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ARTICLE

Histological study of quercus galls of *Neuroterus quercusbaccarum* (Linnaeus, 1758) (Hymenoptera: Cynipidae)

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ABSTRACT The aim of this study is to reveal the histological structure of galls induced by *Neuroterus quercusbaccarum* and to identify accumulated secondary metabolism products and storage materials in gall tissue by histochemical methods. The galls induced by *N. quercusbaccarum* showed a concentrical layer tissue structure under light microsope. Directly next to the chamber, a protein and lipid containing nutritive tissue can be found, which is covered by sclerenchyma layer consisted of two large cell plates in the lenticular galls of the unisexual generation, while the bisexual generation induced grape shaped galls lack lignified sheaths. Our results confirm previous findings. The outer layer of the gall is the voluminous parenchymatic cortex with a supplying vascular network and covered epidermis. We proved with histological methods, that the galls really contain accumulated nutritives -proteins, lipids and starch- in large quantities. The concentration of these nutrients from the chamber toward the border of inner-gall, show a decreasing gradient in the case of proteins and lipids, and an increasing gradient for starch. We present the differences and similarities in histological structure among galls induced by two generations of *N. quercusbaccarum* and the well studied *Biorrhiza pallida.*

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KEY WORDS

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The finest way of manipulation of nutritive plants is done by gall-generating herbivorous insects. These force their nutritive plants for abnormal growing and on this, the plant forms a special formation, so-called gall. Galls have been defined in many ways, but most commonly a gall is: an abnormal cell proliferation or cell size growing in the plant tissue. It is caused by the activity of some sort of living organism to use it as food supply or hiding place. When we define it, it is important that these organisms induce the growth of the gall but they don't create it (Csóka 1997). Formation of cynipid galls is a complex interaction between cynipid gall wasps and host plants (most frequently *Quercus* and *Rosa* species). To understand this interaction we need to study the ecology of gall-inducing insects (Szabó 1992; LeBlanc and Lacroix 2001), the structure and development of the galls and examine the cytological, biochemical and physiological properties of gall tissues (Shorthouse and Rohfritsch 1992; LeBlanc and Lacroix 2001; Harper et al. 2004).

In the case of closed galls of the *Cynipidae* species we discriminate one- and many-chambered galls depending on the number of larvae living in them. Regarding the two species we studied, *Neuroterus quercusbaccarum* prefers the one-chambered galls, while the common *Quercus* species herbivore *Biorrhiza pallida* generates the typical many-chambered galls (Shorthouse and Rohfritsch 1992; Harper et al. 2004). The formation and structure of leaf galls of unisexual generation of *N. quercusbaccarum* is well studied (Rohfritsch 1992). The bisexual generation induces nutrient plants to form grape-shaped leaf or inflorescence galls. We have less information about the formation and structure of these galls (Harper et al. 2004).

It is known that in gall development there are four basic stages: initiation, growth and differentiation, maturation and at last dehiscence (Rohfritsch 1992). It was revealed by the example of *Diplolepis rosae* that in the vicinity of the eggs it is needed to have parenchyma cells which are able to divide, and these generate a callus (called plastem) which will form the chamber by the destruction of cells. The other condition is the presence of a vein from the cells of which a „vascular cambium" develops into the tissue of the plastem and supplies nutrition to the gall by differentiating to vascular tissue elements (Rohfritsch 1992).

The most conspicuous structural characteristic of the differentiated galls of *Cynipidae* is the presence of concentric layers made of different cells around the larval chamber. The nutrient tissue and the lignified sheath constitute the "inner gall" and the "outer gall" is formed by the parenchymatic

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cortical tissue and the epidermis. The size of "outer gall" can vary between taxons (Bronner 1985).

It is known that in the cells surrounding the larval chamber, active protein synthesis takes place and they become nutritive cells which are situated either in patches around the larval chamber or in one region. In the early stage of development, the nutrient tissue is not well structured enough. As the appetite of the larva increases, the nutrient tissue is getting more homogeneous and at the end it surrounds the whole larval chamber. The multiplying cells situated under the nutritive cells (cambial zone) generate radial parenchyma cell layers to grow the gall and renew nutritive layers. By the end of the larval state, the cambial zone and nutritive tissue disappear, only a few residuals of cells border the sclerenchyma sheath (Bronner 1985; Rey 1992; Rohfritsch 1992).

