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Spatial pattern of the density of *Armillaria* epiphytic rhizomorphs on tree collar in an oak stand

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Summary

The density of *Armillaria gallica* epiphytic rhizomorphs on tree collar was mapped in a young stand of pedunculate oaks (*Quercus robur*). A quick method to estimate the rhizomorphs density was developed, investigating 19 trees, and was used in the subsequent study. The method consists of measuring the frequency of rhizomorphs presence on a grid applied to an exposed small area of the tree collar. The pattern in tree collar rhizomorph density was closely related to the pattern of stump colonisation by *Armillaria* and stumps were therefore important as inoculum sources. Rhizomorph density on tree collar showed a strong aggregated spatial pattern which could not be explained by variability in the soil characteristics, in particular waterlogging, or by a spatial pattern in tree vigour. Also, rhizomorph density on tree collar did not depend on their dominance status.

1 - Introduction

Oak forests of Europe have experienced several decline episodes in the 20th century. Those declines were usually attributed to the combined action of several biotic and abiotic stress factors operating in sequences (OLEKSYN and PRZYBYL, 1987; LANDMANN et al. 1993). *Armillaria* root disease has often been one of the biotic factors associated with past oak decline (DELATOUR, 1983; THOMAS et al. 2002). Primarily two species of *Armillaria*, *A. mellea* and *A. gallica*, were shown to be involved in oak decline in Europe (GUILLAUMIN et al. 1985; SICOLI et al. 1998). *A. gallica* is a frequent secondary parasite of hardwoods while *A. mellea* is a more aggressive species, being frequently a primary pathogen on hardwood (WARGO and HARRINGTON, 1991). However, artificial inoculation trials showed that both pathogens are not very aggressive on oaks such as *Q. pubescens*, *Q. frainetto* or *Q. cerris* (SICOLI et al. 2002). The importance of the *Armillaria* role in the decline process is difficult to assess, although the fungus might influence the recovery of weakened trees (GUILLAUMIN et al. 1985). *A. gallica* is almost always present in hardwood forests as epiphytic rhizomorphs, i.e. rhizomorphs attached to the bark surface of the roots and root collars of living trees (PRONOS and PATTON, 1978; MARÇAIS and WARGO, 2000). Healthy trees can usually prevent colonisation of the roots by these rhizomorphs and only limited lesions are observed at points where rhizomorphs are attached to the bark. However, trees weakened by other factors such as defoliation are often killed by the fungus (WARGO and HARRINGTON, 1991).

Inoculum potential, defined by GARRETT (1956) as a combination of rhizomorphs abundance at the host surface and of vitality of those propagules, has been considered as an important feature determining *Armillaria* aggressivity. Indeed, increased *Armillaria* incidence following logging was reported in conifer forests of NW America (KOENIGS, 1969 ; McDONALD et al. 1987) or in the eucalyptus forest of Australia (KELLAS et al. 1987 ; PEARCE et al. 1986).

It was shown that *Armillaria* is able to quickly invade logging stumps from quiescent lesions and subsequently develop an increased inoculum potential in the vicinity of the stumps, resulting in increased infection of the surrounding trees (KELLAS et al. 1987; PEARCE et al. 1986; STANOSZ and PATTON, 1991; CRUICKSHANK et al. 1997; MORRISON et al. 2001). The importance of inoculum potential for aggressivity of secondary pathogen species such as *A. gallica* is by comparison poorly documented. However, HOUSTON and KUNTZ (1964) showed that defoliated sugar maple trees (*Acer saccharum*) were more often killed when they were closer to stumps, suggesting an importance of *Armillaria* inoculum potential.

Verifying the importance of *A. gallica* inoculum potential in oak decline events is complicated. Indeed, as *A. gallica* is a secondary pathogen, one would have to test the ability of the trees exposed to different levels of inoculum potential to overcome a stress. However, methods that have been used to measure the amount of epiphytic rhizomorph on tree collar require extensive digging and thus largely disturb the rhizomorph network at the tree base (MARÇAIS and WARGO, 2000). Moreover, as *A. gallica* is more aggressive on weakened trees, it is possible that the trees exposed to high density of epiphytic rhizomorphs on the collar are in fact trees less vigorous, i.e. trees that were subjected to more past stress and have a lower growth. If this is the case, difference of behaviour between trees subjected to different levels of *Armillaria* inoculum potential might more reflect difference of vigour and comparing high / low inoculum potential trees might be misleading. The objectives of this study were thus to develop a method to measure *A. gallica* inoculum potential at the tree base that does not disturb too severely the rhizomorph network and to determine whether there is a relationship between trees vigour, defined by past growth, and the density of epiphytic *Armillaria* rhizomorphs on their collar.

