Passive entry of fungus spores into wood

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Abstract. Suspensions of *Armillariella* spores were forced through fresh cross sections of wood at a maximum pressure of 0.05 atm. Great variations in the degree of spore penetration were found between different tree species. The wood of ring-porous species allowed the spores to flow readily through 16 cm thick pieces; in diffuse- pored trees the penetration as considerably smaller, and a 1 cm thick piece of conifer wood completely filtered off all the fungus spores. It is concluded that the anatomical structure of wood, in connection with physical phenomena at the wood surface (capillary action, changes in temperature and air pressure, rain splash), may be responsible for differences in the infection process of wood of different tree species.

Introduction

When a spore falls on to a cut wood surface, its position may be changed by several agents before it germinates.

1. Changes in temperature and air pressure produce a flow of air and liquid into and out of tracheas and tracheids. If the temperature falls by 30°C, the volume of the gas in the tracheas decreases by 10 %, producing a subsequent inflow of air into a piece of wood 2 m long, to a depth of 10 cm from each end of the piece. The effect of the air pressure is smaller, and maximum changes of about 40 mm of mercury, which occur extremely rarely, cause changes of about 5 % of the original volume.

2. Capillary action of the tracheas. When a spore falls onto a dry wood surface, which is then moistened, capillary action sucks the liquid in, and possibly the spores, if the structure of the wood is suitable. This is evidently especially effective in horizontal pieces of wood. In addition, uneven drying may cause water movements within the wood.

3. Rain splash. Horizontal surfaces, e.g. stump surfaces, are often exposed to heavy rain splash. In Finland, according to Katajisto (1969) there occurs every second year, heavy rains of 2 mm/min, as measured at 1 min interwals. It is evident that this produces a downward movement of water in the wood.

4. If the wood of living trees is injured, underpressure in the tracheas sometimes produces a distinct inflow of air, which may carry fungus spores rather deep into the wood.

It is evident that the distribution of spores by these agents is largely dependent on the anatomical structure of the wood. The ability of this factor to cause differences in the entry of spores into wood of different tree species is investigated in this paper.

Wood structure in relation to the passive entry of spores

Wood-decomposing basidiomycetes usually have relatively small spores, with a length of under 15 mμ. Fig. 1 indicates the largest length and smallest breadth of spores of 241 polypors and 99 wood-decomposing agarics based on values given by Bondartsev

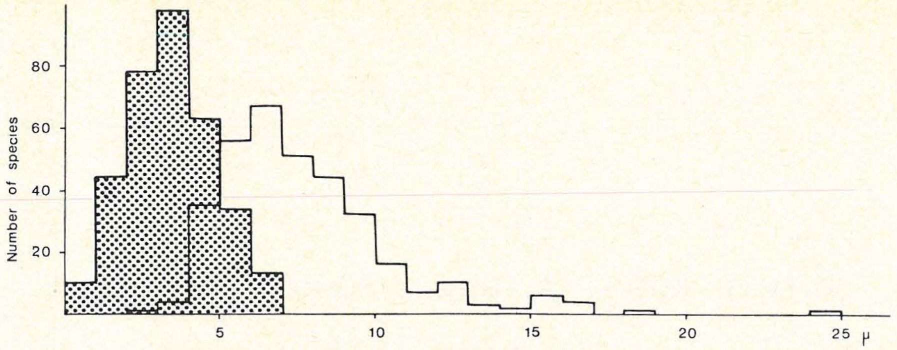

Fig. 1. Basidiospore diameter of 300 wood-decomposing polypore (according to BONDARTSEV 1953) and wood-decomposing agarics (according to MOSER 1967). Shaded: Largest breadth of spores, unshaded: greatets length of spores. Ordinate: number of species, horizontal axis: diameter of spores.

(1953) and MOSER (1967). Thus the shaded part indicates the smallest diameter of a pore through which it is possible for a spore to transverse, and the unshaded area the largest diameter, which may possibly block the throughflow of single spores. *Fomes fomentarius, Polyporus squamosus* and *Ganoderma* and other *Polyporus* species had the largest spores, *Amyloporia, Chaetoporus, Tyromyces, Gloeoporus,* and *Aporpium* species the smallest ones. When compared with soil-inhabiting species, there seems to be no significant difference in the spore size.

