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Modelling the influence of winter frosts on the development of the stem canker of red oak, caused by *Phytophthora cinnamomi*

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Summary — The evolution of trunk cankers induced by *Phytophthora cinnamomi* over a period of about 25–30 years was studied by a dendrochronological method on 20 *Quercus rubra* trees located in four plots in southwest France. In plots as far from each other as 150 km, AE_i, the annual evolution of the cankers, presented similar trends, with enlargement or reduction of the cankers occurring in the same years. This suggests a strong influence of climatic conditions on the disease development. A model describing the influence of winter frost on the evolution of the cankers was developed. This model predicted the AE_i well. No trace of *P cinnamomi* lesions could be found in the growth ring of an individual tree in years for which the model predicted total elimination of the fungus. Moreover, the amount of lesions induced by *P cinnamomi* on the trees studied usually decreased in years for which the model predicted poor survival of the fungus.

***Quercus rubra* / *Phytophthora cinnamomi* / frost / model / canker / winter survival**

Résumé — Modélisation de l'influence des gelées hivernales sur le développement de l'encre de chêne rouge causée par *Phytophthora cinnamomi*. Phytophthora cinnamomi *est l'agent de l'encre du chêne rouge,* Quercus rubra. *La maladie se manifeste par un chancre sur la partie basse du tronc. Par méthode dendrochronologique, nous avons étudié le développement du chancre sur 20 arbres situés dans le sud-ouest de la France sur une période de 25–30 ans. Dans des sites éloignés les uns des autres (Pyrénées-Atlantiques, Hautes-Pyrénées, Gers), l'évolution des chancres présentait des profils similaires, ce qui indique une forte influence des conditions climatiques. D'importantes réductions des chancres actifs étaient liées à des hivers particulièrement froids, notamment en 1985. Nous avons développé un modèle décrivant l'influence du gel sur l'évolution des chancres. Ce modèle prédit correctement l'évolution des 20 chancres étudiés. En particulier, aucune trace de lésions provoquées par* P cinnamomi *ne peut être observée dans le cerne annuel après un hiver où le modèle prédit une élimination totale du champignon des tissus corticaux de l'arbre. Ceci arrive uniquement pour*

la face nord du tronc durant la période étudiée. De plus, la quantité de lésions induites par P cinnamomi *sur les arbres étudiés diminue généralement dans les années pour lesquelles le modèle a prédit une mauvaise survie hivernale du champignon.*

Quercus rubra / Phytophthora cinnamomi / *gel / modèle / chancre / survie hivernale*

INTRODUCTION

Phytophthora cinnamomi Rands causes the ink disease of northern red oak, *Quercus rubra* L. The only obvious symptom of this disease is a cortical canker on the lower part of the trunk, which typically reaches to about 1 m from soil level, but can occasionally reach up to 5–6 m. The canker reduces the economic value of the timber. In some forests of the Basque area, more than 50% of the red oak trees exhibit a trunk canker (Marçais, 1992). Robin et al (1992) studied the aetiology of the canker development. They showed that it was possible to quantify the annual enlargement of the canker over several decades by dendrochronological methods. Dieback of the infected trees did not seem to occur.

The ink disease was first described in France, in the Basque area, in the early 1950s (Moreau and Moreau, 1951). At present, it has only been reported in Europe, in France and in the north of Spain. In France, more than 40 years after its discovery, the disease can only be found in a small area, in the southwest of the country (fig 1). In contrast, after it was first reported in the Basque area in 1880, the ink disease of chestnuts, also caused by *P cinnamomi,* spread throughout the south of France in about 40 years (Grente, 1961). *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 (Vegh and Bourgeois, 1975). Therefore, Delatour (1986) suggested that the distribution of the ink disease might be limited by a meteorological factor.

The most likely factor would be temperature. *P cinnamomi* requires warm conditions to develop. In Europe, Brasier and Scott (1994) showed that the climate was warm enough for the development of *P cinnamomi* only in Mediterranean and Atlantic areas. In Tasmania, temperature explained the distribution of this fungus better than rainfall: dieback induced by *P cinnamomi* in natural forests occurred mostly in areas where the average temperature of the coldest and the hottest months were, respectively, higher than –0.8 and 18.5 °C (Podger et al, 1990). The limit of –0.8 °C for the coldest month should be linked to the limited survival of the fungus at temperatures below 0 °C (Sauthoff, 1967; Benson, 1982). Winter frosts are not a major limiting factor for the development of *P cinnamomi* on chest-