2 - Material and methods

2.1 - Studied stand

The stand was an even-aged, 20-years-old, natural regeneration of *Quercus robur*, the pedunculate oak tree. The trees were 8-12 cm dbh and were located in the stand 7 of the Champenoux communal forest (Meurthe-et-Moselle, NE France). The stand density was about 10000 stem.ha⁻¹. The stand had been thinned 2-3 years before the experiment, leaving small 5-8 cm dbh stumps (10000 ha⁻¹). Oaks were the dominant trees with an understory of mainly hornbeam (*Carpinus betulus*). The soil was an hydromorphic clayed loam with a calcareous clay layer appearing 30-45 cm from soil surface. The soil was fertile with an eutroph mull humus layer and a pH measured in water of 4.7. Stumps from the previous stand had a density of 120 ha⁻¹ and were from oak and hornbeam.

2.2 - Determining epiphytic rhizomorph density on tree collar

The amount of *Armillaria* rhizomorphs was estimated on the collar area of nineteen oaks. The first estimate was done using a grid applied to the tree collar. The grid was a 5.5 X 5.5 cm black plastic sheet with 25 circular holes 6 mm in diameter arranged on a 1 x 1 cm grid. A part of the collar about 7-8 cm wide was exposed, gently washed with a soft brush and water, removing all fine roots and soil present at the bark surface. The plastic sheet was pinned on the cleaned collar area just beneath the soil level. The number of sheet 6-mm diameter holes where rhizomorphs were present was then counted to estimate rhizomorph density. The area exposed represented 15-20 % of the collar perimeter and the grid itself 12-18 %.

After having done this quick estimate of rhizomorph density, a more thorough estimate was done by exposing the total collar of the tree, gently washing it as previously described, and sampling all rhizomorphs that were tightly attached to the collar, discarding the parts that were further than 5 cm from last attachment point to the bark. Rhizomorphs were sampled on the first 10-cm from soil surface and no further than 5 cm from collar on lateral roots. The

sampled rhizomorphs were brought to the laboratory, gently washed in tap water to remove soil and residual fine roots, oven dried at 65 °C for 24 h and weighted. The density of rhizomorph was then computed by dividing the total dry weight by collar area estimated by the collar perimeter at soil surface multiplied by 10-cm, which is the width of the sampled collar band. This density was then related to the quick estimate done with the plastic sheet by linear regression analysis, using SAS (SAS/STAT 8.1, SAS Institute Inc., Cary, NC).

2.3 - Mapping the colonisation of tree collar by epiphytic *Armillaria* rhizomorphs

The density of *Armillaria* epiphytic rhizomorphs on the collar was estimated on 136 dominant pedunculate oak trees scattered within the stand by using the grid method previously developed. The trunk diameters at breast height were recorded. The selected trees represented about 10-20 % of the stand and were selected in order to have trees that were homogeneously distributed in space. To obtain a map of the studied trees, we first mapped the stand stumps, which were large stumps created when the stand was regenerated, 20 years before. They were mapped by measuring the distance and angle between each stump and its 2-4 immediate neighbours using a compass and a laser distance meter (DISTO Classic 10.0, Leica geosystem AG, Heerbrugg, Switzerland). The studied trees were mapped in a second step by measuring the distance and angle to the nearest mapped stump. A Random sample of epiphytic *Armillaria* rhizomorphs was collected on the collar of 37 of the mapped trees for species determination by PCR-RFLP analysis of the IGS region of ribosomal DNA (HARRINGTON and WINGFIELD 1995). DNA was extracted from 3 rhizomorph pieces about 0.5 cm in length and their IGS Alu1 digestion pattern was compared to haploid testers kindly provided by J.J. Guillaumin that were used as reference (3 isolates for each of *A. cepistipes*, *A. gallica*, *A. mellea* and *A. ostoyae*).

