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Preservation of fungi in archaeological charcoal

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ABSTRACT

During the analysis of wood charcoal remains from archaeological sites, it is common to find different microorganisms and different forms of degradation present in the plant tissue. However, one may encounter difficulties when attempting to identify these microorganisms and determine when their attack occurred. This paper focuses on preservation aspects related to the microorganisms in wood and demonstrates the structural changes that take place in different types of decayed wood after it was converted into charcoal. The study seeks to determine whether the microbial attack found in archaeological woods took place before the burning of the wood or after. Burning experiments were conducted using wood that had been decayed by various types of fungi including white-rot, brown-rot, and soft-rot. The laboratory burnt wood samples showed decay patterns that were comparable to those observed in archaeological charcoal samples, indicating that signs of fungal infestation and features of decay can be preserved after burning with micromorphological details of mycelium and cell wall attack evident. This indication may provide important information related to the gathering of deadwood as fuelwood. In addition, examples of decayed wood preserved in archaeological charcoal assemblages are described. Their relationship to the archaeological context and environmental conditions may suggest different interpretative models concerning wood management strategies applied by past societies.

1. Introduction

Anthracology is a discipline that investigates the remains of wood charcoals from archaeological excavations and natural deposits (Chabal et al., 1999). The charcoal is a final product of the carbonization process as well as a result of incomplete combustion during the charring process (Braadbaart and Poole, 2008; Fengel and Weneger, 1983; Smart and Hoffman, 1988). The charcoal retains the anatomical structure of the wood and may permit its botanical identification. Their taxonomic identification depends on anatomical characteristics of the species, the size of the charcoal fragments, and their state of preservation (Chabal et al., 1999; Schweingruber, 1982). In the field of anthracology, a special methodology that advances both palaeoethnographical and palaeoenvironmental information exists that has demonstrated the importance of charcoal analysis in archaeobotany and archaeology (Asouti and Austin, 2005; Badal García, 1992; Chabal, 1997; Chabal et al., 1999; Carrión Marco, 2005; Figueiral and Mosbrugger, 2000; Heinz and Thièbault, 1998; Lityńska-Zając and Wasylikowa, 2005; Marguerie and Hunot, 2007; Ntinou, 2002; Smart and Hoffman, 1988).

One of the purposes of anthracological analysis is to gain palaeoethnographic information about wood used by humans. For example, in the case of fuelwood, there is an assumption that firewood gathering derives from simple necessity based on availability and effort required rather than intentional selection of a particular species of wood, which is called “Principle of Least Effort” (Shackleton and Prins, 1992). Ethnographic studies have shown that this important human activity depends on the wood's abundance, the ease of collecting, and the ability to transport the wood. Deadwood recovered from a forest in the proximity to the habitation site fulfills these requirements, and the documentation of its gathering may lead to the formulation of new hypotheses that permit understanding the management of forest communities by past societies (Asouti, 2005; Asouti and Austin, 2005; Salisbury and Jane, 1940; Théry-Parisot, 2001). Palaeoethnographic information concerning the use of deadwood recovered from forest floor or attached to standing trees may be obtained after observing characteristic features of the decayed wood such as changes in anatomical structure and the presence of microorganisms, and determining if the microbial attack took place before or after burning.

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The main objective of the present study is to confirm that hyphae and other structures produced by microorganisms can be preserved within the wood charcoal after the burning process. In previous work, Schweingruber (1982, p. 204) had indicated that in charcoal, fungal hyphae may be preserved in addition to structural features of the wood. Also, Théry-Parisot (2001) conducted significant experiments related to the detection of rotten wood and driftwood in charcoalified samples. Théry-Parisot had demonstrated that hyphae may be preserved in the charcoal fragments after the burning process. This statement later served as a basis for an assessment of the deadwood present in the anthracological assemblages (Badal, 2004; Carrión Marco, 2005). Reflectance microscopy is a promising method that may help to prove the microbial preservation within the charcoal structure and may also serve as a technique that can distinguish between burnt and uncharred material. In particular, the incidences of microbial and animal organs along with the remnants of the arthropod's fecal pellets were documented in the plant material. The analysis showed that both the aforementioned materials and the charcoals exhibited high reflectance, confirming their charred conditions (Scott et al., 2000). Nonetheless, the way the microbes are preserved in the charcoals still remains unclear. Heiss and Oeggl (2008) recently performed studies on a fuelwood used in prehistoric copper mines in which special attention was paid to fungus-infected charcoal fragments. However, the evaluation of the pre-burning attack was based on the supposition that "wood-decaying fungi are destroyed during the carbonization" (Heiss and Oeggl, 2008, p. 214). Therefore, only the material in which hyphal imprints are observed was taken into account in the gathered—stored wood interpretation while charcoals with fungal hyphae were considered to result from modern contamination.

Also, it was important to examine the charcoal fragments to determine if characteristic patterns were preserved in the anatomical structure of decayed wood. Many studies have demonstrated special features related to the different types of wood degradation observed in xylem (Blanchette et al., 1990; Blanchette, 2000, 2003; Eriksson et al., 1990) and it would be valuable to verify if the same pattern could be documented in the wood structure after charcoalification. It is important to observe whether the changes in microstructure of the cell walls (erosion or cavities) may also be evident after burning, since homogenization of all cell layers happens during this process. This objective may in turn confirm fungal actions in the wood before the burning process and thereby indicate the use of infested wood by the humans in the past.

Finally, some examples of archaeological charcoals that exhibit the characteristics of decayed wood are presented and discussed in relation to their contexts.

2. Background

During the analysis of charcoal fragments, different groups of organisms are usually observed within the anatomical structure of the wood; however, their identifications and mode of attack are difficult to establish. These groups include mainly fungi, bacteria, and animals such as insects or nematodes which are responsible for degradation processes of living and dead plants in almost all environments (Blanchette, 2000, 2003; Caneva et al., 2008; Eriksson et al., 1990; Koestler et al., 2003). The microbial attack observed in the charcoal might have happened at different times and places. First, the infestation could have happened to the wood before the burning process. In this case, the wood may have become infested in its natural environments before being collected by humans or after it was gathered and later stored. Second, the charcoal could have been attacked by microorganisms during a post-depositional period that could have included the deposition in the soil at the archaeological site or in the museum environment after its excavation, or both (Blanchette, 2000; Badal, 2004; Marguerie and Hunot, 2007; Théry-Parisot, 2001). Identification of the species, and knowing their ecological preferences, may help determine the initial moment of attack, e.g., whether living trees, deadwood, charcoal, humid or dry conditions, etc. Nevertheless, many of the microorganisms exhibit similar anatomical characteristics or appear in rather broad natural environments that makes their identification quite uncertain (Alexopoulos et al., 1996; Balows et al., 1992).

