

THE EFFECT OF GALL MITES (ACARIFORMES, ERIOPHYOIDEA) ON LEAF MORPHOLOGY AND PIGMENT CONTENT OF DECIDUOUS TREES IN WEST SIBERIA

Larissa A. Ivanova[1, 2*], Philipp E. Chetverikov[3, 4], Leonid A. Ivanov[1, 2], Shinekhuu Tumurjav[1], Igor V. Kuzmin[1], Alexey G. Desnitskiy[4] and Andrei V. Tolstikov[1]

[1]X-BIO Institute, Tyumen State University, Tyumen, Russia
[2]Institute Botanic Garden, Ural Branch, Russian Academy of Sciences, Ekaterinburg, Russia
[3]Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, Russia
[4]Saint-Petersburg State University, Saint-Petersburg, Russia
[*]corresponding author; e-mail: ivanova.larissa@list.ru

ABSTRACT: Phytophagous mites of the superfamily Eriophyoidea are capable of inducing gall formation on various organs of higher vascular plants. However, the question of how gallogenesis affects leaf assimilation surface and photosynthetic activity of the host plants is poorly understood. We have examined the influence of gall-forming mites from the genera *Eriophyes* and *Acalitus* on leaf size, shape and photosynthetic pigment content in five deciduous tree species near the city of Tyumen, West Siberia. The gall mite infestation resulted in chlorosis, destruction of photosynthetic apparatus in gall-infected leaf parts, leaf deformation and a decrease in leaf area. The magnitude of the effects on leaf size and shape varied among the studied mite–tree systems and did not depend on the infection severity. On the contrary, chlorophyll and carotenoid amounts per leaf decreased in an infection severity-dependent manner in all mite–host plant variants. Mite-induced galls did not influence the pigment concentration in green uninfected gaps between galls. Additionally, the chlorophyll amount in the infected leaves has decreased due to the destruction of the pigment complex in the galled leaf areas and a decrease of the whole-leaf area. As a result, the losses of chlorophylls and carotenoids in leaves of all studied trees were directly related to the infection severity (quantified as the proportion of damaged leaf area to the total leaf area). Our results may help developing an approach to assess the effect of gall mites on the chlorophyll content and the photosynthetic productivity of trees, based on the direct or remote analysis of damaged leaf surface.

KEY WORDS: Mite–host system, galls, *Eriophyes*, *Acalitus,* leaf size, leaf shape, birch, linden, chlorophyll.

DOI: 10.21684/0132-8077-2022-30-1-89-98

INTRODUCTION

Four-legged mites, or eriophyoids (Acari, Eriophyoidea), are microscopic, highly host-specific phytoparasites, permanently associated with higher vascular plants (Lindquist 1996). Among ≈5,000 known species, about 20% induce various galls, or growth abnormalities, on vegetative and generative plant organs (Skoracka *et al.* 2010; Jiang *et al.* 2021). The genus *Eriophyes*, which includes about 300 species, is one of the most diverse eriophyoid mite genera (Soika and Kozak 2013). In the boreal zone, mite species of this genus cause the formation of multiple galls on the leaves of deciduous trees (De Lillo *et al.* 2018). They are especially common and numerous on alder, birch, linden and bird-cherry. In the above tree species, a huge part of leaf canopy can be affected (Kane *et al.* 1997). Infestation by gall inducers (insects, mites, bacteria, viruses) often markedly changes leaf morphology (Tooker *et al.* 2008; Albert *et al.* 2011) and influences the functional activity of affected trees (Dorchin *et al.* 2006; Patankar *et al.* 2013; Jiang *et al.* 2018; Jiang *et al.* 2021). Studies have shown that gall infected leaves modify gas exchange characteristics, such as the photosynthesis rate and stomatal conductance (Patankar *et al.* 2013; Jiang *et al.* 2018; Ye *et al.* 2019). However, the magnitude of effects varies among gall parasite–host systems (Jiang *et al.* 2018). For example, a large decrease in the photosynthesis rate (approximately 60%) of mite-galled leaves of *Acer saccharum* has been reported (Patankar *et al.* 2013), whereas the photosynthesis in *Machilus thunbergia* leaves was not significantly affected by cecidomyiid insect galls (Huang *et al.* 2014). Moreover, climatic conditions can enhance or mask the influence of an infection's damaging agent. Studies examining the effects of gall mites on tree leaf properties have not been carried out in the severe climate of West Siberia.

Gall formation leads to a decrease in the leaf chlorophyll content. In particular, galls change the color of the damaged leaf surface from green to brown, yellow, or red due to the destruction of the chlorophylls, thereby causing decolorization of photosynthetic tissues (Jiang *et al.* 2018, Ye *et al.* 2019). For galls appearing green, the chlorophyll content and the photosynthesis of galled and healthy leaf tissue can be similar (Fernandes *et al.* 2010). However, this mainly concerns insect galls, many of which appear green and contain chlorophyll. The effects of non-green mite galls on the photosynthetic pigments of the host leaves are poorly understood.

An intriguing question in the study of mite–plant interaction is how mite-inducing galls influence the unthreatened (healthy) parts of a leaf. Since chlorophyll content is closely linked with the maximum carboxylation rate—one of the critical parameters of the photosynthetic capacity of plants (Qian *et al.* 2019)—it is clear that more research focused on the effects of mites on the photosynthetic pigments is needed. There is also a lack of quantitative information on the relationship between mite infection severity and the functional response of host plant leaves.

Our study aims to: 1) study the leaf size, shape and the photosynthetic pigment (chlorophyll a, b, carotenoids) content in the healthy and infected leaves of different deciduous trees; and 2) assess the influence of the infection severity on the pigment content per leaf area unit and per whole leaf. In order to achieve these goals, we have examined five gall parasite–host systems infected with *Eriophyes* and *Acalitus* mite species.

MATERIALS AND METHODS

The research was conducted in August 2021 at two study sites: 1) in a birch-spruce-pine forest, near the village of Uspenka, located close to the city of Tyumen (57°02′11.9″N 65°05′04.4″E, alt. 82 m a.s.l.); and 2) a public garden in the city of Tyumen (57°08’13.5″N 65°33′51.7″E, alt. 86 m a.s.l.). The study sites are located in the sub-taiga ecological zone of West Siberia. The climate of the region is cold and continental, with the mean annual air temperature of 2.2°C, the average July temperature of 18.9°C and the mean annual precipitation of 545 mm. Summer starts in late June and ends in September.