The rhizomorphs dry weight per unit area was the computed using the previously established calibration. In order to study the spatial pattern of epiphytic rhizomorph density within the stand, a variogram was computed using the procedure VARIOGRAM of SAS and a lag distance of 2.5 m that enabled to have a minimum 30 pairs of trees per lag. A spherical model was fitted to the variogram: $V = C_0 + C_1 \times (1.5 \times (L/R) - 0.5 \times (L/R)^3)$ if $L < R$ and $V = C_0 + C_1$ otherwise, with C_0 , the nugget, C_1 the sill, R the range and L , the mean distance between the lag pairs.

2.4 - Assessing causes of collar rhizomorph density variability among trees

Ten pairs of neighbour trees 1-2 m apart were selected throughout the stand with one of the pair being a dominant tree and the other a suppressed/intermediate tree. The amount of epiphytic rhizomorphs was determined by sampling and weighting all rhizomorphs on the collar as previously described on the 19 trees. All old stumps from the previous stand within 15 m from the sampled trees were examined for *Armillaria* colonisation and their distance to the trees was recorded. Level of colonisation was rated by the effort needed to find evidence of *Armillaria* colonisation in the form of rhizomorphs firmly attached to the stumps or/and mycelial fans or pockets of decay typical of *Armillaria* in the wood on a zero to four scale: (4) evidence of colonisation was visible without any need to excavate, with rhizomorphs growing out of stump surface, (3) evidence of colonisation after excavation of less than 10% of the stump perimeter, (2) evidence of colonisation found after excavation of 10-50 % of the stump perimeter, (1) evidence of colonisation after excavation of more than 50% of the stump perimeter, (0) no evidence of colonisation. The estimation of the *Armillaria* colonisation of neighbouring stumps was also done as just described for 13 of 19 trees used for the calibration of the grid assessment of collar rhizomorph density. A soil core was extracted with a earth auger at the base of 18 trees as scattered in the stand as possible; 8 trees were selected with very low density of epiphytic rhizomorph on the collar (<1.5 mg.cm⁻² dry weight) and 10 others with high density (> 5 mg.cm⁻²). The 2 main characteristics of the soil that might have shown variability within the stand, i.e. depth of appearance from soil surface of first trace of mottling linked to water logging and of the calcareous clay layer were recorded.

3 - Results

The quick count of the proportion of grid point with rhizomorphs on a small portion of the young oak collar using the 5.5 x 5.5 cm plastic sheet enabled us to have a relatively good estimate of the *Armillaria* rhizomorph density on the whole tree collars (Fig. 1). The relationship between proportion presence of rhizomorphs (Pr, based on the count from the 25 plastic sheet holes of 6 mm diameter) and the dry weight of rhizomorphs per unit collar area (RDW) was: $\text{Log}(\text{RDW}) = 3.043 \times \text{Pr} - 0.514$ ($r^2 = 0.815$).

The density of epiphytic rhizomorphs varied in the same stand from less than 0.5 mg.cm^{-2} dry weight to over 10 mg.cm^{-2} . The *Armillaria* species present on the tree collars all had IGS Alu1 digestion patterns that were identical to the *A. gallica* testers. No other

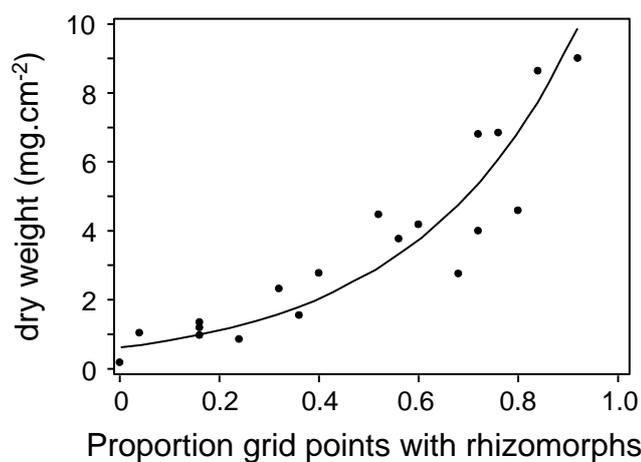


Fig. 1. Relation between the presence of *Armillaria* rhizomorph in 6 mm diameter holes of the 5.5 x 5.5 cm sheet and rhizomorph dry weight per surface area on the entire collar of 20-year-old oak trees. The line represents the curve $\text{Log}(Y) = 3.043 \times X - 0.514$; $r^2 = 0.815$.