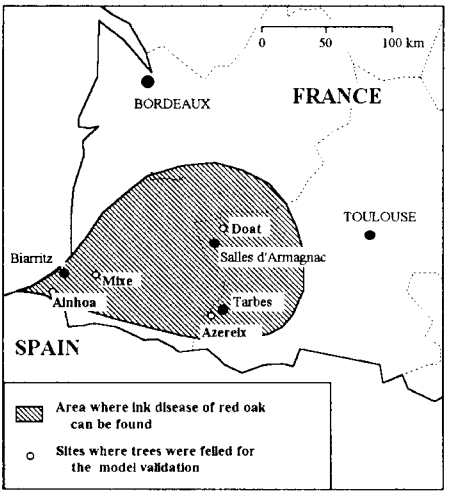

Fig 1. Distribution of the ink disease of *Quercus rubra* in France (from Levy, 1992) and location of the studied sites.

nut trees and on most of its ornamental hosts because it induces a root disease on those plants. Deep layers of the soil seldom freeze in France. In the Netherlands, Van Steekelenburg (1973) showed that *P cinnamomi* was inactivated in the upper layers of the soil during winter, but remained active at depths below 10 cm. Ink disease damages are at first trunk damage. *P cinnamomi* is more exposed to sharp temperature variations in the bark tissues of the trunk than in root tissues, below soil level. Thus, extension of the ink disease to new areas of France could be hampered by the winter temperatures. A model has been constructed which describes the influence of frost on the survival of *P cinnamomi* present in the cortical tissues of the trunk (Marçais, 1992).

The aim of this work was to study the development of *P cinnamomi*-induced trunk cankers on red oaks over a period of many years by dendrochronological methods and to look for relationships between the annual development of the stem cankers and the output of this model.

MATERIALS AND METHODS

Model development

As *P cinnamomi* is more exposed to low temperatures at the trunk level, we assumed, for the model construction, that frost would act primarily on the inoculum present in the trunk cortical tissues. The canker results from an annual vertical spread of *P cinnamomi* in the tissues of the lower trunk of about 15–30 cm a year (Robin, 1992; Marçais et al, 1993). If the fungus is not able to overwinter in the trunk cortical lesions, it will not be able to induce a canker high on the trunk and thus will not have an influence on the economic value of the timber. Thus, the model assumes that *P cinnamomi* has induced cortical lesions on the lower trunk of an oak, and that the fungus inoculum is fully alive at the beginning of the winter. Then, it estimates the influence of frost on the survival of the pathogen present in those lesions. For this, the model estimates the hourly air and bark temperatures for each day from 1 November to 31 March. Then, it computes the sum of bark temperatures below 0 °C for the winter. From this, it computes a survival index for *P cinnamomi*. The main steps of the model are described in table I.

Hourly air temperatures are computed from the maximal and the minimal daily air temperatures, which are input variables. For this, we used equation [2], established by Choisnel (1977, table II). The model then estimates values of the hourly bark temperature for the northern trunk side. Bark temperature variations follow air temperature variations with a latency of about 2 h (Marçais, 1992). The amplitude of the temperature variations is attenuated in the bark compared to the air. The proportion of the air temperature variations which is transmitted to the bark is estimated by *TTC*, the thermic transmission coefficient. *TTC* depends on the trunk diameter, which is an input variable, and on the status of the bark, frozen or unfrozen (eqs [1] and [1'], table II). Equations [1] and [1'] were established for tree diameters at breast height ranging from 13 to 70 cm (Marçais, 1992). These equations can be extrapolated to tree diameters larger than 70 cm. TTC_f, thermic transmission coefficient for frozen bark, is about 0.30 to 0.35 for a trunk of a diameter of 35–70 cm. For diameters smaller than 30 cm, *TTC* increases dramatically. The bark temperature at hour *h* is computed from the bark temperature at hour *h*-1, *TTC*, and from the variation of the air temperature from hour *h*-3 to hour *h*-1 (eq [3], table II). After being computed, the 24 hourly bark temperatures of the day for the northern side of the trunk are checked. For this, the model uses a relation existing between the mean of the maximum and minimum daily temperature of the air and the mean of the maximum and minimum daily temperatures of the bark (steps 7 and 8, table I; eqs [4] and [4'], table II). The model compares *M*bark (mean of the maximum and minimum daily temperature of the bark) computed at step 6, to *M*bark_exp (value expected according to eq [4]). If *M*bark is out of the 95% confidence interval for individual values predicted by equation [4] the difference (*M*bark_ exp – *M*bark) is added to each of the 24 hourly bark temperatures calculated at step 5. Equation [4], has been established for mean air temperatures in the range of –5 to 12 °C. Steps 7 and 8 of the model proved to be necessary because the bark temperature at hour *h* is computed from the bark temperature at hour *h*-1.