As the diameter of tracheas and tracheids is as a rule over 30 mµ, often even up to half a millimeter, it is easy to see that the length of conducting elements, as well as the type of perforation, must play a dominating role in the penetration of spores into wood, and not the size of the spores. In the following discussion it is presumed that no cracks are present in the wood, along which spores could pass deeper into the wood irrespective of the anatomical structure.

Conifer wood. The length of the tracheids in conifer wood as a rule does not exceed 5 mm, and consequently spores cannot passively move into conifer wood more than this distance. Perforated tracheids may occasionally occur, e.g. in *Sequoia* (JANE 1956) and in *Thuja* (BANNAN 1958). The only way, other than through cracks, is by way of resin channels, which may attain considerable lengths; in Scots pine over 100 cm (BÜSGEN 1927) and in lodgepole pine up to 43 cm (REID & WATSON 1966). In living sapwood they are presumed to be filled with resin and not open.

Wood of deciduous trees. According to GREENIDGE (1952), the tracheas of ring-porous hardwood species attain considerable lengths, often up to several meters. These have also the largest diameters, up to half a millimeter. The tracheas of diffuse-pored trees are evidently shorter, but may reach lengths of at least one or two decimeters. In addtion, the type of perforation is an additional factor. According to MØRK (1946) and ILVESSALO-PFÄFFLI (1967), of the Nordic trees, the following have simple perforation: *Populus tremula, Sorbus aucuparia, Tilia cordata, Acer platanoides* and *Prunus padus.* Scalariform perforation plates occur in *Betula, Alnus* and *Corylus.* The distance between the ribs of the perforation plate is in *Betula* about 8 µ, *Alnus* about 4 µ, and in *Corylus* 10—20 µ, thus making a definite barrier against the flow of spores in tracheas.

Experiments

In order to find out the validity of the deductions above, the following experiments were made. The spores of *Armillariella mellea* were chosen as the main subject material, as they are representative of normal wood-decomposing species, 7—9 x 5—6 µ. In nature, the spores of this species are supposed to infect stump surfaces of a very large number of tree species.

The upper surface of a freshly cut piece of a branch, the diameter of which was

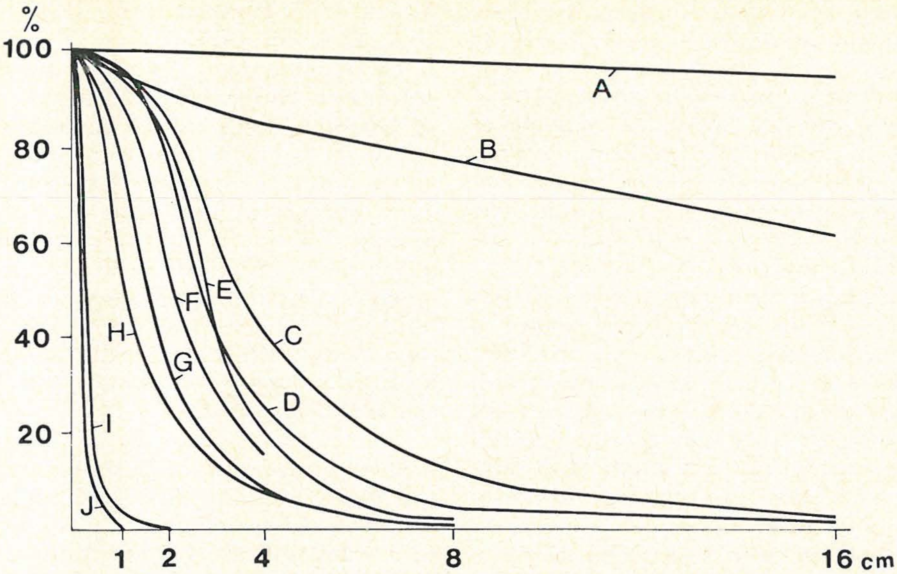

Fig. 2. Ordinate: percentage of spores which passed through a 3 cm ø piece of wood, the length of which is indicated on the horizontal axis. A: *Quercus robur,* B: *Fraxinus excelsior,* C: *Populus tremula,* E: *Acer platanoides,* F: *Corylus avellana,* G and H: *Tilia cordata,* I: *Betula pubescens* and J: *Alnus glutinosa, Pinus silvestris* and *Picea abies.*

