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EXPERIMENTAL ARTICLES

Endophytic Yeasts in Leaf Galls

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Abstract—Yeast abundance and species diversity of endophytic complexes in galls (cecidia) formed on the leaves of *Salix fragilis, Salix caprea, Quercus robur*, *Tilia cordata*, and *Ulmus laevis* and the epiphytic yeast communities of undamaged leaves of these plants were studied. Dynamics of yeast abundance in the galls was significantly different from that of the epiphytic yeast communities. Maximum numbers of endophytic yeast cells in the galls (up to 10^4 CFU/g) were comparable to abundance of epiphytic yeasts. A total of 14 species of endophytic yeasts were isolated from galls of different plants. Ascomycetous yeasts were found to predominate in the insect galls on willows and oak, while basidiomycetous yeasts dominated in mite galls on linden and elm, as well as on plant leaves. These results indicate that gall formation may be considered not only as a bidirectional pathological process of the interaction between plants and invertebrates, but also as a process in which the endophytic microbial population of the galls plays an important role.

Keywords: yeasts, galls, endophytes, *Salix*, *Quercus*, *Tilia*, *Ulmus*, *Pontania*, *Diplolepis*, *Eriophyes*

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Proliferation of plant internal storage tissues as a result of a pathologic process of gall formation caused by insects and mites is a widespread phenomenon. At present, over 132 thousands of invertebrate species are known to induce formation of galls which serve as habitats and food sources (Espirito-Santo and Fernandes, 2007). Galls are formed on all plant organs; this teratogenic results in abnormalities of the organ growth and development and in a decrease in the plant viability (Mani, 1964; Slepyan, 1971).

Gall formation is especially common and abundant in the phyllosphere of trees in anthropogenic ecotopes under unfavorable ecological conditions, mainly in urban green plantations, in park and woodland park zones. In the Moscow agglomeration, it is a natural phenomenon which occurs periodically and is accompanied by considerable foliage damage in many plant species (Chekhonina and Kuznetsova, 2002; Belov, 2008; Ezhov, 2008). In Moscow urban green plantations, gall-forming mites of the family *Eriophyidae* occurring on birch, elm, willow, lime, rowan, and bird cherry tree are the most distinguished in the number of species, abundance, and distribution. Moreover, the gall-forming aphides of the family *Aphididae*, sawflies of the family *Tenthredinidae*, gallflies of the family *Cynipidae*, and gall midges of the family *Cecidomyiidae* are typically revealed in urban plantations (Gusev, 1984; Belov, 2008). Under unfavorable conditions of the Moscow agglomeration, the gall-forming activity of insects and mites has the one of the most negative impacts on trees.

Annually, galls are formed in great amounts on *Salix fragilis, Salix caprea, Quercus robur, Tilia cordata, Ulmus laevis,* and other trees. Tumors on leaves are characterized by increased concentration of simple sugars and lipids, partially, due to translocation of dissolved nutrients from one part of a vascular plant to another one and from the healthy leaves to galls (Motta, 2003; Raghav et al., 2007). It may be assumed that these proliferations of the plant internal tissues containing high concentrations of simple sugars represent specific habitat for endophytic yeasts, which together with some other fungi can be designated as the most copiotrophic representatives of the Fungi Kingdom (Chernov, 2013).

Endophytic development of yeasts is a widespread phenomenon (Isaeva et al., 2010; Doty, 2013). However, until now, galls formed by invertebrates on plant leaves were not distinguished as permanent endophytic habitats for yeasts. According to preliminary studies, specific yeast communities containing previously undescribed species can be formed in plant galls. Thus, a novel species of methanol-assimilating yeasts *Ogataea cecidiorum* from galls formed on willow was isolated (Glushakova et al., 2010).

