Host Specialization in Plant-galling Interactions: Contrasting Mites and Insects

Walter Santos de Araújo 1, Érica Vanessa Durães de Freitas 2,* Ján Kollár 3, Rodrigo Oliveira Pessoa 1, Paulo Henrique Costa Corgosinho 1, Henrique Maia Valério 1, Luiz Alberto Dolabela Falcão 1, Marcio Fagundes 1, Marcio Antonio Silva Pimenta 1, Mauricio Lopes de Faria 1, Waldney Pereira Martins 1 and Magno Augusto Zazá Borges 1

1 Department of General Biology, Universidade Estadual de Montes Claros, 39401-089 Montes Claros, Brazil; walterbioaraujo@gmail.com (W.S.A.); rodrigo.pessoa@unimontes.br (R.O.P.); pcorgo@gmail.com (P.H.C.C.); hmvaler@gmail.com (H.M.V.); luizdolabelafalcao@gmail.com (L.A.D.F.); marcilio.fagundes@gmail.com (M.F.); marcio.pimenta@unimontes.br (M.A.S.P.); fariaml@gmail.com (M.L.d.F.); martinswp@gmail.com (W.P.M.); diptera@gmail.com (M.A.Z.B.)

2 Programa de Pós-Graduação em Biodiversidade e Uso dos Recursos Naturais, Universidade Estadual de Montes Claros, 39401-089 Montes Claros, Brazil

3 Department of Planting Design and Maintenance, Slovak University of Agriculture in Nitra, 949-76 Nitra, Slovakia; jankollar82@gmail.com

*Correspondence: vanessaduraesfreitas@gmail.com; Tel.: +55-38-3220-1466

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Abstract: Gall-inducing arthropods represent one of the most specialized herbivore groups. On an evolutionary scale, different taxa of insects and mites have convergently adapted to a galling lifestyle. In this study, we have used a multi-taxonomic approach to analyze the interaction specialization between gall-inducing mites and insects and their host plants in the Nitra City Park (Nitra, Slovakia). We used four ecological descriptors for describe plant-galling interactions: number of host plant species used by each arthropod species, galling specificity on host plant species (specificity), exclusivity of interactions between galling and plant species (specialization) and overlap of the interactions between arthropod species (similarity). We have found 121 species of gall-inducing arthropods, totaling 90 insects and 31 mites occurring on 65 host plant species. Our results reveal that mites have high specialization and low similarity of interactions in comparison to insects. A multiple-taxonomic comparison showed that these differences are triggered by gall-wasps (Hymenoptera: Cynipidae), the taxon with the lowest levels of specificity of plant-galling interactions (i.e., occurring on different host plant species). Our findings are indicative of different patterns of interaction between distinct gall-inducing arthropods taxa and their host plants, despite the ecological convergence of different taxa to a highly specialized herbivorous habitat.

Keywords: Cecidomyiidae; Cynipidae; Eriophyidae; herbivory; plant-insect interactions

1. Introduction

Gall-inducing organisms are considered to be the most sophisticated herbivores found in nature [1], given that they are the only herbivores capable of manipulating plant tissues inducing the formation of structures called galls [2–4]. Fungi, bacteria, viruses, nematodes, and arthropods are capable of inducing galls in plants, but arthropods are undoubtedly the most diverse and studied galling group [5,6]. The arthropods inducing mechanisms that promote tissue modifications are diverse, ranging from the reaction of plant tissues to the piercing activity of mouthparts, saliva components, hormones released by the female ovipositor at the time of laying eggs, or even substances in the eggshell [4,7]. Consequently,
plant tissues form a capsule that houses totally or partially the gall-inducing arthropod inside [3], offering food to the arthropods, as well as shelter and protection against adverse environmental conditions and natural enemies [7]. Despite the protection provided by gall structures, the performance of gall-inducing insects can be affected by top-down (e.g., predators and parasitoids) and bottom-up (e.g., host plant characteristics) forces [6,8].

