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## DISTRIBUTION AND HOSTS OF *COLLYBIA FUSIPES* IN FRANCE

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### Abstract

Thanks to data collected by two different observation networks, it was possible to clarify the distribution of *Collybia fusipes* in France. It is frequently found in the west and north of France, mainly on *Q. rubra* and *Q. robur*, and to a lesser extent on *Q. petraea*. It has rarely been reported in the south-eastern quarter of France, where *Q. ilex* and *Q. pubescens* are the dominant species. Complementary observations carried out at the National Arboretum of Les Barres would appear to indicate that a large number of oak species are susceptible to being infected by this fungus, particularly those in the section *Erythrobalanus*. These observations are discussed with reference to reports of this fungus throughout France.

Fruit-body clumps were monitored and root damages were assessed on 73 final-crop trees and 40 codominant trees in a red oak stand. The results suggest that *C. fusipes* do not infect more severely weakened trees. The degree of soil water logging significantly affects the severity of the root damage as well as the number of fruit-body clumps produced. This report confirms that *C. fusipes* develops preferentially in soils which are not subjected to a to severe water logging.

### Introduction

*Collybia fusipes* [Bull.:Fr] Quél. was mentioned a long time ago in France by mycologists, on stumps and at the base of various Fagaceae, particularly oak and beech (Romagnesi 1971; Maublanc 1974). This Agaricale produces basidiomes in clumps between spring and autumn. Around 1980, during studies carried out on oak decline, severe damage of the root system caused to this fungus were described, in particular for pedunculate oak under non water logged conditions (Delatour and Guillaumin 1984; Guillaumin *et al.* 1985). Bark lesions were rather typical, orange in colour and located on the large roots and on the collar. The fungus reached the cambium and the wood latter in the infection process. The parasitic behaviour of *Collybia*, already mentioned by Buller (1958) and Kreisel (1961), was confirmed. In addition, *Collybia* aggressiveness appeared to be influenced by host vigour and by site conditions.

Additional field observations were collected before pathogenicity was confirmed under experimental conditions (Marçais and Delatour 1996). Particular attention was paid to the hosts susceptible of being infected. The frequent fruiting of *C. fusipes* at the base of living trees and its seasonal persistence greatly simplifies such tasks. We made observations over a 4-year period in the National Arboretum of Les Barres and compared them to other observations obtained from various pathological and mycological databases. We also collected information in a severely-infected red oak stand on other factors influencing the disease, in particular water logging conditions.

## Materials and methods

### Databases

Two available databases were used: the base managed by the Forest Health Department (DSF: French Ministry for Agriculture and Fisheries) created in 1989, and the base managed by the French Mycology Society (SMF), which was created in 1950.

The DSF database is supplied by reports from a network of people made up of foresters trained in observing pathological and entomological phenomena as well as all types of decline. Over 11,000 cases of disease or decline were reported between 1989 and 1995. Of these reports, 144 mention the presence of *C. fusipes*, either as basidiomes at the base of living trees, or as orange-coloured necrosis on the collar or roots of declining trees.

The information from the SMF database is collected by mycologists, voluntary amateurs for the most part, but without any particular reference to pathology; nor are the abundance of the registered fungi or the host species or the type of support material (stump or living tree) taken into account. Each fungus species is referred to a systematic grid as being present or absent in grid boxes of approximately 10 x 14 km. All the information is collected and synthesised by the Botany Department of the Pharmaceutical and Biological Sciences Faculty of Lille (Co-ordinator R. Courtecuisse).

### Observations at the National Arboretum of Les Barres

The National Arboretum of Les Barres is located in the centre of France (Loiret) (cf. Figure 1). The site characteristics were described by Rol *et al.* (1944). Most of the soils are composed of soft clay covered in places by loamy sands of varying thickness. Those soils prove to be rather variable for depth of the clay horizon and for the depth of the first water logging traces. The average climatic conditions over the four years of observation (1991-1994, Table 1), are characterised by a large water deficit during the first two years compared to the reference period (1936-1990), and by a rather high average temperature. Of the 2,500 tree species and 8,500 individuals which make up the arboretum's botanical collections, all the trees bearing *Collybia* basidiomes were registered between 1991 and 1994. Fagaceae (79 species, 352 individuals) were investigated in more detail, particularly the genera *Castanea* (4, 14), *Fagus* (18,48), *Nothofagus* (4, 12) and *Quercus* (53, 278); the genus *Quercus* itself includes the sub-genera *Cyclobalanopsis* (3, 13), *Erythrobalanus* (12, 49) and *Lepidobalanus* (38, 216).

