

UNIVERSITY OF PÉCS

Biological and Sportbiological Doctoral School

Study of the endosymbiotic bacterial diversity of corn leaf aphid,
Rhopalosiphum maidis Fitch (Hemiptera: *Aphididae*) and its role in
aphid adaptation

PhD thesis

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1. INTRODUCTION

Maize (*Zea mays* L.) is the largest crop in Romania. Some 2 million ha are cultivated every year (average 18.6 million tons/year), making Romania the ninth largest producer in the world. One increasing problem in maize cultivation is the occurrence of the major pest of cereals, the corn-leaf aphid, *Rhopalosiphum maidis* Fitch (Hemiptera: Aphididae) over the last 5 years, especially in Germany, Poland, Hungary and from 2019 onwards in Romania (Banat region), not only as a result of direct physical damage (i.e. sap-feeding), but also due to the transmission of plant pathogenic viruses (Blackman and Eastop, 2000; Emden and Harrington, 2017, 2007).

Aphids are closely associated with microorganisms, the obligate mutualist endobacterium (usually referred to as a primary symbiont), *Buchnera aphidicola*, which is maternally inherited (Russell and Moran, 2006), as well as, other maternally transmitted intracellular bacteria, such as *Rickettsia* spp. (α -Proteobacteria), *Spiroplasma* spp. (Mollicutes) and various γ -proteobacterial microbes (including *Hamiltonella defensa*, *Regiella insecticola*, *Serratia symbiotica* and *Arsenophonus* spp.) (Gómez-Valero et al., 2004). These aphid secondary symbionts are often shared between divergent lineages and seem to undergo both vertical and horizontal transfer among matriline (Russell and Moran, 2006).

Several previous publications suggest that these symbiotic bacterial communities are involved in the expression of different traits related to aphid biology, including resistance to parasitoid wasps (Oliver et al., 2005), tolerance to heat stress (Montllor et al., 2002) and changes in the host plant range (Tsuchida et al., 2010). Overall, the functional role of bacterial endosymbionts have been defined in relation to two main traits: 1) those that confer advantages to the host aphid under specific ecological conditions, often defined as a protective role against abiotic conditions (high temperatures) or natural enemies and 2), the particular role of the endosymbiont in relation to the aphid host's metabolism, in other words, in terms of the specific nutrients that the endosymbionts synthesize and release and that are required by the host (Douglas, 2016).

Objectives: In this light, the present study concerns our efforts to answer the central question, important both from a fundamental as well as potentially an applied point of view (i.e. aphid pest control): Does host plant (here maize) management, i.e. conventionally managed large and medium scale fields, with fertilizer and pesticide input *versus* conventionally managed low input field small scale farming and local gardens, influence corn leaf aphid endosymbiotic bacterial community composition and diversity. If so, what does this teach us about the potential relevance of these symbionts in the life history and life cycle of this aphid

species, from which we may perhaps be able to gain further insights into how these microorganisms can be manipulated to effect better pest control?

2. AIMS OF THE STUDY

Three main objectives were formulated

H1. Has the corn leaf aphid (*R. maidis*), similar or different bacterial symbionts (obligate and facultative) community as it was described at other species?

H2. If these bacterial symbionts are present, they diversity can or cannot be associated with the host plant (maize) management systems?

H3. Has any associations between bacterial symbionts and the nutrient inputs intensity?

3. MATERIALS AND METHODS

3.1 Study areas

Field collection of corn leaf aphid were made from four maize fields, each differing in scale and management, *viz.* large and medium scale fields grown in monoculture and showing low natural landscape diversity due to high and medium input fertilizer and insecticide usage, whilst conventionally-managed systems comprised low input fields farmed on a small-scale and also local gardens, both grown under high agricultural and natural landscape diversity with no chemical and inorganic fertilizers input. From each management system, two maize fields were sampled and inside each one, two sample sites were defined. The two large-scale monoculture fields were placed in Western Romania (Banat region, Timis county), located about 15 km between them. Medium-scale fields were located in Central Romania (Sfantu Gheorghe city area) and were both represented by semi-intensive maize monocultures, located about 10 km apart from one another. Small-scale maize fields were placed also in Central Transylvania (Targu-Secuiesc city area), having a distance of about 8 km between sites. Local gardens were located in the Sighisoara area (Saxon region) of Central Transylvania, Romania, about 5 km distances from each other. This region comprises mostly valleys between mountains with no pesticide and fertilizer usage during maize production, characterized by a landscape mosaic of different land-cover types (approx. 28% forest, 24% pasture, and 37% arable land).