Most of the previous studies on yeast are concerned with analysis of so-called "black galls" (black knot) formed by the fungus *Dibotryon morbosum* on branches of the trees of the families *Rosaceae*, *Salicaceae,* and others (Lachance, 1981; Hutchison et al., 1993, 1994). It is also known that yeasts of the genus *Protomyces* (*P. gravidus, P. lactucaedebilis,* and *P. mac-*

rosporus), as well as the species *Tilletiopsis pallescens* and *Taphrina vestergrenii*, caused damage to the leaves, inducing the gall formation (Mix, 1956; Tubaki, 1957; Valverde and Templeton, 1984; Rodrigues and Fonseca, 2003). The galls are known to be also formed by yeast fungi *Laurobasidium lauri* (on *Laurus azorica*) and *Ustilago maydis* (on maize) (Kurtzman et al., 2011). It should be noted that until now, the galls formed on leaves by invertebrates were not considered as permanent endophytic habitat for yeast fungi.

The goal of the present work was to analyze the abundance and species diversity of epiphytic yeasts in the phyllosphere of undamaged leaves and of endophytic yeasts in the galls formed on leaves of the trees *Salix fragilis, Salix caprea, Quercus robur, Tilia cordata,* and *Ulmus laevis* throughout the whole period of the gall ontogenesis.

MATERIALS AND METHODS

The subjects of the study were galls on the leaves of *Salix fragilis* and *S. caprea* (formed by sawflies of the genus *Pontania*), *Quercus robur* (formed by the gallfly *Diplolepis quercus-folii*), *Tilia cordata* and *Ulmus laevis* (formed by *Eriophyes* sp. mites) as well as undamaged leaves of these trees. Monitoring of yeast abundance and species diversity was carried out in dynamics from the gall formation to their degradation. The sampling was carried out for 2–3 times per month from May to October 2014 and then analyzed within 1–2 days. In total, 2600 samples were analyzed. The studies were carried out in Rublevo (west of Moscow), Karacharovo (east of Moscow), the Kuskovo woodland park (east of Moscow), and in the vicinity of the Lobnya railway station (Dubovaya Roshcha), Mytishchi region, Moscow oblast.

Abundance and species diversity of the yeast population were determined by plating. The samples of undamaged leaves (~1 g) were placed into tubes, suspended in sterile water in a ratio of 1 : 50, and stirred on a MultiReax vortex (Heidolph, Germany) for 15 min. The obtained suspensions were plated in triplicate onto agarized glucose–peptone–yeast extract medium containing the following (g/L): glucose, 20; peptone, 10; yeast extract, 5; agar, 10, supplemented with levomycetin (500 mg/L) to suppress bacterial growth. The plates were incubated at room temperature for 5–7 days; the grown colonies were divided into morphological types and enumerated. Pure cultures were isolated from each of the colony types.

Communities of endophytic yeasts were studied by conventional methods. The gall surface was treated as follows: 70% ethanol, 30 min; sodium hypochlorite (2%), 30 min; 70% ethanol, 30 s, and then washed in sterile distilled water for 10 min. After removing the integumentary tissues with a sterile scalpel, sections of the gall internal tissues were cut out, ground, and suspended in sterile water in a ratio of 1 : 10. The obtained suspensions were stirred on a vortex and plated in triplicate onto agarized glucose–peptone–yeast extract medium.

Identification of the yeast species was carried out by analysis of the nucleotide sequences of the D1/D2 domain of 26S (LSU) rDNA. Isolation of DNA and the polymerase chain reaction (PCR) were carried out according to the previously described methods (Glushakova and Kachalkin, 2017). The DNA sequencing was performed in the Syntol Company (Moscow) using the Big Dye Terminator V3.1 Cycle Sequencing Kit (Applied Biosystems, United States) with subsequent product analysis out on an Applied Biosystems 3130xl Genetic Analyzer. The NL4 primer (5'-GGT CCG TGT TTC AAG ACG G) was used for sequencing. Species identification was carried out using the GenBank NCBI (ncbi.nlm.nih.gov) and the MycoID (www.mycobank.org) databases.