Five species of deciduous trees infected by the gall mites have been examined (Table 1). In the list below, the first three species were collected from the first study site, and the last two—from the second study site:

1) the birch *Betula krylovii* G.V. Krylov (Bk), numerous white erinea on the lower leaf surface caused by *Acalitus rudis* (Canestrini, 1891);

2) the gray alder *Alnus incana* (L.) Moench (Ai), numerous pouch galls on the upper leaf surface caused by mite *Eriophyes laevis* (Nalepa, 1889);

3) the bird-cherry *Prunus padus* L. (Pp), numerous nail galls on the upper leaf surface caused by mite *Eriophyes padi* (Nalepa, 1889);

4) the pear *Prunus ussuriensis* Kovalev and Kostina (Pu), numerous blisters (parenchymatous galls) caused by mite *Eriophyes pyri* (Nalepa, 1881);

5) the linden *Tilia cordata* Mill. (Tc), numerous white erinea between veins on the upper and lower leaf surfaces caused by mite *Eriophyes leiosoma* (Nalepa, 1892).

We have sampled 20–30 leaves from 3–5 individual trees per each plant species and per each variant (healthy, infected). The leaves were selected from 4–5-year-old branches of a tree from the lower third part of the tree crown, at the level of human height. We have measured the leaf area, the leaf shape coefficient, as well as the pigment content. For infected leaves, we have also measured the area of the damaged leaf surface and determined the severity of infection by calculating the share of the damaged surface relative to the area of the whole leaf (ShGall). The areas of individual leaves (LA, cm^2) and the areas of damaged leaf surfaces were measured using the digital image analysis system Simagis Mesoplant (OOO SIAMS, Russia). The leaf shape coefficient (LSh, dimension-loss) was calculated as $LSh = P^2/LA$, where P is the leaf perimeter (cm) (Migalina *et al.*, 2010).

The contents of photosynthetic pigments—chlorophyll a, b and carotenoid—were measured separately in healthy and infected leaves. Three healthy and fully expanded leaves per tree were selected from the lower third of the tree crown. Subsequently, two disks with an area of 0.42 cm^2 each were punched out in the middle part of each fresh leaf while avoiding large vines. In infected leaves, green unthreatened parts between galls were selected. On the surfaces of the galls, the leaf tissues were markedly disturbed, containing no photosynthetically active chlorophyll. The pigments were extracted with 80% acetone and measured using an Odyssey DR/2500 spectrophotometer (Hach, USA). The content of the chlorophylls (Chl) and carotenoids (Car) was estimated according to Wellburn (1994). Using the known areas of leaf disks, the pigment concentration was calculated per leaf area unit (Cab), in g m^{-2}. In infected leaves, the mean concentration of chlorophyll per leaf area unit (Cab_gall) was calculated using the chlorophyll content in green unthreatened parts between galls (Cab) and the share of the damaged surface relative to the area of the whole leaf (ShGall), according to the formula:

$$Cab\_gall = Cab * ShGall$$

In healthy leaves, the total amount of chlorophylls per whole leaf was calculated by multiplying the chlorophyll content per leaf area unit by the leaf area:

$$Chl\_leaf = Cab^* \ LA$$

In infected leaves, the total amount of chlorophylls per whole leaf was calculated by multiplying the mean chlorophyll content per galled leaf area unit by the galled leaf area:

$$Chl\_gall\_leaf = Cab\_gall^* \ LA$$

The losses in the chlorophyll and carotenoid amounts in the infected leaves were calculated as a difference between potential chlorophyll amount per leaf and the real chlorophyll amount per leaf:

$$\text{Losses in chlorophyll} = Cab^* \ LA - Chl\_gall\_leaf$$

Carotenoid contents per leaf area unit and per whole leaf in healthy and infected leaves were calculated in a similar manner. Using the data on the chlorophyll and carotenoid contents, we have calculated the following ratios of pigments: Chl a/b and Chl/Car.

When analyzing data, linear regression analysis was used. In particular, the determination coefficient (R^2) and the Pearson correlation coefficient (r) were calculated. To test for differences between the variants (healthy, infected) and the tree species, we have used the paired t-test and two-way ANOVA. Differences were considered to be significant at $p \leq 0.05$. The tables and graphs show mean values with standard errors. All statistical analyses were carried out using Statistica 13.5 (StatSoft Inc.)

RESULTS

Mite induced galls differed among the studied gall parasite–host systems in their shape, size, color and the amount per leaf (Fig. 1). Quantitative characteristics of the pouch and nail galls caused by the three *Eriophyes* species are shown in Table 1. Galls of *Eriophyes laevis* on alder leaves had maximal sizes whereas galls of *Eriophyes padi* on bird-cherry leaves were four-fold lower. The largest number of galls and the maximum share of damaged leaf area was found on pear leaves infected