Table 1. Rainfall and temperature: mean values from 1991 to 1994 at the National Arboretum of Les Barres

Year	Annual rainfall (mm)	Rainfall from April to October (mm)	Annual average temperature (°C)	Average temperature from April to October (°C)
1991	501	283	10.5	14.7
1992	551	303	11.2	15.2
1993	653	463	10.6	14.7
1994	880	501	12.1*	15.4
Average 1936–90	687	392	unavailable	unavailable
Average 1969–90	708	403	10.6	14.6
Average 1969–98	704	404	10.7	14.8

\* Record year for the reference period 1969–98.

Near the botanical collections at the National Arboretum of Les Barres, a red oak stand (*Quercus rubra* L.) where *Collybia* was abundant was studied in more detail. This stand, referred to as, "La Glandée d'Amérique" originated from natural regeneration which occurred between 1924 and 1928. The soil is similar to that at the Arboretum, in particular in terms of the depth of the clay horizon and water logging characteristics.

The observations were focused on 73 final-crop trees designated in 1974, all of which were dominant and evenly distributed in the stand. These final-crop were favoured by the selective logging

done in the stand each 5 years since 1974. Trees not designated as final-crop trees and not favoured by the selective logging were also observed. Since 1974, the final-crop trees were submitted to identical silviculture practices and their circumferences were measured annually (Ginisty 1994). At the base of each tree, *Collybia* fruiting was monitored every year from 1991 to 1994; the depth of the clay horizon and of the first traces of water logging occurrence was also measured for each tree (2 or 3 measurements per tree).

In March 1995, the heights and circumferences of these 73 trees together with 40 suppressed trees, evenly distributed in the stand, were measured. Their root system was studied for *C. fusipes* infection in the following way described elsewhere (Marçais *et al.* 1999). The root collar was partially excavated to a depth of 20-30 cm and a distance of 80-100 cm from the trunk base. The infection status of each major root was assessed as: 0, no necrosis detected; 1, necrosis present but covering less than half of the root circumference; 2, necrosis entirely covering one side of the root; 3, *C. fusipes* infection over the entire root circumference but root still alive; 4, root dead with wood rotten. The root infection index of a tree was computed as:  $\sum(\text{root diameter} \times \text{root rating}) / \sum(\text{root diameter})$ . This index therefore takes values from 0 to 4. If this index is lower or higher than 1.5, the tree is considered slightly or severely affected.

## Data analysis

The tree height and diameter values were compared using analysis of variance followed by an S.N.K test, and the same was done for the soil characteristics using non parametric tests (Mann-Whitney and Kruskal-Wallis). Correlations were carried out using Spearman rank correlation analysis, and the frequencies were compared using the  $\chi^2$  test. The confidence intervals were calculated at a 95% threshold.

The maximal number of fruit-body clumps counted on each tree during the four years of observation was analysed by generalised linear modelling with the GENMOD procedure using SAS Inc software (SAS Inc, 1989). We assumed the data fitted a Poisson distribution and used the log link function. The root infection index, used as an independent variable, was log-transformed. The model validity was checked by plotting deviance residuals against the linear predictor and with a half normal plot (Collet, 1991).

## Results

### Distribution in France

The surveys carried out by the Société Mycologique de France (Figure 1) and the Département de la Santé des Forêts (Figure 2) give similar picture of *C. fusipes* distribution in France. The parasite is common in much of the country. However, the large number of reports in Franche-Comté, Burgundy and region Centre in both databases should be noted. The DSF mentions *C. fusipes* in the south-west more frequently than the SMF, and the reverse is true for Northern France. On the other hand, *C. fusipes* is barely mentioned at all in the south-east, particularly in the Mediterranean region where pedunculate and sessile oaks are infrequent (Rameau *et al.* 1989).

### Host species

Only the DSF database provides indications on the host species (Table II). All the reports were obtained on oak trees, apart from six cases on chestnut trees. Pedunculate oak, *Quercus robur* L., is the more often reported host, well above sessile oak, *Q. petraea* (Matt.) Liebl, despite the fact that these two species cover similar surface area France. Red oak, *Q. rubra* L., was also often reported as hosting basidiomes although it covers relatively small surface areas. Despite presence on large areas in France, the other oak species, *Q. pubescens* Willd., *Q. ilex* L., *Q. suber* L., are seldom reported as host of the fungus.