In the outer gall radial vascular tissue grows from the peripheral vascular tissue to the cambial area and proceeds toward the chamber. The cambium laces parenchyma cells, which in the beginning, contain starch too. Later mitosis ends and due to cell differentiating, peripheral cells lignify. Sclerenchyma cell layers often differentiate next to the vascular tissue, causing concentric layers in the gall. The mature outer part of the gall (cortex) is made of well-differentiated peripheral vascular tissue, parenchyma and epidermis. The peripheral vascular tissue of the cortex establishes the connection between the host plant and the gall. The mature cortex often stores water or air and also may contain tannin and lignin. Accessories formed on the outer side of the gall (spines, glandular hairs, etc.) probably play a role in defense against parasites (Askew 1984).

The primary goal of this study is tissue examination of galls induced by *Neuroterus quercusbaccarum* and to examine how the original structure changes during gall generation (structural changes of tissues), furthermore the detection of accumulating secondary metabolism products and stored nutrients within gall tissue with histochemical methods. We show the histological structure of galls generated by *N. quercusbaccarum* with the help of models found in literature (*Diplolepis rosae,* Rohfritsch 1992*)*, confirmed by our own experimental results. We will discuss about the bud gall of *Biorrhiza pallida*, another well studied cynipid model (Rey 1992), especially to emphasize the differences.

Materials and Methods

Collecting site and time of plant samples

The galls developed on leaves and catkins of *Quercus robur* induced by the bisexual generation of *Neuroterus quercusbaccarum* were collected in the Botanical Garden of University of Debrecen several times between 04-25.05.2006., 10-25.05.2007. and 10-15.04.2011. We examined the galls induced by the unisexual generation of *Neuroterus quercusbaccarum* on *Quercus robur* leaves collected in the Botanical Garden of the University of Debrecen. Date of collection: 07.09.2007.

The bud galls of the unisexual generation of *Biorrhiza pallida* were collected from nutritive plant *Quercus pubescens* from the "Kőtenger" area of Balaton-highland on 06.05.2006. and in the Botanical Garden of the University of Debrecen on 03.05.2007.

Preparing plant materials

We collected healthy leaves and galls for examination. For the histochemical study, we created preparations from fresh plant matter manually, and with the help of a freezing accessory and microtome (Leica Jung Histoslide 2000 microtome).

We examined the preparations with Olympus BX50 and Olympus Provis AX70/A light microscopes, the microscopic photos were taken by OLYMPUS Camedia 4040 and DIGITAL SP350 cameras.

With microchemical or histochemical methods, we could create chemical reactions which cause differences in some details of the preparation (e. g. in colour). From the quality of the difference, we could draw conclusions from the chemical nature of the cell or tissue structures and detect special products of cells (Sárkány and Szalai 1964).

We used the following histochemical methods in order to

identify proteins: after treatment with potassium-iodide solution, the protein containing cell organelles (aleurone grains) got different shadings of yellow and brown (Sárkány and Szalai 1964, Wanner 2004),

identify starch: potassium-iodide solution caused a violet-blue or bluish-black coloration of starch grains (Sárkány and Szalai 1964, Wanner 2004),

identify tanninic acid: the tanninic acid containing cytoplasm became greyish-blue to 3% ferrichloride solution (Sárkány and Szalai 1964),

identify fatty oil and volatile oil drops: these drops became brick-red to Sudan III treatment, furthermore it coloured the suberinic cell walls too (Mihalik et al. 1999).

We used the method of colouring with congo red to stain the cytoplasm and the cellulose cell wall (Mihalik et al. 1999).

Results

The histological properties of the grape-shaped leaf galls generated by the bisexual generation of *Neuroterus quercusbaccarum*

The unisexual generation of *Neuroterus quercusbaccarum* lays its eggs into the flower-buds of the male catkin or near the still differentiating vein of the developing leaf, ensuring the fast cell multiplying generating a one chambered gall. The galls we studied were generated in leaves (Figs. 1.B-D) and catkin (Figs. 1.F-H) of *Quercus robur.*