Table I. Key processes in the model estimating the influence of winter frost on the stem canker of red oak, caused by *Phytophthora cinnamomi*.

	Step and process	*Derivation* *
Beginning of winter		
1	Read the tree diameter at 0.5 to 0.8 m height	Initializing file
2	Calculate thermic transmission coefficients for the lower trunk of the tree	Equations [1] and [1']
Every day in winter (1 November–31 March)		
3	Read the daily maximum and minimum air temperature	Meteorological file
4	Calculate hourly air temperature for the day	Equation [2]
5	Calculate hourly temperature of the inner bark for the northern side of the lower trunk	Equation [3]
6	Calculate the mean of the daily maximum and minimum temperature of the air and of the inner bark (trunk side toward north)	
7	Calculate an expected value for the mean of the daily maximum and minimum temperature of the inner bark (trunk side toward north) and compare it to the previously calculated one	Equation [4]
8	If the difference is too large (over the standard error of individual values predicted by eq [4]), add this difference to each hourly temperature of the inner bark (trunk side toward north)	Equation [4']
9	Calculate the hourly temperature of the inner bark for the trunk side toward south	Equation [5]
10	Calculate the daily sum of temperature below 0 °C for the inner bark of the lower trunk (for both sides, toward north and south)	
End of winter (31 March)		
11	Calculate the annual sum of temperature below 0 °C for the inner bark of the lower trunk (for both northern and southern sides)	
12	Calculate a *P cinnamomi* survival index for the inoculum present in the cortical lesions of the lower trunk on a cankered tree (for both northern and southern sides)	Equation [6]

* Equations are given in table II.

As a consequence, errors in the estimation of bark temperatures are accumulated over time, which would be a problem if bark temperature was estimated on this basis for several days. Moreover, for the first day of the winter, an initial bark temperature has to be provided for equation [3]. Steps 7 and 8 enabled us to overcome these problems.

The hourly bark temperatures of the southern side of the trunk are computed from the hourly bark temperature of the northern side of the trunk. This is done only if the bark temperature of the

Table II. Equations and variables used in modelling the influence of winter frost on the ink disease of oak, caused by *Phytophthora cinnamomi*.

Equation no	*Equation and definition of the variables*	*Reference*
[1]	$TTC_f = [1 - 0.70 / (1 + 17.82 \times \exp(-0.05 \times \pi \times D))]$	Marçais, 1992
[1']	$TTC_u = [1 - 0.52 / (1 + 26.00 \times \exp(-0.05 \times \pi \times D))]$ *TTC* are thermic transmission coefficients for frozen (TTC_f) or unfrozen (TTC_u) inner bark; *D* is, in cm, the diameter under the bark of the second disk from the base of the trunk (0.5–0.8 m from soil level).	Marçais, 1992
[2]	$T\text{air}\ [h] = (\ T\text{min} + (\ T\text{max} - T\text{min}\ ) \times K\ [h]$ *T*air *[h]* is the air temperature on hour *h*, in °C; *T*max and *T*min are the daily maximum and minimum temperature, in °C; *K [h]* is a coefficient which depends on the hour *.	Choisnel, 1977
[3]	$T\text{bark}\ [h] = T\text{bark}\ [h\text{-}1] + TTC \times [(T\text{air}\ [h\text{-}1] - T\text{air}\ [h\text{-}3]\ ) / 2\ ]$ *T*bark *[h]* is the temperature of the inner bark for the trunk side toward north at hour *h* (in °C); *TTC* is TTC_f if *T*bark [*h*-1] is below 0 °C or TTC_u if *T*bark [*h*-1] is higher than 0 °C	Marçais, 1992
[4]	$M\text{bark\_exp} = 0.84 \times M\text{air} - 0.33$ *M*air is the mean of the daily maximum and minimum temperature of the air. *M*bark_exp is the expected means of the daily maximum and minimum temperature of the inner bark (trunk side toward north).	Marçais, 1992
[4']	if $\lvert M\text{bark\_exp} - M\text{bark} \rvert > 1.5$: $T\text{bark}\ [h] = T\text{bark}\ [h] + (\ M\text{bark\_exp} - M\text{bark}\ )$ *M*bark is the mean of the daily maximum and minimum temperature of the inner bark (trunk side toward north). *M*bark_exp ± 1.5 are the upper and lower limits of the 95% confidence interval for the individual values predicted by equation [4]	Marçais, 1992
[5]	if $h > 10$ or $h < 20$: *T*bark_south *[h]* > 0 if $h <= 10$ and $h >= 20$: *T*bark_south *[h]* = *T*bark *[h]* + 0.3 *T*bark_south *[h]* is the inner bark temperature on hour *h* for the trunk side toward south	Marçais (unpublished)
[6]	$I_j = 1 - 1 / (\ 1 + 14.7 \times \exp (\ 0.007 \times AST_j))$ I_j is the *P cinnamomi* survival index for canker part located on the trunk side toward south (I_s) or north (I_n); AST_j is the annual sum of temperature below 0 °C for inner bark on the trunk side toward south (AST_s) or north (AST_n)	Marçais, 1992