An insight of the relative susceptibility of the host species could be obtained by considering the number of reports compared to the surface covered by a given species. According to this index, it appears that red oak is a very frequent host, and that pedunculate oak is found infected more often than sessile oak (Table II). Mortality associated with the presence of *C. fusipes* is very frequent for all oak species (Table II).

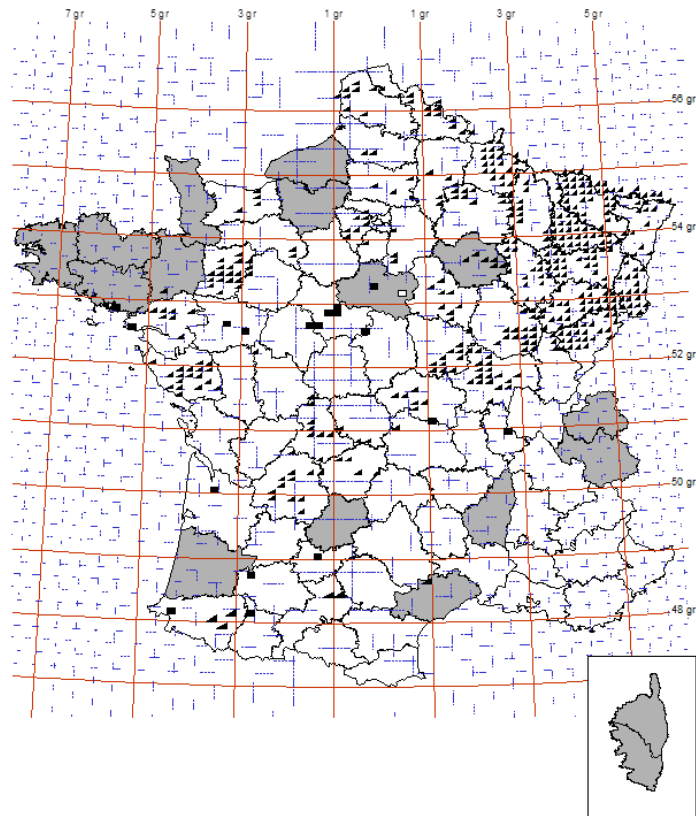


Fig. 1. Distribution of *Collybia fusipes* according to the French Society of Mycology (SMF) database 1950–2000

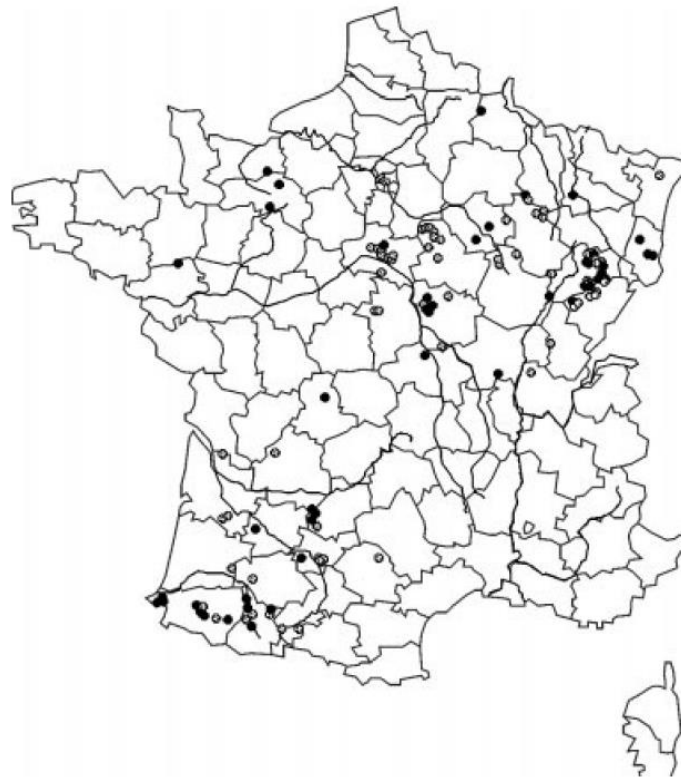


Fig. 2. Distribution of *Collybia fusipes* according to the French Forest Health Service (DSF) database 1989–95. , case reported not associated with tree mortality; d, case reported in association with tree mortality