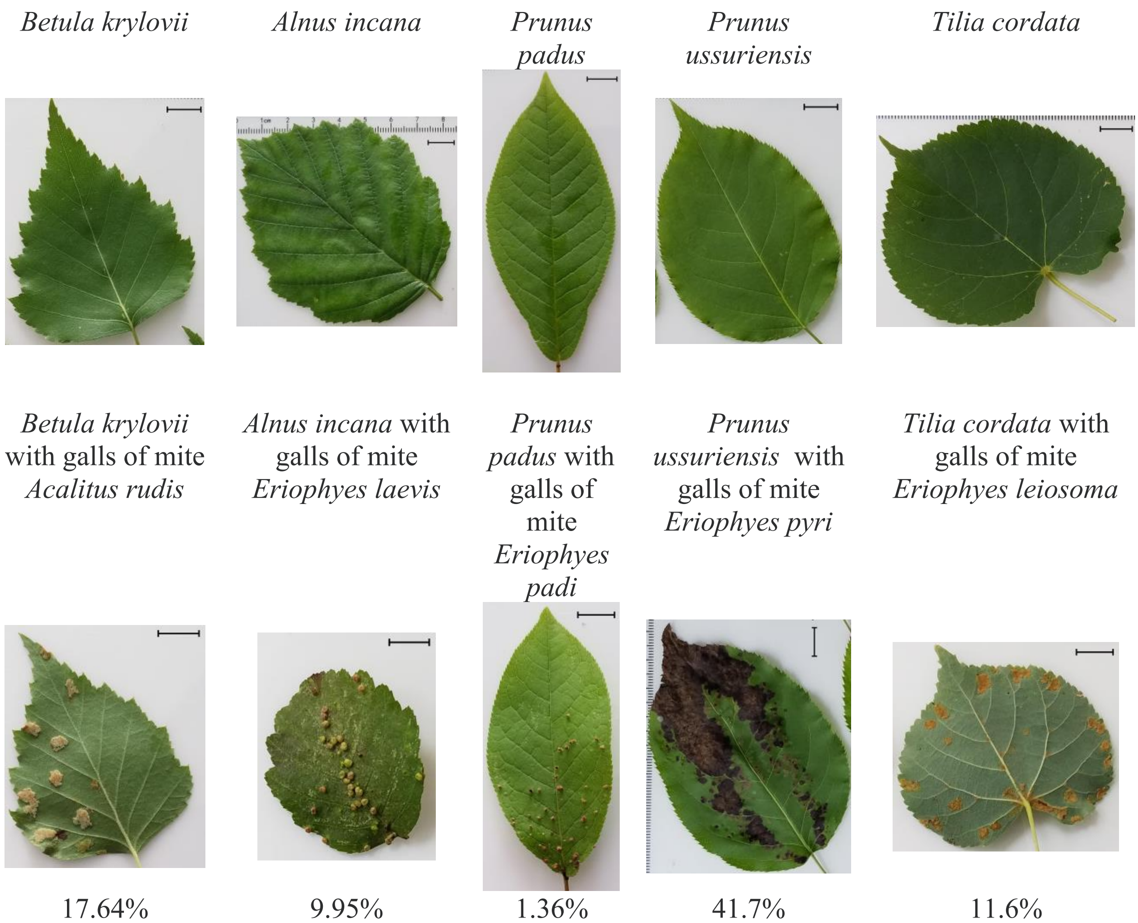

Fig. 1. Images of uninfected leaves (upper row) and leaves infected by different species of gall-forming mites (lower row) of the studied tree species. The scale is 1 cm. Mean share of damaged leaf surface in percent is shown under the images of infected leaves. 20–30 leaves from 3–5 trees per each species were measured.

by *Eriophyes pyri* (Fig. 1). In the four of five studied tree species, galled leaves were 20–40% smaller than the healthy leaves of the same species. However, pear leaves did not change in size (Fig. 2). Gall mite infection significantly affected leaf shape in all tree species (Fig. 2). In comparison with healthy leaves, infected leaves had a 5% lower leaf shape coefficient inside each tree species, i.e., leaf shapes became simpler and rounder. The largest change in leaf shape was found in bird-cherry leaves (*Prunus ussuriensis*). The magnitude of the decrease in leaf size and shape did not depend on the infection severity among the tree species.

The analysis of the chlorophyll and carotenoid content showed that gall formation caused a decrease in both pigment content per leaf area unit and per whole leaf in all plant species (Fig. 2). The reason for the decrease in the pigment content in all studied tree species was similar: the infection of leaves with mites did not affect the pigment content in the green parts of the leaves between galls (Fig. 3). Instead, the decrease in the pigment amount per leaf occurred due to the loss of chlorophylls and carotenoids in the galled areas of the leaf surface. Actually, the chlorophyll and the carotenoid content in the uninfected parts of infected leaves remained stable, close to the values