* *K [h]* are from Choisnel (1977).

northern side of the trunk falls below 0 °C. As the trunks are unshaded during the winter, the difference in the bark temperatures between the southern and northern sides can be critical during the afternoon, with values sometimes superior to 10 °C during frost events. As a consequence, it can be assumed that bark at the southern side of the trunk do not freeze from 1100 to 900 hours (eq [5], table II). From 2000 to 1000 hours, the difference is much smaller and has an average value of 0.3 °C. Equation [5] has been established for bark temperature in the range of 0 to –8 °C.

Equations [1], [1'], [3], [4] and [5] were established from investigations on mature red oaks in forest conditions (Marçais, 1992; Marçais, unpublished results).

At the end of the winter, the annual sum of bark temperatures below 0 °C, *AST*, is computed for both the northern (AST_n) and southern (AST_s) aspects of the trunk. *P cinnamomi* survival index I_n and I_s are calculated from AST_n and AST_s (eq [6], table II). *P cinnamomi* is not more resistant to frost after a hardening treatment (Benson, 1982; Marçais, unpublished results). Variability in frost resistance could not be detected among 12 *P cinnamomi* isolates from France (Marçais, 1992). Equation [6] was derived from experiments where the recovery of *P cinnamomi* from infected oak bark tissues was determined after exposure to frost in laboratory conditions. The *P cinnamomi* survival index, *I*, is therefore a frequency of *P cinnamomi* recovery from bark lesions. It ranges from 1, for full survival, to 0, for total death of the fungus. Equation [6] has been established at –5 °C. It can be used with little error for temperatures ranging from 0 to –12 °C (Marçais, 1992; Marçais, unpublished results). Figure 2 shows the relationship between the survival index and the sum of temperatures below 0 °C. It was assumed that *I* is representative of the proportion of inoculum which is still active in the lesions at the end of the winter. Thus, when *I* is low, the proportion of lesions from the previous years from which *P cinnamomi* is able to grow and to infect new host tissues is low and the amount of lesions induced on the trunk that year should be less than in the previous one. As survival of *P cinnamomi* should be better on the southern side of the trunk, I_s is likely to be higher than I_n for characterizing overwintering of the fungus in the trunk lesions. If I_s and I_n are equal to 0, the tree should heal the wounds and no active cortical lesions induced by *P cinnamomi* should be found in the following years. I_s and I_n were considered to be equal to 0 when they were below 0.01.

Model validation

Studied plots

Severely infected plots were selected in four stands located in southwest France (fig 1). The percentage of trees exhibiting a trunk canker ranged from 15 to 50%. The least infected plot was Azereix. Ink disease has been reported in the two western stands (Ainhoa and Mixe) since 1948, whereas it was only reported in the eastern stands (Azereix and Doat) in 1984 (Pilard-Landeau, 1984). The presence of *P cinnamomi* in each studied site was checked: samples were taken from active stem lesions on some of the trees and plated on selective medium (20 g x L^{-1} agar; 15 g x L^{-1} malt extract; 400 µL x L^{-1} pimaricin; 250 mg x L^{-1} ampicillin; 10 mg x L^{-1} rifampicin; 30 mg x L^{-1} of 50% benomyl). Trees in the Ainhoa, Doat and Azereix plots were on low-lying land, whereas the Mixe plot was located on a hilltop. Doat was a severely hydromorphic site. The age of these planted stands were 33 years for Ainhoa, 45 years for Mixe and Doat and 61 years for Azereix.