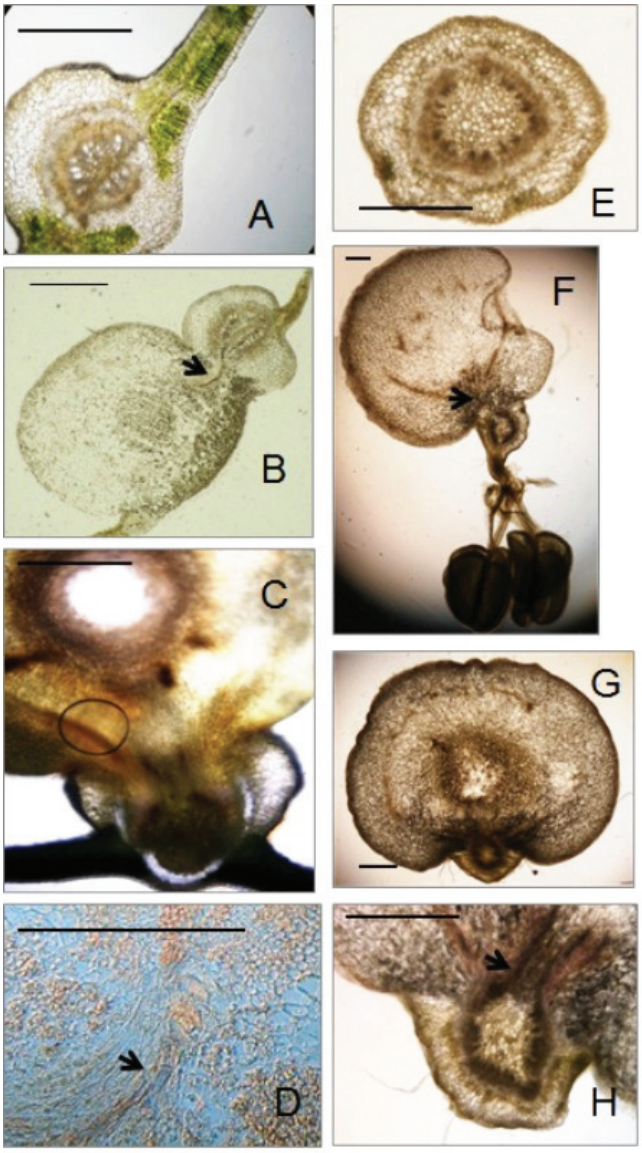

Figure 1. Formation of leaf and flower galls generated by the bisexual generation of *Neuroterus quercusbaccarum* on *Quercus robur*. Cross section of untouched leaf (A) and inflorescence axis (E) of *Quercus robur.* Gall generation next to (B) and above (C) the vein of leaf. Gall generating on the inflorescence axis opposite to flower (F) or replacing flower (G). Differentiation of vascular elements to ensure the transport between the vascular system of leaf/ inflorescence axis and the gall (D and H, arrows). Bars: 400 μm.

The untouched leaves of *Quercus robur* show a typical dorsiventral structure, the chloroplast (chlorophyll) content of the chlorenchyma is very high. The epidermis cells are large, covered by a thick cuticle, but no epidermal accessories can be seen (Fig. 1A). The extended vascular tissue (xylem and phloem) of the main vein is braced by sclerenchyma, and under the epidermis, collenchyma too. The vascular tissue of xylem is made of two direction-differentiated tracheal rows, which refers to secondary thickening and presumes the presence of meristema (cambium). However the vein grid of the leaves is usually built of collateral-closed bundles.

Our leaf samples showed two types of gall-generation (Figs. 1B and C). In the first type, the gall generated directly next to the main vein (Fig. 1B), while in the second type, above the vein (Fig. 1C). Both types have the two conditions of gall-generation: first, the presence of multiplying parenchyma cells near the eggs, in this case the clorenchyma of the leaf, second, the presence of a vein, from which a "vascular cambium" develops into the tissue of plastem (Rohfritsch 1992), which ensures the nutrition of the gall by differentiating into vascular bundles (Figs. 1.B and D, black arrows).

In the parenchymatous tissue of the axis of male catkin there is a good development of vascular system with many rows of tracheal elements, which seemed to grow by new elements produced by the ring-formed cambium (Fig. 1E). The vascular system of catkin axis is in connection with the bundles of flower peduncles (Fig. 1F). This connection can form as well, when a gall replaces completely a flower (Fig. 1G and H, black arrow) or when it develops opposite to a flower (Fig. 1F, black arrow).

