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## Prediction and mapping of the impact of winter temperature on the development of *Phytophthora cinnamomi*-induced cankers on red and pedunculate oak in France

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### Abstract

*Phytophthora cinnamomi* is the causal agent of a perennial canker that develops on the lower bole of northern red oak and pedunculate oak. The disease has a limited range in Europe, being reported only in south-west France. This limited distribution is probably linked to the susceptibility of *P. cinnamomi* to frost. A model was developed in previous work to estimate the impact of temperatures <0°C on the winter survival of *P. cinnamomi* in trunk cortical tissues and on the subsequent development of cankers. In this article, we report the use of this model to simulate canker development in 503 locations across France during a 30-year period. The predicted canker extension decreased sharply when the median *P. cinnamomi* winter survival index decreased from 0.95 to 0.65, with cankers that poorly developed when the median survival index was lower than 0.5-0.6. The actual incidence of the disease in 192 stands located across south-west France was compared to model outputs. Both presence of disease in stands and frequency of cankered trees in infected stands, but not canker size on infected trees was strongly related to the median *P. cinnamomi* survival index. No disease was present in stands with median survival index lower than 0.65, and the frequency of cankered trees in infected stands remained very low in stands with a median survival index between 0.65 and 0.70. Aspect was an additive factor explaining disease incidence, while the effect of elevation was likely due to its effect on winter temperatures. Maps of winter suitability to *P. cinnamomi*-induced cankers on oaks in France are presented.

**Additional Keywords:** *Quercus rubra*, *Quercus robur*

### Introduction

Northern red oak, *Quercus rubra* L., an exotic tree species in Europe, has been extensively planted in south-west France during the 20<sup>th</sup> century, in part to replace stands impacted by exotic pathogens introduced at the beginning of the century. In particular, black oak, *Quercus pyrenaica* Willd, was severely impacted by powdery mildew *Microsphaera alphitoides* Griffon et Maublanc (8) and sweet chestnut, *Castanea sativa* Mill. by *Phytophthora cinnamomi* Rands (1). Indeed, *Q. rubra* was reported as tolerant to European powdery mildew and not affected by *P. cinnamomi* in its natural distribution area (6; 18). In the early 1950s, the ink disease of northern red oak, induced by *P. cinnamomi*, was described in the Basque area around Biarritz (1; 16). In infected stands, as much as 30-40 % of the trees can be infected (11). The disease has since also become a problem on *Q. robur*, the indigenous pedunculate oak, especially in young stands that have been planted (15). Presence of ink disease on pedunculate oak is especially worrying, as this species is much more important than northern red oak in Europe both economically and

ecologically. It is feared that the disease has been introduced into planted stands with infected seedlings and that it might be presently spreading on a large scale by infected nursery stock. The main symptom of the disease on red and pedunculate oak is a bleeding canker on the lower bole of the tree that can reach up to 4-5 m high. The canker drastically reduces the value of the timber. Although the pathogen infected the trees via roots and attacks also the fine roots, *P. cinnamomi* does not appear to affect the general health of the trees, at least for red oak. Infected trees do not appear to decline and their radial growth is not reduced (20). The development of the canker can be studied retrospectively by dendro-chronological methods, and cankered trees with apparently healthy crowns were shown to have been infected for several decades (14; 20). This contrasts strongly with the situation that has been described for other oak species and for chestnuts where *P. cinnamomi* induces a decline presumably because the infection of the root system is more severe (3; 6; 23). In the south of France, *P. cinnamomi* also causes ink disease on mediterranean oak species, *Q. ilex* and *Q. suber*, inducing either trunk cankers or decline symptoms (3; 21). However, as our work focuses on red oak, “ink disease” will here refer only to the presence of cankers.

About 50 years after its first mention, ink disease of red and pedunculate oak is still present only in a small part of south-west France and adjacent areas of Spain, mainly in the Pyrenean Piedmont, in an area where it was probably already present in the 1950s (10; 11; 14). This is in contrast with the rapid extension reported for the ink disease of chestnuts, caused by the same pathogen, from its first report in 1848 in the Basque country (9; 17). Ink disease has since been reported on chestnuts in most areas where this species is present, in places where, despite widespread occurrence of pedunculate and red oaks, no ink disease was reported on those species. *P. cinnamomi* has also been reported on various ornamental plants in a large part of the country, far beyond the limited area in which the ink disease of *Q. rubra* can be found in natural conditions (25). Delatour (7) hypothesized that the high susceptibility of *P. cinnamomi* to frost might explain the geographic distribution of the disease. Indeed, the parasite has a limited survival at temperatures below 0°C (2; 22), and cold winters were shown to have a major impact on canker development in infected red oak stands of south-west France (14). A lower impact of frosts is expected on hosts such as chestnut and ornamental plants where *P. cinnamomi* causes primarily a root disease, as deep layers of the soil seldom freeze in France.