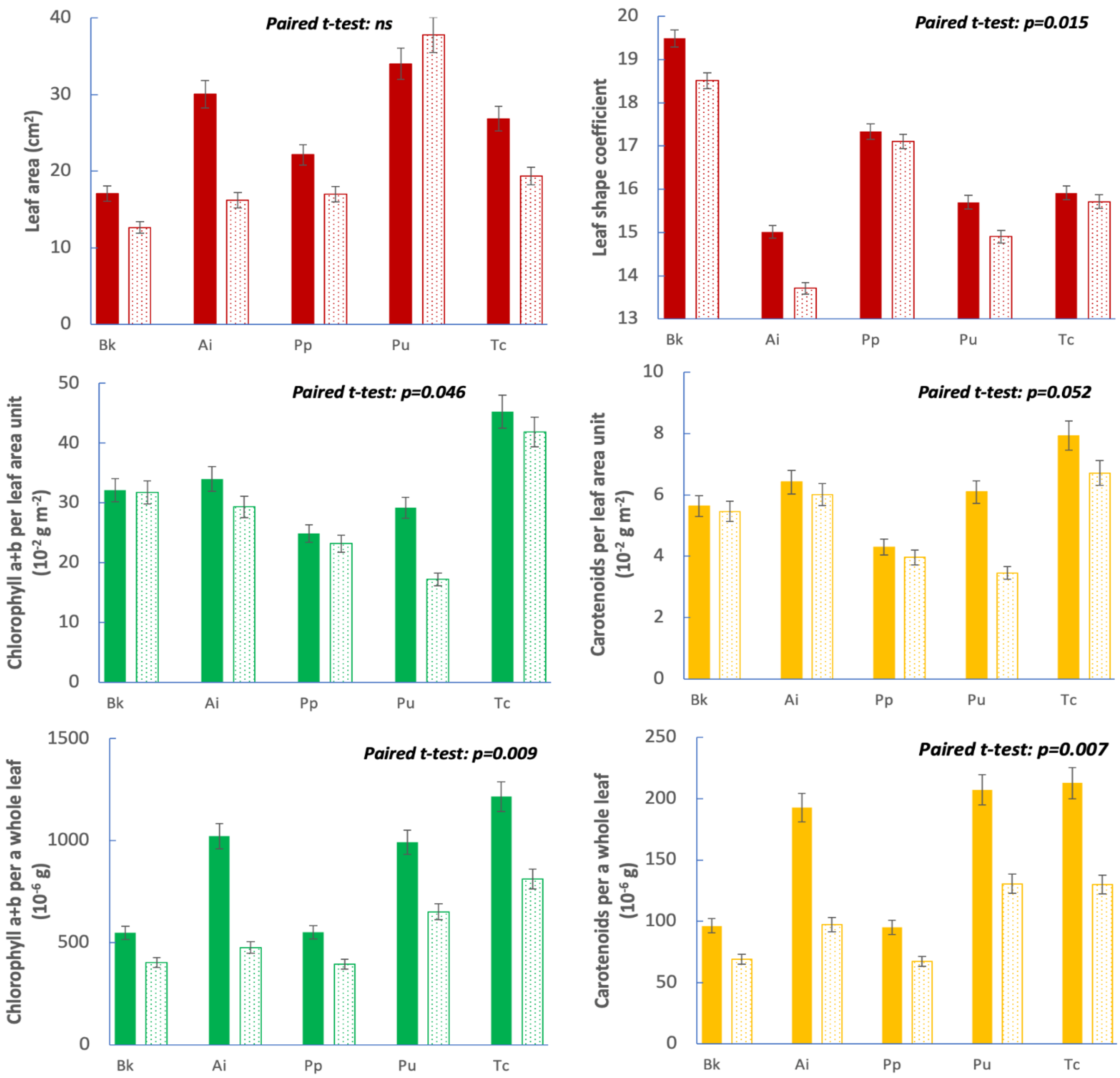

Fig. 2. Functional traits of infected (colored columns) and uninfected (light columns with dots) leaves in different tree species: *Betula krylovii* (Bk), *Alnus incana* (Ai), *Prunus padus* (Pp), *Prunus ussuriensis* (Pu) and *Tilia cordata* (Tc). The values of paired t-test are shown. Differences at $p<0.05$ are significant.

characteristic of uninfected leaves of the same species.

The content of photosynthetic pigments varied significantly between plant species. Linden was characterized by the maximum amount of chlorophylls and carotenoids in leaves, whereas bird cherry leaves had 1.5 times less pigments. Tree species also differed significantly in the ratio of chlorophylls a/b, which was the highest in birch and the lowest in bird cherry. In addition, the mite infestation did not change the ratio of pigment forms (Chl/Car, Chl a/b) in any of the studied plant species (Fig. 3).

Interspecific correlation analysis revealed a direct dependence of losses in the amount of chlorophylls and carotenoids on the severity of infection (Fig. 4). The relative share of the damaged leaf area was the main determining factor in the decrease in the total amount of pigments per whole leaf. The decrease of the total area of infected leaves was another factor contributing to the decrease of pigment mass in leaves.

DISCUSSION

In this study, we have investigated the functional characteristics of the mature leaves of 5 species of deciduous trees (Betulaceae, Rosaceae and Tiliaceae families) infested by 5 species of gall mites of the Eriophyidae family. A significant influence of mite activity on the leaf morphology and pigment content was found in all of the examined plants. The influence of gall mites on the leaf size and shape is one of the most interesting results of this study. The differences in the size and shape of healthy and infected leaves were practically invisible in the field conditions. However, our quantitative analysis of healthy and galled leaves showed: 1) a decrease in the shape coefficient (indicating simplification of leaf shape) in all 5 model species, and 2) a significant decrease of the leaf area in 4

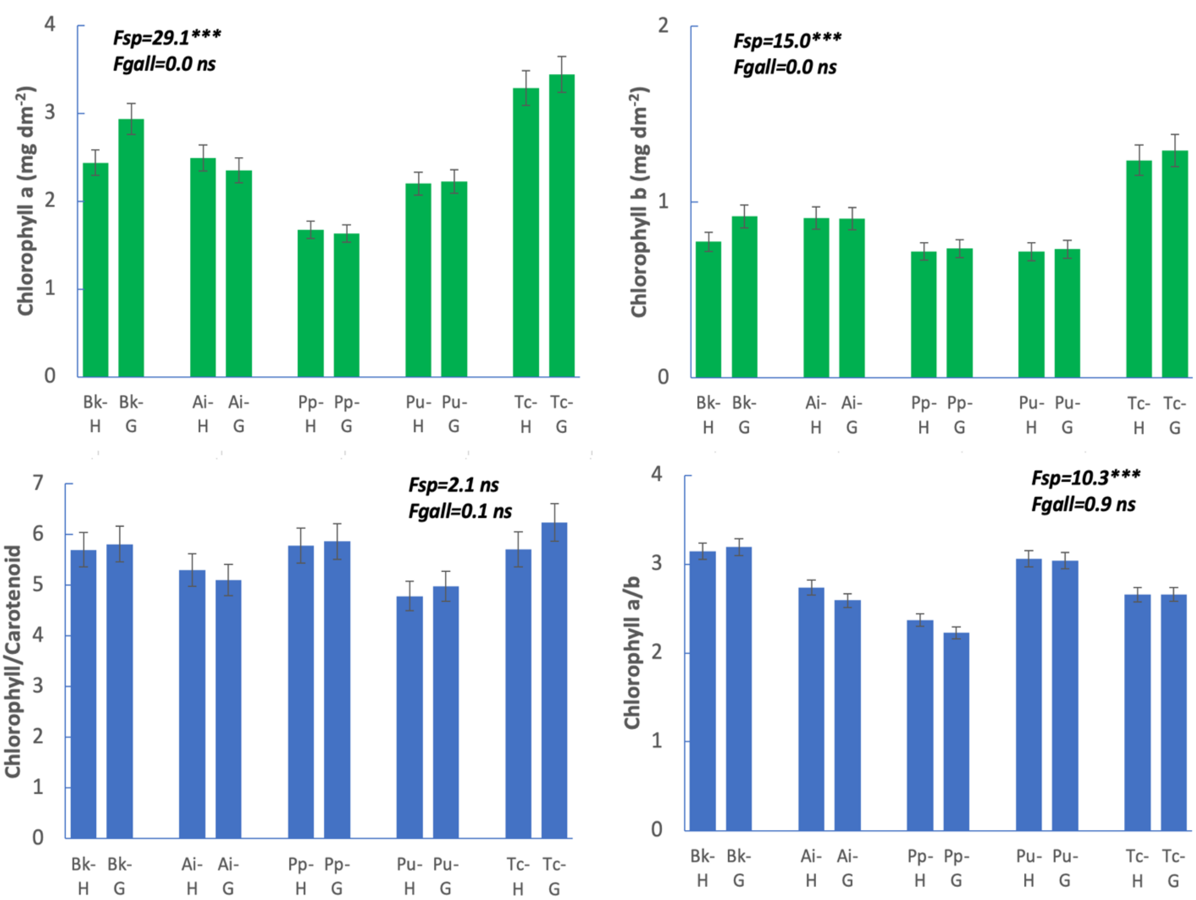

Fig. 3. The content and ratios of photosynthetic pigments in green parts of gall-infected (uninfected areas between galls) (G) and uninfected (H) leaves in different tree species: *Betula krylovii* (Bk), *Alnus incana* (Ai), *Prunus padus* (Pp), *Prunus ussuriensis* (Pu) and *Tilia cordata* (Tc). The values of F-criterion are shown depending on tree species (Fsp) and gall infection (Fgall).

of 5 tree species as a result of gallogenesis. The effect of mites on leaf size was not detected in pear (*Prunus ussuriensis*), which can be explained by the peculiarities of the morphology of parenchymatous galls in this plant (Fig. 1, Table 1).