In most cynipid galls it is possible to find three kinds of tissues surrounding the larval chamber; a nutritive tissue lining the larval chamber, a sheath of lignified cells, and a parenchymatous zone (or cortex). This structure could be seen at the bud galls induced by the bisexual generation of *Biorrhiza pallida* (Rey 1992). In the case of this type of gall, the parenchyma grows significantly and makes the gall soft and spongy. The gall becomes spherical, will turn from red to white. The nutritive tissue and the starch containing cell layers (nutritive parenchyma) around the larval chamber are closed by sclerenchyma cells (Fig. 2E), and this inner-gall is surrounded by the above mentioned spongy parenchyma. However, we did not find the layer of sclerenchyma cells in the leaf galls and flower galls generated by the bisexual generation of *Neuroterus quercusbaccarum* (Figures 2A-D). The layer of lignified cells (sclerenchyma) is missing from both the still multiplying (Figs. 2A and C) and the differentiated galls (Figs. 2B and D). The chamber is surrounded only by a parenchymatic nutritive tissue. The outer- and inner-galls can be still distinguished, because differentiation of a cambial zone is characteristic in the growing gall to ensure hyperplasia (Figs 2A and B., marked by red arrows).

According to cytological examinations, in the grape shaped gall of the bisexual generation of *N. quercusbaccarum,* the cells between the larva chamber and the gall cortex showed similar cytological features (Rohfritsch 1992). This seems to be true to the young leaf galls (Fig. 2A.) and the ones developed in the catkin inflorescence (Fig. 2C). However, in galls from the end of May, the inner gall is divided into at least 2 different concentric layers. It is easy to distinguish the lighter part of nutritive cells around the chamber which

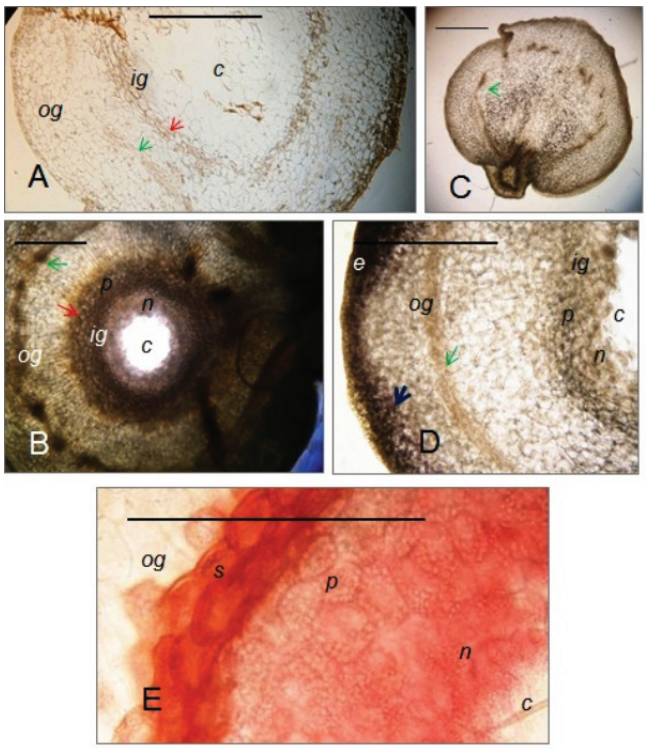

Figure 2. The growth and maturation stages of cynipid gall formation induced by the bisexual generations of *Neuroterus quercusbaccarum* (A-D) and *Biorrhiza pallida* (E). Formation of leaf gall induced by *N. quercusbaccarum* at the beginning of May (A) shows that the chamber (*c*), inner gall (*ig*) and outer gall (*og*) start separating. Later, in the middle of May (B), within the epidermis and the wide parenchymatic cortex (*og*) in the inner gall (*ig*) around the chamber (*c*) the layers of nutritive parenchyma cells (*p*) and of inner nutritive cells (*n*) are differentiated. In differentiated galls the inner and outer galls are separated (A and B, red arrow) by brownish cells with thin cell-walls instead of sclerenchymatised cells. In the cortex, the differentiating tracheal elements form a new transport system (A and B, green arrow). Galls on the catkin-axes induced by the bisexual generation of *N. quercusbaccarum* show the same stages of formation and layers of differentiated cells. They were collected at the end of April (C) and at the beginning of May (D) and have the concentric layers of epidermis (*e*), cortical parenchyma (*og*) with starch grains in the outer part (blue arrow) and with transport network (green arrow), the layers of nutritive parenchyma cells (*p*) and the inner nutritive cells (*n*) of the inner gall (*ig*) around the chamber (*c*). The gall with multilocular larval chambers induced by bisexual generation of *Biorrhiza pallida* in the flower-bud of *Quercus pubescens* (E) has good detectable layers of different cells around the chambers: outer gall (*og*), sclerenchyma (*s*), parenchyma cells with starch (*p*), nutritive tissue (*n*), chamber (*c*). The roughly thickened and sclerenchymatised cell walls became dark-red stained by congo red solution. Bars: 400 μm.