The information collected in arboretums gives insight in *C. fusipes* host range (Table III). At the National Arboretum of Les Barres, with the exception of one reported case concerning *Castanea crenata* Sieb and Zucc., all the others reported concerned the genus *Quercus*. Twenty-one oaks out of the 278 examined (i.e. 7.6%), belonging to 11 species and 3 hybrids, exhibited *C. fusipes* basidiomes during the observation period. This list is undoubtedly not an exhaustive one, as shown by the presence of basidiomes at the base of *Q. cerris* trees at the Arboretum of Pézanin. Within the genus *Quercus*, the species belonging to the section *Erythrobalanus* appear to be infected the most frequently (18.4% of individuals in this section were infected in Les Barres) compared to those of the section *Lepidobalanus* (5.1%).

Table 2. Tree species infected by *Collybia fusipes* (from the DSF database 1990–94)

Species	Number of reports				Area in France (1000 ha)	No. reports (per 10 000 ha)
	Total		With mortality			
	n	(%)				
<i>Quercus robur</i> L.	69	48 <sup>1</sup>	33		2421 <sup>2</sup>	0.3
<i>Q. rubra</i> L.	34	24	21		16 <sup>3</sup>	20.2
<i>Q. petraea</i> (Matt) Liebl.	20	14	14		1776 <sup>2</sup>	0.1
<i>Q. robur</i> or <i>petraea</i>	14	10	11		–	–
<i>Castanea sativa</i> Mill	6	4	2		484 <sup>2</sup>	0.1
<i>Q. pubescens</i> Willd	1	1	1		855 <sup>2</sup>	0.01
<i>Q. ilex</i> L.	0	0	0		342 <sup>2</sup>	–
<i>Q. suber</i> L.	0	0	0		64 <sup>2</sup>	–
Total	144		82		5962	

<sup>1</sup> Reports of the species as a percentage of the total number of reports.  
<sup>2</sup> In 'Les indicateurs de gestion durable des forêts françaises' (ANONYMOUS 1995).  
<sup>3</sup> In 'An overview of ecology and silviculture of indigenous oaks in France' (TIMBAL and AUSSENAC 1996).

Table 3. Fagaceae with *Collybia fusipes* clumps at the National Arboretum of Les Barres (1991–94)

Genus	Species	Sub-genus	Section	Origin
<i>Castanea</i>	<i>crenata</i> Sieb. and Zucc.	–	–	Japan
<i>Quercus</i>	<i>myrsinifolia</i> Bl.	<i>Cyclobalanopsis</i>	–	Japan
	<i>imbricaria</i> Michx. × <i>heterophylla</i> Michx. f.	<i>Erythrobalanus</i>	<i>Phellos</i>	North America
		<i>Erythrobalanus</i>	<i>Phellos</i>	North America
	<i>coccinea</i> Muenchh.	<i>Erythrobalanus</i>	<i>Rubrae</i>	North America
	<i>palustris</i> Muenchh.	<i>Erythrobalanus</i>	<i>Rubrae</i>	North America
	<i>rubra</i> L.	<i>Erythrobalanus</i>	<i>Rubrae</i>	North America
	<i>velutina</i> Lam.	<i>Erythrobalanus</i>	<i>Rubrae</i>	North America
	<i>bicolor</i> Willd.	<i>Lepidobalanus</i>	<i>Albae</i>	North America
	× <i>bebbiana</i> Schneid.	<i>Lepidobalanus</i>	<i>Albae</i>	North America
	<i>glandulifera</i> Bl.	<i>Lepidobalanus</i>	<i>Albae</i>	Asia
	<i>acutissima</i> Carruth.	<i>Lepidobalanus</i>	<i>Cerris</i>	Asia
	<i>pyrenaica</i> Willd.	<i>Lepidobalanus</i>	<i>Robur</i>	Europe
	<i>robur</i> L. × <i>vilmoriniana</i> Camus	<i>Lepidobalanus</i>	<i>Robur</i>	Europe
			' <i>Dentatae</i> × <i>Robur</i> '	–
Total	15 taxons			
Additional observations at the Arboretum of Pézanin (Saône et Loire)				
<i>Quercus</i>	<i>phellos</i> L.	<i>Erythrobalanus</i>	<i>Phellos</i>	North America
	<i>cerris</i> L.	<i>Lepidobalanus</i>	<i>Cerris</i>	Europe



