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## Soil factors associated with infection by *Collybia fusipes* and decline of oaks

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### Summary

*Collybia fusipes* is the cause of a root rot of oaks in Europe. Infection by the pathogen is site dependent and inconsistently correlated with crown deterioration. This study aimed at clarifying the relationship between soil factors and *C. fusipes* impact on tree health. The database of the Département de la Santé des Forêts, the forest health survey service, collected over the French forest during the last 12 years allowed us to perform a large scale study dealing with soil textures in which *C. fusipes* was reported to induce problems on *Quercus robur* and/or *Q. petraea*. Furthermore, a specific survey from 30 plots in north eastern France was carried out to determine which of the soil factors, such as texture, degree of waterlogging, presence and nature of a layer limiting rooting, carbon/nitrogen ratio, cation exchange capacity, or pH could be related to an increased risk of decline of pedunculate oaks infected by *C. fusipes*. The main results were that *C. fusipes* is preferentially distributed on coarse textured soils and that its impact on tree crown appearance also increased with the soil sand content.

### 1. Introduction

*Collybia fusipes* (Bull.:Fr) Quéél. is the cause of an oak root rot in Europe. This fungus has been first mentioned in association with the decline of pedunculate oak in 1983 (DELATOUR and GUILLAUMIN 1984, GUILLAUMIN *et al.* 1985). *C. fusipes* is widespread throughout the French oak forests (MARÇAIS *et al.* 1998-a, PIOU *et al.* 2002). Its basidiomes are frequent from spring to autumn, occurring in clumps at the base of living trees. The basidiome clumps are connected to infected roots through a perennial organ, the pseudorhiza (BULLER 1958). Based on field surveys, MARÇAIS *et al.* (2000) and PIOU *et al.* (2002) have shown that *C. fusipes* basidiomes are good indicators of root infection. A research program was initiated 10 years ago to determine the role of this pathogen in the oak decline syndromes and to find in which type of site it could be an important factor involved in the decline process.

*C. fusipes* is a slow primary parasite able to induce typical orange lesions located on large roots and root collar. It can induce a drastic destruction of the root system (MARÇAIS and DELATOUR 1996, MARÇAIS *et al.* 1999). Disease frequency is higher in pedunculate (*Quercus robur* L.) and red oak stands (*Q. rubra* L.) as compared to the sessile oak ones (*Q. petraea* Liebl.) (MARÇAIS *et al.* 1998-a, PIOU *et al.* 2002), reflecting different susceptibility of these three oak species to the parasite (MARÇAIS and CAËL 2000). Field observations also showed that this parasite has a higher incidence in coarse textured soils (unpublished data). A field study carried out in five oak stands, evidenced that severe *C. fusipes* root infection could not always be correlated with deterioration of oak crown. The causes of this inconsistent relationship between infection of the oak and their decline still remained unclear, although it appeared that it could be related with coarseness of the soil texture, and possibly to the water holding capacity of the soil (MARÇAIS *et al.* 2000). However, although severe root infections induced by *C. fusipes* were not always associated with a deterioration of the tree

crown, they were associated with a reduction in tree growth in all the stands studied (MARÇAIS and CAËL 2001). Soil conditions, in particular soils with coarse texture have been mentioned to be related with increasing impact and incidence of root rot diseases, such as those induced by *Armillaria ostoyae* (MALLETT and MAYNARD 1998, Whitney 1984, WIENSCYK *et al.* 1997) or *Heterobasidion annosum* (ALEXANDER *et al.* 1975, BAKER *et al.* 1993, FROELICH *et al.* 1966).

This study aimed at clarifying which soil conditions promote *C. fusipes* incidence in oak stands. At first, the relationship between soil texture, decline of oaks and *C. fusipes* was studied at a large scale using data collected during the last 12 years by the Département de la Santé des Forêts (DSF), the French forest health survey service. Thereafter, a specific survey was carried out in north eastern France to determine which soil factors could be related with an increased risk in the decline of pedunculate oaks infected with *C. fusipes*.

## 2. Materials and methods

### 2.1. Analysis of the database of the French forest health survey service (DSF)

#### 2.1.1. Information available in the DSF database

The database of the DSF was used to study in which type of site *C. fusipes* root rot was reported to cause problems in France on *Q. robur* and/or *Q. petraea*. This database, created in 1989, is a compilation of reports made by a network of foresters who are trained to diagnose all types of forest health problems *i.e.* abiotic, entomological or pathological. Health problems of *Q. robur* and/or *Q. petraea* were reported 10 000 times between 1989 and 2001, with 161 reports involving *C. fusipes* root rot. The majority of reports in the database refers to defoliation by insects (61 %), powdery mildew (8 %), decline (8.5 %) and frost damages (5 %). Site characteristics used in this study were stand age, soil texture, degree of soil waterlogging and the dominant oak species. Soil textures were reported as clay, loam or sand as dominant and secondary textures. They were grouped in the following categories according to the overall frequency: (1) clay as dominant and clay or loam as secondary textures, (2) loam as dominant and clay as secondary texture, (3) loam as both dominant and secondary texture, (4) loam as dominant and sand as secondary texture and (5) sand as dominant and loam or sand as secondary textures. Waterlogging was reported as severe or non severe logging. Not all reports contained the necessary information, so only those including this information were considered in the analysis.