is covered by a zone of darker cells - this can be the layer of starch containing cells – followed by radially elongated parenchyma cell layers belonging to the outer-gall/cortex. The parenchymatic wide cortex is divided into two equal parts by the layer of brownish cells (Fig. 2A-D, green arrows). This could be the peripheral differentiating vascular network, because they are in connection with the vascular bundles of the leaf and catkin axis (Figs. 2B and C). In the spherical gall of another cynipid, *Liposthenes glechomae* similar vascular bundles were detected by Bronner (1992).

With the aid of histochemical methods, we found that the cells next to the chamber store lipids in higher quantities (Fig. 3A), but large drops of lipids can be found in the parenchyma cells of the inflorescence galls creating plastem as well (Fig. 3B). Potassium-iodide staining shows proteins in the cells around the chamber and starch in the cells of outer layers (Fig. 3C). We experienced that during the formation of galls (leaf- and inflorescence-galls as well) starch grains firstly appear in the cells under the epidermis, where the normal subepidermal cells are rich in chloroplasts (Fig. 3D). The histochemical staining of fresh preparations showed that the galls really do accumulate spare nutritives: lipids, proteins and carbohydrates equally.

According to literature, the galls have a high concentration of starch, which depletes toward the larval chamber, the typical nutritive tissue does not contain starch. Lipid gradient shows the opposite tendency. The lipid content depletes in all *Cynipidae* galls toward the periphery of the nutritive tissue, while the nutritive cells around the larva contain many lipid drops (Bronner 1977). This observation was affirmed by the preparations of galls induced by the bisexual generations of *Neuroterus quercusbaccarum* (Figs. 2B, D and Figs. 3A-D) and *Biorrhiza pallida* (Fig. 2E, further data not shown). The lipid drops are the mixtures of unsaturated triglycerides and oil bodies and are not spherosomes. While the larva is alive, there is no starch in the inner layers of the nutritive tissue, but after the larva dies, starch soon appears and the lipids form large drops (Bronner 1980).

It can be traced in older, mature galls, that the nutritive tissue of the chamber is getting used up during the larva development (Figs. 3E and G) and the wall of parenchymatic cells thicken unevenly around the chamber (Figs. 3E-H). But from the chamber towards the epidermis the walls of parenchymatic cells stay thinner. The wall of the epidermic cells are also thin, there can be groups of cells accumulating anthocyanins among them, which make the surface of the gall spotted (Fig. 3F).

Properties of the disk shaped gall induced by the unisexual generation of *Neuroterus quercusbaccarum*

The stages of the development and the histological structure of lenticular galls caused by the unisexual generation of *N. quercusbaccarum* is well studied (Rohfritsch 1992). The larval chamber develops near a vein between the palisade and the spongy clorenchyma of the dorsiventral leaf. In the differentiated lenticular gall around the chamber, narrow nutritive tissue and parenchyma covered by sclerenchyma layers are characteristic (Rohfritsch 1992).