Insects and mites are the gall-inducing arthropods [3,4]. Insect galls are very common in many parts of the world (Europe, Asia, Australia, Africa, and America) [9]. Among the gall-inducing insects are the well-known species of the orders Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, and Thysanoptera [3,9,10]. Among these, the highest number of gall-inducing species belongs to the orders Diptera and Hymenoptera [11]. Previous studies have documented the great variety of gall structures induced by numerous insect species belonging to the dipteran gall-midges of the family Cecidomyiidae [12,13], hymenopteran gall-wasps of the family Cynipidae [14], and sawflies of the family Tenthredinidae [10,15]. Within Acarina, it is known that gall-inducing mites’ species belong to the families Eriophyidae and Phytoptidae [16]. Mites of the superfamily Eriophyoidea are amongst the smallest herbivorous arthropods and their degree of association with plants varies from free-ranging, refuge-seeking, and gall inducing, some of them economically important as agricultural pests [17]. Gall-inducing mites occur in angiosperms, conifers, and ferns throughout the world, but exhibit great specificity, the result of an intimate relationship with their host plant [18].

The great diversity of gall-inducing taxa shows that the galling life-style evolved repeatedly within and among arthropod groups [7]. Despite the convergence of these taxa to a highly specialized guild of sessile endophytic herbivores, different groups of gall-inducing animals may have different patterns of interaction with their host plants [5,10,19]. Previous studies suggest that plant-galling interactions can vary between distinct galling taxa [19,20] and between galling species within the same taxon [21]. Nevertheless, no previous study has systematically evaluated how the specialization of interactions differs between different groups of gall-inducing arthropods. In this study, we have inventoried the diversity of arthropod galls in an urban garden in the city of Nitra, Slovakia. Our main objective is to investigate whether plant-galling interactions specialize differently between insects and mites. Additionally, we have compared the specialization of interactions of distinct orders and families of gall-inducing arthropods.

2. Materials and Methods

2.1. Study Area

The investigations were carried out from 2004 to 2008 in Nitra City Park in the city of Nitra, Slovakia (48°19'7” N, 18°4’5” E, 144 m a.s.l.). The climate of the area is characterized as semi-arid and humid with an average annual total precipitation of 600 mm and the average annual temperature of 9.5 °C [16]. The park is bordered by the Nitra River and is composed by woody plants of various ages. The dominant woody plant species in the park are oaks (Quercus robur, Q. cerris, and Q. pubescens) and hornbeam (Carpinus betulus).

2.2. Sampling of Plant-galling Arthropods Interactions

All host woody plants of the Nitra City Park were actively searched for gall-inducing species. The identification of arthropod species was determined in the field whenever possible according to morphological characteristics of the gall. Some galls were collected to be reared in the laboratory for better identification of the gall-inducing species. Gall-inducing arthropods were identified using the taxonomic keys of Csóka [22]. The Fauna Europaea database [23] was used for the taxonomic classification and correct terminology of gall-inducing insects. Plant species were identified using flora catalogs, and the correct nomenclature and possible synonyms were checked against The Plant List database [24].
2.3. Data Analyses

For the characterization of the interactions between the arthropod galling species and their host plant species, we have used the number of host plant species and three species-level measures of interaction (specialization, specificity, and similarity) for each galling species. These four ecological descriptors measure distinct aspects of the interactions between arthropods and plants, which are the number of host plant species used by each arthropod species (number of host plant species), galling specificity on host plant species (specificity), exclusivity of interactions between galling species and plant species (specialization), and overlap of the interactions between arthropod species (similarity). We have calculated the specialization for each galling species using the index $d'$ of Blüthgen et al. [25]. This index ranges from 0 to 1, with 0 indicating maximum generalization and 1 indicating maximum specialization. For each arthropod species, we have additionally calculated the specificity of the interactions using the coefficient of variation of interactions proposed by Poisot et al. [26], normalized to values between 0 (low specificity) and 1 (high specificity). Finally, the dissimilarity between used resources (number of used host plant species) and their availability (number of potential host plant species) [27] was employed to calculate the similarity of interactions for each galling species. All species-level indices were calculated using the bipartite package [28] within the software R [29].