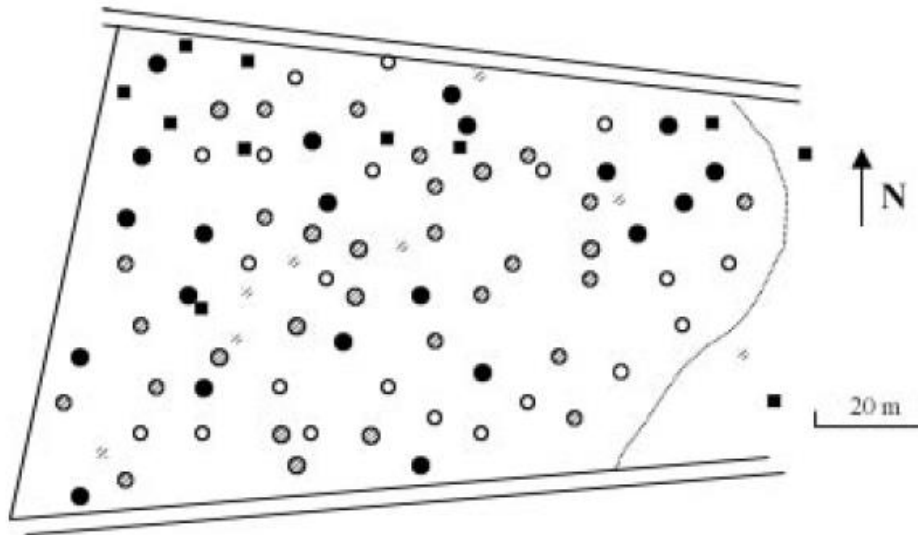


Fig. 3. Location of the red oak trees investigated at the Glandée d'Amérique site. Dominant trees: open circle, healthy; shaded circle, slightly infected; black circle, severely infected. Codominant trees: open square, healthy; shaded square, slightly infected; black square, severely infected

Table 4. Growth characteristics of red oaks in the infected stand of La Glandée d'Amérique

Category of tree in 1994 according to root infection by <i>C. fusipes</i>		No.	Root infection index	Girth in 1994 (cm)	Height in 1994 (m)	Girth in 1974 (cm)
Final-crop trees	not infected	21	0	96.4 ± 8.3 <sup>a</sup>	22.7 ± 1.0 <sup>a</sup>	55.8 ± 3.9 <sup>a</sup>
	slightly infected	31	0.5 ± 0.1	99.5 ± 5.5 <sup>a</sup>	23.3 ± 0.7 <sup>a</sup>	59.8 ± 3.6 <sup>ab</sup>
	severely infected	21	2.4 ± 0.4	97.9 ± 9.9 <sup>a</sup>	22.5 ± 1.2 <sup>a</sup>	63.4 ± 6.3 <sup>b</sup>
Codominant trees	not infected	20	0	70.3 ± 3.4 <sup>a</sup>	22.0 ± 1.6 <sup>a</sup>	–
	infected	20	1.80 ± 0.4	77.6 ± 5.4 <sup>b</sup>	21.4 ± 0.8 <sup>a</sup>	–

<sup>a,b</sup> Values with different letters are significantly different within a column.

### Conditions for the expression of the fungus in a red oak stand

The annual monitoring of red oak trees between 1991 and 1994 in the Glandée d'Amérique stand made it possible to observe how regularly *C. fusipes* basidiomes appeared, in relation with tree growth and soil characteristics on the one hand and the severity of root infection on the other.

After examining the root systems, it appeared that 52 final-crop trees out of 73 (71%) exhibited root necrosis attributable to *C. fusipes* (Marçais *et al*, 2000) as opposed to 50% for the trees not favoured by the selective logging, which is a significantly lower value ( $\chi^2=4.37$ ;  $p=0.04$ ). The infected final-crop trees were scattered within the healthy ones (Figure 3). Infected final-crop trees did not exhibit significantly different root infection index compared to the infected trees not favoured by the selective logging (Table IV).

In 1974, when the final-crop trees were selected, their trunk circumferences was positively correlated with the depths at which first traces of water logging appeared ( $r=0.24$ ;  $p=0.04$ ) and the 21 most infected trees had significantly larger circumferences than those which were not infected (Table IV). None of the other tree growth parameters measured in 1994 (circumference, height, crown height, H/D ratio) differed significantly between healthy trees and trees infected by *C. fusipes*. For these 73 trees, the root infection index was also positively correlated with the depth at which first traces of water logging appeared ( $r=0.27$ ;  $p=0.03$ ; Figure 4).