We compared our preparations to the study about the for-

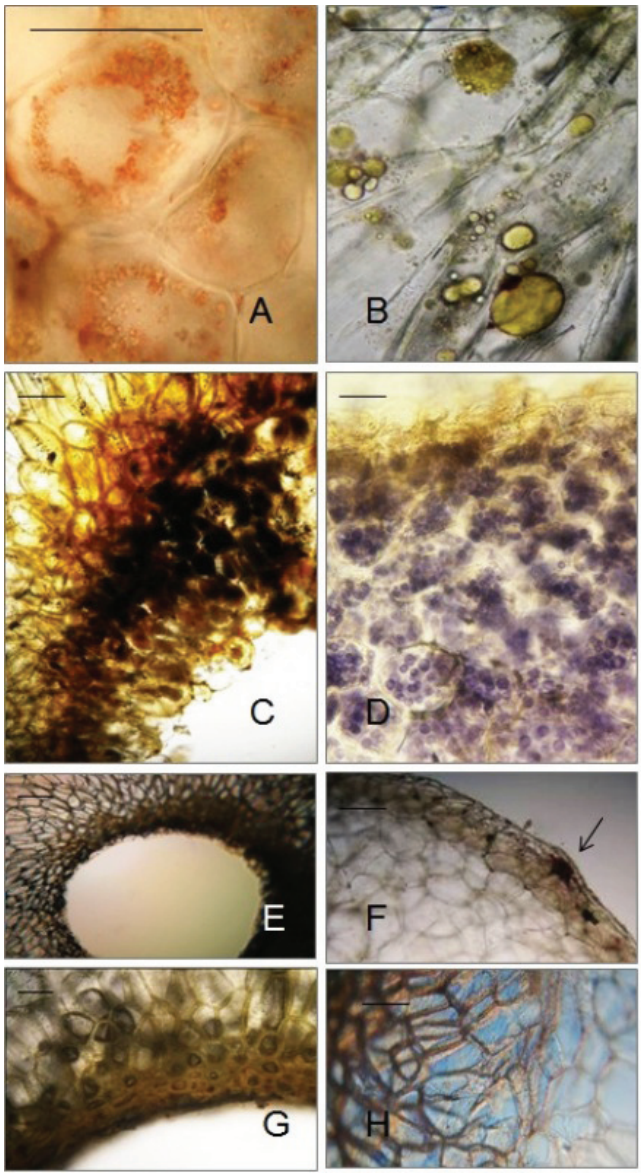

Figure 3. Differentiation- and accumulation processes in the galls on leaves (A, C, E, G) and on catkin-axes (B, D, F, H) induced by the bisexual generations of *N. quercusbaccarum.* Cross sections coloured by potassium iodide (C, D, G) and Sudan III. solutions (A), the other ones are native preparations. Lipid drops in the cells around the chamber coloured red by Sudan III (A) in a leaf-gall, and the large drops of lipids in parenchyma cells of the inflorescence-galls creating a plastem (B, uncoloured preparation). Cells around the larval chamber in reaction with potassium-iodide (C): the protein bodies are stained yellow, the starch grains dark-purple. We experienced that starch firstly appears in the cells under the epidermis in inflorescence galls (D). In the matured galls the cells around the larval chamber are empty (E and G) and the galls consist mainly of parenchyma cells with reticulate secondary cell walls. The walls are less thickened from inner gall (E and G) toward the periphery of the gall (H and F). The epidermis cells on the gall surface contain anthocyanins (F, arrow). Bars: 20 μm.