From the calculated measurements for each species of galling arthropod, we have calculated the average values for different taxonomic levels (class, order, and family). Firstly, we have used general linear models (GLMs) followed by ANOVA to compare the number of host plants, specialization, specificity, and similarity of galling species between arthropod classes (insects and mites). All models had a Gaussian error distribution assumed. In sequence, we have used GLMs followed by ANOVA to contrast if the measures of interaction at the species-level differ between orders and families of gall-inducing arthropods. In these analyses, only orders (Acarina, Diptera, Hemiptera, and Hymenoptera) and families (Adelgidae, Aphididae, Cecidomyiidae, Cynipidae, Eryophyidae, and Tenthredinidae) which had at least three species of gall-inducing arthropods were contrasted. Additionally, we have performed post-hoc contrast tests to highlight the differences between galling orders and families. All statistical analyses were performed in the software R version 3.4.1 [29].

3. Results

In total, we have sampled 121 species of gall-inducing arthropods occurring on 65 host plant species (Appendix A), totaling 90 species of insects and 31 species of mites (Table 1). We have recorded six galling orders among which the most speciose were Hymenoptera (32 species), Acarina (31), and Hemiptera (31). Gall-inducing insects were represented by nine families, with Cynipidae (Hymenoptera) with 27 species, Aphididae (Hemiptera) with 25 species, and Cecidomyiidae (Diptera) with 24 species appearing as the most specious taxa. For Acarina, we recorded the families Eryophyidae with 29 species and Phytoptidae with two species. The most speciose galling genera were Andricus (Cynipidae) with 15 species, Aceria (Eryiophyidae) with 13, and Dasineura (Cecidomyiidae) with seven gall-inducing species.

The number of host plants ($F < 0.001; p > 0.05$) and the interaction specificity ($F = 0.186; p > 0.05$) did not differ between insect and mite species (Figure 1A). However, species specialization was higher for galling mites (mean 0.661 ± SD 0.234) than for galling insects (0.484 ± 0.369) ($F = 6.233; p = 0.013$). The similarity of interactions was greater for insect species (0.072 ± 0.068) than for mite species (0.031 ± 0.024) ($F = 10.772; p = 0.001$).

The specialization and similarity of the plant-galling interactions varied widely among the galling orders (Figure 1B). Hymenoptera was less specialized (0.148 ± 0.294) than Acarina (0.661 ± 0.234), Diptera (0.596 ± 0.294) and Hemiptera (0.710 ± 0.222) ($F = 30.689; p < 0.001$). A higher level of similarity was observed for the hymenopteran species (0.142 ± 0.059), with lower values recorded for the other orders (values < 0.050) ($F = 58.360; p < 0.001$). In contrast, galling orders did not differ in the number of host plants and the interaction specificity (all $F$ values < 2.300 and $p$ values > 0.05).
When contrasting the different families of gall-inducing arthropods, we found a lower specialization ($F = 24.045; p < 0.001$) and a higher similarity in the interactions ($F = 60.441; p < 0.001$) of Cynipidae when compared to the other families. Cynipidae species had a mean specialization of 0.076 ($\pm 0.236$), whilst species of other galling families had specialization mean values higher than 0.533 (Figure 1C). Instead, the number of host plants and the interaction specificity did not differ between distinct galling families (all $F$ values < 1.700 and $p$ values > 0.05).
Table 1. Diversity of galling arthropods and host plants recorded in the Nitra City Park (Nitra, SW, Slovakia).