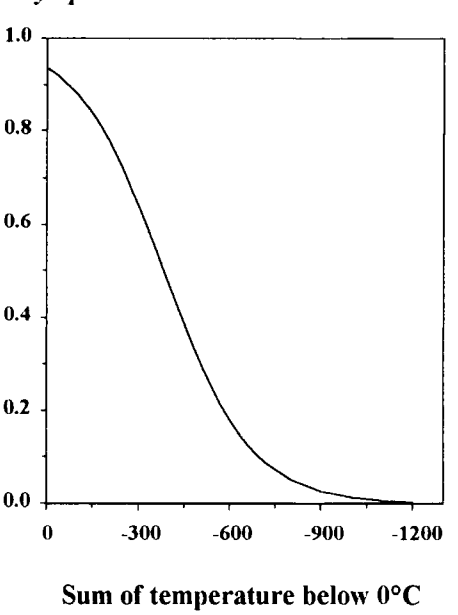

Fig 2. Influence of frost on *Phytophthora cinnamomi* survival (Marçais, 1992).

Sampling of the trees

Five infected trees per plot were selected and felled in December 1988 at Ainhoa, in February 1990 at Doat, in November 1990 at Azereix and in March 1991 at Mixe. The selected trees were among the most severely attacked by *P cinnamomi*: they exhibited large cankers which extended high up the trunk and were present on a percentage of the lower trunk circumference as high as possible. Mean diameter at breast height of the sampled trees was 29.8 cm in Ainhoa, 45.3 cm in Azereix, 45.3 cm in Doat and 46.4 cm in Mixe. Five trunk disks, 5–10 cm thick, were sampled per tree with a chain saw. One was located at the collar, another at the upper part of the canker, at 1.5–2.5 m height, and the three others at regular intervals in between. Disks were therefore taken every 30–60 cm. Only three to four disks were sampled on three trees of the Azereix plot because they had a canker of less than 1.5 m height. The disks were air-dried at room temperature and then sanded.

Quantification of the annual development of the trunk cankers

Figure 3a shows an infected trunk disk of a red oak tree. *P cinnamomi* develops in the inner cortical tissues, causing the necrosis of the cambium (fig 3b). The oak heals most of the wounds and includes the lesion inside the wood by producing xylem-callus curls or a new cambium in the living cortical tissues (Barriéty et al, 1951; fig 3b). We assumed a lesion had occurred during the last year for which the earlywood was present (fig 3b). The earlywood starts to develop early in the spring, before bud break in April (Zasada, 1968). For each disk, all the lesions were dated. Their width was traced on a plastic film as shown in figure 3b and was measured with a digitizer. For each disk, we added the width of all the lesions which occurred during the same year. Each of those annual sums of lesion widths were then divided by the annual perimeter of the disk, giving a parameter we will call hereafter the *percentage of perimeter attacked (PPA)*. The perimeter of the disk was computed for each year from the annual wood ring diameter. For each year, the mean *PPA* of the tree was calculated.

The annual evolution of a canker for year *i* (AE_i) was calculated as:

$$AE_i = (PPA_i - PPA_{i-1}) / PPA_{i-1}$$

where PPA_i and PPA_{i-1} are the mean *PPA* of the five disks for the years i and *n*-1. Therefore, a positive AE_i indicates an increase in *PPA* on the disks already attacked or/and the colonisation of a disk previously free of *P cinnamomi*. The AE_i was calculated only if the canker in the year *i*-1 was sufficiently developed, ie, if PPA_{i-1} was greater than 1.

A specific study on the orientation of the lesions was realized in Azereix. This plot was chosen because it has the coldest winters among the four studied plots. Moreover, the low level of ink disease in this stand suggested, a priori, that frost might be an important epidemiological factor there. The study was realized for the years 1980 to 1989 because the cankers were sufficiently