RESULTS AND DISCUSSION

Yeast abundance in the galls varied during the whole period of the gall development until their complete decay. The minimum number of endophytic yeasts corresponded to the stages of the gall formation and decay (Fig. 1). The maximum yeast number was observed in mature galls and depended on the gall-forming agents. In the galls formed on willows *Salix fragilis* and *S. caprea* by sawflies of the genus *Pontania*, the yeast number was the maximum and in August was in some samples up to 2.5×10^4 CFU/g (Fig. 1a). Yeast abundance in the galls formed on oak by the gallfly *Diplolepis quercus-folii*, as well in the galls formed by insects on willows reached 2.2×10^4 CFU/g (Fig. 1b); in the mite-formed galls on the leaves of *Tilia cordata* and *Ulmus laevis,* the yeast number was an order of magnitude lower and reached in certain samples the maximum up to 4.5×10^3 and 2.3×10^3 CFU/g depending on the plant species (Fig. 1b).

The maximum yeast number in the galls on different plants was observed in summer, the period of active gall formation. This period occurred in June for mite-formed galls on lime and elm and in July–August for sawfly-formed galls on willow and gallfly-formed galls on oak (Fig. 1). In the galls formed on leaves of *S. fragilis, S. caprea,* and *Q. robur,* the number of endophytic yeasts was highest in the peak of the gall development and then sharply decreased. In the galls formed on leaves of *T. cordata* and *U. laevis,* the yeast number reached the maximum in June, remained constant until October, and then declined. A decrease in the number of endophytic yeasts was typical of all the studied galls during their transition to the stage of destruction and decay.

On the whole, the yeast number on leaves of all studied plants was characterized by a regular increase from spring to autumn. In autumn, the leaves entered

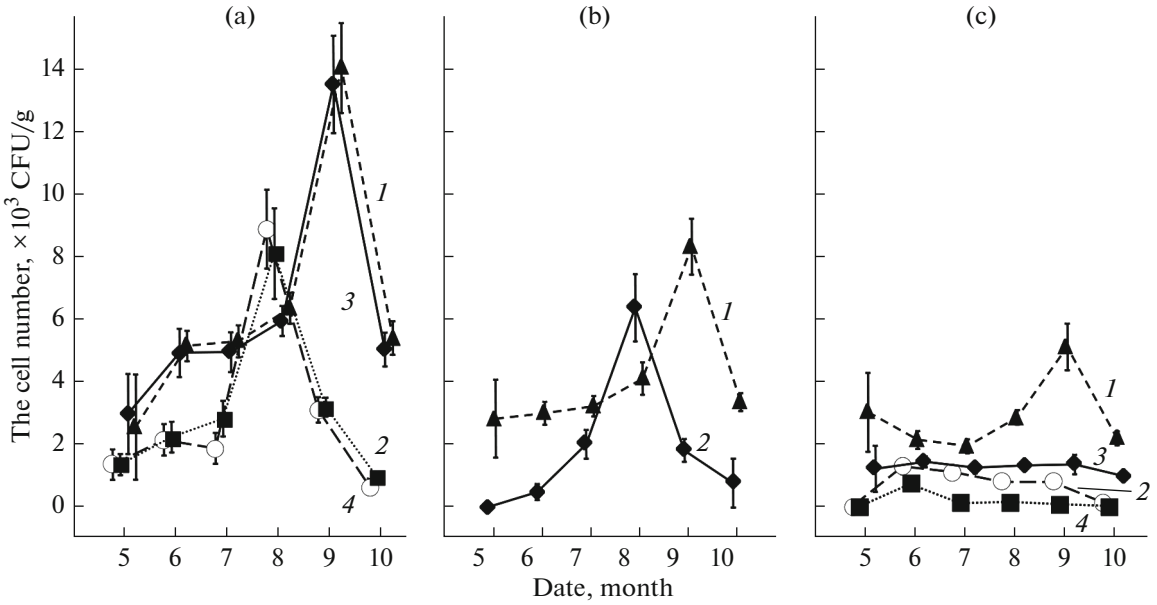

Fig. 1. Dynamics of the average monthly values of the total number of endophytic yeasts in the galls and of epiphytic yeasts on the leaves of the studied plants: (a) *Salix caprea* ((*1*), leaves, (*2*), galls) and *Salix fragilis* ((*3*), leaves, (*4*), galls); (b) *Quercus robur* ((*1*), leaves, (*2*), galls); (c) *Tilia cordata* ((*1*), leaves, (*2*), galls) and *Ulmus laevis* ((*3*), leaves, (*4*), galls).

into subsenile and senile stages, in which the cuticle integrity was disrupted and concentrations of simple sugars available to yeast growth increased. This event appeared to be the main reason for an increase in the number of yeasts in the phyllosphere during the autumn period (Glushakova and Chernov, 2007).