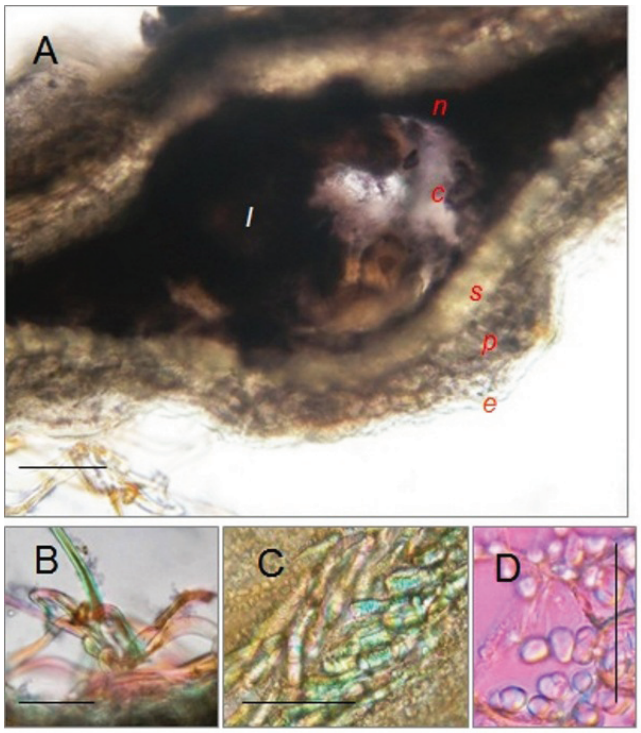

Figure 4. Disk shaped/lenticular leaf gall induced by the unisexual generation of *Neuroterus quercusbaccarum*. A: Our preparation shows a mature gall on the leaf: larva (*l*), chamber (*c*), nutritive tissue (*n*), sclerenchyma (*s*), parenchyma (*p*), epidermis (*e*). It may be more than 7 weeks after oviposition. Cross section made in the middle of the gall and coloured by $FeCl_3$-solution, the dark colour shows the high tanninic acid content. Bar: 300 μm. B: Typical stress-response of the host-plant is the abnormal hair accessory on the gall surface. C: Differentiation of sclerenchyma cells around the chamber in polarized light. D: Chloroplasts turned into starch grains in the chlorenchyma of the host-leaf, examined in polarized light. Bars: 30 μm.

mation of this gall by Rohfritsch (1992).We concluded that the development of galls we collected show the mature state, before falling (Figs. 4A-D). *Quercus* species are very rich in tannins and they can be detected with histochemical methods around the chamber in galls induced by *N. quercusbaccarum* (Fig. 4A) and *B. pallida* (data not shown) as well. On the surface of lenticular gall, abnormal hairs appeared (Fig. 4B), in the middle of leaf mesophyll cells showing sclerification could be seen (Fig. 4C) and starch grains instead of chloroplasts were detected (Fig. 4D).

Discussion

From the four basic stages of gall development we focused on the growth with differentiation and maturation of cynipid galls. The best examples of prosoplasmic galls are those induced by cecidomyiids and cynipids, because these well organized and differentiated galls are the results of defensive reactions of host plants and specific adaptations to the requirements of the insects (Rohfritsch 1992). The "oak apple" a multilocular, spongy, spring gall formed on buds of *Quercus pubescens* by the bisexual generation of *Biorrhiza pallida*

was used as reference, being perhaps the best known cynipid model (Rey 1992; Harper et al. 2004) to compare the galls of the two generations of *Neuroterus quercusbaccarum.* The most prominent structural characteristic of cynipid galls is the presence of concentric layers of differentiated cells around the larval chamber (nutrient cells, nutrient parenchyma and sclerenchyma), that can be shown on our preparation from gall of bisexual generation of *B. pallida* (Fig. 2E).

The bisexual generation of *N. quercusbaccarum* develops in the spherical, monolocular, spring gall, called "currant gall" induced on *Quercus* leaf and in male catkin (Figs.1A-H. and Figs. 2A-D). The lenticular autumn leaf galls of the unisexual generation of *N. quercusbaccarum* are also developed near veins of *Quercus* leaves. Both have nutritive tissue and nutritive parenchyma around the larval chamber, but the parenchyma of the lenticular gall is much thinner (Figs. 2B, D and Fig. 4A). The spherical galls of *N. quercusbaccarum,* similarly to the oak apple of *B. pallida,* develop an extended callus-like parenchymatic tissue via realignment of the cells of clorenchyma tissue. In the growing plastem, chloroplasts transform into amyloplasts, and a vascular cambium produces tracheal elements for a vascular network (Figs. 1, 2A-D, Fig. 3D).