3.2 Field collection of corn leaf aphids

Aphid samples were collected from the four maize fields, both in two replicates during the same time period (June and July, 2019-2020) when all plots were in flowering stages R2 to R3.

Inside all maize fields two semi fields (sites) were sampled, except local gardens, from which only two separate small plot were sampled. Aphids were collected from maize plants inside the field; this was done to minimize the possible effects of field margins. Similar sampling methods were used in all sites, asexual lineages of wingless (apterous) individuals were collected as follows: Ten maize plants per semi-field were randomly selected at each sampling date, with first instar aphid nymphs (five from each colony / plant) collected and stored in 0.5 mL Eppendorf tubes containing 99% ethanol prior to DNA analysis.

3.3 Aphid associated bacterial community analysis

The bacterial communities associated with aphids were studied with Illumina amplicon sequencing of the V3-V4 region of the 16S rRNA gene using OTUs (operational taxonomic units) defined at 97% nucleotide sequence similarity level. For DNA extraction and subsequent PCR amplification, aphids (five asexual individuals from each colony sampled / one semi field /field) were first washed twice with 70% ethanol to remove surface-attached microbes. Analysis was based on amplicon sequencing of the 16S rRNA gene, as in our previous works (Benedek et al., 2019; Csorba, n.d.). Briefly, total genomic DNA was extracted using the DNeasy PowerSoil Kit (Qiagen), where after a part of the 16S rRNA gene was amplified using primers with the Bacteria-specific sequences Bakt_341F (5'-CCT ACG GGN GGC WGC AG-3' (Herlemann et al., 2011)) and Bakt_805NR (5'-GAC TAC NVG GGT ATC TAA TCC-3' (Apprill et al., 2015)). DNA sequencing was performed on an Illumina MiSeq platform using MiSeq standard v2 chemistry as a service provided by the Genomics Core Facility RTSF, Michigan State University, USA.

3.4 Data analyses

Methodological details and the applied bioinformatics and statistical analyses were as described in (Benedek et al., 2019), except that the resulting sequence reads were processed using the mothur v1.41 software (Schloss, 2020). This was based on the MiSeq standard operating procedure (downloaded on 03/04/2020), with the removal of chimeric sequences performed using VSEARCH (Rognes et al., 2016). and a taxonomic assignment based on the ARBSILVA SSU reference database (Quast et al., 2013). Raw sequence data were submitted to NCBI under BioProject ID PRJNA647165.

For statistical analysis of amplicon sequencing data, the subsampling of reads was performed to the read number of the smallest dataset (n=56.288). Microbial diversity indices

and species richness values (using the Chao1 and the ACE richness metrics) were calculated using mothur v1.41.

Linear regression was used to assess the variation in total bacterial diversity indices (Shannon & Simpson indices, as above) under different management systems were computed using PAST version 4.02 (Hammer et al., 2001).

Relative abundance patterns of the endosymbiotic taxa present on all maize fields were performed at the level of taxonomic paths (resolved up to the genus level). Community patterns were compared by cluster analysis in PAST 4.02 using UPGMA as clustering algorithm and calculation of Bray–Curtis similarity indices. Endosymbiotic taxa were sorted by their abundance (total genomic DNA) in relation to the differences noted between managements systems. Data are shown for taxa with >0.1% contribution.

Principal Components Analyses (PCA) were used to identify the proportion of variation in each PCA axis (bacterial DNA diversity and management) that was explained by the most frequent obligate and facultative bacterial distribution. The average count of each bacterial DNA reads numbers detected and \log_{10} transformed from each sample grouping as response variables as component 1 (PCA axis1) and management systems as component 2 (PCA axis 2) scores were used.