A model was developed that describes the influence of frost on the winter survival of *P. cinnamomi* in the trunk cortical tissues of the host (12). The model outputs were in good agreement with the annual development of natural cankers in red oaks (14). In particular, it was shown that the pathogen may be eliminated from cankers during exceptionally severe frosts with subsequent total healing of cankers. This suggests that once *P. cinnamomi* is present in a site, the development of a perennial canker is strongly dependent on the local winter climate. However, if the model predicts the influence of pathogen overwintering for single winters, we need to be able to assess the integrated impact of successive winters on the enlargement of these perennial cankers that develop over several decades.

The aim of this work was to extrapolate the previous model over long periods by simulations of canker development in order to determine which winter temperature regimes are favorable to the ink disease of red oak. Model outputs were also compared with the actual distribution of ink disease of oak in south-west France in order to validate the method. Finally, a climatic hazard map for ink disease on oaks was constructed.

## Material and Methods

### Mapping of pathogen survival

*P. cinnamomi* survival indices ( $I_n$ ) were computed for each year of the period 1969-98 for the 503 meteorological stations of France from the Météo-France network having 30 years of temperature data and an elevation of <1000 m.  $I_n$  was computed as a function of the annual sum of temperature under 0°C in the bark, as explained in Marçais *et al* (14). Bark temperatures were computed hourly from air temperatures using a thermal transmission coefficient that represents the proportion of the air

temperature variations which is transmitted to the bark, and the sum of temperatures  $<0^{\circ}\text{C}$  in the bark was computed from those values. The calculation was done for the southern facing part of a large red oak tree of 50 cm trunk diameter to be conservative, as  $I_n$  increases with tree size and is larger on the southern aspect of the trunk.  $I_n$  values were computed for the same stations and the same period for pedunculate oak. The bark transmission coefficients used for red oak were 0.48 and 0.30 for unfrozen bark and frozen bark respectively (14). Lower bark transmission coefficients of 0.16 and 0.07 for unfrozen and frozen bark, respectively, were used for pedunculate oak, due to the different bark structure, (Marçais, *unpublished results*). Median  $I_n$  values were then calculated for each meteorological station and oak species. These parameters were mapped using the GIS Arcview software, with a 4 x 4 km grid. The value for each grid point was computed as the mean of the 5 nearest meteorological stations weighted by  $1/d^2$ ,  $d$  being the distance between the grid point and the station.

### Influence of winter temperature on canker enlargement

To determine whether a canker will develop on an oak tree under a given winter temperature regime if *P. cinnamomi* is present at the tree base, we used data from Marçais *et al* (14). In this previous study, the enlargement of natural cankers was studied retrospectively for about 25 years, using the signs of past cambium infections left in the wood, and was compared to the annual *P. cinnamomi* survival index  $I_n$  computed for each tree. The data were here re-analyzed to simulate canker enlargement in a given winter temperature regime. The canker development was described as follows:

$$(1) P_n = a + b \times \text{Log}(I_n \times P_{n-1}) \times I_n \times P_{n-1}$$

with  $P_n$  the width of trunk perimeter attacked at the cambium level in year  $n$ , in cm, and  $a + b \times \text{Log}(I_n \times P_{n-1})$  the canker growth rate.  $I_n \times P_{n-1}$  represents the proportion of the previous year's canker lesions where *P. cinnamomi* is still active in the spring. The density-dependence of canker growth was described by the relation  $a + b \times \text{Log}(I_n \times P_{n-1})$ , and the parameters  $a$  and  $b$  were estimated by non linear regression by the Gauss-Newton method using the procedure NLIN of SAS (SAS/STAT 6.0, SAS Institute Inc., Cary, NC) based on the data reported in Marçais *et al.* (14).