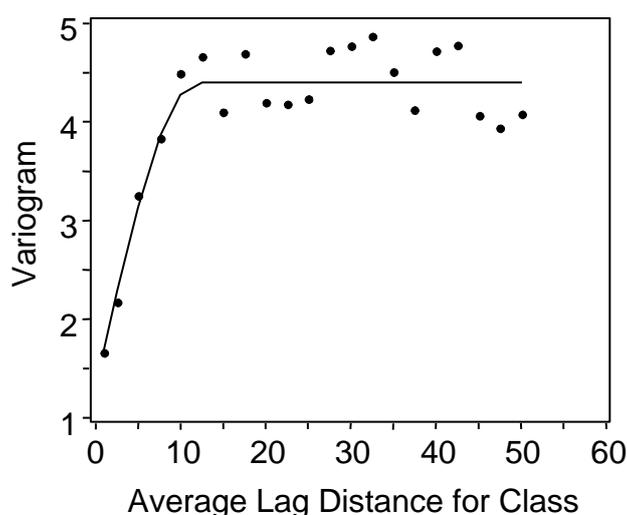


Fig. 2. Variogram of epiphytic rhizomorph dry weight on tree collar. The line represents a spherical model with a range of 12 m, a sill of 3.1 and a nugget of 1.3. The variogram at k represent half of the mean value of $(V_i - V_j)^2$, V_i and V_j being the rhizomorph dry weight on all pairs of i and j

trees that are at a distance of $k \pm 1.25$ m apart.

Armillaria species were detected on the tree collars. Altogether, there was no relationship between tree dbh and the density of epiphytic rhizomorphs on the tree collar (Spearman's $r = 0.086$, $p = 0.371$). The plotted variogram showed that the rhizomorph density on tree collar exhibited within the studied stand a strongly aggregated spatial pattern with a range of about 12 m, a sill of 3.1 and a nugget of 1.3 (Fig. 2). This means that trees that are less than 12 m apart tend to be alike while this is not anymore the case for trees further than 12 m apart. It can be seen on Figure 3 that patches of trees with a high density of rhizomorphs on tree collar alternate with patches of trees poorly colonised by the epiphytic rhizomorphs.