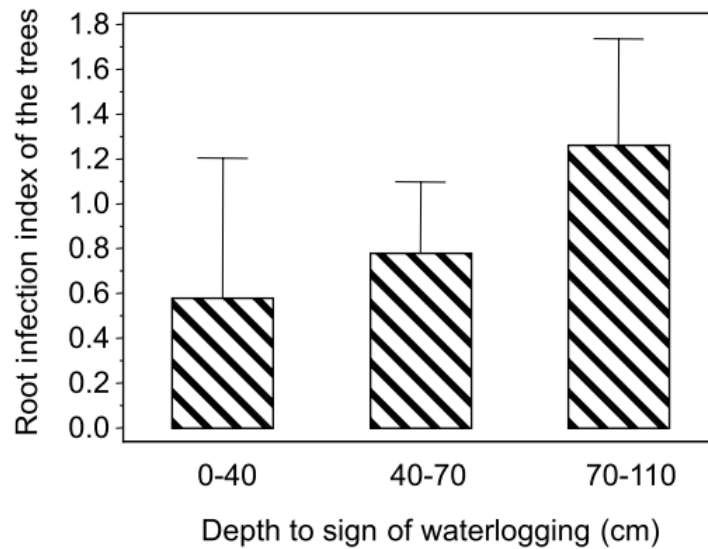


Fig. 4. Relation between waterlogging and root infection by *Collybia fusipes* in red oak

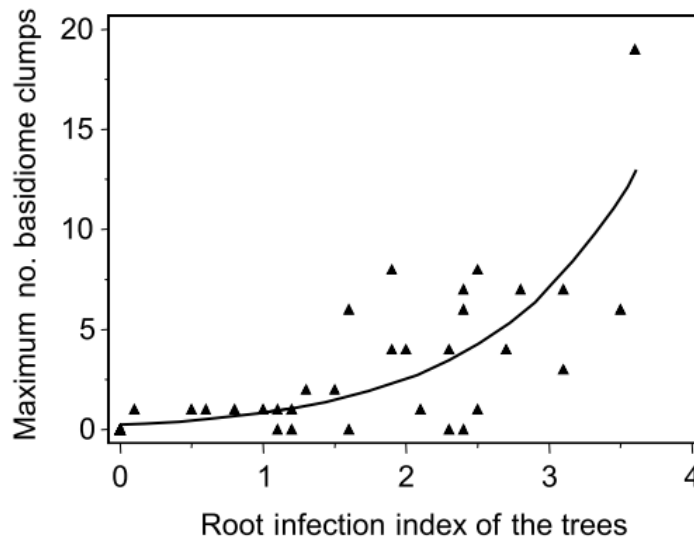


Fig. 5. Relationship between fruiting of *Collybia fusipes* and root infection in red oaks. (Maximum number of clumps observed during the period 1991–94). The curve was adjusted using generalized linear model and assuming a Poisson distribution

Out of the 52 infected final-crop trees, 31 exhibited *C. fusipes* basidiomes between 1991 and 1994. A total of 259 basidiome clumps was counted (83 in 1991, 58 in 1992, 53 in 1993 and 65 in 1994). The total number of *C. fusipes* clumps at the base of each tree during the 4-year observation period significantly depends on the degree of root infection (Table V). *C. fusipes* fruiting was also linked to water-logging, even after the severity of the root infection was taken into account. This could be explained by poor fruiting on a few severely infected trees that had evidence of water-logging close to the soil surface (Figure 4B). The frequency at which fruit-body clumps appear is also linked to this factor. For low root infection index (<0.5), *C. fusipes* does not bear any basidiomes, or if it does so only one year in four. On the other hand, trees hosting basidiomes each year all had root infection index of over 1.5 (cf. Figure 5).