Gall mites induce a wide variety of damage on plant leaves (Westphal and Manson 1996; Chetverikov *et al.* 2015). Usually, the growth of eriophyoid galls on leaves is associated with the initiation of the growth processes in young leaf tissues. As a result, the new cellular material forms a three-dimensional structure (gall) rising above the leaf lamina and containing a polyploid parenchyma tissue. Galls usually have a voluminous internal chamber, where mites can reproduce (Paponova *et al.* 2018; Desnitskiy, Chetverikov 2022). In this case, part of the cell mass of a young growing leaf is removed from the leaf lamina. This can explain the reduction in size and the deformation of leaves, bearing sac-like and horn-shaped galls observed by us. The formation of erineum is associated with active cell divisions, leading to the formation of numerous epidermal trichomes. Therefore, the observed reduction in leaf size connected with erinea on linden and birch can also be explained in terms of the "3D loss of cellular material".

The blisters (="parenchymatous galls") caused by *Eriophyes pyri* on pear leaves are characterized by the intense necrosis of the parenchyma within the leaf, which leads to the formation of black areas of the leaf, visible to the naked eye. Weak cell proliferation occurs only in the inner tissues of the leaf, in the early stages of parenchymatous gall formation, while all the cellular material remains in the plane of leaf lamina, thereby preventing new three-dimensional structures from forming (Kołątaj 2016). This apparently explains the lack of influence of *E. pyri* mites on the sizes of pear leaves. If our assumptions are correct, then the reduction in leaf size is a common effect that accompanies the formation of mite galls of certain types: erinea and galls containing a chamber (e.g., pouch, nail and bead galls). This hypothesis needs further testing using more extensive material.

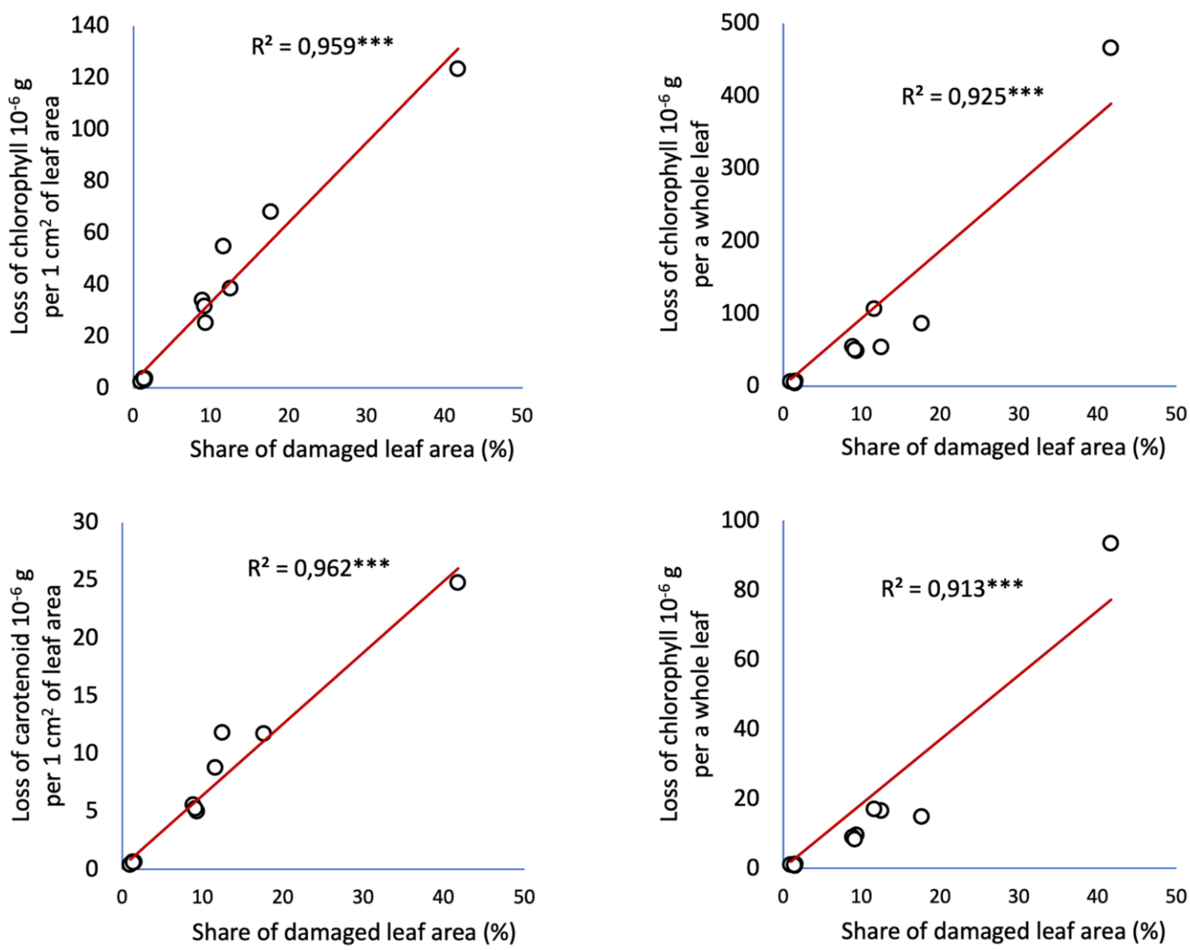

Fig. 4 Relationships between the losses in leaf pigment content and the gall infection severity in the studied tree species. Determination coefficients and significance of Pearson correlation coefficient are shown.

Table 1

Characteristics of the galls induced by different mite *Eriophyes* species on the leaves of studied deciduous trees. N—the number of measured leaves, n—the number of measured galls.