| Galling Taxa       | Number of Galling Species | Number of Galling Genera | Number of Plant Species | Number of Plant Genera |
|--------------------|----------------------------|--------------------------|-------------------------|------------------------|
| Order Acarina      | 31                         | 11                       | 24                      | 16                     |
| Family Eryophyidae | 29                         | 10                       | 23                      | 15                     |
| Family Phytoptidae | 2                          | 1                        | 2                       | 2                      |
| Order Coleoptera   | 1                          | 1                        | 1                       | 1                      |
| Family Cerambycidae| 1                          | 1                        | 1                       | 1                      |
| Order Diptera      | 24                         | 16                       | 22                      | 17                     |
| Family Cecidomyiidae| 24                       | 16                       | 22                      | 17                     |
| Order Hemiptera    | 31                         | 19                       | 29                      | 20                     |
| Family Adelgidae   | 3                          | 2                        | 5                       | 2                      |
| Family Aphididae   | 25                         | 14                       | 23                      | 17                     |
| Family Psyllidae   | 2                          | 2                        | 2                       | 2                      |
| Family Triozidae   | 1                          | 1                        | 1                       | 1                      |
| Order Hymenoptera  | 32                         | 9                        | 7                       | 3                      |
| Family Cynipidae   | 27                         | 6                        | 5                       | 2                      |
| Family Tenthredinidae| 5                        | 3                        | 3                       | 2                      |
| Order Lepidoptera  | 2                          | 2                        | 5                       | 1                      |
| Family Tortricidae | 2                          | 2                        | 5                       | 1                      |

4. Discussion

Gall-inducing arthropod fauna recorded in Nitra City Park was composed of distinct and important gall-inducing groups such as eriophyids (Eriophyidae), gall-wasps (Cynipidae), gall-midges (Cecidomyiidae), and aphids (Aphididae). Galling eriophyids constitute the most specialized group of phytophagous arachnids [30] and can induce galls in more than 500 host plant species [22]. Similarly to what we have found in this study, the gall-wasps constitute one of the most numerous groups of galling insects in the old world, inducing galls in trees of the family Fagaceae, usually oaks (Quercus) or roses (Rosa) [31]. Gall-midges are considered the most diverse group of gall-inducing insects in the world [13] and are usually characterized by monophagous species with larvae that develop within a single plant [12,21]. In turn, aphids can induce galls in several host plants and can cause indirect damage to the hosts by the transportation of viral diseases [16]. Other taxa were also present with fewer representatives (e.g., cerambycids, psyllids, tortricids). The occurrence of this taxonomically diverse assemblage of galling arthropods provides a rather interesting setting for multi-taxon comparisons.

We have found that the interaction patterns differ between different arthropod taxa. Mite species had more specialized and less similar interactions than insect species. However, both mites and insects have a similar number of host plants and interaction specificity. Eriophyids depend on the wind to disperse and tend to preferentially colonize trees rather than transient plants (e.g., grasses and herbs), which can influence their host specificity [32]. In Nitra City Park, we have also found a high diversity of mites parasitizing the trees. We have also found that the orders and families of gall-inducing arthropods differ in their specialization and similarity of interactions, but did not differ in the number of host plants and specificity. Similarly to previous studies, our data indicate that galling arthropods tend to be quite specific [7,21]. However, we offer new evidence that the galling taxa may vary accordingly to the way that their hosts are used and shared.

The index of specialization that we have used (index $d'$) measures the specialization of each species based on its discrimination of random selection of partners [25]. In other words, it measures how much the plant-galling interactions are more exclusive than expected by chance. A high degree of specialization indicates that the interactions of a species of gall-inducing arthropods tend to be exclusive, that is, the galling species “A” only consumes a single species of plant “B”, and that this species of plant “B” is only consumed by the galling species “A”. Therefore, specialization of a species is inversely proportional to their host sharing with other galling species (i.e., the similarity in the plant-galling interactions).
Our results show that the differences between mites and insects, and between orders and families of gall-inducing arthropods, are highly influenced by the presence of gall-wasps (Hymenoptera: Cynipidae). Corroborating previous studies, the family Cynipidae had low specialization and high similarity of their interactions, as a consequence of the high specificity of gall-wasp species on oak species (Quercus), [14]. In this study, we found a high overlap of cynipid species on the species Quercus robur, which hosts 25 gall-wasp species. The Cynipid family of gall-wasps comprises approximately 1300 species distributed worldwide, 1000 of which occur on oaks [14]. Price et al. [10] discuss that the great diversity of gall-wasps is the result of high adaptive radiation on Quercus species (600 species distributed worldwide). Although each recorded species of gall-wasp occurred on one or two host plant species (mean of 1.07 host plant species), the high levels of different species occurring on the Quercus super-hosts have generated low specialization and high similarity of their interactions. Consequently, the pattern observed for Cynipidae influenced the values obtained for the order Hymenoptera and insects in general.