The differentiated currant galls show the concentric layered histological structure of inner-gall, which are mostly layers of lipid-, protein- and starch accumulating cells (Figs. 2.B-E, Figs. 3A-C, Figs.4A and D). Harper et al. (2004) investigated the cytological and biochemical background of formation of cynipid galls. Among the inner-gall proteins the putative carboxyl carrier protein, which is involved in triacylglycerol lipid synthesis gave a rich source of energy in the inner-gall cells, revealed differential expression throughout development (Harper et al. 2004). They claimed that the spherical galls of *B. pallida, N. quercusbaccarum* and *Cynips quercusfolii*s have the same patterns of development, including sclerenchyma layers. However we found that in the spherical galls induced in *Quercus* leaf and in male catkin of *N. quercusbaccarum* these sclerenchyma layers do not differentiate. In the young gall only a row of small parenchymatic cells marks the border between the differentiating inner- and outer-gall (Fig. 2A, red row), maybe it is a cambial zone characteristic on several cynipid galls (Rey 1992). We can read that in case of the galls with no sclerenchyma, a layer of tannin containing cells can appear (Rohfritsch 1992). Synthesis of tannins is general in *Quercus* species and we can detect them in a wide stripe round the chamber in galls induced by both generations of *N. quercusbaccarum* (Fig. 4A) and *B. pallida* (data not shown) as well. We believe that our results are in good agreement with the notice of Rohfritsch (1992) about the missing of a lignified sheath in the grape shaped gall of the bisexual generation of *N. quercusbaccarum.* The cambial zone appearing near larval chamber organizes the compensation of the nutritive parenchyma and nutritive cells. We proved by different histochemical methods that the galls really contain nutriments: proteins, lipids and starch in large quantities. The concentration of lipids and proteins shows a decreasing gradient toward the periphery of the gall, while the concentration of starch shows an increasing gradient from the chamber to the periphery (Figs. 3A-D). The results of histological studies of these galls and the histological identifying of accumulated nutrition and secondary tannins altogether were compatible with the common statements about *Cynipidae* galls (Bronner 1977). In differentiated galls around the inner-gall an extended, spongy tissue of large parenchyma cells with vascular network is the characteristic outer-gall structure (Figs. 2B-D). The vascular elements that can be found in the gall are either the remains of the original vascular bundles or products of the cambium generated during gall formation and are essential for gall development. We detected typical plant stress responses during the gall formation induced by wasps (Figs. 3F and 4.A-C). We confirm that during the stages of gall development, active cell multiplying (hyperplasia), cell growing (hypertrophy), differentiating and cell destruction jointly shape the gall structure.

Little data can be found in literature about the grape shaped galls of *Neuroterus quercusbaccarum* compared to other types. Therefore our results might contribute to a better understanding of the structure of this gall type.

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References

Askew RR (1984) The biology of gall wasps. In Ananthakrishnan TN, ed., Biology of Gall Insects. Oxford and IBH, New Delhi, India, pp. 223-271.

Bronner R (1977) Contribution a l'étude histochimique des tissus nourriciers des zoocécidies. Marcellia 40:1-134.

Bronner R (1980) Ultrastructural observations on lipid globules in nutritive cells of cynipid galls (Hymenoptera). Cecidol Int 1:127-135.

Bronner R (1985) Anatomy of the ovipositor and ovipositional behavior of the gall wasp *Diplolepis rosae* (Cynipidae:Hymenoptera). Can Entomol 117:849-858.

Bronner R (1992) The role of nutritive cells int he nutrition of Cynipids and Cecidomyiids. In Shorthouse DJ, Rohfritsch O, eds., Biology of Insect-Induced Galls. Oxford University Press, New York, pp. 118-139.

Csóka Gy (1997) Gubacsok – Plant Galls. Agroinform Kiadó, Budapest.

Harper LJ, Schönrogge K, Lim KY, Francis P, Lichtenstein CP (2004) Cynipid galls: insect-induced modifications of plant development create novel plant organs plant. Plant Cell Environ 27:327-335.

LeBlanc DA, Lacroix CR (2001) Developmental potential of galls induced by *Diplolepis rosafolii* (Hymenoptera: Cynipidae) on the leaves of *Rosa virginiana* and the influence of *Periclistus* species on the *Diplolepis rosaefolii* galls. Int J Plant Sci 162(1):29-46.

Mihalik E, Nyakas A, Kálmán K, Nagy E (1999) Növényanatómiai praktikum. JATEPress, Szeged, p. 155.

Rey LA (1992) Developmental morphology of two types of Hymenopterous galls. In Shorthouse DJ; Rohfritsch O eds., Biology of Insect-Induced Galls. Oxford University Press, New York, pp. 87-101.

Rohfritsch O (1992) Patterns in Gall Development. In Shorthouse DJ; Rohfritsch O eds., Biology of Insect-Induced Galls. Oxford University Press, New York, pp. 60-86.

Sárkány S, Szalai I (1964) Növényrendszertani Gyakorlatok. Tankönyvkiadó Budapest, pp. 590-610.

Shorthouse DJ, Rohfritsch O (1992) Biology of Insect-Induced Galls. Oxford University Press, New York, pp. 1-285.

Szabó L. (1992) Interleaf and intraleaf distribution of gall formers on *Quercus cerris*: the organization of the leaf galling community. Acta Oecol 13(3):269-277.

Wanner G (2004) Mikroskopisch-Botanisches Praktikum Georg Thieme Verlag, Stuttgart, New York, pp. 82-91, 108-109.