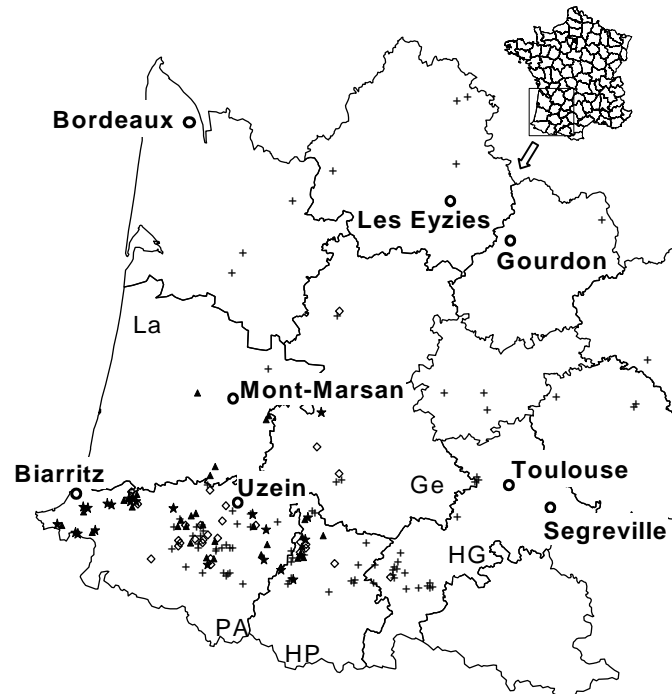
The ability of *P. cinnamomi* to induce a canker on an oak tree, provided it is present in soil at the base of the tree, was then estimated across France using the 503 series of 30 annual  $I_n$  values computed in the previous section. At the beginning of the period, in 1969,  $P_n$  was set to 1, which is close to the value observed the first year of infection for a sample of naturally infected trees (14) and equation 1 was used to simulate the canker extension. Whenever  $P_n$  reached a value  $<1$ , it was reset to 1 to take into account the possible initiation of new cankers from root or collar infections. The maximal enlargement reached by the cankers during the 30-year period was then compared with the median  $I_n$ .

### Validation data

During the period 1990-94, 192 red oak stands located in the south-west of France were surveyed for incidence of ink disease by technicians of the Département de la Santé des Forêts (DSF), the French forest health survey. The stands were selected in two ways depending on the location. In the Pyrénées-Atlantiques and Hautes-Pyrénées, where red oak is frequent and the disease known to be widespread, about one  $>20$ -year-old stand was sampled for each 10 ha of red oak forest, taking care in each forest, whenever possible, to select stands in all aspects and all topographic positions. In the rest of the area, all known  $>20$ -year-old stands were selected for the study. In each stand, 30 to 100 trees depending on stand size were examined for ink disease symptoms, i.e., a typical bleeding canker starting at the bottom of the tree. Each tree was rated as 0, no canker; 1, canker  $<1$  m above ground; 2, canker 1-2 m above ground; 3, canker  $>2$  m above ground. An index of canker development for infected trees of each stand was computed as:

$$(3) CD = (0.5 \times N_1 + 1.5 \times N_2 + 2.5 \times N_3) / (N_1 + N_2 + N_3)$$

where  $N_i$  is the number of trees with a disease rating of  $i$  in the stand. The coefficients 0.5, 1.5 and 2.5 correspond to the mean canker height of disease rating 1, 2 and 3. This index is proportional to the volume loss on infected trees due to the canker.



**Figure 1.** Distribution of Ink disease caused by *Phytophthora cinnamomi* on red oak in the south-west of France. PA, Pyrénées-Atlantiques; HP, Hautes-Pyrénées; HG, Haute-Garonne; Ge, Gers; La, Les Landes. Frequency of cankered trees: +, none;  $\diamond$ , 1-3 %;  $\square$ , 3-10 %;  $\triangle$ , > 10 %.

In each stand, co-ordinates in longitude and latitude, elevation, topography, and slope aspect as north to north-west, west to south-west, south to south-east, east to north-east and no slope were noted. This survey has been reported elsewhere (10; 11) and more information on relationships between ink disease and site conditions can be found in those reports. The results of this survey showing the distribution of ink disease on oaks in south-west France are presented in Figure 1. The disease has not been reported from other areas so far.

### Model validation

The  $I_n$  values computed in the previous section for 1969 to 1994 and for the 503 meteorological stations of France were used to compute the 26 annual  $I_n$  values by kriging for each of the 192 red oak stands surveyed for presence of ink disease. Data for years 1995-1998 were not used because the stand survey was done in 1990-94. The data from all meteorological stations were used to establish the variograms, while the data from the 87 meteorological stations that were located in south-west France were used for kriging. The variograms were modeled by spherical functions. The computations were done in BLUEPACK software (Delfiner, Delhomme, Chiles, Ecole des mines de Paris). The median  $I_n$  was computed for each surveyed stand.