The largest groups of fungi which are responsible for wood degradation belong to the Basidiomycetes, which attack both angiosperms and gymnosperms, and can even decompose the heartwood of living conifers. Other groups are representatives of Ascomycetes and Deuteromycetes. In addition, bacteria may degrade the wood, especially in environments which exclude fungal competition. Bacteria may also take part in multi-organism decomposition processes. On the basis of morphological changes in wood caused by microbial attack, three major types of decay are distinguished: brown-rot, white-rot, and soft-rot. Wood structure and chemical composition have a major influence on microbial attack since different microorganisms specialize in degrading different wood components. The main structural components of wood cell walls are polymeric which include cellulose, hemicellulose, lignin, and other minor polymeric substances. They are located in different areas of the cell walls and their proportions vary significantly depending on cell types, plant group (angiosperms or gymnosperms) or species. Brown-rot fungi preferentially decompose cellulose and hemicellulose (polysaccharides) as a source of carbohydrates, which are mainly located in secondary cell wall layer. Some groups of them may also cause limited degradation of lignin. In advanced states of decay, the cells lose rigidity but the main structure of the wood is unchanged. Also, shrinkage of the cells in the brown-rotted wood occurs and results in cracking into cubical pieces. White-rot fungi may preferentially degrade lignin, which is principally concentrated in the middle lamella region (lignin-selective fungi) or some white-rot fungi may degrade all cell wall components simultaneously. White-rot fungi are characterized by a great diversity of wood-decay types and all of them produce a white color in the wood due to extensive lignin alteration or removal from the cells. Soft-rot fungi are Ascomycetes that show preference for cellulose and hemicellulose, but they do not appear to degrade lignin within the middle lamella. Some soft-rot fungi may erode the secondary wall completely while others produce cavities within the secondary walls. The distinctive appearance of these cavities is related to the cellulolytic microfibrillar orientation that changes in different layers of cell walls (Blanchette et al., 1990; Blanchette, 2000, 2003; Eriksson et al., 1990; Fengel and Weneger, 1983; Zabel and Morrell, 1992).

Among all groups of fungal-decayed wood, the most common are the microbes responsible for white and brown rot, whereas the soft-rot fungi usually appear in restricted environments of very wet or dry conditions. In natural environments, two main groups (white-rot or brown-rot fungi) dominate, but they are hardly represented in ancient wood collections while soft rot dominates in archaeological wood. This is consistent with the preservation of wood over time since in favorable conditions a variety of microorganisms quickly decompose all kinds of organic matter. The wooden material may be preserved in extremely dry or waterlogged conditions in which a limited group of microorganisms thrive. These habitats favor soft-rot fungi and exclude mostly white- and brown-rot competitors (Rayner and Boddy, 1988; Blanchette, 2000, 2003). In archaeological charcoal, all of the fungal groups may be found, although their presence is directly related to the archaeological context. In the charcoal assemblages that result from domestic fuelwood, white-rot and brown-rot fungi are prevalent in the deadwood gathered from the forest. These microbes may also appear in the remains of burnt wooden constructions, especially when the material was previously in contact with the ground. It is less probable but not impossible to find soft-rot fungi in the charcoals, but their presence could be limited depending on the environmental conditions.

Three major groups of wood-rot fungi may appear together in the process of wood deterioration and may be accompanied by other organisms such as bacteria and insects that may contribute to wood deterioration processes. This presents additional difficulties when trying to identify the cause of wood degradation. The nature of these relationships presents very wide diversity from symbiosis to parasitic associations, and the major food sources may constitute the wood itself as well as insect feeding on fungi in wood (i.e., mycophagous insects) (Blanchette et al., 1990; Blanchette, 2000, 2003; Eriksson et al., 1990; Gilbertson, 1984; Harrington, 2005; Zabel and Morrell, 1992). When studying deadwood that was gathered from the forest floor, different organisms related to forest soil ecology should be of special interest, and one group of microorganisms is particularly worth mentioning: filamentous bacteria of Actinomycetales order. This group may deteriorate the wood components and play an important role in the decomposition of organic matter in the soil. Hyphae and spore chains that belong to this group are present within the charcoals and may occasionally be incorrectly identified as fungi. However, their hyphae may be generally distinguished from fungal hyphae on the basis of their smaller dimensions (Eriksson et al., 1990; Kutzner, 1981; Lechevalier and Lechevalier, 1981; Rayner and Boddy, 1988).

Another problem with regard to the fungi found in the charcoals is related to the possibility of observing the agents of post-burning attacks. Charcoal is the most ubiquitous plant material found in archaeological sites because of its lack of valuable nutrients after burning for microbiological decomposers. There is a group of fungi that grow on burnt areas and may be responsible for charcoal degradation. They belong mainly to the class of Discomycetes of the Ascomycotina subdivision but some may also represent Basidiomycotina. All of the various names of these microorganisms, such as anthracobionts, carbonicolous, pyrophilous, fireplace fungi or phoenicoid fungi, indicate their appearance after burning, in the substrates rich in charcoal material. However, these fungi are not specialized in charcoal decomposition and their preferred habitat is related to the heat-treated soils that stimulate their germination. Some of them may appear on the tree after partial burning and the presence of injuries can favor the development of a new community. Also, these unoccupied substrates provide great opportunity for rapid colonization that excludes competition (Alexopoulos et al., 1996; Carpenter and Trappe, 1985; Petersen, 1974; Rayner and Boddy, 1988).

3. Material and methods

3.1. Wood samples

Six wood samples that represent the major fungal degradation groups were prepared for conversion to charcoal. The first group included two samples, a coniferous wood *Tsuga* sp. (Fig. 1) and a hardwood (*Populus* sp.), infected with brown-rot. The second group of hardwoods was infected with white-rot fungi and included one sample from a deciduous oak (*Quercus* sp.; Fig. 2) and two poplar samples (*Populus* sp.; Fig. 3). All of these woods were collected from downed trees on the ground in a natural forest. The last group consisted of pine wood from a prehistoric great house dwelling in New Mexico (Blanchette et al., 2004) that had advanced stages of soft-rot decay (*Pinus* sp.; Fig. 4). Moreover, in the case of the brown-rot coniferous sample, it was possible to identify *Fomitopsis pinicola* as the fungal species responsible for the wood decay since the sample was taken directly behind a basidiocarp. Fruiting bodies were not found on the other samples so the specific fungus causing the attack was not known. However, anatomical observations were made on these decayed wood samples to characterize the specific type of decay that was present.

3.2. Burning process

Small pieces of infected wood (3–5 cm) were burned at temperatures between 300 and 350 °C. Each sample was divided into two parts for charcoal making; the first sample was burned wrapped in aluminum foil in order to reduce the oxygen supply while the second one was burned with unlimited oxygen. Many different factors such as fire temperature, length of exposure, location of the fire, position of the wood in the fire, diameter of the wood, and humidity of the wood can influence the charcoalification processes (Braadbaart and Poole, 2008; Panshin and de Zeeuw, 1980; Smart and Hoffman, 1988; Théry-Parisot, 2001). The design of representative burning experiments becomes particularly difficult when there is limited availability of historic wood samples. Both the foil-wrapped and unwrapped samples are designed to simulate charcoal making in an open-air fireplace. The first group may represent the charcoal produced with partly restricted oxygen supply, such as under other burnt wood and ashes in the center of the fire (Smart and Hoffman, 1988). The second group may correspond to the wood and charcoal located in the periphery of the fire. The relatively low temperature is also associated with the charring process, where the charcoal is usually preserved when the temperature of the fire goes below 350 °C (Braadbaart and Poole, 2008). Again, the size and condition of the wood has influence on the low temperature rate of charring. Small and dried pieces of wood began to burn with flames shortly after reaching 280–300 °C and their exterior surfaces started converting quickly into ashes. For this reason, wood beginning to convert to ash was sprayed with water in order to stop the combustion.