4. Results and discussion

4.1 Results from 2019

A total of 259,878 high-quality bacterial 16S rRNA gene sequences were obtained from the samples ($86,626 \pm 15,031$ reads per sample). Good's coverage values were higher than 0.99 in all cases, indicating that sequencing depth was sufficient to recover all major taxa. The average length of sequences was ~450 nt, which allowed genus-level taxon identification. In total, 213 bacterial genera were identified. A high abundance of primary symbionts *Buchnera* and secondary symbionts including uncultured *Enterobacteriaceae* were detected in all aphid samples tested, although there were no significant differences in these bacterial distribution between aphids (Figure 1). While other bacterial genera (*Bacillus*, *Pseudomonas*, *Salipaludibacillus*, *Pantoea*, *Sphingomonas*, and uncultured members of “*Candidatus Moranbacteria*” and “*Candidatus Falkowbacteria*”) were recorded, mostly from aphids collected from conventionally managed (high input) fields, along with other bacteria detected with very low relative abundance from sample T2_3 (Figure 1).

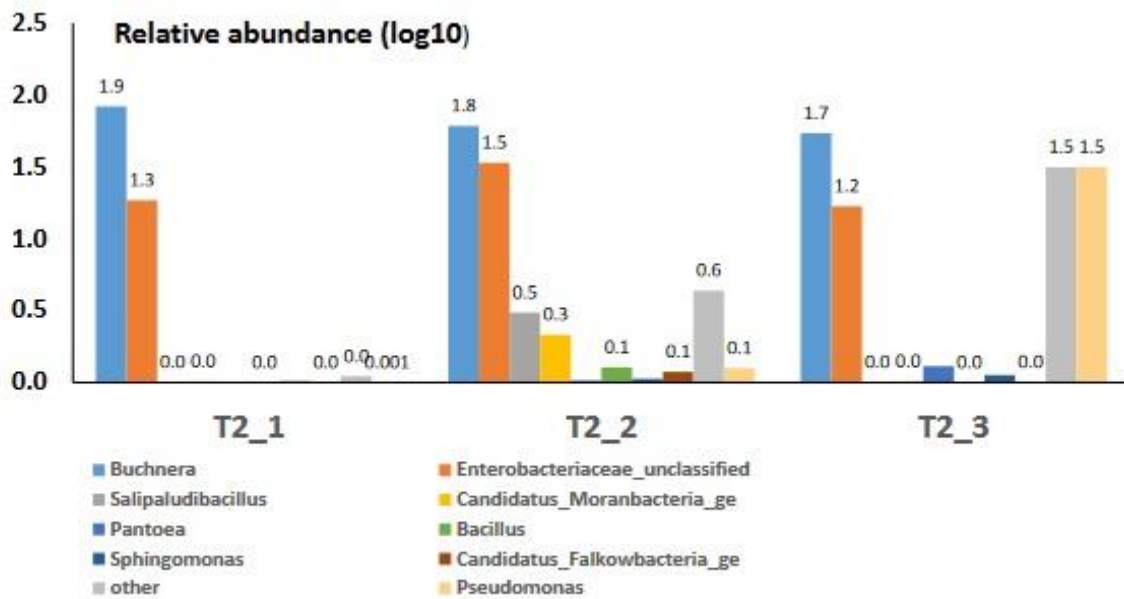


Figure 1: Bacterial abundance (dominant taxa) associated with corn leaf aphids (log10) in differently treated maize fields.

4.2 Results from 2020

Altogether 365 genus-level bacterial taxa were identified related to corn leaf aphids under the four management systems. The total bacterial diversity by using linear regression analyses related to corn leaf aphid differed even within management systems; the highest taxonomic numbers were detected at large-scale farming field A12 with 166 species, while the lowest also at large-scale farming site A11 were observed with 28 species. An average of 50 to 53 species of total bacteria per management systems were detected during the study. Diversity indices also revealed that several bacterial species were found in low frequency, and only a few species from total bacterial community were dominant.

Considering only the endosymbiotic bacterial taxa, these varied between management systems, with six genera from six phyla being detected. The obligate symbiont *Buchnera* was present at all sites, but with different frequencies according to the total genomic DNA analyzed. Aphids collected from large-scale crops site A12 were related with four bacterial endosymbionts, while in many cases the number of symbionts were less, only one that was the obligated symbiont *Buchnera*.