Among the species of gall-inducing arthropods found in this study, gall-wasps have distinct evolutionary histories, evolving from parasitoids of galler-arthropods inside plant tissues [33]. Instead, mites, hemipteroids, gall-midges, and sawflies are descendants of phytophagous ancestors [4,30]. This reflects in the way of initiation of the gall, whether by lesions of the plant tissues by the gall wasp’s ovipositor or by lesions caused by the mouthpieces during the feeding in the other groups [34]. These different evolutionary origins of the galling arthropod groups may have given rise to different ways of interacting with the host plants, which in turn enriches the patterns of interaction of the gall-inducing arthropods.

The number of host plant species and the interaction specificity did not vary among the different groups of galling arthropods analyzed. Specificity is a measure of how much a species of herbivore tends to be endemic to its host plant [26]. The specificity was high and varied little among mites and insects, and also among the different orders and families analyzed. This absence of difference can be explained by the monophagous behavior of most of the galling species. Our results revealed that 79.3% of the galling species were recorded on a single host plant species (i.e., monophages). For oligophagous species (20.7%), most of them were recorded on phylogenetically related host plant species (i.e., congeneric species). Similarly to previous studies, our data reveal a high level of monophagy and specificity in galling arthropods [7,19,21].

5. Conclusions

The ability to induce galls is one of the most elaborate and complex mechanisms developed by herbivores [1]. Due to the high degree of intimacy that the gall inducers have with the cells and tissue of their host plants [4], there is a great restriction in the possibility of interactions within the plant-galling assemblages [19,20]. Here we have multi-taxis plant-galling assemblage very well resolved taxonomically, which is usually very rare to find in the literature. Our results provide evidence that supports the high specificity and specialization of plant-galling interactions, regardless of whether insects or mites are involved. Only cynipid gall-wasps presented a low level of specialization (i.e. few exclusive interactions), with different species sharing host plants of the genus Quercus, despite having high interaction specificity (i.e., many monophagous species). Although we have not provided comparisons related to host plant species, our findings suggest a strongly conservative phylogenetic pattern of the interactions between the assemblages of host plants and galling arthropods. This is evidenced by the low number of host plant species and the high specificity of interactions of each galling species with their hosts, a pattern that is constant when comparing distinct classes, orders and families of arthropods. Future studies may investigate whether there is a phylogenetic signal in plant-galling interactions, as well as whether the strength of this signal differs between species of galling arthropods and host plants.
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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Species of host plants and galling arthropods recorded in Nitra City Park (SW Slovakia).

