4), 1061–1075. [CrossRef]

Sasaki, T., & Ishikawa, H. (1995). Production of essential amino acids from glutamate by mycetocyte symbionts of the pea Aphid, *Acyrthosiphon pisum*. *Journal of Insect Physiology*, *41*(1), 41–46. [CrossRef]

Scarborough, C. L., Ferrari, J., & Godfray, H. C. J. (2005). Aphid protected from pathogen by endosymbiont. *Science*, *310*(5755), 1781–1781. [CrossRef]

Sharma, G., Malthankar, P. A., & Mathur, V. (2021). Insect–Plant Interactions: A multilayered relationship. *Annals of the Entomological Society of America*, *114*(1), 1–16. [CrossRef]

Shigenobu, S., Watanabe, H., Hattori, M., Sakaki, Y., & Ishikawa, H. (2000). Genome sequence of the endocellular bacterial symbiont of aphids *Buchnera* sp. APS. *Nature*, *407*(6800), 81–86. [CrossRef]

Skaljac, M. (2016). Biology and Ecology of Aphids. (Ed. Andreas Vilcinskas), CRC Press.

Smith, C. M., & Chuang, W. P. (2014). Plant resistance to aphid feeding: Behavioral, physiological, genetic and molecular cues regulate aphid host selection and feeding. *Pest Management Science*, *70*(4), 528–540. [CrossRef]

Thomas, F., Adamo, S., & Moore, J. (2005). Parasitic manipulation: Where are we and where should we go? *Behavioural Processes*, *68*(3), 185–199. [CrossRef]

Thorpe, P., Cock, P. J. A., & Bos, J. (2016). Comparative transcriptomics and proteomics of three different aphid species identifies core and diverse effector sets. *BMC Genomics*, *17*(172), 172. [CrossRef]

Tsuchida, T., Koga, R., Matsumoto, S., & Fukatsu, T. (2011). Interspecific symbiont transfection confers a novel ecological trait to the recipient insect. *Biology Letters*, *7*(2), 245–248. [CrossRef]

Tsuchida, T., Koga, R., Meng, X. Y., Matsumoto, T., & Fukatsu, T. (2005). Characterization of a facultative endosymbiotic bacterium of the pea aphid *Acyrthosiphon pisum*. *Microbial Ecology*, *49*(1), 126–133. [CrossRef]

van Bel, A. J. E., & Will, T. (2016). Functional evaluation of proteins in watery and gel saliva of aphids. *Frontiers in Plant Science*, *7*, 1840. [CrossRef]

van Ham, R. C. H. J., Kamerbeek, J., Palacios, C., Rausell, C., Abascal, F., Bastolla, U., Fernández, J. M., Jiménez, L., Postigo, M., Silva, F. J., Tamames, J., Viguera, E., Latorre, A., Valencia, A., Morán, F., & Moya, A. (2003). Reductive genome evolution in *Buchnera aphidicola*. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(2), 581–586. [CrossRef]

Wang, J., Chung, S. H., Peiffer, M., Rosa, C., Hoover, K., Zeng, R., & Felton, G. W. (2016). Herbivore oral secreted bacteria trigger distinct defense responses in preferred and non-preferred host plants. *Journal of Chemical Ecology*, *42*(6), 463–474. [CrossRef]

Wilkinson, T. L., & Douglas, A. E. (1995). Aphid feeding, as influenced by disruption of the symbiotic bacteria: An analysis of the pea aphid (*Acyrthosiphon pisum*). *Journal of Insect Physiology*, *41*(8), 635–640. [CrossRef]

Wittstock, U., & Gershenzon, J. (2002). Constitutive plant toxins and their role in defense against herbivores and pathogens. *Current Opinion in Plant Biology*, *5*(4), 300–307. [CrossRef]

Yao, I. (2019). Seasonal changes in the density of the symbionts *Buchnera* and *Wolbachia* of the aphid *Tuberculatus macrotuberculatus* on *Quercus dentata*. *Entomologia Experimentalis et Applicata*, *167*(3), 261–268. [CrossRef]

Zepeda-Paulo, F., & Lavandero, B. (2021). Effect of the genotypic variation of an aphid host on the endosymbiont associations in natural host populations. *Insects*, *12*(3), 217. [CrossRef]

Zhang, F., Li, X., Zhang, Y., Coates, B., Zhou, X. J., & Cheng, D. (2015). Bacterial symbionts, *Buchnera*, and starvation on wing dimorphism in English grain aphid, *Sitobion avenae* (f.) (Homoptera: Aphididae). *Frontiers in Physiology*, *6*(155). [CrossRef]