Species diversity of the yeast population. In total, 14 yeast species were isolated from the studied substrates; half of them were represented by ascomycetes (table). The structure of the yeast communities formed in galls of different origin varied considerably. A share of the ascomycetous yeasts in the insect-formed galls on the leaves of willow and oak reached 50–70%. Basidiomycetous yeasts predominated both in the galls formed by mites on lime and elm and on the leaves of all the studied plants, whereas ascomycetes comprised only 2–6%.

In the yeast community of the phyllosphere of all the studied trees, typical epiphytic yeasts of the genera *Rhodotorula, Filobasidium,* and *Cryptococcus* s. l. prevailed. The dominant species in all samples was *Rhodotorula mucilaginosa;* this eurybiontic yeast species is widespread in different geographic regions in both natural and anthropogenic substrates, e.g., soils, plants, plant residues, natural water, food products, and clinical samples. In the Moscow region, *Rh. mucilaginosa* is the most commonplace species, which is found in various substrates; it is especially abundant in the phyllosphere of all biogeocenoses. This species reached the maximum in the community in summer due to its high tolerance to insolation and drying (Glushakova et al., 2015).

The endophytic yeast communities in mite-formed galls on leaves of *T. cordata* and *U. laevis* were not different between each other and were identical to the epiphytic yeast complexes of the phyllosphere. The small mite-formed galls (1.5–5.0 mm) were probably unable to accumulate a sufficient amount of simple sugars to provide the endophytic growth of ascomycetous yeast species. On the contrary, the endophytic yeast communities from relatively large **galls formed by insects** differed considerably in yeast species diversity from the epiphytic communities. For instance, the galls formed on leaves of both willow species were similar; they were characterized by the highest diversity of ascomycetous yeast species. The following species of ascomycetous yeasts were isolated only from the galls formed on willow leaves: *Candida fructus* (revealed in juicy fruits before), *Metschnikowia henanensis* (isolated from decayed wood in China and described in 2013) (Hui et al., 2013), and *Pichia fermentans* (occurred in very diverse substrates, which are often associated with humans and animals; it was isolated from food products). Strains of the ascomycetous yeast species *Candida railenensis* were abundant in the galls on *Q. robur* leaves; this species was shown to prevail in the endophytic yeast community of acorns (Isaeva et al., 2009). Strains of this species were isolated from various natural substrates, such as decaying wood, *Quercus rubra* exudate, fruit surface, etc. Moreover, this species was repeatedly isolated from black knot formed by the fungus *Dibotryon morbosum* on *Prunus avium* and *P. virginiana* in Canada. The basidiomycetous yeast species *Dioszegia changbaiensis* occurred only in the galls formed on oak leaves; which

The average relative abundance (%) of endophytic yeasts in the galls and of epiphytic yeasts in the phyllosphere

Species	*Salix fragilis* galls	*Salix caprea* galls	*Quercus robur* galls	*Tilia cordata* galls	*Ulmus laevis* galls	Leaves
Candida fructus	16.50	17.78	–	–	–	–
Candida railenensis	9.21	6.90	15.53	0.01	–	0.01
Dioszegia changbaiensis	–	–	11.76	–	–	0.04
Dothiora cannabinae	–	–	36.70	–	–	0.01
Filobasidium magnum	5.61	3.99	3.55	16.75	24.17	14.46
Filobasidium wieringae	6.08	3.98	5.04	5.14	12.60	4.01
Hanseniaspora uvarum	9.45	9.29	–	5.17	1.21	0.51
Metschnikowia henanensis	8.77	9.23	–	–	–	–
Metschnikowia pulcherrima	12.55	12.78	–	1.02	0.71	1.13
Papiliotrema flavescens	1.62	0.91	–	8.40	10.87	6.29
Pichia fermentans	15.30	12.70	–	–	–	–
Rhodotorula mucilaginosa	14.91	22.43	27.23	59.24	45.26	68.61
Vishniacozyma carnescens	–	0.02	–	0.14	0.05	2.07
Vishniacozyma victoriae	–	–	0.20	4.12	5.13	2.86
Ascomycetes/Basidiomycetes	71.8/28.2	68.7/31.3	52.2/47.8	6.2/93.8	1.9/98.1	1.7/98.3