3.3. Scanning electron microscopy sample preparation

Wood and charcoal fragments were first examined using a reflected light microscope and then pieces of three anatomical sections were prepared: transverse (T.S.), longitudinal tangential (L.T.S.), and longitudinal radial (L.R.S.). All fragments were manually broken, and put on the aluminum stubs with adhesive tabs. Samples were coated with gold/palladium and later examined using scanning electron microscopy (Hitachi model S-3400N VP-SEM; Hitachi model S-4100).

4. Results and discussion

4.1. Experimental results

Observations of wood and charcoal samples under the microscope show similarities in decay patterns, and hyphae were identified in both types of samples, the foil-wrapped and unwrapped samples (Figs. 1–4).

4.1.1. Brown rot

In the coniferous wood sample attacked by brown-rot fungi, the typical “wavy” appearance of degraded cells can be observed in the T.S. of wood and charcoal samples (Fig. 1a and d). Fungal hyphae are also present in both samples and are numerous in all anatomical sections (Fig. 1a–f). In the L.T.S. the hypha penetrates tracheids via bordered pits and also enters a ray directly through the cell wall

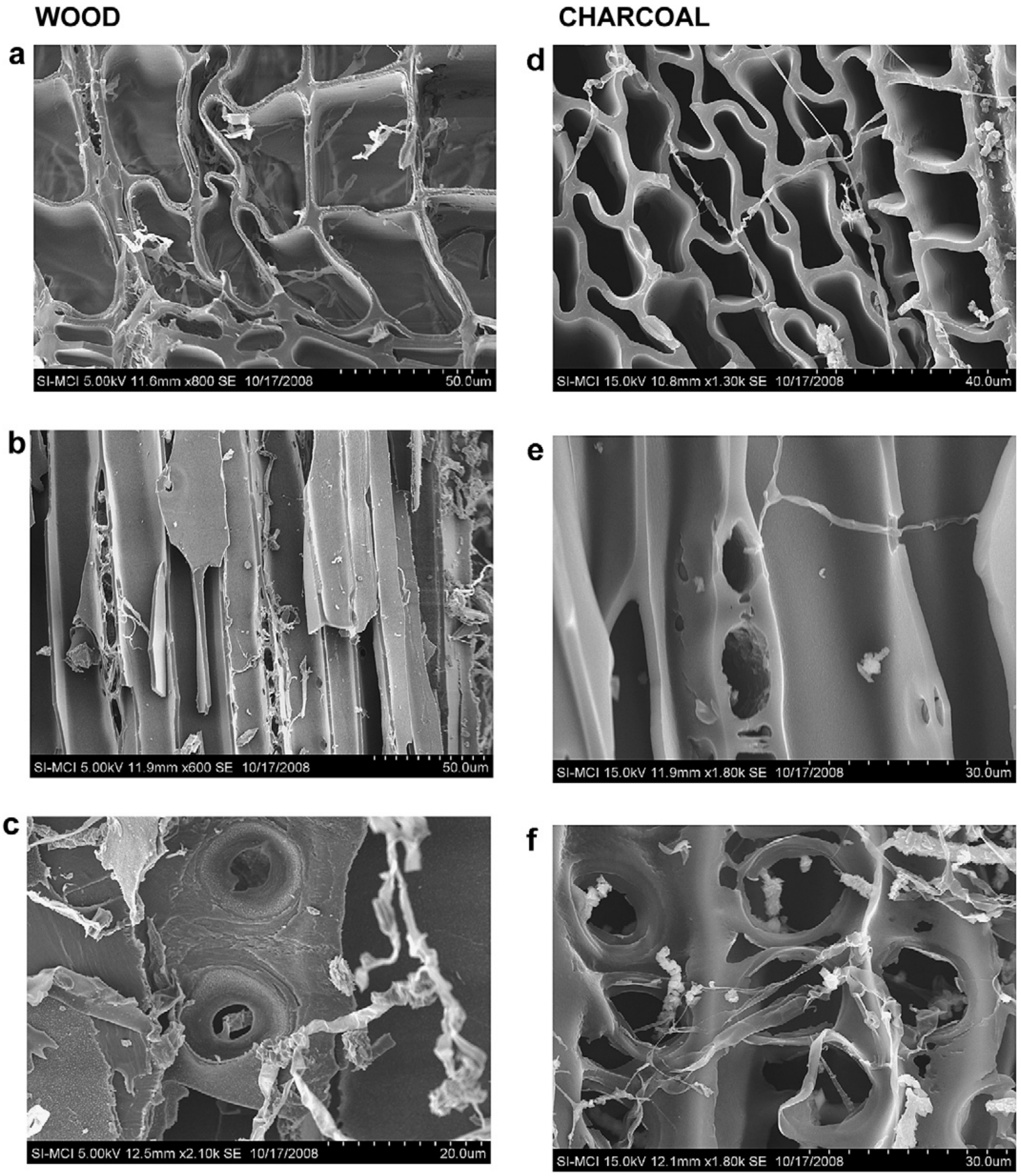

Fig. 1. Wood (a–c) and charcoal (d–f) fragments with brown-rot fungi: *Tsuga* sp. Transverse section (a and d), longitudinal tangential section (b and e), longitudinal radial section (c and f).

(Fig. 1b and e). The fine structure of fungi is preserved in the charcoal after burning and even calcium oxalate crystals that are associated with the hyphae remain clearly visible (Fig. 1c and f). These crystal structures may be related to hyphal metabolism products and some fungi may produce different types of deposits (Eriksson et al., 1990). Elemental analysis of these samples showed the presence of mainly calcium and potassium. In the L.R.S., a more deteriorated structure of the wood was seen in some areas of the fragments. This is the result of an extensive removal of cell content, producing holes in their walls, and is a result of consumption of the polysaccharides together with lignin (Fig. 1c and f). Moreover, the wood was infested by *F. pinicola*, a species that has been reported as capable of causing lignin modification (Eriksson et al., 1990, p. 53). The comparison between two kinds of samples – burnt with limited oxygen and open to the air – showed no differences in preservation of microbes in the charcoal.

In hardwood samples (*Populus* sp.), the same pattern of wood decay was observed since the loss of strength resulting from fungal attack caused distortion of plant tissue and the presence of a thin framework of lignified tissue. Also, fungal hyphae were well preserved and were mainly observed within the vessels. Once again, the same characteristics were observed in samples from both types of charcoalification processes.