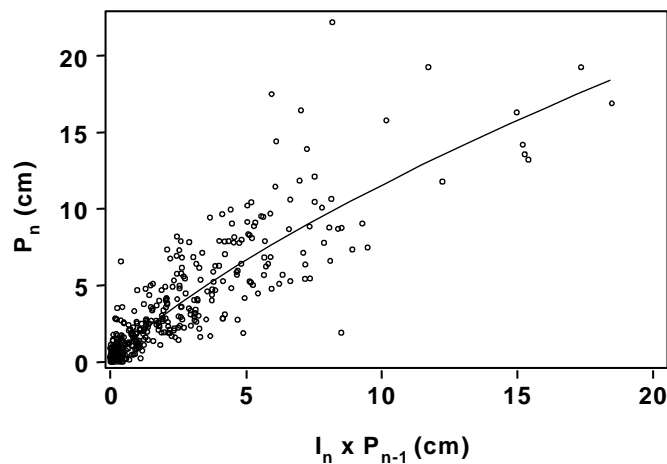
The relationship between median  $I_n$  and absence / presence of ink disease in a stand, called hereafter 'presence of disease in stands', was analyzed by logistic regression using the GENMOD

procedure of SAS. A similar analysis was conducted for the frequency of cankered trees in stands where the disease was present. The model used was the following:

$$\text{Log}(p_i / (1 - p_i)) = \mu + \alpha \times \text{Elevation}_i + \beta \times \text{median } I_i + \gamma \times \text{Aspect}_i + \rho \times \text{median } I_i \times \text{Aspect}_i$$

where  $p_i$  is the likelihood of either disease presence in a stand or of canker presence on a tree. Model validity was checked using the deviance/degree of freedom ratio when group binary data were analyzed, by plotting deviance residuals against the linear predictor, and by using a half-normal plot (5). The model for the frequency of cankered trees in stands with presence of the disease showed some overdispersion, as evidenced by a ratio deviance / degree of freedom higher than expected and thus the model was fitted with an overdispersion parameter of 0.056 computed according to the method of Williams (5).

The relationship between the index of canker development CD and median  $I_n$  was studied by regression analysis.



**Figure 2.** Relation between the canker size at the end of year  $n$ ,  $P_n$ , and canker size at the end of the previous winter  $I_n \times P_{n-1}$ .  $I_n$  is an index indicating overwinter survival of *Phytophthora cinnamomi* in oak cortical tissues. The line represents the relation:  $P_n = (1.69 - 0.22 \times \text{Log}(I_n \times P_{n-1})) \times I_n \times P_{n-1}$  ( $r^2 = 0.743$ ,  $p < 0.001$ ).

## Results

### Influence of winter temperature on canker enlargement

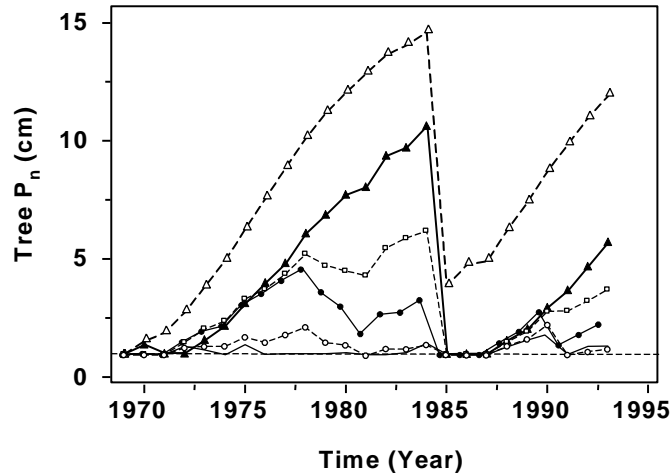
The relationship between the canker size in year  $n$  and its size in year  $n-1$  was:

$$P_n = (1.69 - 0.22 \times \text{Log}(I_n \times P_{n-1})) \times I_n \times P_{n-1} \quad (r^2 = 0.743, p < 0.001)$$

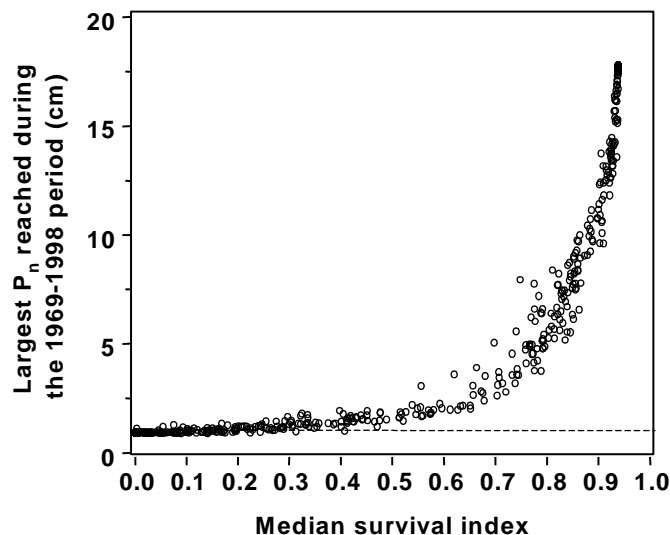
Figure 2 shows the relationship between  $P_n$  and  $(I_n \times P_{n-1})$ .