"–'', species was not found.

was isolated before from dry leaves of *Brachybotrys paridiformis* in China (Wang et al., 2003). Until now, no other isolates of this species are known. The species *Dothiora cannabinae* was isolated only from the galls on oak leaves. We have earlier revealed this species in Moscow region on the surface of fruits of *Malus domestica* and *Pyrus communis* (Glushakova and Kachalkin, 2017). The yeasts belonging to the group of opportunistic species, which usually occurred in the plant yeast communities of anthropogenic biotopes

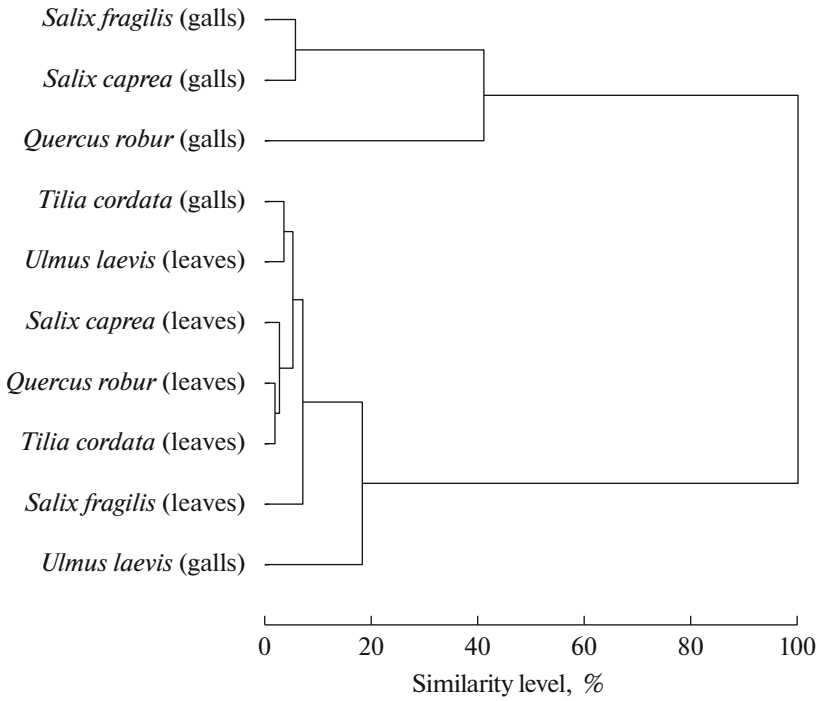

Fig. 2. Dendrogram of resemblance (Euclidean distance was determined by the Ward method) of the yeast communities of the galls and leaves of the studied plants.