Table 5. Host species and frequency of *Collybia fusipes* in Europe and North Africa

Country	Host species	Frequency of reporting	Reference
Algeria	<i>Q. ilex</i>	very rare	MALENÇON and BERTAULT (1975)
Bulgaria	<i>Quercus</i> sp.	reported	KUTHAN and KOTLABA (1981)
Canary Islands	–	reported as being terrestrial	BANARES et al. (1994)
Finland		rare	NANTA and VELLINGA (1995)
Great Britain	<i>Quercus</i> sp. <i>Quercus robur</i>	very widespread but rare reported	HARK 1983 R.G. STROUTS (personal comm.)
Germany (West) (former Federal Republic)	<i>Quercus</i> (90% of reported cases) <i>Fagus, Corylus, Castanea</i> <i>Quercus, Corylus, Fagus, Castanea</i>	very widespread infrequent reported (Palatinat)	KRIEGLSTEINER 1991 KRIEGLSTEINER 1991 KREISEL 1961
Germany (East) (former Democratic Republic)	<i>Quercus, Carpinus</i> <i>Quercus, Fagus</i>	reported reported as saprophyte and parasite	FISCHER W. (1987) KREISEL H. (1987)
Italy	<i>Corylus, Carpinus</i> (substrate not mentioned) <i>Q. ilex, Q. cerris, Q. robur</i> <i>Quercus</i> sp.	rare reported (Sardinia) reported (Tuscany) reported (Naples region)	KREISEL H. (1987) BALLERO et al. (1987) INTINI (1990) VOLANTE and SORIENTE (1986)
Luxembourg	<i>Quercus</i> sp.	reported	M.U.C.L (personal comm.)
Morocco	<i>Quercus pyrenaica</i>	very rare	MALENÇON and BERTAULT (1975)
Poland	<i>Quercus</i> sp. <i>Quercus robur</i>	reported reported	LAWRYNOWICZ (1973) K. PRZYBYL (personal comm.)
Romania	<i>Quercus robur</i>	reported	DELATOUR and GUILLAUMIN 1984
Spain	<i>Quercus</i> sp. <i>Q. pubescens, Q. ilex, Q. suber</i>	reported frequent (Catalonia)	MARCHAND 1973 MARCHAND 1973
Spain and Portugal	<i>Q. faginea, Q. ilex</i> ssp. <i>rotundifolia</i> , <i>Q. pyrenaica, Q. suber</i>	frequent	MORENO et al. 1986
Switzerland	<i>Quercus</i> sp., <i>Fagus</i> sp.	widespread	BREITENBACH and KRÄNZLIN 1991
Sweden	(substrate not mentioned)	rare	NANTA and VELLINGA (1995)
The Netherlands	<i>Quercus</i> <i>Quercus</i> sp. (71% of reported cases) <i>Fagus sylvatica</i> (24%) Other broadleaved trees ( <i>Betula</i> sp., <i>Corylus avellana</i> , <i>Carpinus carpinifolia</i> ) (5%) <i>Quercus, Fagus, Acer, Betula, Corylus</i>	quite rare infrequent reported	SUNHEDE (1977) NANTA and VELLINGA (1995) ARNOLDS et al. (1995)

## Discussion

### Distribution

At the present time, *Collybia fusipes* is known from Europe and North Africa only. Reports are quite frequent there although often difficult to compare (Table V). It is considered to be common in Great Britain<sup>1</sup>, Germany, Switzerland, and in the Iberian Peninsula ('widespread' or 'very widespread').

In France it also appears to be widespread throughout the oak forest area, with the exception of much of the south-east of the country. Despite the problems about the reliability and homogeneity of observations made within a network (Bouhot, 1991), it appears that two independent networks give a

<sup>1</sup> Eight isolates of *C. fusipes* from the Forestry Commission (FCRA), all of which were obtained from necrotic roots of rapidly declining pedunculate oaks, confirm the presence of the fungus in its parasitic state in the south of England.

similar picture of the fungus distribution. Consequently, the absence of cases reported in the south-east of France could indicate that the fungus is relatively rare in the Mediterranean region, which would be consistent with the few cases reported in Italy and North Africa, or even in south-east Europe. Moreover, *C. fusipes* is infrequently isolated from declining oak of various species in southern Italy (Luisi *et al.*, 1996). Nonetheless, the frequent reports of *C. fusipes* in Spain, particularly in Catalonia (Marchand, 1973), disagree this analysis, as do the ancient observations made in the South of France (Gillet, 1878; Moyon 1889).

## Hosts

The observations made in France, and particularly those made on Fagaceae of the National Arboretum of Les Barres, confirm the hypothesis that *Collybia fusipes* is mainly associated with the genus *Quercus*. Numerous oak species have been shown to be host of the fungus, regardless of their geographical origin. It would seem, however, that species in the section *Erythrobalanus*, originating from North America, are the most particularly concerned (Table IV). The very frequent report of *C. fusipes* on *Q. rubra* in forests conditions is in agreement with this hypothesis (Table III).