Plant species	Mite species	N	n	Gall number on the leaf	Gall diameter, µm	Gall area, mm^2
Alnus incana	*Eriophyes laevis*	25	58	33.6±2.8	1,757±50	2.3±0.1
Prunus padus	*Eriophyes padi*	30	71	41.1±3.6	828±26	0.5±0.0
Prunus ussuriensis	*Eriophyes pyri*	15	25	85.4±12.0	1,530±86	1.8±0.3

The activity of the gall-forming mites on the studied plants resulted in the leaf shape simplification. On the one hand, this simplification may be of an adaptive nature, e. g., an adaptation to climate factors. For instance, it was shown that more severe climatic and weather conditions had resulted in the leaves of two birch species—*Betula pendula* and *B.pubescens*—having lower shape coefficients, i. e., having a simpler shape (Migalina *et al.* 2010). On the other hand, leaf shape simplification may be due to the reduction in resources necessary for the formation of normal leaf shape. After all, the increase in the complexity of leaf shape is correlated with the complexity of leaf venation and the coordinated development of all leaf tissues (Dengler and Kang 2001). Finally, the simplification of leaf shape may indicate a distortion in normal leaf development, since mites initiate gallogenesis at the earliest stages of leaf development, when plant tissues are still poorly differentiated and extremely susceptible to the transforming influence of mite saliva (Desnitskiy and Chetverikov 2022). The shape of a leaf is determined by the interaction of all the tissues and cells that make up the leaf. Therefore, the change in shape observed in this study implies that the effect of the gall-forming mite activity involves not only the gall tissues and small areas adjacent to the galls, but also the entire leaf lamina, including peripheral parts of the leaf. This conclusion is in accordance with the results of recent comparative metabolomic study performed on the model system "strawberry *Fragaria viridis*—gall mite *Fragariocoptes setiger*" (Chetverikov *et al.* 2018). In the above work, the differences in metabolomic profiles between the tissues of galls and the green leaf gaps between galls were shown to be most pronounced at the very beginning of the gall growth, in the spring, gradually disappearing by mid-summer. This result indicates the effect of gallogenesis on the entire leaf area and suggests similarity of gallogenesis induced by eriophyoid mites with systemic plant diseases at the metabolomic level.

Galls act like metabolic sinks (Ajoykumar and Subitha 2019). Accordingly, galls are considered a significance drain on a leaf's resources (Fay *et al.* 1993; Nyman and Julkunen-Tiitto 2001). We can conclude that the disposal of resources necessary for gall formation can lead to a reduction in leaf area in deciduous trees. At the same time, leaf area is a relevant predictor of the functional state and the productivity of trees. For example, in birch trees, leaf area was a reliable indicator of tree productivity in different climatic conditions of the Urals and West Siberia (Migalina *et al.* 2009). Therefore, a decrease in leaf size resulting from mite infection allows suggesting the reduction in the overall tree productivity. The magnitude of such decline could be gall mite–host specific. It is important to note that leaf size reduction and shape simplification were not proportional to the degree of damage to the species. For instance, the maximum reduction in the leaf area of *Alnus incana* was associated with a small (≈10%) degree of damage, whereas in *Prunus ussuriensis,* maximum degree of leaf damage (≈42%) was associated with no changes in leaf area. This means that the magnitude of the effect on the leaf shape and size depends on the specifics of a gall mite–host system rather than on the infection severity.

Despite the obvious effect of mites on the whole leaf traits, the results of our study showed the stability of the pigment apparatus in green intact areas of infected leaves. We did not find any differences in the content of photosynthetic pigments between healthy leaf gaps of infested leaves and non-infested leaves of the same tree species. Regardless of the mite species and the shape and size of galls, gallogenesis induced by eriophyoid mites did not affect the structure of pigment complexes—chlorophyll/carotenoid and chlorophyll a/b ratios. This suggests the predominant importance of the adaptation of the photosynthetic apparatus to the external ecological factors, first and foremost, to sunlight intensity (Lichtenthaler *et al.* 2007; Poorter *et al.* 2019). A given plant species needs to have a certain amount of pigments per unit of leaf area in order to maintain the required photosynthesis rate to survive in given environmental conditions (Lichtenthaler *et al.* 2007; Ivanov *et al.* 2013, 2020). Indeed, pigment content per leaf area markedly differed among the studied tree species (Fig. 3) due to their ecological and morphological peculiarities. However, none of the studied tree species changed its chlorophyll and carotenoid content in the intact parts of the galled leaves.

In general, the analysis of the pigment amount at the level of a whole leaf showed a significant decrease in the chlorophyll and carotenoid mass per leaf area in the infected leaves of all tree species (Fig. 2). Earlier, it has been reported that with an increase in the growth of the gall, chlorophyll content in the gall tissue decreased in a small tropical Asian tree *Alstonia scholaris* (Apocynaceae) (Albert *et al.* 2011). This loss of chlorophyll is responsible for the decolorization of the threatened area of the leaf, where galls form (Moghe 1980). The decrease in the chlorophyll content of the galled tissues was due to the loss of photosynthetic tissues and the disappearance of chloroplasts (Moghe 1980). Since the content of chlorophylls is directly proportional to the photosynthesis intensity (Lichtenthaler *et al.* 2007; Lambers 2008; Ivanova *et al.* 2018, 2019; Qian *et al.* 2019), the loss of pigments in infected leaves denotes a decrease in the photosynthesis of plants. It has been shown that the net assimilation rate per area and the stomatal conductance strongly decrease with the increasing severity of infestation by *Eriophyes* gall-forming mites in *Alnus glutinosa* and *Tilia cordata* (Jiang *et al.* 2021). The above plant parameters also inversely correlated with the severity of infection by gall wasp species (Jiang *et al.* 2018). In the leaves of *Salix* species, galled leaves also showed significant declines in the maximum photosynthetic capacity, photosystem II efficiency and stomatal conductance (Patankar *et al.* 2013). The severity-dependent manner of decrease in photosynthesis found in many studies confirms that the formation of galls does not affect the photosynthetic activity in intact areas between galls. Thus, infection with gall mites can reduce the photosynthesis of the host plant, and one of the reasons for photosynthesis reduction is a loss of chlorophyll in the leaf areas occupied by mite galls.