#### 2.1.2. Database investigations

As *C. fusipes* is known to be mainly a problem of mature trees (MARÇAIS *et al.* 1998-a) and as no mention of the pathogen was made in young stands, only reports referring to mature stands, or to stands older than 80 years, or higher than 15 m where taken into account. Care was also taken to consider stands only once when problems were reported in the same stand over several years.

In the DSF database, the characteristics of the stands where *C. fusipes* was reported were first compared to those of stands where health problems other than *C. fusipes* were reported (respectively 119 and 2402 stands). This was done using chi-square tests.

The distribution of soil textures in stands where *C. fusipes* is mentioned in the DSF database was also compared with the one observed in the 154 *Q. robur* / *Q. petraea* stands of the French part of the European forest health monitoring network (ICP-Forests, International Co-operative Programme on Assessment and Monitoring of Effects of Air pollution on Forest), hereafter called 'European network'. This network is established in a systematic way, on a 16 km x 16 km grid and was used to establish the reference distribution of soil texture over the French oak forest. Because the trained foresters of the DSF are very

unevenly distributed throughout the whole territory, it induces a bias in the distribution of the *C. fusipes* reports which differs significantly from the oak stand distribution observed in the

**Table1.** Description of plot characteristics of the plot survey

Plot	Region	Number of oaks (%) infected	Stand	Soil layer limiting rooting	%sand	pH	<i>Quercus</i> species
Adelans	Haute-Saône	41 (27)	Old coppice with beech and oak standards	None until 120 cm	7.8	4.8	<i>Q. robur</i>
Ainvelle 1	Haute-Saône	38 (32)	Old coppice with oak standards	None until 120 cm	17.8	4.5	<i>Q. robur</i>
Ainvelle 2	Haute-Saône	42 (36)	Old coppice with oak standards	Gravel layer 80 cm	47.2	4.1	<i>Q. robur</i>
Ainvelle 3	Haute-Saône	40 (38)	Old coppice with oak standards	None until 120 cm	65.2	4.3	<i>Q. robur</i>
Amance	Meurthe-et-Moselle	34 (32)	Old coppice with oak standards	Clayey hardpan 70 cm	10.5	5.7	<i>Q. robur</i>
Saint Aubin 1	Jura	40 (38)	Old coppice with oak standards	Fragipan 50 cm	9.5	4.8	<i>Q. robur</i>
Saint Aubin 2	Jura	38 (42)	Old coppice with oak standards	Fragipan 50 cm	9.5	4.8	<i>Q. robur</i>
Les Aynans 7	Haute-Saône	33 (45)	Old coppice with oak standards	Clayey hardpan 70 cm	20.1	4.2	<i>Q. robur</i>
Les Aynans 28	Haute-Saône	39 (33)	Coppice with oak standards	Gravel layer 70 cm	57.5	4.1	<i>Q. robur</i>
Les Aynans 35	Haute-Saône	42 (40)	Old coppice with oak standards	Gravel layer 80 cm	56.2	4.5	<i>Q. robur</i> + <i>Q. petraea</i>
Champagney	Haute-Saône	39 (28)	Beech and oak standards	None until 120 cm	46.4	4.2	<i>Q. robur</i>
Champenoux	Meurthe-et-Moselle	40 (33)	Old coppice with oak standards	Clayey hardpan 60 cm	8.7	5	<i>Q. robur</i>
Equevilley	Haute-Saône	42 (38)	Old coppice with beech and oak standards	None until 120 cm	40.6	4.5	<i>Q. robur</i>
Filain	Haute-Saône	50 (8)	High forest of oaks	Clayey hardpan 75 cm	3.6	5.8	<i>Q. robur</i> + <i>Q. petraea</i>
Gouhenans	Haute-Saône	32 (31)	Old coppice with beech and oak standards	None until 120 cm	8.1	4.7	<i>Q. robur</i>
Gremecey	Meurthe-et-Moselle	38 (39)	Old coppice with oak standards	Clayey hardpan 50 cm	2.3	4.4	<i>Q. robur</i> + <i>Q. petraea</i>
Hautevelle	Haute-Saône	42 (33)	Old coppice with beech and oak standards	Clayey hardpan 80 cm	17.3	5.3	<i>Q. robur</i> + <i>Q. petraea</i>
Saint Hilaire	Doubs	28 (50)	Old coppice with beech and oak standards	Fragipan 80 cm	11.2	4.9	<i>Q. robur</i> + <i>Q. petraea</i>
Lure	Haute-Saône	38 (47)	Old coppice with beech and oak standards	Gravel layer 60 cm	47.5	4.7	<i>Q. robur</i>
Mailleroncourt	Haute-Saône	41 (39)	High forest of beech and oaks	Gravel layer 70 cm	8.6	4.8	<i>Q. robur</i>
Mersuay 36	Haute-Saône	41 (44)	Old coppice with oak standards	Gravel layer 70 cm	62.5	4.5	<i>Q. robur</i>
Mersuay 5	Haute-Saône	50 (22)	Old coppice with oak standards	Gravel layer 70 cm	26.7	5.2	<i>Q. robur</i>
Roye	Haute-Saône	47 (53)	High forest of oaks and beeches	None until 120 cm	16.1	4.5	<i>Q. robur</i>
La Tour de Sçay	Doubs	35 (31)	Old coppice with beech and oak standards	Gravel layer 90 cm	32.3	4.4	<i>Q. petraea</i> + <i>Q. robur</i>
Vauvillers 1	Haute-Saône	39 (26)	Old coppice with beech and oak standards	Clayey hardpan 70 cm	7.8	5.2	<i>Q. robur</i>
Vauvillers 2	Haute-Saône	40 (33)	Old coppice with beech and oak standards	Clayey hardpan 70 cm	10.2	5	<i>Q. robur</i>
Villers Grélot	Doubs	38 (34)	Old coppice with beech and oak standards	None until 120 cm	3.7	4.8	<i>Q. robur</i> + <i>Q. petraea</i>
Villey St Etienne	Meurthe-et-Moselle	51 (41)	Old coppice with oak standards	Gravel layer 60 cm	68.4	4.3	<i>Q. robur</i>
Vitrimont	Meurthe-et-Moselle	43 (51)	High forest of oaks and beeches	Gravel layer 80 cm	64.2	4.1	<i>Q. robur</i> + <i>Q. petraea</i>
Vy les Lures	Haute-Saône	41 (44)	Coppice with oak standards	Fragipan 90 cm	10.7	5.4	<i>Q. robur</i>