| Host Plant Species | Galling Species          | Galling Family | Galling Order |
|--------------------|--------------------------|----------------|---------------|
| Abies alba         | Dreyfusia nordmannianae   | Adelgidae      | Hemiptera     |
| Abies concolor     | Dreyfusia piceae          | Adelgidae      | Hemiptera     |
| Acer campestræ     | Dasineura rubella         | Cecidomyiidae  | Diptera       |
| Acer campestræ     | Drisina glutinosa        | Cecidomyiidae  | Diptera       |
| Acer campestræ     | Aceria cephalonea        | Eryphidae      | Aracina       |
| Acer campestræ     | Aceria macrorrhynchos     | Eryphidae      | Aracina       |
| Acer campestræ     | Aceria macrocelis         | Eryphidae      | Aracina       |
| Acer montspessulanum | Aceria macrorrhynchos     | Eryphidae      | Aracina       |
| Acer pseudoplatanus | Aceria cephalonea        | Eryphidae      | Aracina       |
| Acer pseudoplatanus | Aceria pseudoplatani     | Eryphidae      | Aracina       |
| Acer pseudoplatanus | Aceria macrorrhynchos     | Eryphidae      | Aracina       |
| Acer saccharinum   | Vasates quadripes        | Eryphidae      | Aracina       |
| Alnus glutinosa    | Aceria breitarsa          | Eryphidae      | Aracina       |
| Alnus glutinosa    | Eriophyes laevis          | Eryphidae      | Aracina       |
| Alnus glutinosa    | Eriophyes inaequalis      | Eryphidae      | Aracina       |
| Alnus incana       | Eriophyes inaequalis      | Eryphidae      | Aracina       |
| Betula pendula     | Anisostephus betulinus    | Cecidomyiidae  | Diptera       |
| Buxus sempervirens | Monarthropalus flavus     | Cecidomyiidae  | Diptera       |
| Buxus sempervirens | Psylla buxi              | Psyllidae      | Hemiptera     |
| Carpinus betulis   | Zygobia carpini          | Cecidomyiidae  | Diptera       |
| Carpinus betulis   | Aceria tenellus           | Eryphidae      | Aracina       |
| Carpinus betulis   | Aculops macrotrichus      | Eryphidae      | Aracina       |
| Cornus sanguinea   | Cramebia corni           | Cecidomyiidae  | Diptera       |
| Corylus colurna    | Phytoptus atellanae      | Phytoptidae    | Aracina       |
| Crataegus monogyna | Dysaphis crataegi        | Aphididae      | Hemiptera     |
| Crataegus monogyna | Phyllocoptus goniotherax  | Eryphidae      | Aracina       |
| Euonymus europaeus | Aphis fabae              | Aphididae      | Hemiptera     |
| Euonymus europaeus | Stenacis euonymi         | Eryphidae      | Aracina       |
| Fraxinus excelsior | Dasineura acrophila      | Cecidomyiidae  | Diptera       |
| Fraxinus excelsior | Dasineura fraxini        | Cecidomyiidae  | Diptera       |
| Fraxinus excelsior | Prociphilus bunelae       | Aphididae      | Hemiptera     |
| Fraxinus excelsior | Psyllopsis fraxini       | Psyllidae      | Hemiptera     |
| Host Plant Species | Galling Species | Galling Family | Galling Order |
|--------------------|----------------|---------------|---------------|
| Fraxinus excelsior  | Aceria fraxinivora | Eryophyidae | Acarina |
| Fraxinus ornus      | Dasineura fraxini | Cecidomyiidae | Diptera |
| Fraxinus ornus      | Aceria fraxinivora | Eryophyidae | Acarina |
| Gleditsia triacanthos | Dasineura gleditchiae | Cecidomyiidae | Diptera |
| Hibiscus syriacus   | Myzus persicae    | Aphididae | Hemiptera |
| Juglans regia      | Aceria tristriata | Eryophyidae | Acarina |
| Juglans regia      | Aceria erinea     | Eryophyidae | Acarina |
| Juniperus communis | Oligotrophus juniperinus | Cecidomyiidae | Diptera |
| Larix decidua      | Adelges laricis | Aphididae | Hemiptera |
| Larix decidua      | Dasineura kellneri | Cynipidae | Hymenoptera |
| Ligustrum vulgare   | Myzus ligustri   | Aphididae | Hemiptera |