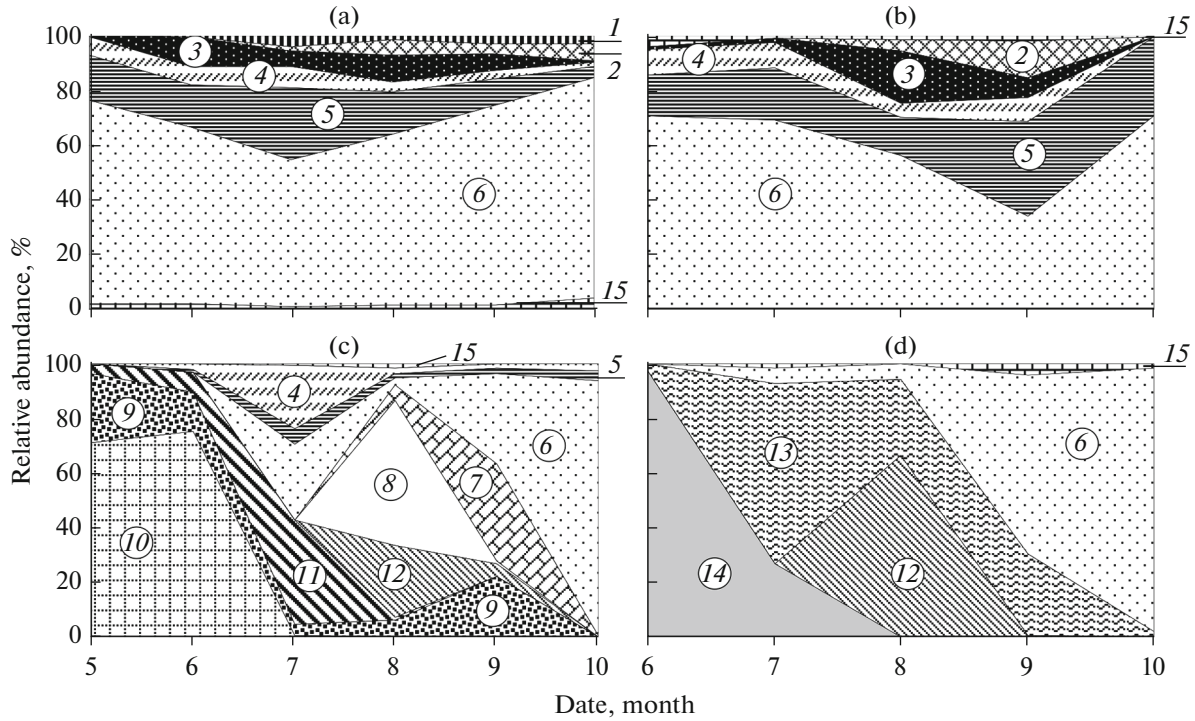

Fig. 3. Dynamics of the average monthly values of relative abundance of the yeast species on leaves (a) in the galls formed by *Eriophyes* mites (b) in the galls formed by *Pontania* sawflies (c); and in the galls formed by gallfly *Diplolepis quercus-folii* (d). Yeast species: *Vishniacozyma carnescens* (*1*), *Vishniacozyma victoriae* (*2*), *Papiliotrema flavescens* (*3*), *Filobasidium wieringae* (*4*), *Filobasidium magnum* (*5*), *Rhodotorula mucilaginosa* (*6*), *Hanseniaspora uvarum* (*7*), *Pichia fermentans* (*8*), *Metschnikowia pulcherrima* (*9*), *Candida fructus* (*10*), *Metschnikowia henanensis* (*11*), *Candida railenensis* (*12*), *Dothiora cannabinae* (*13*), *Dioszegia changbaiensis* (*14*), and others (*15*).

(pollen of wind-pollinated trees and juicy fruits), were not found in tree galls and phyllosphere, although the studied plants grew in a large megalopolis.

The similarity and difference between all the studied substrates were demonstrated by their clusterization on the basis of species diversity of the yeast communities; in particular, endophytic populations from the galls formed on different willow species were characterized by a high level of similarity (Fig. 2). The yeast populations of the mite-formed galls on lime and elm were also similar and resembled the epiphytic population inhabiting the leaves of the studied plants. The epiphytic yeast communities formed on leaves of different plant species were characterized by low variability.

Dynamics of species diversity of the yeast communities. It had been earlier shown that different yeast species grown on different plant substrates were characterized by different types of seasonal dynamics of their relative abundance. Therefore, combination of the yeast species dynamics together with ontogenetic cycles of plants made the pattern of the yeast population dynamics, which was unique for each plant species or the type of plant substrate (Chernov, 2013). Plant substrates similar in ontogenetic cycles and physiological features are characterized by similar dynamics of the relative abundance of yeast species. However, investigation of dynamics of the number and species diversity of yeasts in the studied samples suggests the key role of the gall-forming agents.