4.1.2. White rot

Two examples of white-rot fungi that show different stages of wood decay are presented. The first one, (*Quercus* sp. deciduous, Fig. 2) illustrates an exceptionally advanced stage of decay that originated from simultaneous degradation of all cell wall components. The infected wood was characterized by a spongy appearance and showed an extensive growth of mycelia, which filled most of the fragile and deteriorated oak tissues, as observed under the reflected light microscope (also seen in SEM images Fig. 2a–c). After burning, both the charring and the carbonization processes left all characteristic patterns of decay previously observed in the wood (Fig. 2d–f). In the T.S. (Fig. 2d) and L.R.S. (Fig. 2f), earlywood vessels were filled with fungal mycelium and fungal attacks were concentrated in the area of uniseriate and multiseriate rays that caused

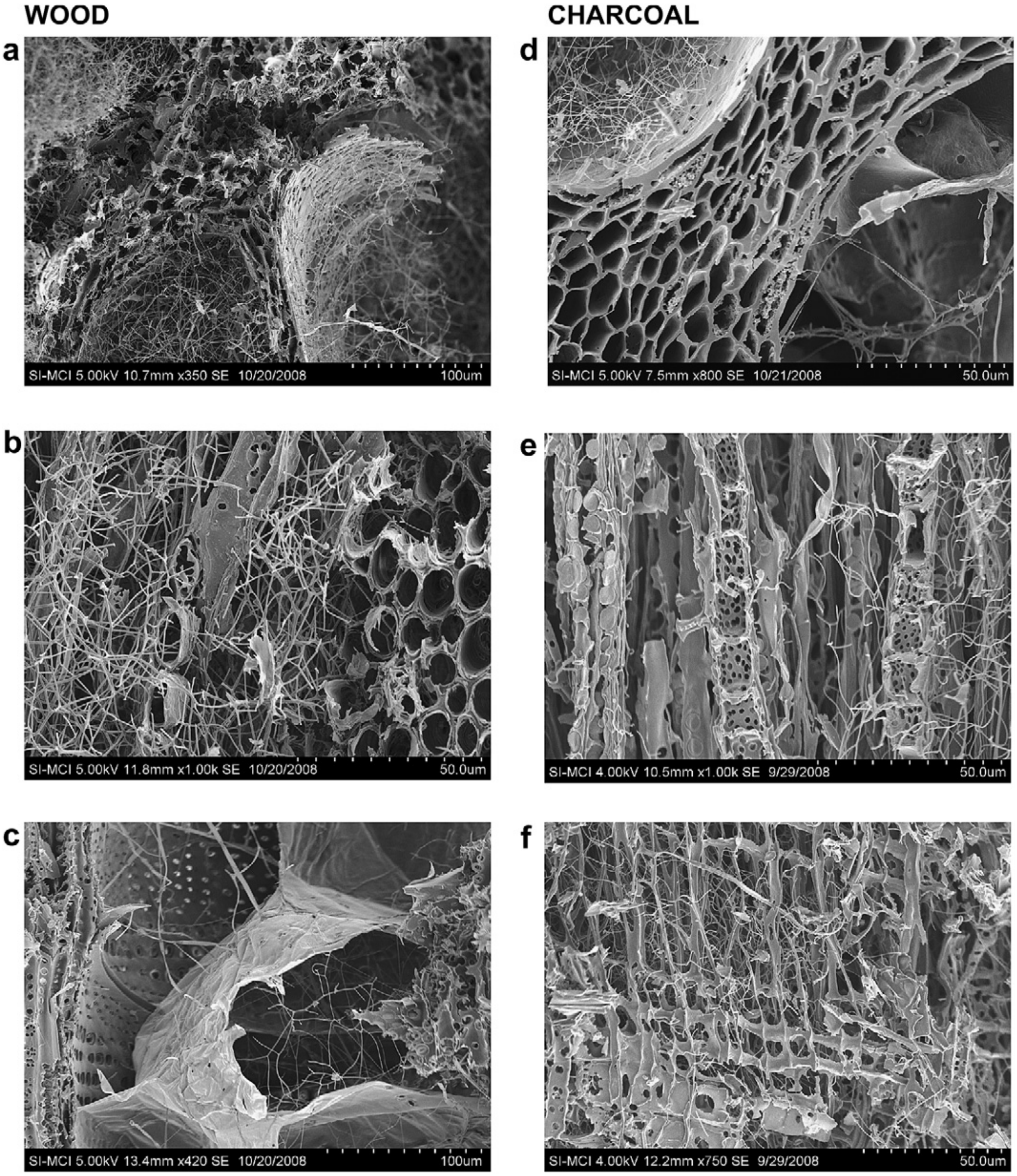

Fig. 2. Wood (a–c) and charcoal (d–f) fragments with white-rot fungi: *Quercus* sp. deciduous. Transverse section (a and d), longitudinal tangential section (b and e), longitudinal radial section (c and f).

erosion of the cell walls and large voids. Also in the L.T.S., the attack of ray parenchyma was observed together with the degradation of all cell wall components (Fig. 2e). Widespread fungal mycelia were also seen in the L.R.S. that at lower magnification showed remnants of wood structure (Fig. 2f).

In the second piece of wood (*Populus* sp.), the attack by white-rot fungi was less developed (Fig. 3). The charcoals showed evidence of fungal preservation after charcoalification, and the image of the decayed wood was very comparable to that obtained from the charcoal. The fungal hyphae were grouped mainly in the vessels and their metabolic products, in the form of crystal oxalate salts, were also observed (Fig. 3a, c, d, e, and f). White-rot fungi that commonly decayed the sapwood of various angiosperms, such as *Odontia bicolor*, commonly produce these calcium crystals in early stages of decay. In the L.R.S., selective degradation of lignin was observed in the region of ray-vessel intersections where the middle lamella was not present (Fig. 3b and e), whereas in the L.T.S. lignin removal resulted in separation of axial tissues (Fig. 3f). Also, the ray parenchyma in the L.T.S. was more deteriorated and this suggesting that these cells, which are rich in polysaccharides, were the first colonized. In some regions of the vessels, a simultaneous degradation was documented as hyphae eliminated all cell components and produced holes around the pitting (Fig. 3b, e and f). Another poplar wood sample attacked by white-rot fungi showed similarities regarding the preservation of fungal hyphae and the indication of a wood-decay pattern of similar degradation type.

4.1.3. Soft rot

In the T.S. of coniferous wood and charcoal, the cavities completely fill the cell walls of tracheids leaving areas of middle lamella untouched (Fig. 4a and d). The typical pattern of the cavities was more evident in the longitudinal sections, especially in the L.R.S. in which there were cavities of cell walls and around bordered pits in diverse orientations (Fig. 4c and f). The ray parenchyma cells were also colonized as was observed in both transverse and longitudinal tangential sections (Fig. 4a, b, d and e). Furthermore, after burning took place, fungal hyphae in all charcoal fragments were preserved in the form of hyphal imprints and were present in