The simulation of canker enlargement in six contrasted sites of south-west France over the period 1969-1998 is shown in Figure 3. In Biarritz, located in the Basque area, winter temperatures are almost never limiting for the disease. As stations are located farther from Biarritz, the limitation of canker development by poor overwintering was more frequent, and in Gourdon and Les Eyzies, cankers poorly developed. The enlargement was not prevented by severe frosts with  $I_n < 0.05$  that kill the pathogen in all the cankers as those occurred in the six locations only in 1969-71 and 1985-87. A 20-year period with little frost limitation was enough in locations like Uzein and Mont-Marsan for significant cankers to

develop. By contrast, years with moderate survival with  $I_n$  in the 0.3 to 0.5 range efficiently hampered the canker enlargement in Segreville and Gourdon in the 1975-1984 period. Indeed, a small canker of  $P_n = 1$  will enlarge only if  $(1.69 - 0.22 \times \log(I_n)) \times I_n$  is larger than 1, i.e. for values of  $I_n > 0.55$ . Accordingly, the largest  $P_n$  reached during the simulation in the 503 locations studied across France decreased quickly when median  $I_n$  decreased from 0.9 to 0.6 (Figure 4). When median  $I_n$  was lower than 0.5 to 0.6, cankers poorly developed, with maximal extension  $< 2$ , which means they did not even double in size in a 30-year period compared to the initial value.



**Figure 3.** Simulation of the development of *P. cinnamomi* induced cankers on red oak in six weather stations of south-west France with different median survival index,  $I_n$ : ( $-\Delta-$ ) Biarritz, 0.93; ( $-\blacktriangle-$ ) Uzein, 0.86; ( $-\square-$ ) Mont-Marsan, 0.78; ( $-\bullet-$ ) Segreville, 0.76; ( $-\circ-$ ) Gourdon, 0.61; ( $-\text{—}$ ) Les Eyzies, 0.46.  $P_n$ , the canker size in year  $n$ , was computed as  $P_n = (1.69 - 0.22 \times \log(P_{n-1} \times I_n)) \times P_{n-1} \times I_n$ , with  $P_n = 1$  at the beginning of the simulation.



**Figure 4.** Relation between maximal canker size on red oak reached during the simulation and median *Phytophthora cinnamomi* survival index  $I_n$  in the 30-year period (1968-98) for 503 meteorological stations of France.



**Table 1.** Comparison between modeled *Phytophthora cinnamomi* overwintering survival,  $I_n$ , and incidence of Ink disease of red oak in south-west France.

| Median $I_n$ <sup>a</sup> | No. of stands |                  | Frequency of               |   | Index of canker development <sup>b</sup> |
|---------------------------|---------------|------------------|----------------------------|---|--|
|                           | total         | with ink disease | stand with ink disease (%) | cankered trees (% in stands with ink disease) |  |
| < 0.55                    | 8             | 0                | 0                          | -   | -  |
| 0.55-0.65                 | 10            | 0                | 0                          | -   | -  |
| 0.65-0.70                 | 18            | 2                | 11                         | 2 ± 1   | 1.0 ± 0.1                                |
| 0.70-0.75                 | 16            | 5                | 31                         | 14 ± 7  | 1.3 ± 0.2                                |
| 0.75-0.80                 | 35            | 25               | 71                         | 8 ± 4   | 1.1 ± 0.2                                |
| 0.80-0.85                 | 25            | 10               | 40                         | 6 ± 4   | 0.8 ± 0.2                                |
| 0.85-0.90                 | 68            | 48               | 71                         | 8 ± 2   | 1.0 ± 0.2                                |
| 0.90-0.95                 | 12            | 12               | 100                        | 22 ± 6  | 1.2 ± 0.1                                |

<sup>a</sup>  $I_n$  is an index indicating *P. cinnamomi* overwinter survival in trunk cankers of red oak trees (14).

<sup>b</sup> The index of canker development measures the volume loss on infected trees due to the canker.

### Relation between incidence of ink disease in surveyed red oak stands and *P. cinnamomi* survival index

The median  $I_n$  was significantly linked to both the presence of disease in stands and to the frequency of cankered trees in infected stands (Table 1 and 2). No ink disease was found in the stands where median  $I_n$  was lower than 0.65. By contrast, disease was present in all of the 12 stands with a median  $I_n$  > 0.95. The relationship between median  $I_n$  and the frequency of cankered trees in infected stands was less favorable, and still 8 to 14 % of the trees were cankered in the infected stands with a median  $I_n$  of 0.7 to 0.8. However, stands with the highest median  $I_n$  (>0.95) had a very high percentage of infected trees (22% as compared to 6-14% in the other classes).