The genus *Castanea* can also harbour the fungus as reported in Germany (Kreisel, 1961; Krieglsteiner, 1981). A similar observation has been reported in France as shown by DSF observations on *C. sativa* and those made at the National Arboretum of Les Barres on *C. crenata*.

Reports of *Fagus* or species other than Fagaceae (*Acer*, *Betula*, *Carpinus*, *Corylus*) have been made in several European countries, particularly in the Netherlands in the case of beech. To our experience, presence of *C. fusipes* on these species is not very frequent in France, although we observed the disease sporadically in infected oak forests on hornbeam and hazel trees. Bigeard and Guillemain (1909) reported *Collybia* on *Populus tremula* L. which appears to be a unique case.

Mediterranean oaks (*Q. suber*, *Q. ilex*, *Q. pubescens*.) which are abundant in the National Arboretum of Les Barres and which cover large surface areas in France, do not appear to be frequent *C. fusipes* hosts in our study, (only one case reported on *Q. pubescens* in the Dordogne in 1993). The fungus is nevertheless frequently reported in Spain on several Mediterranean oak species (cf. Table VI). Moreover, Gillet (1878) and Moyon (1889) reported a *Collybia* variety (*C. illicina* D.C.) growing at the base of holm oak, which they considered to be synonymous with *C. fusipes* and which, at the time, was "of interest" in the South of France.

## Pathogenicity

In the case of the Glandée d'Amérique, the frequency and abundance of basidiomes at the tree base is linked to the degree of root infection. This result confirms those of Marçais *et al.* (in press). Consequently, the recording of *C. fusipes* basidiomes present at the base of trees, such as done by the DSF or by ourselves, can give an insight on the tree infection status. The case of the red oak stand of 'La Glandée d'Amérique' is a good exemple. Indeed, the information collected in this stand shows that the trees subjected to more severe water logged conditions had initially a slower radial growth than the others (until 1974). This can be explained by the well-known sensitivity of that the species to that factor (Dreyer and Colin-Belgrand, 1994). Despite of that, *C. fusipes* did not develop on these trees. Similarly, it developed less frequently on trees not favoured by the selective logging. Conversely, *C. fusipes* developed well on the final-crop trees subjected to less water logged conditions, which were those that grew the best. The radial growth of these trees decreased significantly latter and in the last years these trees had become the less vigorous. *Collybia* should therefore not be considered as a weakness parasite. Our observations suggest that *Collybia* influence the growth of severely infected trees. Red oak appears particularly susceptible to it, which is consistent with the extensive observations made by the DSF, even in a region such as the south-west where climate is favourable to red oak (Timbal *et al.*, 1994). Besides, the presence of a near-surface water table may be detrimental not only to the development of the fungus itself in the root system, as suggested by Guillaumin *et al.* (1985) for pedunculate oak, but also to the fruiting capacity of the fungus. In the Netherlands, Nanta and Vellinga (1995) also reported preferential distribution of *C. fusipes* on dry soil.

Following inoculation, *Q. robur* and *Q. petraea* appear to be less susceptible than red oak (Marçais and Caël, 2000). Under natural conditions, apparently healthy trees of both species, *Q. robur* and *Q. petraea*, may show *Collybia* root infections. Nonetheless, the disease is far more frequent on *Q. robur* than in *Q. petraea* (Marçais *et al.*, 1998). It has been suggested that the development of root lesions may be enhanced by poor vigour or host stress as water shortage, resulting over a probably long

time-period in destruction of part of the root (Guillaumin *et al.*, 1985; Delatour, 1990). This could have explained the more frequent occurrence of *C. fusipes* on pedunculate oak because this oak species is present under unfavourable situation in France. This hypothesis should probably be reconsidered in the light of the results presented in this article. Also, vigorous seedlings of pedunculate oaks have proved to be more susceptible to inoculation than seedlings weakened by summer defoliation (Marçais and Delatour, 1996). The fact that the parasite is observed more frequently on pedunculate oak than on sessile oak, as shown by the DSF database, may also be due to the fact that this species is relatively more sensitive (Marçais and Caël, 2000).

Whatever the case, the greater susceptibility of red oak to *Collybia fusipes* may be due, in the genus *Quercus*, to a characteristic of the section *Erythrobalanus* and not only of *Q. rubra* alone. The risks ran by this group of species should be evaluated more closely in Europe where the parasite is widespread.

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