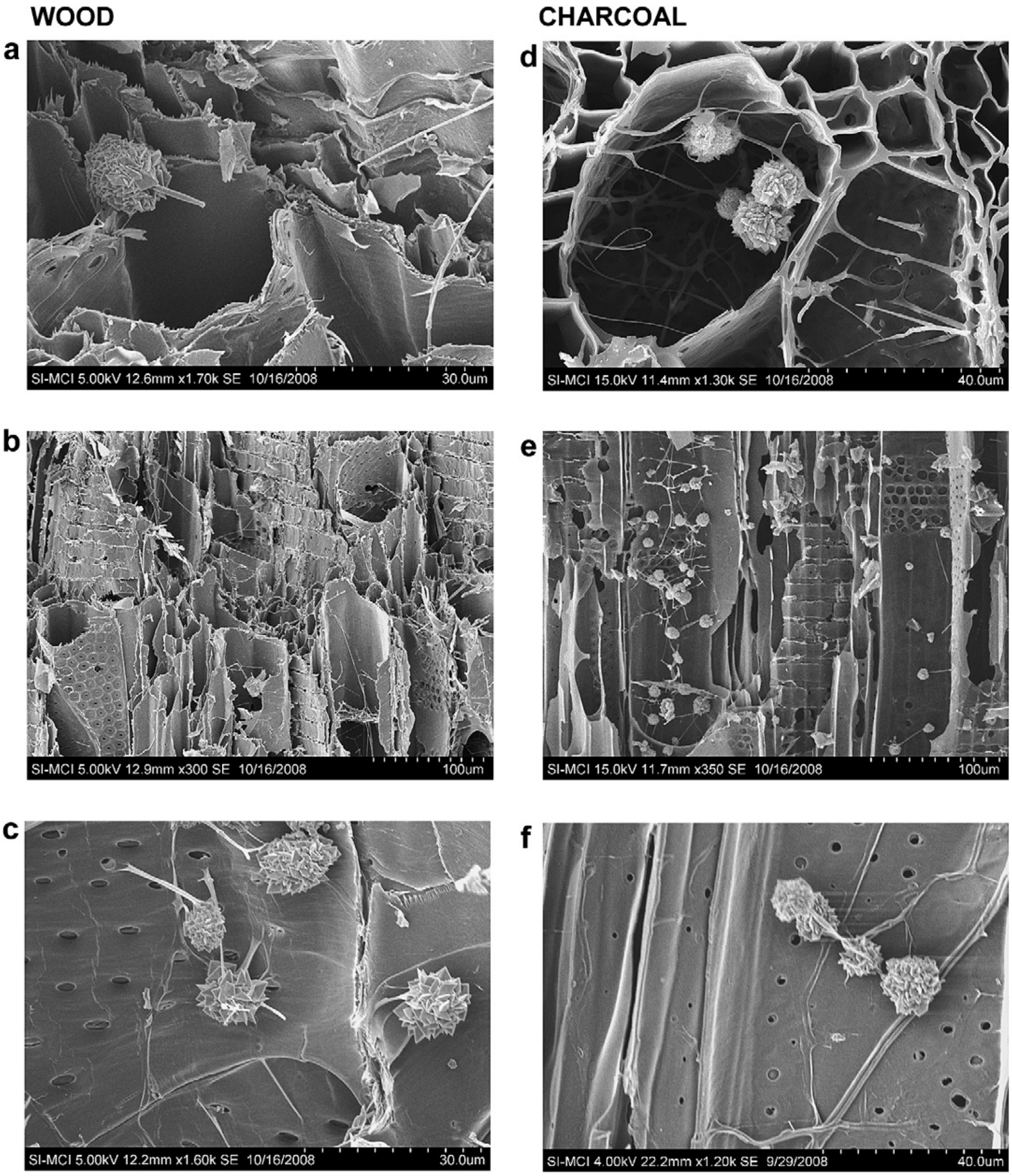

Fig. 3. Wood (a–c) and charcoal (d–f) fragments with white-rot fungi: *Populus* sp. Transverse section (a and d), longitudinal tangential section (b and e), longitudinal radial section (c and f).

the cell lumen as individual hypha or as a mass of mycelia. Since, this was from a sample of prehistoric wood, the hyphae present and responsible for causing the decay may have been very old and only residual imprints of the fungal cells remained in the wood before burning.

The experiments have demonstrated the preservation of fungal mycelium in test charcoals after the burning process. The fungi were present in all anatomical wood sections, mainly as hyphae that penetrated cell walls and formed accumulations of mycelia. Apart from individual hyphae, many fungal imprints were also observed. It was noticed that if hyphae colonized the cell lumen, after burning they were preserved in the lumen (Figs. 1–4), and if they were older collapsed hyphae, they occurred as imprints (Fig. 3c and f). Therefore, the results suggested that hyphae are preserved in the charcoal exactly as they appear in the wood before charcoalification. Consequently, it is possible to deduce prior attack on the wood by the presence of fungi in both forms as hyphae and as imprints. Furthermore, the way the hyphae occur within the lumen is also significant. Only the hyphae that appear attached directly to the cell walls and emerge from behind the cell wall surface should be taken into account as evidence for pre-burning activities. It is not possible to identify the fungus producing the decay by observing only the fungal hyphae since there are no structural differences among most species or genera. At times hypha can be accompanied by spores or calcium oxalate crystals but many fungi classified as white- and brown-rot Basidiomycetes can produce them.

In many cases the pattern of wood deterioration may help in the characterization of the wood-decaying organisms. Observing the macrostructure of the wood may help significantly in determining its decay type. In brown rot, the fungi cause the characteristic wavy appearance due to the lack of strength, particularly visible in the transverse section but also seen in longitudinal ones. The same group is distinguished by forming cubical cracks in the wood. In some advanced stages of decay, the cell walls begin to have a porous aspect as polysaccharides are extensively removed. Some