**Table 2.** Relationship between presence of Ink disease in the studied stands or frequency of cankered trees in the infected stands and aspect, elevation, and median *Phytophthora cinnamomi* survival index<sup>a</sup>.

| Effect                    | df | Presence of ink disease |       | Frequency of cankered trees in infected stands |       |
|---------------------------|----|-------------------------|-------|--|-------|
|                           |    | $\chi^2$                | P     | $\chi^2$                                       | P     |
| Aspect <sup>b</sup>       | 4  | 12.7                    | 0.013 | 23.4   | 0.001 |
| Median $I_n$ <sup>c</sup> | 1  | 16.5                    | 0.001 | 4.8  | 0.001 |
| Median $I_n$ x Aspect     | 4  | 0.2                     | 0.996 | 3.1  | 0.550 |
| Elevation (m)             | 1  | 3.7                     | 0.055 | 2.0  | 0.160 |

<sup>a</sup> Results based on logistic regression. Likelihood ratio statistics are of type 3., which means that the contribution of each variable is computed after the others have been entered in the model.

<sup>b</sup> Aspect classes are east and northeast; north and northwest; west and southwest; south and southeast; or flat topography.

<sup>c</sup>  $I_n$  is an index indicating *P. cinnamomi* overwinter survival in trunk cankers of red oak trees (14).

Other factors known to be linked to ink disease incidence, such as aspect and elevation (11), were tested to determine whether impact of winter temperature on overwintering of *P. cinnamomi* in trunk tissues could act as a confounding factor in the relationship. The aspect of stands was significantly associated with both presence of the disease in stands and frequency of cankered trees in infected stands, even when median  $I_n$  was already introduced in the model (Table 2). Stands with an aspect toward the south, WSW and SSE, had both a higher frequency of ink disease presence and a higher



incidence of cankered trees in infected stands (Table 3). There was no median  $I_n$  x aspect interaction for these two disease variables. When entered in a model not including median  $I_n$ , elevation was significantly linked to both the presence of ink disease in a stand and to the frequency of cankered trees in infected stands ( $\chi^2 = 31.1$  and 28.0 respectively,  $p < 0.001$ ). However, when it was entered in a model already including the median  $I_n$  and the stand aspect, it did not contribute any additional information (Table 2).

**Table 3.** Incidence of Ink disease caused by *Phytophthora cinnamomi* on red oak according to site aspect in stands with suitable winter climate <sup>a</sup>.

| Aspect <sup>b</sup> | No | Frequency of            |   | Index of canker development <sup>c</sup> |
|---------------------|----|-------------------------|---|--|
|                     |    | stands with ink disease | cankered trees (in stands with ink disease) |  |
| ENE                 | 22 | 55 %                    | 7 %   | 1.3                                      |
| NNW                 | 27 | 52 %                    | 4 %   | 0.9                                      |
| WSW                 | 15 | 70 %                    | 18 %  | 1.1                                      |
| SSE                 | 28 | 85 %                    | 9 %   | 0.9                                      |
| None                | 79 | 53 %                    | 9 %   | 1.0                                      |

<sup>a</sup> Locations with  $I_n$ , an index indicating *P. cinnamomi* overwinter survival in trunk cankers of red oak trees (14), greater than 0.65.

<sup>b</sup> ENE, east and northeast; NNW, north and northwest; WSW, west and southwest; SSE, south and southeast; None, flat topography.