Phyllosphere of all the studied trees during the whole period of leaf growth contained the same yeast species with predominance of basidiomycetous yeasts *Filobasidium magnum, F. wieringae, Papiliotrema flavescens, Rh. mucilaginosa,* and *Vishniacozyma victoriae*, as well as an insignificant number of ascomycetous species, such as *Metschnikowia pulcherrima* and *Hanseniaspora uvarum*. The relative abundance of *Rh. mucilaginosa* in the epiphytic community increased from May to June, declined in July, and steadily increased in autumn until the end of sampling (Fig. 3a). The relative abundance of *F. magnum,* on the contrary, increased in July. Other species were characterized by insignificant variation in their relative abundance in the tree phyllosphere during the sampling period.

Mite-formed galls on the leaves of lime and elm did not differ from each other in the species diversity of the yeast populations (Fig. 2); moreover, they were characterized by similar dynamics of endophytic yeasts (Fig. 3b). Dynamics of relative abundance of endophytic yeasts in the **sawfly-formed galls** on the leaves of

S. fragilis and *S. caprea* were similar. The species *Rh. mucilaginosa* occurred in willow galls during the whole period of ontogenesis; its share both in the galls and in the phyllosphere increased in autumn (Fig. 3c). Ascomycetous yeast species were constantly present in the willow galls. Different species of ascomycetes were characterized by the maximum relative abundance in different stages of the gall formation. Thus, during the initial stage (in June), *C. fructus* and *M. pulcherrima* showed the maximum relative abundance; then an increase in the share of *M. henanensis* and finally of *C. railenensis* and *P. fermentans* was observed. At the final stage of the gall formation and destruction, the abundance of *M. pulcherrima* and *H. uvarum* was enhanced again. An increase in the relative abundance of ascomycetous species *M. pulcherrima* and *H. uvarum* at the final stage of ontogenesis was typical of endophytic communities inhabiting fruits (Glushakova and Chernov, 2009; Glushakova and Kachalkin, 2017). In the galls formed on oak leaves, as well as in all studied substrates, the share of *Rh. mucilaginosa* increased in autumn (Fig. 3d). At the initial stage of gall formation (May–June), the oak galls contained a high share of basidiomycetous yeast *D. changbaiensis;* in the period of active gall development (July–August), the relative abundance of ascomycetous yeast *C. railenensis* was increased. Throughout the whole period of gall formation and development on oak leaves, the presence of *Dothiora cannabinae* was revealed with the maximum level in summer.

It is obvious that development of the endophytic yeast population in the galls is mainly determined by the gall-forming agents, which penetrate into internal tissues of leaves, infect the plant, and initiate the process of gall formation. At the initial stages of gall formation, species diversity of endophytic yeasts is essentially different from that of the epiphytic community, especially in the insect-formed galls (Fig. 3). During the subsequent gall development, when the concentration of simple sugars increased, the yeast number and diversity in the galls inceased, probably due to repeated penetration of microorganisms inside the galls, e.g., with the help of some inquiline species of invertebrates, as well as because of growth of the previously inactive yeast species. At this stage, we revealed ascomycetes *C. railenensis, H. uvarum,* and *P. fermentans*, which were not detected during the initial stages of gall formation. The final stage of gall development, beginning at the leaf dying, was characterized by a sharp decrease in the yeast number and domination of the typical epiphytic species *Rh. mucilaginosa* in the endophytic community.

It has been earlier shown that yeasts form associations with a number of invertebrates, especially with phytophages (Terenina and Chernov, 2001). The distinguishing feature of such associations is predominance of widespread ascomycetous yeasts, for which invertebrates create favorable habitats by excretion of sugars, readily utilizable by yeasts. On the other hand, endophytic yeasts were shown to have a direct positive effect on plants due to synthesis of various biologically active metabolites and phytohormones, including plant growth regulators (Streletskii et al., 2016). Thus, our results indicate that gall formation may be considered not only as a bidirectional pathological process of the interaction between plants and invertebrates, but also as a process in which the endophytic microbial population of the galls, including yeasts, plays an important role.

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