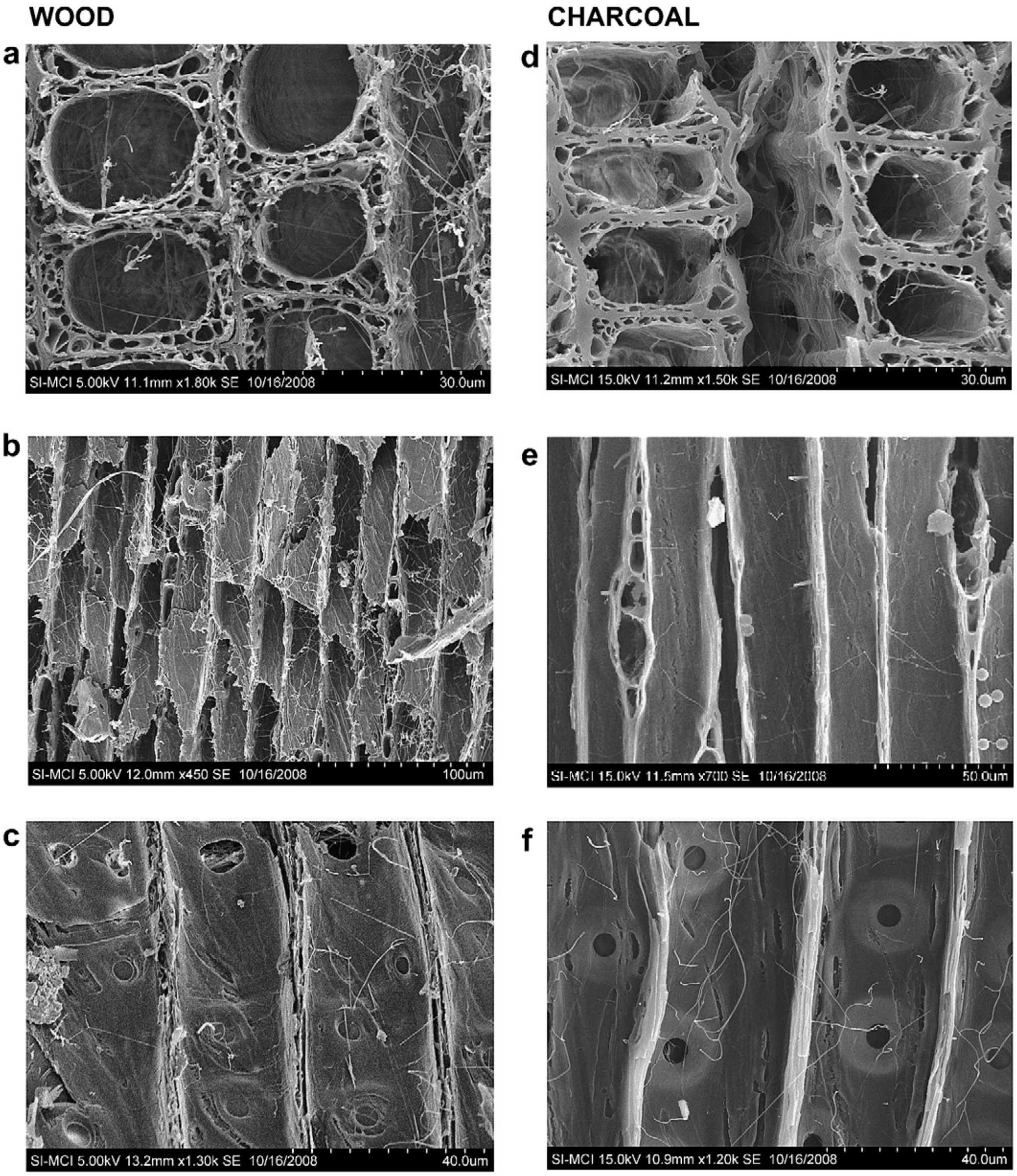

Fig. 4. Wood (a–c) and charcoal (d–f) fragments with soft-rot fungi: *Pinus* sp. Transverse section (a and d), longitudinal tangential section (b and e), longitudinal radial section (c and f).

of the brown-rot fungi also decompose some lignin that may result in the destruction or an extremely fragile middle lamella that appears degraded. This could mimic some stages of a white rot. Soft-rot fungi are characterized by forming biconical and cylindrical cavities in the secondary cell walls but some forms of soft rot such as the erosion of the secondary wall can appear similar to early stages of attack by a white-rot fungus (Blanchette et al., 1990; Blanchette, 2000, 2003; Eriksson et al., 1990; Schwarze, 2007). As a result, it is important to remember that some features characteristic for one rot group may also be characteristic of another group. Moreover, wood can be a source of nutrition for different groups of wood-rot fungi, and combination of attack such as brown rot following a white rot or soft rot (Blanchette, 2003; Eriksson et al., 1990; Rayner and Boddy, 1988). Therefore, identification of microorganisms preserved in charcoal on the basis of wood-decay patterns may be difficult since features such as color of the wood are not observable. Nonetheless, all the above-described microscopic characteristics serve as tools for compiling general information that may indicate possible uses of decayed wood.

In archaeological charcoal there may also be modern fungal hyphae coming from plant roots or soils that frequently overgrow the ancient material and use the structure of the charcoal as support. Modern attack also can take place in the storage area after excavation. This is especially true for charcoal samples after flotation methods or water sieving recovery techniques are employed, or if the charcoals are kept together with uncharred roots or other plant material that are not completely dried out. In these cases, anthracological analysis of the sample may also help distinguish between possible pre-burning attack and modern infected samples. Some microbial uncharred mycelia may exhibit characteristic colors observable under the reflected light microscope. For example, the surface of a few charcoals from the same sample from a Bronze Age necropolis of Kokotów (Poland) was covered by fresh mycelia of white color that under higher magnification showed violet and green colors (Moskal-del Hoyo, unpublished data). Taking into considerations the morphology of these microorganisms, it is possible that they correspond to some filamentous bacteria of Actinomycetales order and especially to the Streptomycetaceae family (Kutzner, 1981). Streptomycetes are very ubiquitous but they are most typical in the soil habitats where they act as decomposers (Kutzner, 1981; Williams et al., 1984). They may also colonize and degrade wood (Eriksson et al., 1990) but in the case of charcoals from Kokotów, the colored mycelia may suggest their post-burning activities. The growth of microbes on these charcoals might have been favored by the recovery of the soil samples and their storage under conditions that may have favored their growth. Finally, it can be stated that modern fungal infestation most likely covers the surface of charcoals and only fungi found inside freshly broken charcoal fragments could be the result of pre-burning activities. Nevertheless, the phenomenon of possible modern attack by different agents requires more detailed studies.

4.2. Archaeological results

A few examples of archaeological charcoal that showed symptoms of pre-burning fungal attack were compared to the above-described wood-decay patterns (Fig. 5). The first charcoal came from an eastern Hungarian site (Nagykörű) that belonged to the early Neolithic Körös culture (Raczky et al., in press). This charcoal of ivy (*Hedera helix*) in the T.S. showed insect attack in the form of round axially situated holes within the plant tissue (Fig. 5a) that were also filled with fungal hyphae; however, in this section the ultrastructure of the wood did not present obvious fungal degradation. On the other hand, in the L.R.S. some hyphae and hyphal imprints occurred in the vessels (Fig. 5b). The attack caused holes around the pitting that demonstrated their ability to degrade all cell wall components. The attack was not at an advanced stage and the wood-decay pattern was not very evident, nevertheless the pre-burning microbial activity in the wood may be seen. This charcoal fragment was found within an apparent disposal pit together with other remnants of domestic fuelwood, burnt animal bones, fragments or lithic material and pottery. In general, the charcoal assemblage from Nagykörű is characterized by the presence of wood of small diameter that may correspond to branch woods or twigs of different arboreal and bushy taxa (oak, elm, ivy, plum, buckthorn), and the majority shows clear evidence of