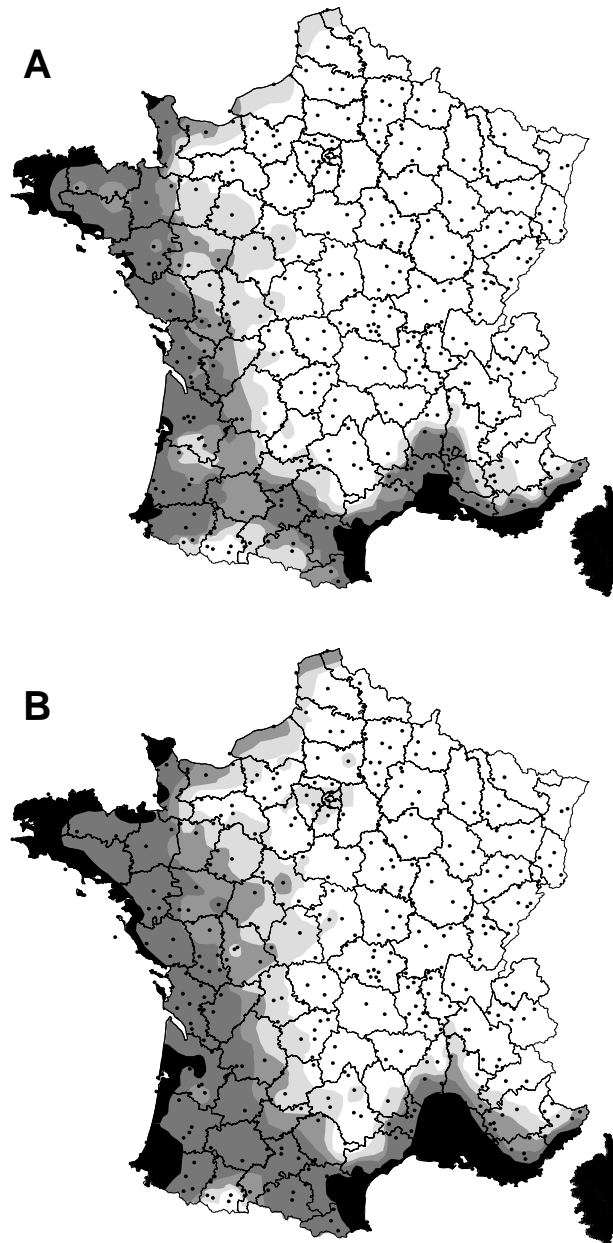
<sup>c</sup> The index of canker development measures the volume loss on infected trees due to the canker.

Unlike the presence of disease in stands or the frequency of cankered trees, disease severity on trees, estimated by the mean index of canker development, CD, on infected trees, depended neither on median  $I_n$  nor on stand aspect (Tables 1 and 3). Pearson correlation between CD and median  $I_n$  was 0.054 ( $p = 0.592$ ). CD, remained around 1, which meant that most infected trees had a canker between 0.5 and 1 m high.

### Mapping of pathogen survival in cankers

The map of median  $I_n$  distribution in France for red oak is shown in Fig. 5A. The areas with winter temperature regime favorable to pathogen survival correspond to western and southern coastal areas of the country with median  $I_n > 0.7$ . In three areas, winter temperature regime are extremely favorable (median  $I_n > 0.9$ ). They correspond to the actual area of the disease in the south-west corner of the country, to Brittany, in the north-west of France, an area free of the disease until now, and to the Mediterranean coast, where *P. cinnamomi* is present on other oak species. The ink disease hazard is very low in most of the rest of the country, with  $I_n$  above 0.5. The map for pedunculate oak is different (Fig. 5B), with larger areas with winter temperature regime favorable to canker development (high  $I_n$ ).

The distribution of the ink disease in south-west France shown in Fig. 1 closely matches the distribution of the median  $I_n$  (Fig. 5). Indeed, in both cases there is a west to east gradient in the Pyrenean Piedmont, from the Basque area, around Biarritz, to the east of Hautes-Pyrénées and south of Haute-Garonne. Also, median  $I_n$  values are smaller north of the line from Bordeaux to Toulouse and disease is absent in that area.



**Figure 5.** Mapping of ink disease hazard in France, based on the median predicted survival of *Phytophthora cinnamomi* in oak trunks. A. median  $I_n$  for *Quercus robur*. B. median  $I_n$  for *Quercus rubra*. median  $I_n < 0.5$  (□), 0.5 to 0.7 (◻), 0.7 to 0.8 (◼), 0.8 to 0.9 (◼), >0.9 (◼). Closed circles represent meteorological stations used in the study.

## Discussion

The median  $I_n$  enabled us to adequately predict the distribution of the disease in south-west France. The simulation of canker development predicted that cankers will fail to develop in areas where median  $I_n$  is lower than about 0.5 to 0.6, and indeed no disease is found in stands where median  $I_n$  is  $< 0.65$ . The prediction was especially good for presence of disease in stands. The frequency of moderately cold winters was more important for preventing canker enlargement than the occasional occurrence of very severe frosts. Winter temperature regime appears to be the predominant factor in the distribution of ink disease in south-west France and, in particular, the west-to-east gradient in disease incidence that can be observed in the Pyrenean piedmont. The Gers, Landes, and Lot-et-Garonne areas also have favorable winter temperature regimes. However, in these areas, the forest is mainly a pine

forest and few red oak stands are present. As a consequence, the approach used in this work to estimate the suitability of climate for ink disease development as far as winter temperature regime is concerned can be considered valid.