According to our calculations, when about 10% of the leaf area is damaged by gall mites, a deciduous tree in the climate of West Siberia loses from 250 mg (in alder) to 550 mg (in linden) of chlorophyll per 1 m^2 of leaf canopy (Fig. 4). We have previously shown that in West Siberian birches, 1 g of chlorophyll ensures the assimilation of 20–25 μmol CO_2 per second in full light (Kalashnikova *et al.* 2021), which corresponds to 880–1,100 μg CO_2 per 1 g of chlorophyll per second, or about 1 g of carbon (C) per 1 g of chlorophyll per hour. Therefore, the gall damage to 10% of leaf surface results in a carbon uptake loss of 250 to 550 mg of C per 1 m^2 of leaf surface per hour. If 50% of the leaf surface is damaged by galls, the carbon fixation by the plant will reduce by 1 g of C per 1 m^2 per hour at full sunlight. Thus, a decrease in the chlorophyll content by gall mite infection can cause a significant decrease in the photosynthesis and the productivity of trees proportional to the infection severity. We have not assessed the assimilation activity of chlorophyll in healthy and infested trees. However, future studies in this direction can potentially help test the effect of mites on the photosynthesis and the carbon balance of plants, which can significantly affect the carbon balance of natural and urban ecosystems as a whole. The obtained results on the infection severity-dependent character of chlorophyll changes indicate the possibility of assessing the effect of gall mites on the chlorophyll content and the photosynthetic productivity of trees based on the direct or remote analysis of damaged leaf surface.

ACKNOWLEDGEMENTS

The reported study was performed within the framework of the state assignment FEWZ-2020-0009 from the Ministry of Education and Science of the Russian Federation, in accordance with the budget themes of the Botanic Garden UB RAS and of the Zoological Institute RAS 122031100263-1, as well as the Russian Foundation for Basic Research (RFBR) grant No. 21-54-46003 CT_a.

REFERENCES

Ajoykumar, K.N. and Subitha, P.P. 2019. Physiochemical changes associated with foliar gall formation by a psyllid insect *Trioza pallida* Haupt. in

Mallotus philippensis Muell. Arg. *International Journal of Research in Advent Technology*, 7(2): 721–728.

Albert, S., Padhiar, A., Gandhi, D. and Nityanand, P. 2011. Morphological, anatomical and biochemical studies on the foliar galls of *Alstonia scholaris* (Apocynaceae). *Rev Bras Bot*, 34: 343–358.

Chetverikov, P.E., Vishyakov, A.E., Dodueva, I.T., Osipova, M.A., Sukhareva, S.I. and Shavarda, A.L. 2015. Gallogenesis induced by eryophyoid mites (Acariformes: Eriophyoidea). *Entomological Review*, 95(8): 1137–1143. DOI: 10.1134/S0013873815080217

Chetverikov, P.E., Dodueva, I.E., Pautov, A.A., Krylova, E.G., Paponova, S.S. and Shavarda, A.L. 2018. Metabolomic changes in a model system of gallogenesis induced by eriophyoid mites. In: *Abstract Book of XV International Congress of Acarology*. Antalya, Turkey, p. 210.

De Lillo, E., Pozzebon, A., Valenzano, D. and Duso, C. 2018. An intimate relationship between eriophyoid mites and their host plants—a review. *Frontiers in Plant Science,* 9: 1786.

Dengler, N.G. and Kang, J. 2001.Vascular patterning and leaf shape. *Current Opinion in Plant Biology*, 4: 50–56.

Desnitskiy, A.G. and Chetverikov, P.E. 2022. Induction of leaf galls by four-legged mites (eriophyoidea) as a problem of developmental biology. *Russian Journal of Developmental Biology*, 53(1): 6–14. DOI: 10.1134/S1062360422010039

Dorchin, N., Cramer, M.D. and Hoffmann, J.H. 2006. Photosynthesis and sink activity of wasp-induced galls in *Acacia pycnantha*. *Ecology*, 87: 1781–1791.

Fay, P.A., Hartneet, D.C. and Knapp, A.K. 1993. Increased photosynthesis and water potentials in *Silphium integrifolium* galled by cynipid wasps. *Oecologia* 93: 114–120.

Fernandes, G.W., Coelho, M.S. and Lüttge, U. 2010. Photosynthetic efficiency of *Clusia arrudae* leaf tissue with and without Cecidomyiidae galls. *Brazilian Journal of Biology*, 70: 723–728.

Huang, M.Y., Chou, H.M., Chang, Y.D. and Yang, C.M. 2014. The number of cecidomyiid insect galls affects the photosynthesis of *Machilus thunbergii* host leaves. *Journal of Asia-Pacific Entomology*, 17: 151–154.

Ivanov, L.A., Ivanova, L.A., Ronzhina, D.A. and Yudina, P.K. 2013. Changes in the chlorophyll and carotenoid contents in the leaves of steppe plants along a latitudinal gradient in South Ural. *Russian Journal of Plant Physiology*, 30: 812. DOI: 10.1134/S1021443713050075

Ivanov, L.A., Ronzhina, D.A., Yudina, P.K., Zolotareva, N.V., Kalashnikova, I.V. and Ivanova, L.A. 2020. Seasonal dynamics of the chlorophyll and carotenoid content in the leaves of steppe and forest plants on species and community level. *Russian Journal of Plant Physiology*, 67(3): 453–462. DOI: 10.1134/S1021443720030115

Ivanova, L.A., Yudina, P.K., Ronzhina, D.A., Ivanov, L.A. and Hölzel, N. 2018. Quantitative mesophyll parameters rather than whole-leaf traits predict response of C3 steppe plants to aridity. *New Phytologist*, 217(2): 558–570. DOI: 10.1111/nph.14840

Ivanova, L.A., Ivanov, L.A., Ronzhina, D.A., Yudina, P.K., Migalina, S.V., Shinehuu, T., Tserenkhand, G., Voronin, P.Yu., Anenkhonov, O., Bazha, S.N. and Gunin, P.D. 2019. Leaf traits of C3- and C4-plants indicating climatic adaptation along a latitudinal gradient in Southern Siberia and Mongolia. *FLORA*, 254: 122–134. DOI: 10.1016/j.flora.2018.10.008

Jiang, Y.F., Veromann, L.L., Ye, J.Y. and Niinemets, Ü. 2018. Oak gall wasp infections of *Quercus robur* leaves lead to profound modifications in foliage photosynthetic and volatile emission characteristics. *Plant Cell Environ*, 41: 160–175.