NOTE: the sand content was evaluated at 30 cm below the soil surface with the sulfochromic method. The pH at 10 cm below the soil surface was measured using 10 g of dry soil in 50 ml of deionized water.

European network. To take this ‘observer bias’ into account, France was divided into five areas and a weight was attributed to DSF reports of each areas. This weight for each area was computed as  $PA_{en} / PA_{r-dsf}$ , where  $PA_{en}$  is the proportion of the oak stands found in the European network for a specific area and  $PA_{r-dsf}$  the proportion of DSF reports concerning

*Q. robur* / *Q. petraea* for this area. This way a large weight was attributed to reports coming from areas with few reports compared to their importance in the french oak forest. The European network was used to generate a theoretical soil texture distribution in the oak forest and the distribution of *C. fusipes* reports in the soil texture categories was compared to it by chi-square tests, each reports being weight by  $PA_{en} / PA_{r-dsf}$ .

In the DSF database, the soil texture of stands where *C. fusipes* was associated with oak decline was also compared to soil texture of stands where *C. fusipes* was not associated with decline, using chi-square tests. A report of *C. fusipes* was considered to be associated with a decline problem whenever either a decline was explicitly reported, mortality or secondary organisms such as *Agriolus* sp. or *Armillaria* sp. were reported and when the report was stated to concern more than only isolated trees.

## 2.2. Relationship between soil factors and decline risk of *C. fusipes* infected trees

### 2.2.1. Plot survey

Thirty oak stands with at least 25% of the trees infected by *C. fusipes* were selected in north eastern France. Twelve of these plots were also reported in the DSF database. Half of the plots were pure stands of pedunculate oaks, while the other half were stands of pedunculate oaks mixed with sessile oaks or beech (*Fagus sylvatica* L.). Stands were all older than 90 years. Soil textures, pH and the vertical rooting limits were variable between plots (Table 1).

In each plot, a group of 28 to 51 contiguous pedunculate oaks located in an area of about 5000 m<sup>2</sup> was selected (Table 1). All the pedunculate oaks present were selected, independently of their social status. The oak species was determined based on leaf morphology observed with binoculars. In mixed oak stands, sessile oaks were not included in the sample. During the period of basidiome production, presence/absence of *C. fusipes* infection was assessed for each tree. The root collar and the major roots were carefully inspected for presence of basidiomes or pseudorhiza. Pseudorhizae are persistent dark stroma-like fungal structures of 2-5 cm diameter that connect *C. fusipes* basidiome clusters with the root (BULLER 1958).