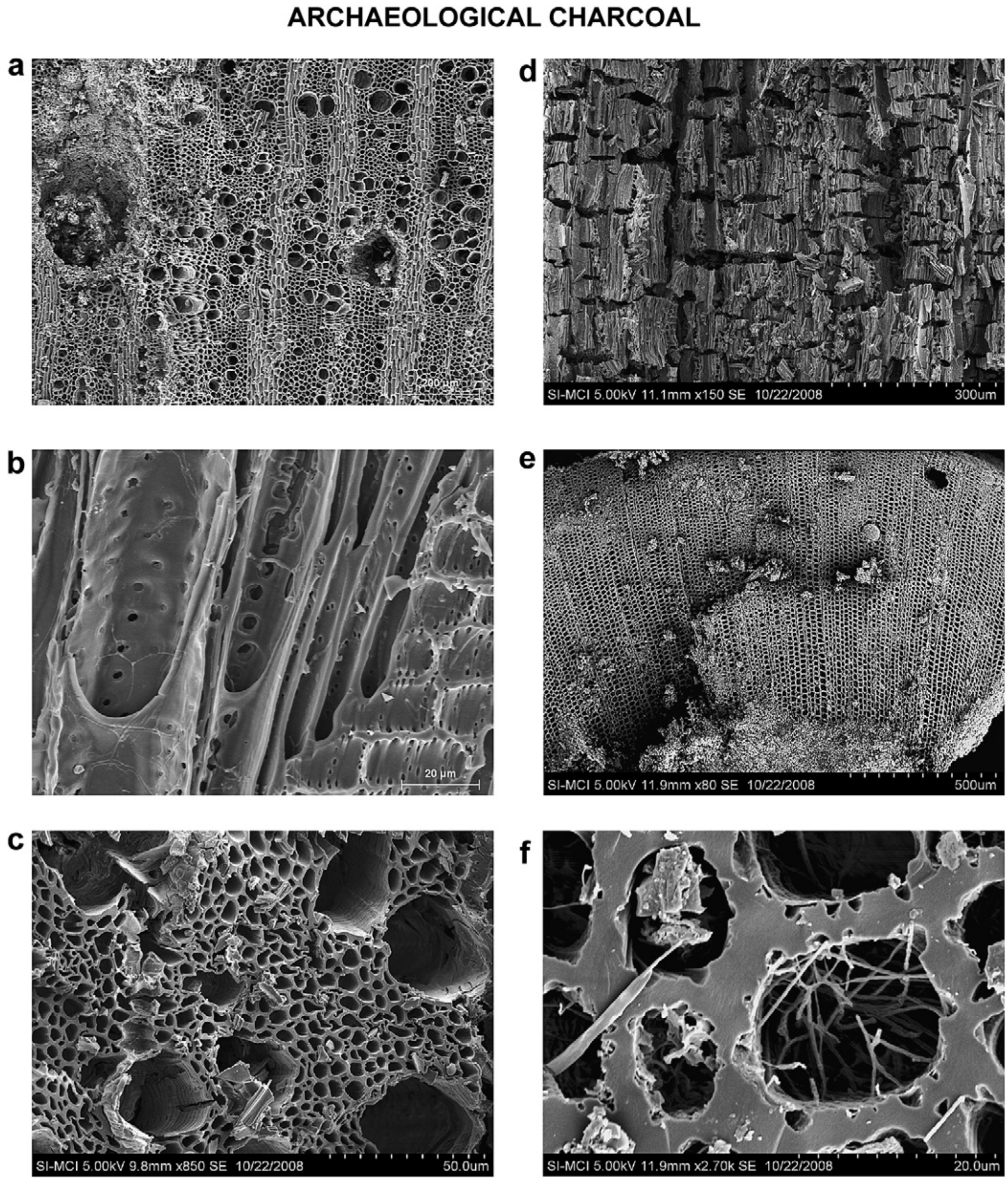

Fig. 5. Archaeological charcoal samples with pre-burning microbial attack: a. *Hedera helix*, transverse section; b. *Hedera helix*, longitudinal radial section; c. *Prunus* sp., transverse section; d. *Prunus* sp., longitudinal tangential section; e–f. *Pinus sylvestris*, transverse section.

microbial and insect attack (Moskal-del Hoyo, in press). This settlement represents the group of northernmost sites of the first Neolithic cultures in Tisza River valley and in the proximity of the site there are no traces of previous Mesolithic occupation detected (Raczky et al., in press). As a consequence, this new site was located in an area of unexploited woodland which shows an abundance of different kinds of fuelwood. The large amount of dry wood is expected at this site since it was a typical mature forest in which deadwood forms an important part of the tree biomass (Rayner and Boddy, 1988). Therefore, the management of wood resources at the settlement corresponds to the first situation in the "Principle of Least Effort" model testified by Shackleton and Prins (1992). In this case, the gathering of firewood corresponded to very little collection effort based on high availability of dry wood. Usually the deadwood formed in the forest litter or attached to standing trees requires prolonged periods of time and good ecological conditions of humidity and temperature to be colonized by decomposers (Rayner and Boddy, 1988) and have significant micromorphological changes present that are characteristic of decayed wood. It is possible that the charcoal assemblage coming from Nagykörü, in which a great quantity of attacked wood of small diameter is detected, represents the model of easy collectable deadwood for domestic fires. Diversity of taxa that exhibit a pattern of decayed wood may also confirm this hypothesis and indicate the preference for dead older wood found on the ground.

The second charcoal fragment (Fig. 5c and d) came from the late Neolithic settlement of Polgár-Csőszhalom located in eastern Hungary (Raczky and Anders, 2008). This fragment was very fragile and was characterized by distortion of wood tissues, particularly vessels and fibers (Fig. 5c). The rays were also deteriorated, but it was still possible to identify it as *Prunus* sp. In longitudinal sections, all charcoal fragments were cracked into cubical pieces (Fig. 5d), but this pattern was different from the cracks usually found in charcoal as a result of a burning process (Carrión Marco, 2005; Marguerie and Hunot, 2007; Théry-Parisot, 2001). All the features of the *Prunus* fragment indicated that brown-rot fungi probably degraded it. The Polgár-Csőszhalom site represents the northernmost tell settlement known from the Carpathian Basin which together with another external horizontal settlement constitutes an important complex center of the Upper Tisza River region, extended along an area of 28 ha (Raczky and Anders, 2008). The late Neolithic occupation of the site is divided into three main phases that correspond to a duration of about 500 years (ca. 4940–4500 cal. BC: Raczky et al., 2007). The *Prunus* charcoal fragment described above was found together with the remnants of other tree taxa (oak, elm and dogwood/cornelian cherry) within sediments of one of the houses dated to the oldest phase of the tell. The exact provenance of this charcoal sample (domestic firewood *versus* construction elements) is not well defined due to the leveling of layers before the preparation of the subsequent construction in the tell, thus the interpretation of the meaning of the presence of decayed wood is not obvious. However, it is possible that it was used previously as construction material and the brown rot is decay that occurred in the structure. This type of decay dominates in building wood (Rayner and Boddy, 1988, pp. 453–460, Table 12.2). Moreover, it should be added that the charcoal assemblage from different archaeological features located in diverse contexts (refusal pits, floors of houses, hearths, ditches) from other two recent phases constitutes a sample of wood used in the settlement in the apogee of human occupation in the region (Moskal-del Hoyo, unpublished data). In those phases, the woodland area should have manifested some changes following systematic and continued gathering of wood for different purposes. In contrast with the Nagykörű site, it is probable that in the vicinity there was very little dry wood available and probably some fresh wood was also regularly used. This condition may correspond to the situation described by Shackleton and Prins (1992) as typical for long-established occupation areas. Particularly in recent phases of the Polgár-Csőszhalom tell in the charcoals there are almost no signs of decayed wood. This may confirm the progressive lack of dry wood. Probably the deadwood still selected in the vicinity of the site was gathered before the advanced development of a decay community could expand. The only example of decayed wood was observed in the context of houses, associated with ash and oak charcoal. In this case, it likely represents remnants of some reused timber used for construction as both of these woods were preferentially used for these purposes. The possibility of wood recycling has been previously noted in archaeological sites and is known from ethnographic examples (Asouti, 2005).