| Lonicera xylosteum  | Hyadaphis tataricai | Aphididae | Hemiptera |
| Lonicera xylosteum  | Rhyacionia buolina | Tortricidae | Lepidoptera |
| Philadelphus coronarius | Aphis fabae   | Aphididae | Hemiptera |
| Picea abies        | Adelges laricis | Aphididae | Hemiptera |
| Picea abies        | Sacchiphantes viridis | Adelgidae | Hymenoptera |
| Picea glauca       | Sacchiphantes viridis | Adelgidae | Hymenoptera |
| Picea pungens      | Sacchiphantes viridis | Adelgidae | Hymenoptera |
| Pinus contorta     | Rhyacionia buolina | Tortricidae | Lepidoptera |
| Pinus nigra        | Rhyacionia buolina | Tortricidae | Lepidoptera |
| Pinus ponderosa    | Rhyacionia buolina | Tortricidae | Lepidoptera |
| Pinus sylvestris   | Retinia resinella | Tortricidae | Lepidoptera |
| Pinus sylvestris   | Rhyacionia buolina | Tortricidae | Lepidoptera |
| Pinus sylvestris   | Thecodiplosis brachyntera | Cecidomyiidae | Diptera |
| Populus alba       | Aceria populii   | Aphididae | Hemiptera |
| Populus canescens  | Saperda populnea | Cerambycidae | Coleoptera |
| Populus nigra      | Chaitophorus populicola | Aphididae | Hemiptera |
| Populus nigra      | Pemphigus borealis | Aphididae | Hemiptera |
| Populus nigra      | Pemphigus bursarius | Aphididae | Hemiptera |
| Populus nigra      | Pemphigus populii | Aphididae | Hemiptera |
| Populus nigra      | Pemphigus populinigras | Aphididae | Hemiptera |
| Populus nigra      | Pemphigus spirothecae | Aphididae | Hemiptera |
| Populus nigra      | Thecabius affinis | Aphididae | Hemiptera |
| Populus simonii    | Pemphigus spirothecae | Aphididae | Hemiptera |
| Prunus avium       | Myzus cerisi     | Aphididae | Hemiptera |
| Prunus avium       | Eriophyes padi   | Eriophyidae | Acarina |
| Prunus padus       | Eriophyes padi   | Eriophyidae | Acarina |
| Pseudotsuga menziesii | Gillettella cooleyi | Aphididae | Hemiptera |
| Pyracantha coccinea| Aceria pyracanthi | Eriophyidae | Acarina |
| Quercus cerris     | Andricus cydoniae | Cynipidae | Hymenoptera |
| Quercus hispanica  | Andricus anthracina | Cynipidae | Hymenoptera |
| Quercus robur      | Andricus anthracina | Cynipidae | Hymenoptera |
| Quercus robur      | Andricus conglomeratus | Cynipidae | Hymenoptera |
| Quercus robur      | Andricus coriarius | Cynipidae | Hymenoptera |
| Quercus robur      | Andricus curvator | Cynipidae | Hymenoptera |
| Quercus robur      | Andricus fasciculatus | Cynipidae | Hymenoptera |
| Quercus robur      | Andricus grossulariae | Cynipidae | Hymenoptera |
| Quercus robur      | Andricus hungaricus | Cynipidae | Hymenoptera |
| Quercus robur      | Andricus hungaricus | Cynipidae | Hymenoptera |
| Host Plant Species     | Galling Species       | Galling Family | Galling Order |
|------------------------|-----------------------|----------------|---------------|
| Quercus robur          | Andricus inflator     | Cynipidae      | Hymenoptera   |
| Quercus robur          | Andricus kollari      | Cynipidae      | Hymenoptera   |
| Quercus robur          | Andricus lucidus      | Cynipidae      | Hymenoptera   |
| Quercus robur          | Andricus mayri        | Cynipidae      | Hymenoptera   |
| Quercus robur          | Andricus solitarius   | Cynipidae      | Hymenoptera   |
| Quercus robur          | Andricus testaceipes  | Cynipidae      | Hymenoptera   |
| Quercus robur          | Biorrhiza pallida     | Cynipidae      | Hymenoptera   |
| Quercus robur          | Cynips caputmedusae    | Cynipidae      | Hymenoptera   |
| Quercus robur          | Cynips disticha       | Cynipidae      | Hymenoptera   |
| Quercus robur          | Cynips divisa         | Cynipidae      | Hymenoptera   |
| Quercus robur          | Cynips longiventris   | Cynipidae      | Hymenoptera   |
| Quercus robur          | Cynips quercusfolii   | Cynipidae      | Hymenoptera   |