Crown health status was assessed for each tree. It was rated in two categories, *i.e.* heavily or not declining according to an adaptation of the rating system proposed by NAGELEISEN (1995): (0) crown healthy or moderately declining, with less than 50% defoliation; (1) crown severely declining, with large dead limbs in the upper part of the crown and/or loss of more than 50% of fine branches.

On each plot, a pit was dug near a tree located in the middle of the sampled oaks to observe soil characteristics. Soils were described specifically for the degree of waterlogging, *i.e.* depth at which appear the first signs of hydromorphia (reddish traces of insoluble oxidized iron deposition and / or discoloration indicating iron depletion) and for the presence and nature of a soil layer susceptible to limit vertical root growth. The vertical rooting limits were rated in 4 categories: absence of limits, presence of a gravel layer, a clayey hardpan or a fragipan (compacted silt). These soil parameters were also described at the base of two oaks located on opposite sides of the tree group by observation of a soil core extracted with an earth auger. The depth to waterlogging signs and to the layer limiting vertical root growth was taken into account as the mean of the three values observed in each group of trees. In each plot a sample of soil from a depth of 10 cm was analysed for carbon and organic matter (sulfochromic method), total nitrogen (Kjeldahl method), cation exchange capacity (cobaltihexamine method) and pH (10 g of dry soil in 50 ml of deionized water). Another soil sample, from a depth of 30 cm, was analysed in the laboratory for texture (%sand). All these soil analyses were carried out following the AFNOR norms for soil quality assessment (AFNOR 1999).

### 2.2.1. Statistical analysis of the plot survey

The likelihood of oak decline was analysed using logistic regression based on soil factors (sand content, depth at which appear the first waterlogging signs hereafter called waterlogging depth, soil pH, presence and nature of a soil layer limiting rooting, carbon/nitrogen ratio or cation exchange capacity) and presence of signs of *C. fusipes* infection (binary variable) as independent variables (genmod procedure) (SAS 1989). At first, each soil factor was tested individually, together with the presence or absence of infection signs by *C. fusipes* and the interaction between the studied soil factor and the infection variable. The model used was:

$$(1) \quad \text{Log} (p / (1-p)) = \alpha + \beta \text{ soil factor} + \gamma \text{ infection} + \delta (\text{soil factor} \times \text{infection})$$

where  $p$  is the likelihood of a tree being declining, 'soil factor' is the soil characteristic studied and 'infection' is the presence or absence of infection signs by *C. fusipes*. A sequence of nested models were fitted, beginning with the simplest model with only the intercept term and continuing through models of increasing complexity *i.e.* type 1 analysis. Residual deviances were computed for each successive model and the significance of the last introduced variable was assessed by computing the Pvalue of the deviance decrease associated with the introduction of the new variable (COLLETT, 1991). The model validity was checked using the deviance/degrees of freedom ratio, by plotting deviance residuals against the linear predictor and using a half-normal plot (COLLETT, 1991). Whenever a significant interaction 'soil factor x infection' was observed, *i.e.* whenever the impact of infection on tree decline status depended on the soil characteristic, the odds ratio  $\exp ((\gamma + \delta \times \text{soil factor}) \times \text{infection})$  was computed with "infection" taking the value of 1. This odds ratio is an estimate of the relative risk of decline for infected oaks, *i.e.* the increase in the likelihood of oaks showing signs of *C. fusipes* infection to be declining as compared to oaks without infection signs.

Then, the model (1) with the percent of sand content as a soil factor was compared with 2 more complex models: (i) the model (1) with waterlogging depth and the interaction infection x waterlogging depth as additional variables; (ii) the model (1) with the surface soil pH and interaction infection x soil pH as additional variables. The collinearity between the soil factors was assessed by comparing the residual deviance of model (i) or (ii) with the one of model 1 and testing whether the introduction of additional variables in those 2 models was associated with a significant drop in deviance.

## 3. Results

### 3.1. Analysis of the database of the French forest health survey service (DSF)

In the DSF database, presence of *C. fusipes* was mainly reported in *Q. robur* stands (67 %) and to a lower extent in *Q. petraea* or mixed *Q. robur/Q. petraea* stands (16-17% each). This distribution is significantly different from the one found for reports concerning health problems other than *C. fusipes*. Indeed, *C. fusipes* reports represent 8.5 % of the overall reports for *Q. robur*, 3.9 % for *Q. petraea* and 1.8 % for mixed *Q. robur/Q. petraea* stands ( $\chi^2 = 56.05$ ,  $df = 2$ ,  $p < 0.001$ ). The difference is even greater if one consider the *C. fusipes* reports associated with decline: they represent 5.4 % of the reports for *Q. robur*, 1.2 % for *Q. petraea* and 0.9 % for mixed *Q. robur/Q. petraea* stands. For the following analysis *C. fusipes* reports on *Q. petraea* and mixed *Q. robur/Q. petraea* were grouped together because of too low frequencies.