Previous reports of the field survey (10; 11) indicated that disease incidence is linked to elevation: at elevations above 440 m no disease can be found. The hypothesis was that at higher elevations, winters are unfavorable to the survival of *P. cinnamomi*. Indeed, once the impact of frost was taken into account by the median  $I_n$ , elevation did not bring any additional information in our analysis. The lower incidence of the disease in stands on northern aspects might also have been linked to winter temperature conditions. However, there was no interaction between median  $I_n$  and aspect: incidence of ink disease remains low on northern aspects even in the Basque area where winter temperature regime is almost never limiting for canker development, with  $I_n > 0.9$  in >80 % of the years. Alternatively, the difference in incidence of ink disease on different aspects could be linked to the water regime. The susceptibility of red oak to *P. cinnamomi* is increased by water stress (13). A higher incidence of ink disease on southerly aspects could be due to higher evapotranspiration during summer and more frequent water deficit. Indeed, the disease is also more severe on other locations that are prone to water deficit, i.e., hill tops and upper slopes compared with flat topography and lower slopes (10; 11; 12).

The modeling approach only considers the ability of the pathogen to cause cankers once it is present at the tree basis. The underlying hypothesis is that the pathogen is introduced into forests by planting infected, nursery-raised oaks and is quite well distributed in infected stands. We thus did not consider the spread of the pathogen in soil within the stand. This assumption appears to be justified by the close agreement between ability of the pathogen to survive in trunk canker in a location and the incidence of ink disease in this area. The mapping of disease hazard would also need to be improved by including other environmental effects that may act on canker enlargement at a regional scale such as temperature during the growing season. Such information would be important in particular in Brittany where summer temperature might not be high enough to enable proper canker development. Unfortunately, the variability in summer temperature was not high enough during the studied period in south-west France, and we did not have enough data to include this effect in the model. In any case, in locations where median  $I_n$  was <0.5, the winter temperature regime was not favorable to the ink disease of red oak. For  $I_n$  between 0.5 and 0.7 the winter temperature regime was moderately unfavorable to the disease and its development should be strongly hampered. By contrast, in locations where median  $I_n$  was >0.7, winter temperatures were not limiting for disease development.

The median  $I_n$  was much better linked to the likelihood of disease presence in a stand than to frequency of cankered tree in infected stands. It appears that once climate enables some overwintering of *P. cinnamomi* in the tree cortical tissues, the development of the disease in some stands may be severe. It is likely that the local site conditions such as aspect, topography, and soil are then major factor determining the local incidence of the disease (10; 11; 12), which explains the looser relationship with median  $I_n$ . It has to be pointed out that the relationship between  $P_n$  and  $I_n \times P_{n-1}$  was loose (Fig 2), which suggests that many significant factors, in particular tree variability in susceptibility and site effects, were not taken into account.

Since soil seldom freezes at depths >10 cm in south-west France, *P. cinnamomi* is less exposed to temperature <0°C in the soil than in trunks. As a consequence, we anticipated that in areas with winter temperature regime moderately unfavorable to ink disease development on oak, very small cankers would occur resulting only from root infection each year. Thus, the first limiting effect of frost on disease would have been a limited canker height. However, frequent years with unfavorable winter temperature appeared to have an impact mainly on the proportion of trees cankered per stand. No relation could be seen with the canker size on infected trees. Other important stand factors such as aspect and topography were also shown to have a much higher impact on the proportion of cankered trees per stand than on canker size on infected trees (10; 11). Obviously, the establishment of *P. cinnamomi* on the lower bole of an oak tree is a key step in disease development. Perhaps in stands where frost limits disease incidence, only trees very susceptible to *P. cinnamomi* are cankered, while in stands where winter conditions are favorable to the disease, many trees with limited susceptibility to *P. cinnamomi* get cankered.

Climatic factors, especially winter temperature, may also explain the absence of ink disease of red oak in its natural range in the eastern United States. Indeed, severe *P. cinnamomi* damage has been reported on chestnuts and pines in the southern part of the red oak range. However, red oak, at those latitudes, is generally found at much higher elevations than chestnuts and pines (24). Mortality of chestnuts was especially high in bottom lands and at lower elevations (6).

To our knowledge, this is the first hazard mapping for a disease caused by *P. cinnamomi*, based on the modeling of a key epidemiological process, i.e. the winter survival of the parasite in trunks. *P. cinnamomi* has been known to be susceptible to frost for many years (2; 22) and other mappings have been based on correlation analysis and climate matching (4; 19). As expected, temperature, especially the minimum, was among the most discriminatory variables. Our results are in good agreement with the CLIMEX analysis performed by Brasier and Scott (4) for Europe. They show that the disease could develop in many areas of France where it is not present yet, especially in the west of the country. Moreover, high risk of ink disease on pedunculate oak could exist in a wider area than for red oak. It is therefore very important to avoid the introduction of *P. cinnamomi* in areas or stands presently free of the parasite, especially via infected nursery seedlings when plantations are established.

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