| Quercus robur          | Macrodiplotis pustularis | Cecidomyiidae | Diptera       |
| Quercus robur          | Neuroterus laevisculus| Cynipidae      | Hymenoptera   |
| Quercus robur          | Neuroterus quercus-baccarum | Cynipidae | Hymenoptera   |
| Quercus robur          | Trigonaspis megaperta | Cynipidae      | Hymenoptera   |
| Ribes aureum           | Aphis idaei           | Aphididae      | Hemiptera     |
| Robinia pseudoacacia   | Acericccis vitrina    | Cecidomyiidae  | Diptera       |
| Robinia pseudoacacia   | Aphis craccivora      | Aphididae      | Hemiptera     |
| Robinia pseudoacacia   | Aphis fabae           | Aphididae      | Hemiptera     |
| Robinia pseudoacacia   | Obolidiplotis robiniae| Cecidomyiidae  | Diptera       |
| Rosa canina            | Blennocampa pusilla   | Tenthredinidae | Hymenoptera   |
| Rosa multiflora        | Dasineura rosa        | Cynipidae      | Hymenoptera   |
| Rosa multiflora        | Diplolepis rosae      | Cynipidae      | Hymenoptera   |
| Salix alba              | Aphis farinosa        | Aphididae      | Hymenoptera   |
| Salix alba              | Eura americana        | Tenthredinidae | Hymenoptera   |
| Salix alba              | Pontania proxima      | Tenthredinidae | Hymenoptera   |
| Salix alba              | Pontania vesicator    | Tenthredinidae | Hymenoptera   |
| Salix alba              | Rabdophaga rosaria    | Cecidomyiidae  | Diptera       |
| Salix alba              | Rabdophaga salicis    | Cecidomyiidae  | Diptera       |
| Salix alba              | Aculus laevis         | Eryophyidae    | Acarina       |
| Salix alba              | Aculus craspedobius   | Eryophyidae    | Acarina       |
| Salix alba              | Stenacis triradiatus  | Eryophyidae    | Acarina       |
| Salix purpurea          | Pontania viminalis    | Tenthredinidae | Hymenoptera   |
| Sambucus nigra          | Epitrimerus trilobus  | Eryophyidae    | Acarina       |
| Taxus baccata           | Taxomyia taxi         | Cecidomyiidae  | Diptera       |
| Taxus baccata           | Cecidophyopsis psilaspis | Eryophyidae | Acarina       |
| Tilia cordata           | Contarinia tiliarum   | Cecidomyiidae  | Diptera       |
| Tilia cordata           | Dasineura tilae       | Cynipidae      | Hymenoptera   |
| Tilia cordata           | Eriophyes tilae       | Eryophyidae    | Acarina       |
| Tilia cordata           | Eriophyes leiosoma    | Eryophyidae    | Acarina       |
| Tilia cordata           | Eriophyes exilis      | Eryophyidae    | Acarina       |
| Tilia platyphyllos      | Contarinia tiliarum   | Cecidomyiidae  | Diptera       |
| Tilia platyphyllos      | Dasineura tilae       | Cynipidae      | Hymenoptera   |
### Table A1. Cont.

| Host Plant Species | Galling Species  | Galling Family | Galling Order |
|--------------------|------------------|----------------|--------------|
| Tilia platyphyllos | Didymomyia tiliacea | Cecidomyiidae | Diptera      |
| Tilia platyphyllos | Eriophyes tiliae  | Eryophyidae   | Acarina      |
| Tilia platyphyllos | Eriophyes leiosoma | Eryophyidae | Acarina      |
| Tilia platyphyllos | Eriophyes exilis  | Eryophyidae   | Acarina      |
| Tilia platyphyllos | Phytoptus tetratrichus | Phytoptidae | Acarina      |
| Ulmus glabra       | Eriophyes tiliae  | Eryophyidae   | Acarina      |
| Ulmus laevis       | Tetraneura ulmi   | Aphididae     | Hemiptera    |
| Ulmus minor        | Tetraneura ulmi   | Aphididae     | Hemiptera    |
| Viburnum lantana   | Aphis viburni     | Aphididae     | Hemiptera    |
| Viburnum opulus    | Aphis viburni     | Aphididae     | Hemiptera    |
| Vitis vinifera     | Colomerus vitis   | Eryophyidae   | Acarina      |

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