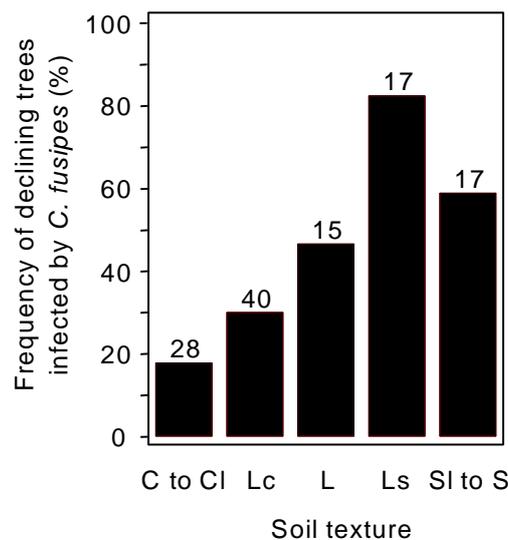
Only 87 reports (3.5 %) give information about the degree of waterlogging. So, the severity of waterlogging was not available for most of the reports. No significant relationship could be established between waterlogging and the incidence of *C. fusipes*, although 1.7% of the reports dealing with waterlogged soil were associated with the occurrence of *C. fusipes* and 3.6% with health problems other than *C. fusipes* (Fisher's exact test of 0.92,  $p = 0.144$ ).

For *Q. robur*, Table 2 shows that *C. fusipes* reports were distributed in categories of soil texture differently than the reports dealing with other kind of problems ( $\chi^2 = 89.22$ ,  $df = 4$ ,  $p < 0.001$ ). This was due to the infrequent mention of *C. fusipes* in fine textured soils (clay to loamy clay) and its high frequency in coarse textured ones (loamy sand to sand). A similar tendency was observed for the distribution in the soil texture categories of *C. fusipes* reports on *Q. robur* as compared with that of *Q. robur* European network stands, although the difference was not significant ( $\chi^2 = 7.61$ ,  $df = 4$ ,  $p = 0.107$ ). By contrast, for *Q. petraea* and mix *Q. robur/Q. petraea* stands, no difference in frequency distribution in terms of soil texture was observed between DSF reports of *C. fusipes* problems or of other problems ( $\chi^2 = 4.83$ ,  $df = 4$ ,  $p = 0.305$ , Table 2). The DSF reports of *C. fusipes* were more frequent than expected in fine textured soils as compared to oak stand frequency distribution in the European network (table 2,  $\chi^2 = 16.02$ ,  $df = 4$ ,  $p = 0.003$ ).

**Table 2.** Soil texture distribution for the DSF reports on oak concerning *C. fusipes* or other health problems, as well as the soil texture distribution observed for the oak stands of the European network. Textures are given as dominant (C: clay, L: loam or S: sand) and secondary (c: clay, l: loam or s: sand).

Reports of :	Soil texture					Number of stands.	
	C to Cl	Lc	L	Ls	Sl to S		
<i>Q. robur</i>	<i>C. fusipes</i> (DSF)	10.1 %	25.5 %	13.2 %	8.4 %	42.8 %	81
	Other problems than <i>C. fusipes</i> (DSF)	34.0 %	29.2 %	15.4 %	12.6 %	8.8 %	879
	European Network	10.4 %	33.3 %	16.7 %	10.4 %	29.2 %	48 <sup>a</sup>
<i>Q. petraea</i> and mixed <i>Q. robur / Q. petraea</i>	<i>C. fusipes</i> (DSF)	48.4 %	25.4 %	5.3 %	6.7 %	14.2 %	38
	Other problems than <i>C. fusipes</i> (DSF)	33.1 %	33.3 %	10.6 %	10.7 %	12.3 %	1523
	European Network	21.9 %	29.2 %	12.5 %	11.4 %	25.0 %	96 <sup>a</sup>

<sup>a</sup> No information was available on the presence or absence of *C. fusipes* in European Network stands



**Fig. 1.** Frequency of *C. fusipes* DSF database reports associated with oak decline in relation with soil textures. C, clay; Cl, loamy clay; L, Loam; Ls, sandy loam; Sl, loamy sand; S, sand. The total number of reports on which the frequency was computed are indicated above the bars

The frequency of *C. fusipes* reports associated with decline symptoms increased with the coarseness of the soil texture (Fig. 1) ( $\chi^2 = 22.65$ ,  $df = 4$ ,  $p < 0.001$ ). The relationship was similar for all types of stands (*Q. robur*, *Q. petraea* or mixed *Q. robur*/*Q. petraea*), so data of all stand types were pooled. The cases of oak decline associated with *C. fusipes* represented 9.3 % of the oak declines reported in the data base. However, if one take into account only decline reports on coarse soils (sandy loam to sandy texture) where *C. fusipes* root rot was shown to be more narrowly associated with decline, they represent 4.5 % of the decline reports over all oak species and 7.4 % of the decline reports on *Q. robur*.