A third charcoal fragment was from the wood used in a funerary pyre and came from the Bronze Age necropolis of Kokotów (Kraków, Poland) (Matoga, unpublished; preliminary results: Matoga et al., 2009). This fragment belonged to a small branch or a young shoot of common pine (*Pinus sylvestris*) (Fig. 5e). At higher magnification, the cell walls of the majority of tracheids were eroded and cells had holes near the lumen surface (Fig. 5f). Hyphae of various diameters were preserved in the wood structure. It is probable that this wood was infested by a white-rot fungus that simultaneously removed all cell wall components. Moreover, the biodeterioration of the branch wood also confirmed its source among the litter, since this part of wood is typically more resistant to microbial attack. This is especially true in gymnosperms, in which compression wood is formed (Blanchette, 2000, 2003). The charcoal analysis from the necropolis of Kokotów comprises more than 100 graves (Moskal-del Hoyo, unpublished data; preliminary results: Moskal-del Hoyo, 2008) in which 15 taxa and different types of gathered wood were documented: trunks, branch woods, twigs, barks, and conifer cones. Also the presence of many branch woods that showed microbial deterioration may indicate that part of the wood prepared for the rituals of cremation was obtained from deadwood found in the forest. These observations together with taxonomical analysis may demonstrate a special pattern of wood selection for funerary purposes. In this case, the data suggest a more opportunistic model of wood selection of funerary fuel, which was probably motivated by the need for collection of a large amount of wood that was generally required for cremation, as shown by modern analogy (e.g. Sikandar et al., 1989).

Three examples presented above correspond to white-rot or brown-rot fungi but on basis of the presence of hyphae or decay patterns, the exact place in which the attack occurred cannot be indicated as the same characteristics may represent considerable number of diverse fungi. Moreover, the fungi that cause white or brown rot play an important role in wood decomposition of different habitats in the woodland. They invade the deadwood that is accumulated in the forest floor but they also colonize dead branches or twigs attached to standing trees. The same fungi also decompose remains of dead standing trees. Some Basidiomycetes that are mainly responsible for wood decomposition in the forest have also developed different strategies to colonize a living tree. This usually constitutes a very hostile habitat for fungi growth due to its high content of water in the sapwood, unfavorable aeration and formation of mechanical barriers and allelopathic chemicals. Compared to the decomposers of deadwood, these organisms represent a minor group of fungi. They mostly take advantages of some disturbance produced to a tree (fire scars, insect wounds, mechanical injuries, etc.) which allow them to enter the heartwood, avoiding the barriers composed by the bark and sapwood, but they may also behave as active pathogens. The action of fungi in a living tree may be lethal but the plant may also recover depending on the type of fungal attack and the degree of damage (Rayner and

Boddy, 1988; Schwarze et al., 2000). Furthermore, the same wood-decay pattern is also associated with fungi inhabiting wood outside of woodland communities, in wood either utilized as timber and raw material or stored (Rayner and Boddy, 1988). Even though the exact habitat of decayed wood found in archaeological assemblages cannot be stated, its presence indicates the selection of dry wood of different origins, from the forest floor or above-ground parts of trees and stored wood (Théry-Parisot, 2001, p. 50, Fig. 12). The differences in deadwood and living trees attacked by fungi cannot be easily discerned. However, in either case, their recovery may be related to the selection of wood that is easier to collect compared to the labor-intensive processing of wood from a healthy tree.

The presence of white-rot or brown-rot fungi in these three archaeological sites is not unexpected since they are ubiquitous in temperate regions. In general, the climatic zone should be taken into consideration when trying to investigate the importance of gathering of deadwood for domestic purposes. This is because in temperate ecosystems the rate of wood decay is relatively high compared to desert or tundra communities and is relatively slow compared to a tropical rainforest (Rayner and Boddy, 1988). For example, for a fallen tree in some temperate forests the microbial colonization phase is about two years and it takes approximately 15 years for the advanced decomposition (Théry-Parisot, 2001, p. 39); in tropical forests, a big tree can completely decompose in 10 years; in sub-Alpine forests this process may take more than 70 years (Rayner and Boddy, 1988, p. 308). Despite some general macro-environmental trends, the wood-decay rate cannot be easily determined since it is a dynamic and complex process. In the same environment, characteristics such as wood diameter, exposure of the surface or presence of bark and different microclimatic conditions influence and modify the processes of wood decay (Rayner and Boddy, 1988). Therefore, the presence of pre-burning activities of fungi in wood coming from temperate regions might be easier observed than in other zones. It is also important to remember that deadwood does not necessarily represent decayed wood. For example, in the Tucson area (Arizona, USA) the radiocarbon datings of deadwood recovered from the vicinity of the archaeological sites demonstrated that due to the climatic conditions unfavorable for fungi growth (high temperature and low moisture) linked with characteristics of local wood (dense and hard), deadwood may be preserved for more than a millennium in the environment (Schiffer, 1996, pp. 310–312). However, some fungi, such as soft rot, do grow and degrade the wood (Blanchette et al., 2004), and if that is the case, decay patterns even in this location may help to identify the type of wood used as fuelwood.

The observation of fungi in charcoal assemblages as part of anthracological analysis of archaeological charcoals may give additional information concerning the models of wood management by past societies (Asouti and Austin, 2005; Théry-Parisot, 2001) and thus is related mostly to palaeoethnographic aspects of wood usage. The aforementioned observations and case studies (Théry-Parisot, 2001; Asouti, 2005) have demonstrated that the presence or absence of wood attacked by fungi within a particular charcoal assemblage should be interpreted individually as it depends on different archaeological contexts which introduce many variables of interpretation. First, a geographic situation of the site (lowland, mountains, temperate zones, deserts, proximity of the rivers, etc.) and climatic period (Interpleniglacial, maximum of Ice Age, Atlantic period, Subatlantic period, etc.) indicate different woodland communities (boreal forest, temperate broad-leaved forest, temperate needle-leaved evergreen forest, riverine forests, unexploited woodland, etc.). Second, a type of site (mobile hunter-gatherers campsite, seasonal site, settlement, long-term multiphase site, industrial area, etc.) related to a type of activities concerning the use of fire (domestic, industrial or ritual hearths, funerary pyre, etc.) constitute a remarkable difference when interpreting charcoal assemblages. Third, some taphonomic problems should also be taken into account for the formulation of different hypotheses and finally, the charcoal sampling strategies during archaeological excavations may influence the results. It is important to emphasize that the search for decayed wood should be integrated in the charcoal analysis at the beginning of the study because the detection of fungi and their activities may require more detailed observations during the identification (Asouti, 2005, p. 219). Finally, if the charcoal assemblages that are characterized by the abundance of decayed wood form the basis for further palaeoecological interpretation, it should be additionally analyzed according to its ecological representativeness (Godwin and Tansley, 1941; Théry-Parisot, 2001).

5. Conclusions

The biodeteriorated structure of wood and the fungi responsible for its decay exhibit similar characteristics in both wood and charcoal samples. Charcoal produced using a limited or unlimited oxygen supply seems to have little influence on the preservation of fungi because in both kinds of samples hyphae were documented as individual hypha, mass of mycelia or as hyphal imprints. The patterns of decayed wood attacked by the three major wood-rot groups may be a valuable source of information when conducting an anthracological analysis since the preservation of altered wood structure is found in the macrostructure of archaeological charcoals as well as the ultrastructure of the wood. Archaeological charcoal shows evidence of microbial/insect presence and one of the main problems is to determine the initial moment of their attack and whether the attack occurred before or after burning. The results presented here show the possibility of recognizing pre-burning microbial activity because of the preservation of both fungal hyphae and wood deteriorated structures after burning. Although the identification of the fungal agent is often possible by examining the type of decay present, difficulties can be encountered if mixed decayed patterns occur.

The recognition of the decayed wood in the archaeological charcoal assemblage as part of the anthracological analysis may be a source of relevant palaeoethnographic information but there is an archaeological context at each site that indicates the possibility of further models of interpretation.

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