Jiang, Y., Ye, J., Veromann-Jürgenson, L. and Niinemets, Ü. 2021. Gall- and erineum-forming Eriophyes mites alter photosynthesis and volatile emissions in an infection severity-dependent manner in broad-leaved trees *Alnus glutinosa* and *Tilia cordata*. *Tree Physiology,* 41(7): 1122–1142. DOI: 10.1093/treephys/tpaa173

Kalashnikova, I., Migalina, S., Ronzhina, D., Ivanov, L. and Ivanova, L. 2021. Functional response of Betula species to edaphic and nutrient stress during restoration of fly ash deposits in the Middle Urals (Russia). *Environmental Science and Pollution Research*, 28: 12714–12724. DOI: 10.1007/s11356-020-11200-5

Kane, N.A., Jones, C.S. and Vuorisalo, A.T. 1997. Development of galls on leaves of *Alnus glutinosa* and *Alnus incana* (Betulaceae) caused by the eriophyid mite *Eriophyes laevis* (Nalepa). *International Journal of Plant Sciences,* 158: 13–23.

Kołątaj K.T. 2016. Leaf blister mites (*Eriophyes* sp.) as significant pests in orchards. In: *Scientific Proceedings of the 5th International Scientific Horticulture Conference*, pp. 55–59.

Lambers, H., Chapin, F.S., III and Pons, T.L.. 2008. *Plant Physiological Ecology*. Springer, New York. 605 pp. DOI: 10.1007/978-0-387-78341-3

Lichtenthaler, H. K., Ač, A., Marek, M. V., Kalina, J. and Urban, O. 2007. Differences in pigment composition, photosynthetic rates and chlorophyll fluorescence images of sun and shade leaves of four tree species. *Plant Physiology and Biochemistry*, 45: 577. DOI: 10.1016/j.plaphy.2007.04.006

Lindquist, E.E. 1996. Chapter 1.1 External anatomy and systematics 1.1.1. External anatomy and notation of structures. In: E.E. Lindquist, M.W. Sabelis and J. Bruin (Eds.). *World Crop Pests*. Elsevier, pp. 3–31.

Migalina, S.V., Ivanova, L.A. and Makhnev, A.K. 2009. Size of the leaf as a marker of birch productivity at a distance from the climatic optimum. *Russian Journal of Plant Physiology*, 56 (6): 857–861.

Migalina, S.V., Ivanova, L.A. and Makhnev, A.K. 2010. Changes in leaf morphology in *Betula pendula* Roth and *B. pubescens* Ehrh. along a zonal–climatic transect in the Urals and Western Siberia. *Russian Journal of Ecology*, 41 (4): 263–271.

Moghe, M. 1980. Studies on the insect gall of *Ficus racemosa* Linn. Ph.D. Thesis. The Maharaja Sayajirao University, Vadodara.

Nyman, R. and Julkunen-Tiitto, R. 2001. Manipulation of the phenolic chemistry of willows by gall-inducing sawflies. *Proceedings of the National Academy of Sciences*, 97: 13184–13187.

Paponova, S.S., Chetverikov, P.E., Pautov, A.A., Yakovleva, O.V., Zukoff, S.N., Vishnyakov, A.E., Sukhareva, S.I., Krylova, E. G., Dodueva, I.E. and Lutova, L.A. 2018. Gall mite *Fragariocoptes setiger* (Eriophyoidea) changes leaf developmental program and regulates gene expression in the leaf tissues of *Fragaria viridis* (Rosaceae). *Annals of Applied Biology*, 172 (1): 33–46. DOI: 10.1111/aab.12399

Patankar, R., Starr, G., Mortazavi, B., Oberbauer, S.F. and Rosenblum, A. 2013. The effects of mite galling on the ecophysiology of two arctic willows. *Arctic, Antarctic, and Alpine Research*, 45 (1): 99–106. DOI: 10.1657/1938-4246-45.1.99

Poorter, H., Niinemets, Ü., Ntagkas, N., Siebenkäs, A., Mäenpää, M., Matsubara, S. and Pons, T.L. 2019. A meta-analysis of plant responses to light intensity for 70 traits ranging from molecules to whole plant performance. *New Phytologist,* 223: 1073–1105.

Qian, X., Zhang, Y., Liu, L. and Du, S. 2019. Exploring the potential of leaf reflectance spectra for retrieving the leaf maximum carboxylation rate. *International Journal of Remote Sensing* 40: 5411–5428.

Skoracka, A., Smith, L., Oldfield, G., Cristofaro, M., Amrine, J.W. 2010. Host-plant specificity and specialization in eriophyoid mites and their importance for the use of eriophyoid mites as biocontrol agents of weeds. *Experimental and Applied Acarology,* 51: 93–113. DOI: 10.1007/s10493-009-9323-6

Soika, G. and Kozak, M. 2013. Eriophyes species (Acari: Eriophyoidea) inhabiting lime trees (*Tilia* spp.: Tiliaceae)—supplementary description and morphological variability related to host plants and female forms. *Zootaxa*, 3646: 349–385.

Tooker, J.F. and De Moraes, C.M. 2008. Gall insects and indirect plant defenses: a case of active manipulation? *Plant Signaling and Behavior,* 3: 503–504.

Wellburn, A.R. 1994. The spectral determination of chlorophylls a and b, as well as total carotenoids, using various solvents with spectrophotometers of different resolution. *Journal of Plant Physiology*, 144 (3): 307–313. DOI: 10.1016/S0176-1617(11)81192-2

Westphal, E. and Manson, D.C.M. 1996. Chapter 1.4.6. Feeding effects on host plants: Gall formation and other distortions. In: E.E. Lindquist, M.W. Sabelis and J. Bruin (Eds.). Eriophyoid Mites: Their Biology, Natural Enemies and Control. *World Crop Pests*. Elsevier Science Publishing, Amsterdam, The Netherlands, vol 6, pp. 231–242. DOI: 10.1016/S1572-4379(96)80014-5

Ye, J., Jiang, Y., Veromann-Jürgenson, L.L. and Niinemets, Ü. 2019. Petiole gall aphid (*Pemphigus spyrothecae*) infestation of *Populus × petrovskiana* leaves alters foliage photosynthetic characteristics and leads to enhanced emissions of both constitutive and stress-induced volatiles. *Trees: Structure and Function,* 33: 37–51.