### 3.2. Plot survey : influence of soil factors on the relative decline risk for oaks infected with *C. fusipes*

On average, 17% of oaks that showed signs of *C. fusipes* infection were rated as severely declining. However, this percentage varied between 0 and 60% among plots. By contrast, the average percentage of oaks with no signs of infection that were severely declining was 5% and varied between 0 and 13%.

The likelihood of decline was significantly influenced by signs of *C. fusipes* infection, soil sand content, pH and waterlogging depth (Table 3). Cation exchange capacity, carbon/nitrogen ratio or the nature of soil layer limiting rooting did not interact with *C. fusipes* infection (*i. e.* the interaction ‘soil factor x *C. fusipes* infection’ was not significant for these soil characteristics; results not shown). Conversely, the interaction between *C. fusipes* infection and soil factors such as sand content, waterlogging depth or pH was significant (Table 3). Indeed, Fig. 2 shows that the frequency of declining oaks with signs of *C. fusipes* infection increased with soil sand content, waterlogging depth and decreasing soil pH. These soil characteristics did not influence the decline frequency of oaks showing no signs of *C. fusipes* infection.

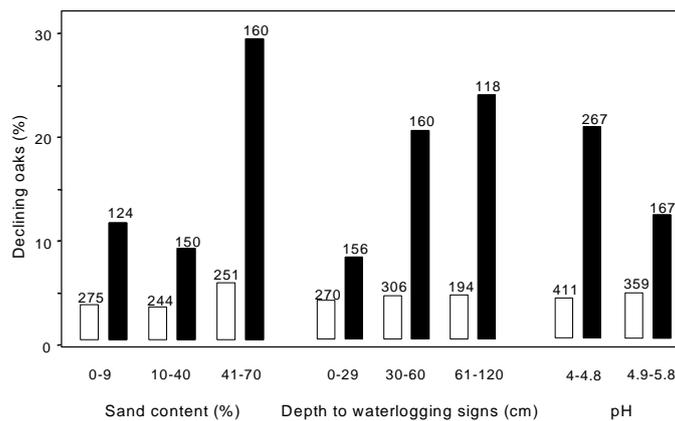
**Table 3.** Logistic regression analyses showing relationships between oak crown health status (rated as severely declining or healthy to moderately declining) and presence of *C. fusipes* infection signs, soil sand content, depth to waterlogging signs (traces of oxydized or depleted iron) and soil pH.

Model	Source	Deviance	Df	Chi-Square	Pr > Chi-Square
<b>1</b>	intercept	151.6	-	-	-
	infection	101.3	1	50.29	< 0.001
	sand content	77.4	1	23.88	< 0.001
	infection X sand content	70.4	1	7.02	0.008
<b>2</b>	intercept	151.6	-	-	-
	infection	101.3	1	50.29	< 0.001
	waterlogging	94.3	1	7.01	0.008
	infection X waterlogging	89.8	1	4.50	0.034
<b>3</b>	intercept	151.6	-	-	-
	infection	101.3	1	50.29	< 0.001
	pH	97.2	1	4.05	0.044
	infection X pH	62.1	1	5.15	0.023

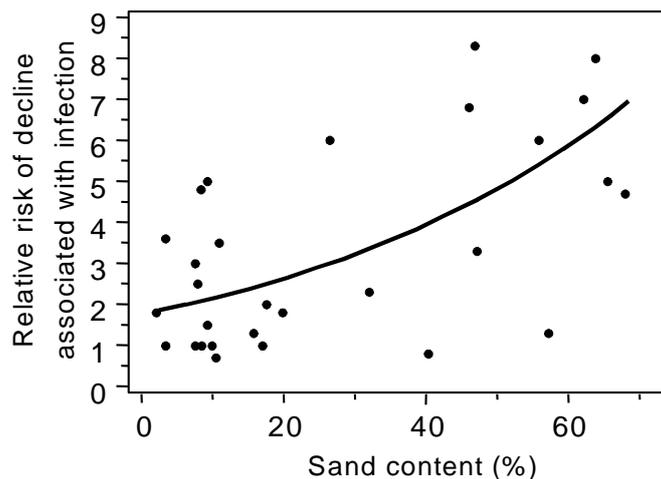
There was a strong collinearity between these three soil factors. Significant correlations were observed between soil sand content and the waterlogging depth as well as with soil pH (Pearson’s  $r$  of 0.52 and  $-0.62$  respectively,  $p < 0.003$ ) while waterlogging depth and soil pH were not significantly correlated ( $r = -0.28$ ,  $p = 0.131$ ). Adding the variable ‘waterlogging’ and the interaction ‘infection x waterlogging’ to model (1) (Table 3) did not reduce significantly the

deviance (likelihood Chi-Square of 0.8,  $p = 0.67$ ). Similarly, adding the variables 'soil pH' and the interaction 'infection x soil pH' to this model did not result in a significant drop in deviance (likelihood Chi-Square of 1.6,  $p = 0.45$ ).