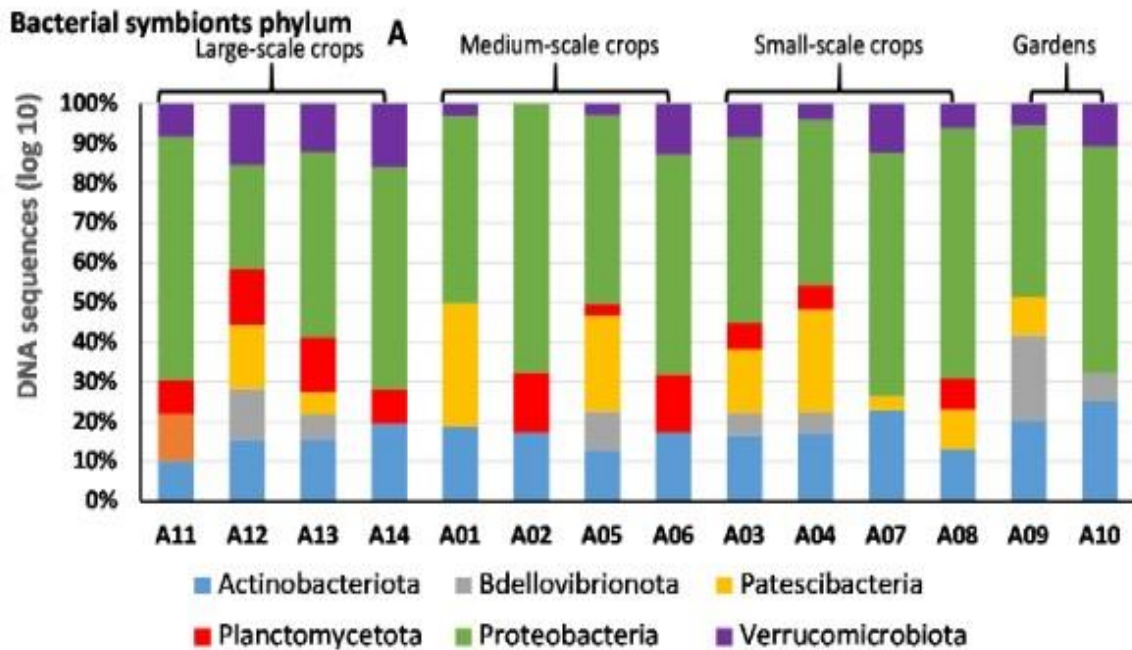


Figure 2: Dominant bacterial phylum variations by sites according to the DNA sequences frequency

At a phylum level, *Proteobacteria* were dominant in all aphid colonies (Figure 2). Among symbionts, at genus level after the obligate symbiont *Buchnera*, the facultative symbiont *Serratia* was also frequent, followed by *Wolbachia*. *Serratia* was present in aphids collected from all large scale-crops, but it was also present in another crops with lower frequency. *Wolbachia* were not detected in medium-scale crops and in gardens (Figure 1B). *Candidatus Hamiltonella* was present only in one large-scale crop. *Rickettsiales* other than genus *Spiroplasma* were detected at very low frequency in aphids in only one medium-scale maize field. *Spiroplasma* was present in aphids colonies collected from large-scale fields and from gardens (Figure 3).