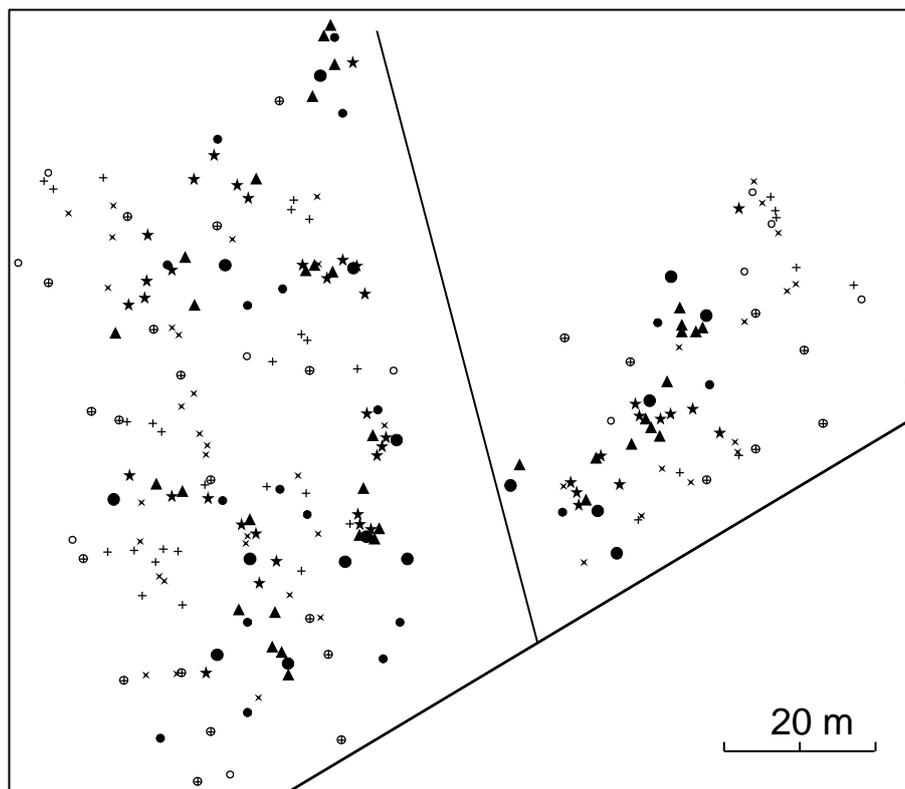


Fig. 3. Map of *Armillaria* rhizomorphs density on tree collar: location of the studied trees and stumps in the plot. Density of epiphytic collar rhizomorphs: +, $< 1.1 \text{ mg.cm}^{-2}$; ×, $1.1 - 2.8 \text{ mg.cm}^{-2}$; ★, $2.8 - 4.7 \text{ mg.cm}^{-2}$; ▲, $> 4.7 \text{ mg.cm}^{-2}$. Stump colonisation: ○, 0; ⊕, 1; ●, 2; ●, 3. The lines represent paths.

The density of rhizomorphs on the collar was not different between the dominant and the suppressed/intermediate trees ($2.5 \pm 0.9 \text{ mg.cm}^{-2}$ and $3.1 \pm 1.6 \text{ mg.cm}^{-2}$ respectively, paired $t = 0.84$, $p = 0.424$). No differences in the soil characteristics could be evidenced between trees with high or low density of rhizomorphs on the collar. The mean depth of appearance of the first traces of mottling were 9 ± 2.8 cm for trees with a collar rhizomorphs dry weight of over 5 mg.cm^{-2} and 8.1 ± 3.1 cm for those with less than 1.5 mg.cm^{-2} (student $t = 0.48$, $p = 0.638$). The difference was also not significant for depth of calcareous clay appearance (respectively 36 ± 3.3 cm and 34 ± 5.2 cm, student $t = 0.82$, $p = 0.430$). By contrast, the density of epiphytic rhizomorphs on a tree collar was significantly related to the sum of neighbour stumps colonisation rating weighted by the inverse of their distance to the tree (Pearson's $r = 0.575$, $p < 0.001$, Fig. 4). Thus, the more stumps well colonised by

Armillaria were present close to a tree, the denser epiphytic rhizomorphs were on the tree collar. Indeed, it can be seen on Figure 3 that the patches of trees with dense rhizomorph colonisation of the collar correspond to places where the stumps were well colonised and that by contrast, locations where the density of epiphytic rhizomorphs on the collar is scarce are locations where the colonisation of the nearby stumps is low.

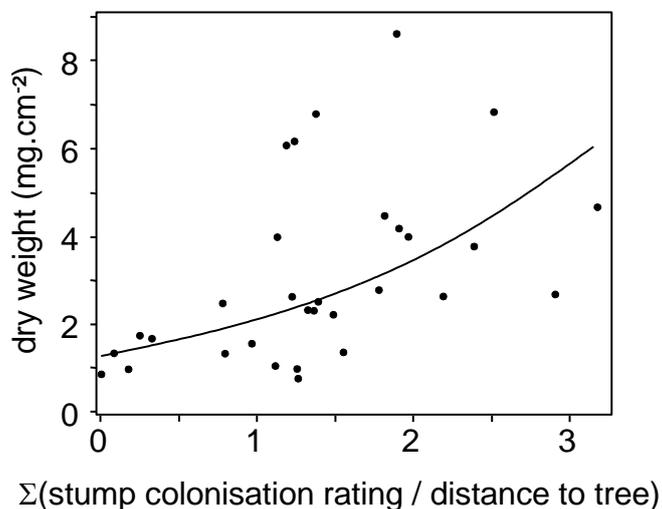


Fig. 4. Relation between rhizomorph density on the collar and number and degree of colonisation by *Armillaria* of stumps in the vicinity. The line represent the curve $Y = \exp(0.49 \times X + 0.24)$; $r^2 = 0.331$.

4 - Discussion

This work thus presents a relatively precise and quick way to estimate the amount of epiphytic rhizomorphs on a tree collar. Although it is invasive, it does not disturb the *Armillaria* rhizomorph system on tree collar too much, especially as tree becomes large. Even on the young about 20-years-old trees used in this study, the collar area exposed and thus potentially disturbed represented only 15-20 % of the total collar perimeter.