The estimates of the odds ratio (OR) for the soil sand content, the waterlogging depth or the soil pH are given by the following equations:  $OR(\text{sand}) = \exp(0.57 + (0.025 \times \text{sand content}))$  (Wald test for  $\delta$  of 6.81,  $p = 0.009$ );  $OR(\text{waterlogging}) = \exp(0.69 + (0.02 \times \text{depth waterlogging}))$  (Wald test for  $\delta$  of 5.17,  $p = 0.023$ );  $OR(\text{pH}) = \exp(6.67 - (1.13 \times \text{soil pH}))$  (Wald test for  $\delta$  of 4.29,  $p = 0.038$ ). The increase with soil coarseness in relative decline risk for oaks showing signs of *C. fusipes* is illustrated in Figure 3.



**Fig. 2.** Percentage of declining pedunculate oaks for different soil sand content, depth to first waterlogging signs (traces of oxydized iron or depleted iron) or pH. Oaks non infected (□) and infected (■) by *C. fusipes*. Sand content of soil, depth to waterlogging signs and soil pH have been categorised. The total number of oaks in each category is given above the bars.



**Fig. 3.** Estimation of the relative decline risk for pedunculate oaks infected by *C. fusipes* in relation to soil textures. The line represents the odds ratio computed as:  $\exp(0.57 + 0.025 \times \text{sand content})$ . The fitted logistic model equation was:  $\log(p / (1 - p)) = -3.17 + 0.006 \times \text{sand content} + 0.57 \times \text{infection} + 0.025 \times \text{sand content} \times \text{infection}$ . To compute the relative risk, whenever no declining tree was present among trees without signs of *C. fusipes* infection, the frequency of decline for non infected was taken as 4 % which represent the mean decline rate of non infected trees for all studied plots.

## 4. Discussion

Our results clearly show that *C. fusipes* is preferentially distributed in coarse textured soils and that its impact on trees, evaluated through the likelihood of crown decline for infected trees, also increases with the soil sand content.

The DSF database was used to determine the relation between *C. fusipes* incidence and soil textures. Such a comparison is difficult to establish due to the lack of a proper reference. Taking as a reference the problems other than *C. fusipes* reported in the DSF database have the advantage that all site characteristics are readily comparable. However, this reference is potentially biased as it refers to sites with health problems. The European network represents a better view of the French oak forest due to its systematic nature. However, it is very difficult to use as a reference because of the very uneven distribution of DSF trained foresters in France and also because of the fact that site characteristics are not measured exactly in a similar way in each database. However, both comparisons yielded similar results.

These results agree with a previous study which showed that, at the plot scale, the severity of root damages induced by *C. fusipes* on *Q. robur* increased with an increase in soil sand content but decrease with the degree of waterlogging (CAMY *et al.* 2003-a). Furthermore, our results are in agreement with those of different field surveys concerning other root rot fungi, such as *A. ostoyae*, *H. annosum*, *Inonotus tomentosus* or *Phellinus noxius*. These pathogens appear to have, in sandy soils, a higher incidence (BERNIER and LEWIS 1999; FROELICH *et al.* 1966; CÔTÉ and DESSUREAULT 1994), a preferential distribution (MC LAUGHLIN 2001; TERMORSHUIZEN and ARNOLDS 1994; CHANG and YANG 1998; BLODGETT and WORRALL 1992) or to induce more damages in terms of root infection severity, rate of decline or mortality (ALEXANDER *et al.* 1975; WHITNEY 1984; MALLETT and MAYNARD 1998). Inoculation experiments under controlled conditions also showed that the proportion of infected seedlings by *Armillaria* spp. increased in sandy soils (REDFERN 1978). BAKER *et al.* (1993) also showed that the risk of lethal root rot on *Pinus* after inoculation with *H. annosum* increased in soils with low silt, high sand content and low pH.