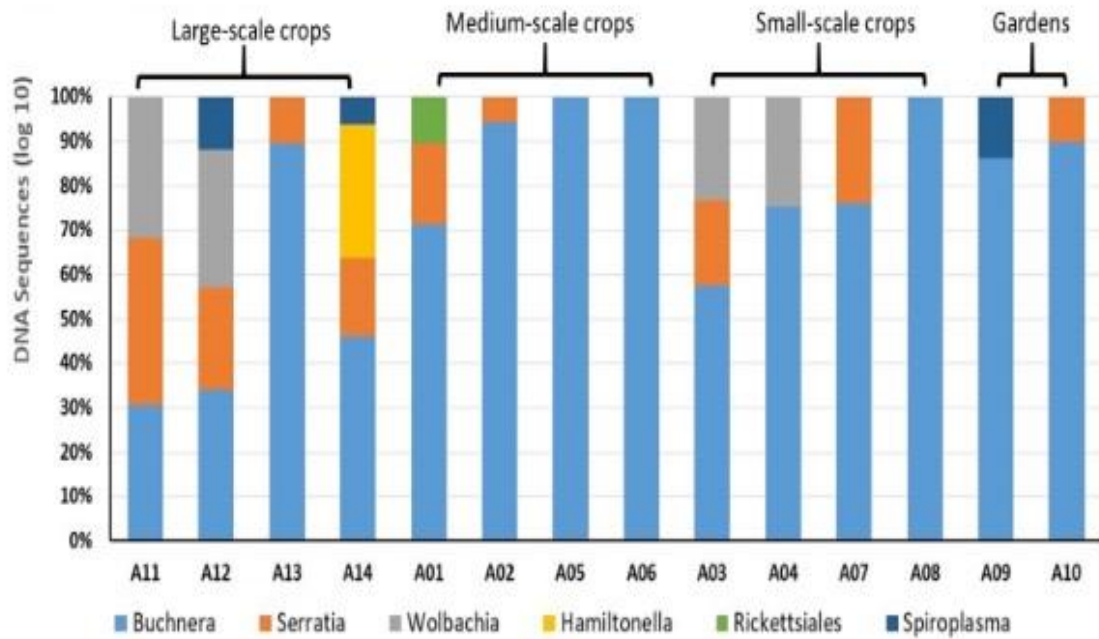


Figure 3: Endosymbiotic bacterial genera variations by sites according to the DNA sequence frequency

In the present study, 365 bacterial genera were identified, of which six endosymbionts were detected and identified as being associated with corn leaf aphid populations infesting maize crops grown under different management systems. Other than our study, only a few previous published studies have presented the detailed species composition of endosymbiotic bacterial communities associated with particular aphid species (McLean et al., 2011).

Primary and secondary symbionts (*Buchnera* and uncultured members of the family Enterobacteriaceae) dominated these communities in all maize fields and management systems. *Buchnera* is generally required for the survival of aphids and provides essential amino acids that are rare in their phloem sap diet (Shigenobu et al., 2000) but also has significant role in aphids heat tolerance (Zhang et al., 2019). Facultative endosymbiotic *Wolbachia* dominated large-scale crops and was also present in small-scale fields. Furthermore, *Serratia* was relatively more frequent in large-scale crops than in other crops. *Candidatus Hamiltonella* was present only in one large-scale site.

To our knowledge, this is the first account to describe the diversity of endosymbiotic bacteria inhabiting corn leaf aphids infesting maize crops under different management systems. By using a high resolution molecular (DNA) approach, it is clear that whilst the aphids are not ‘free agents’ in terms of their biology and life style, including host plant adaptation (Brown and Blackman, 1988; Loxdale et al., 2020; Loxdale and Balog, 2018), nor indeed are the bacterial

endosymbionts inhabiting these insects free of constraints, here abiotic constraints (i.e. management systems including plus or minus synthetic fertilizer and insecticide application). Hence, these factors may well have – and indeed probably do have – a significant influence on endosymbiotic bacterial diversity.

5. SUMMARY

In this study, different maize fields cultivated under different management systems were sampled to test corn leaf aphid, *Rhopalosiphum maidis* populations in terms of total and endosymbiotic bacterial diversity.

Corn leaf aphid natural populations were collected from traditionally managed maize fields grown under high agricultural and natural landscape diversity as well as conventionally treated high-input agricultural fields grown in monoculture and with fertilizers use, hence with low natural landscape diversity.

Total bacterial community assessment by DNA sequencing was performed using the Illumina MiSeq platform. In total, 365 bacterial genera were identified, and six endosymbiont taxa. A high abundance of the primary endosymbiont *Buchnera* and secondary symbiont *Serratia* and *Wolbachia* were detected in all maize crops.

Their frequency was found to be correlated with the maize management system used, probably with fertilizer input. Three other facultative endosymbionts ("*Candidatus Hamiltonella*", an uncultured *Rickettsiales* genus and *Spiroplasma*) were also recorded at different frequencies, under the two management regimes.

Principal Components Analyses revealed that the relative contribution of the obligate and dominant symbiont *Buchnera* to the aphid endosymbiotic bacterial community was 72%, whereas for the managed system, this was only 16.3%. When facultative symbionts alone were considered, the effect of management system revealed a DNA diversity of 23.3%.

These findings strongly suggest that most of the endosymbionts harbored by corn-leaf aphids are less associated with management systems per se, but rather, are more related to special adaptations involving both abiotic and biotic factors, as we discuss.

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