We used this method to study the variability of epiphytic rhizomorph density on the collar of oak trees in a single stand. Despite the fact that the stand was rather homogeneous, as far as the soil and stand structure are concerned, the density of *Armillaria* rhizomorphs on tree collar presented a very high variability within the stand, with a highly clumped spatial pattern. This variability could not be related to tree characteristics such as dominance or vigour. Obviously, tree to tree variability such as dominance status can not be the factor underlying the spatial pattern with clumps of a range of 12 m. However, as the variogram shows a nugget effect, some tree to tree variability in density of epiphytic rhizomorphs might occur. Alternatively, this nugget effect could be due to experimental error in the collar rhizomorph density measure. The spatial pattern of a 12-m range could also not be related to a factor that would have strongly impacted tree vigour as reflected by past tree growth. Indeed, no relation could be evidenced between tree dbh and epiphytic rhizomorph density on the collar. Also, no spatial pattern in tree dbh could be evidenced in the stand when a variogram was computed (result not shown). In agreement with this result, the variability in collar rhizomorph density could not be related to any variability in the soil characteristics. Thus, although less vigorous trees, in particular suppressed ones, are known to be more susceptible to *A. gallica* (REDFERN, 1978; DAVIDSON and RISHBETH 1988), we could not evidence a greater colonisation of the less vigorous oak trees by epiphytic rhizomorphs of that pathogen.

By contrast, the density in epiphytic rhizomorphs could be strongly related to the presence of *Armillaria* food base in the vicinity of the tree. This was expected in the light of the abundant literature that shows that abundance of rhizomorphs in soil strongly increases nearby wood pieces and in particular stumps colonised by *Armillaria* (PRONOS and PATTON 1978; TWERY et al. 1990; STANOSZ and PATTON 1991; MARÇAIS and WARGO 2000). It would thus appear that the former stand history, and in particular the pattern of stump colonisation at the final felling of the previous stand, was the main factor determining the spatial pattern of collar colonisation by the *A. gallica* epiphytic rhizomorphs in that stand. The pattern of stump colonisation could have been affected by many factors including the presence of *Armillaria* genotypes of differing aggressivity, and species and history of the previous crop trees, in particular the way they died (BURRILL et al. 1999).

The consequences of the variability of *A. gallica* inoculum potential for the trees remain difficult to evaluate. It has been well demonstrated that trees subjected to a high inoculum potential of aggressive species such as *A. ostoyae* or *A. luteobubalina* are at greater risk of developing *Armillaria* root disease (CRUICKSHANK et al. 1997; KELLAS et al. 1987; MORRISON et al. 2001; PEARCE et al. 1986). However, *A. gallica* is a weak pathogen and, on oaks, is not likely to severely damage trees unless they have been weakened by some other stress factors (DAVIDSON and RISHBETH 1988; SICOLI et al. 2002; WARGO and HARRINGTON 1991). It is thus possible that inoculum potential is not of the same importance for this pathogen as it is for *A. ostoyae*. It is likely however that trees with abundant epiphytic rhizomorphs on the root collar are more readily colonised by *A. gallica* when they are cut down. Stands such as the one studied in this work where *A. gallica* inoculum potential shows a high variability within a relatively homogeneous environment are suitable places to assess its consequences for the trees.

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Résumé

Patron spatial de densité de rhizomorphes épiphytes sur les collets des arbres dans un peuplement de chênes

Nous avons cartographiés la densité des rhizomorphes épiphytes d'*Armillaria gallica* (Marxm. & Romagn.) sur le collet des arbres dans un jeune peuplement de chênes pédonculés (*Quercus robur*). Une méthode rapide pour estimer la densité de rhizomorphes a été mise au point sur 19 arbres et a été utilisée ultérieurement. Cette estimation a été faite en comptant la fréquence des rhizomorphes épiphytes sur une grille appliquée sur une petite zone du collet qui avait été dégagée. Le patron spatial de densité de rhizomorphes était étroitement relié au patron spatial de colonisation des souches par l'*Armillaire*; celles-ci ont donc représenté une source d'inoculum importante. La densité de rhizomorphes épiphytes sur le collet des arbres présentait un patron spatial agrégé qui ne pouvait pas être expliqué par une hétérogénéité dans les caractéristiques du sol, en particulier l'hydromorphie, ou par un patron spatial de la vigueur des arbres. La densité de rhizomorphes ne dépendait pas non plus du statut social des arbres.

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