The fact that coarse soils are favourable to the presence and the impact of *C. fusipes* could result either from a direct effect on the fungus itself or from an effect on the host tree. Indeed, it could be related to the way *C. fusipes* infects trees. *Collybia* appears to grow along roots mainly through ectotrophic mycelium and to infect bark secondarily (MARÇAIS and DELATOUR 1996). Lesion development is thus strongly subjected to soil conditions. Such an influence of soil conditions on disease evolution have been suggested by RISHBETH (1951) who hypothesised that *H. annosum* incidence decreased in soils rich in organic matter due to the competition with other fungi that are abundant in such soil types. BLENIS *et al.* (1989) showed a direct and positive effect of sandy texture on *A. ostoyae* through a better survival of inoculum in such soils. Similar results were obtained with *C. fusipes* (CAMY *et al.* 2003-b). *C. fusipes* could also be favoured by the good availability in oxygen in sandy textures of soils. Indeed, its growth appeared to be strongly reduced by hypoxia compared to other root rot fungi (CAMY *et al.* 2003-c). Anoxic conditions induced by waterlogging are very unfavourable to *C. fusipes* (PIOU *et al.* 2002, CAMY *et al.* 2003-c). Another hypothesis was expressed by ALEXANDER *et al.* (1975) who demonstrated that conidiospores of *H. annosum* could migrate deeper into soils of high sand content, which might also explain the higher disease incidence in those soils. Indeed, deeper migration of inoculum could increase the probability of spores to reach and infect roots. This hypothesis could well fit *C. fusipes* biology as this pathogen spreads essentially by the way of basidiospores (MARÇAIS *et al.* 1998-b).

However, the difference in distributions of *C. fusipes* reports on *Q. robur* and *Q. petraea* that we evidenced might indicate that soil texture does not only favour the pathogen itself, but may influence the host-pathogen interaction specifically for *Q. robur*. This might suggest an effect of soil coarseness on the tree itself. Such soils are often poor in

nutrients and prone to water shortage in case of drought. These conditions could weaken the host and increase its susceptibility to *C. fusipes*. This could be especially relevant because *Q. robur* was often introduced in sites beyond its optimal ecological range, i.e. in soils poor in nutrients and/or with low water holding capacity (BECKER and LÉVY 1990). Nevertheless, *C. fusipes* is considered to be a primary parasite, since MARÇAIS and DELATOUR (1996) evidenced that young oak seedlings defoliated for two years were less susceptible to *C. fusipes* infection as compared to not defoliated ones. CAMY (2002) was not able to evidence an increased susceptibility of inoculated saplings of *Q. robur* submitted to drought as compared to well watered controls. Also, artificially inoculated mature *Q. robur* growing on coarse textured soils did show a higher susceptibility to *C. fusipes* compared to oaks growing on fine textured soils (CAMY et al. 2003-b). It could also be possible that infected oaks with root systems severely reduced are more prone to water stress in coarse textured soils with low water holding capacity. This lower tolerance of *Q. robur* to *C. fusipes* infection on coarse textured soil could lead to more frequent reports of the pathogen on these soils.

This study showed that sites where *C. fusipes* could be a cause of oak decline are sites where mature *Q. robur* occur on coarse textured soils. These situations represent 7.4 % of the *Q. robur* declines reported in the DSF database. These soil types are not considered to be within the normal ecological range of *Q. robur*. In coarse textured soils, where *Q. robur* are suffering decline problems due to *C. fusipes*, the replacement of pedunculate oaks by *Q. rubra* should be avoided, since this species is more susceptible to *C. fusipes* (MARÇAIS and CAËL 2000). By contrast, the replacement of pedunculate oaks by *Q. petraea* could be considered in specific situations, since this species is less susceptible to *C. fusipes* and more resistant to water stress and low nutrient availability (BECKER and LÉVY 1990).

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### Résumé

#### *Facteurs édaphiques, dépérissement du chêne et infection par Collybia fusipes*

*Collybia fusipes* est à l'origine d'une pourriture racinaire sur chêne en Europe. Les dommages racinaires induits sont corrélés de façon inconstante avec une détérioration de la couronne selon le peuplement. Cette étude a pour but de clarifier les relations entre l'impact de *C. fusipes* sur les chênes, évalué grâce à l'état du houppier, et les facteurs du sol. Pour ceci, la base de données du DSF (Département de la Santé des Forêts Françaises), sur les 12 dernières années, nous a permis d'étudier à large échelle dans quelles textures de sol *C. fusipes* était plus particulièrement liée à des problèmes sanitaires. Une étude plus spécifique, portant sur 30 placettes du nord-est de la France nous a permis de déterminer quels facteurs du sol, texture, degré d'engorgement, présence et nature d'un horizon limitant l'enracinement des arbres, ratio carbone/azote, capacité d'échange cationique ou pH, pouvaient être corrélés à une augmentation du risque de dépérissement chez les chênes infectés par *C. fusipes*. Les résultats ont montré que *C. fusipes* était préférentiellement distribuée sur les sols à textures grossières et que son impact en terme de dépérissement des arbres augmentait avec la teneur en sable du sol.

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