about 3 cm, was fitted on to a rubber tube. A spore suspension of *Armillariella* was prepared by mixing about 12.5 mg of spores from a deposit 100 ml of distilled water with a Sorwall homogenisator and diluting the solution to one litre. The spore concentration was determined by means of a haemocytometer. The suspension used contained about 100 spores per µl. 20 ml of this suspension, well stirred, was pipetted into the rubber tube, and the suspension was forced through the wood piece at a maximum pressure of 0.05 atm. The ends of the wood piece were made even with a razor blade prior to the experiment. The number of spores in the through-flowing liquid was determined in the same way as at the beginning of the experiment, and compared with the initial values. Results are given in Fig. 2. The clogging of the tracheas by spores was studied by allowing 50 ml of concentrated (2100 spores per 1 µl) suspension to flow through pieces of maple wood. At the end of the experiment the wood was as permeable to spores as in the beginning fractions, thus indicating that the spores had not clogged the tracheas to any great extent.

Orientative experiments were made by pressing a starch suspension or a suspension of *Lycoperdon* spores (spherical, diameter 4—4,5 mµ) through wood of different trees after which the wood was split and the position of any starch clogs was determined, or else the outcoming liquid was studied under the microscope for the presence of spores. Coloration of starch by iodine and the labelling of spores with fluorescent Uvitex was carried out. The following values were obtained for the maximum penetration of spores or of starch granules (size over 6 mµ): conifer wood *(Pinus, Larix, Picea)* only a few mm, *Betula verrucosa* 2 cm, *Alnus incana* 0.5 cm, *Populus tremula* and *Salix caprea* 8—10 cm, *Sorbus aucuparia* 10—15 cm, *Prunus padus* about 15 cm, and *Acer platanoides* up to 20 cm.

Results and Discussion

From Fig. 2 it can be seen that between different tree species there were very great differences in the degree of penetration by the spores. As expected, conifer wood did not allow any spores to flow through it, and a 1 cm long piece filtered off practically all the spores. Wood of deciduous trees with scalariform perforation plates *(Betula pubescens, Alnus incana)* gave almost comparable results, except for *Corylus avellana,* the wood of which was penetrated to a depth of 4 cm by about 20 % of the spores. A 8 cm long piece of *Populus tremula* let about 10 % of the spores through. Wood of ring-porous trees, *Quercus robur* and *Fraxinus excelsior* allowed spores to penetrate very readily, evidently because of their wide tracheas. The result agrees with the condentivity of the xylem of different trees (PEEL 1965).

On the basis of the results, it seems evident that when a freshly cut surface is exposed to spores, the infection process varies in different tree species. In the case of conifer wood, the spores remain at the outer surface, but in oak wood the wood may become indected throughout its length to a depth of at least 20—30 cm, when e.g. rain splash forces spores into the wood.

That spores of vascular pathogens may move in tracheas, especially in the wood of ring-porous trees, is well known (BROOKS & MOORE 1923, BANFIELD 1941, 1968, CROWDY 1952, CAMPANA 1967).

The spore surface of the investigated species is dry. However there are some species of blue-stain fungi, which have a strongly gelatinous layer on their spores, which may be of advantage in penetrating the wood when changes in the temperature and air pressure occur. In addition, it would be interesting to investigate, whether the curved spores of certain species of wood-decomposing fungi, are adapted to the crossing of scalariform perforation plates. This type occurs, however, in fungi which colonise both conifer and deciduous wood.

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