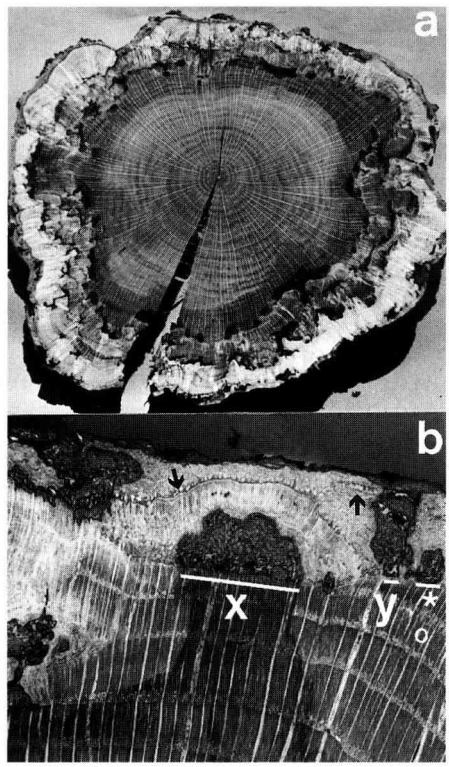

Fig 3. Features of a *Phytophthora cinnamomi*-infected red oak trunk. (**a**) Disk; (**b**) detailed view of an included lesion. The lesion of width *X* developed the year *O* whereas the lesion of width *Y* developed the next year (✱). Wood present inside the inner bark (➜) results from a new cambium activity.

developed during this period. Each disk was divided into two areas, one facing the southwest and the other facing the northeast. The *PPA* was determined separately for each of those two areas, using the method previously described.

Comparison of the model outputs with the AE_i

For each tree, the model was run for all the years where the second disk from the base of the trunk (40–80 cm from soil level) had a perimeter of more than 30 cm (diameter of 10 cm). The annual diameter of this disk was used as the input variable for computing *TTC*. Daily maximal and minimal temperatures were provided by the Bureau inter-régional Sud-Ouest (Météo-France) and originated from the meteorological station of Biarritz for Ainhoa and Mixe, Tarbes-Ossun for Azereix and Salles d'Armagnac for Doat. The distance from the site to the meteorological station was 20 km for Ainhoa, 34 km for Mixe, 3.5 km for Azereix and 15 km for Doat. The *P cinnamomi* survival index, *I*, for both sides of the trunk (southern and northern) were compared to the annual evolution of the canker AE_i.

RESULTS

Evolution of the percentage of the trunk perimeter attacked

Figure 4 shows the annual evolution of the mean percentage of perimeter attacked by *P cinnamoni (PPA)* in each of the four plots studied. A similar general trend can be observed in all the plots. That is a progressive enlargement of the cankers from 1965 to 1984, followed by a steep decrease after 1984.

P cinnamomi stem infections had been present in each of the four plots for at least 25 to 30 years before our study. Indeed, the oldest infections on one of the studied trees dated back to 1958 at Mixe, to 1959 at Azereix, to 1964 at Ainhoa and to 1967 at Doat. Seventy-five percent of the oaks studied were infected on the trunk for the first time between 1965 and 1973. The enlargement of the cankers was slow in Azereix compared with the other plots: the mean *PPA* remained lower than 2.5% until 1982 (fig 4).

The annual evolution of the mean *PPA* per plot was somewhat irregular (fig 4). First order autocorrelation of the annual evolution of the *PPA* (AE_i) was not significant in any of the four plots. In some years, the *PPA* increased simultaneously in all the plots. The increase in *PPA* was especially important in 1982 (fig 4), with the highest AE_i recorded in all the plots for the studied period (result not shown).

In contrast, *PPA* decreased in all the plots in 1985. In that year, annual growth rings of previously attacked disks were frequently completely free of traces of *P cinnamomi* infection ('healed' disks). This occurred in other years, in particular 1963 and 1964, but was specially important between 1985 and 1987 (65.8% of all the 'healed' disks). During this period, 12% of the previously attacked disks 'healed' on the Ainhoa trees, 53% on the Mixe trees, 77% on the Azereix trees and 86% on the Doat trees. With most of the trees, *P cinnamomi* infections could still be observed in the annual growth rings of 1985, 1986 and 1987 on some disks. A new colonisation of the 'healed' disks then occurred in the following years, either downward from upper disks, upward from lower disks or from the roots. For three of the trees studied, located in Azereix, Doat and Mixe, all the previously attacked disks 'healed'. These trees did not show any new *P cinnamomi* infection on the trunk until the felling, in 1989 or 1990. In 1963, just four trees in Azereix and Mixe were infected on the stem. Fifty percent of the disks which were infected in 1962 'healed' in 1963 or in 1964.

During the period between 1980 and 1989, the cankers of the Azereix plot trees were more developed on the southwest side

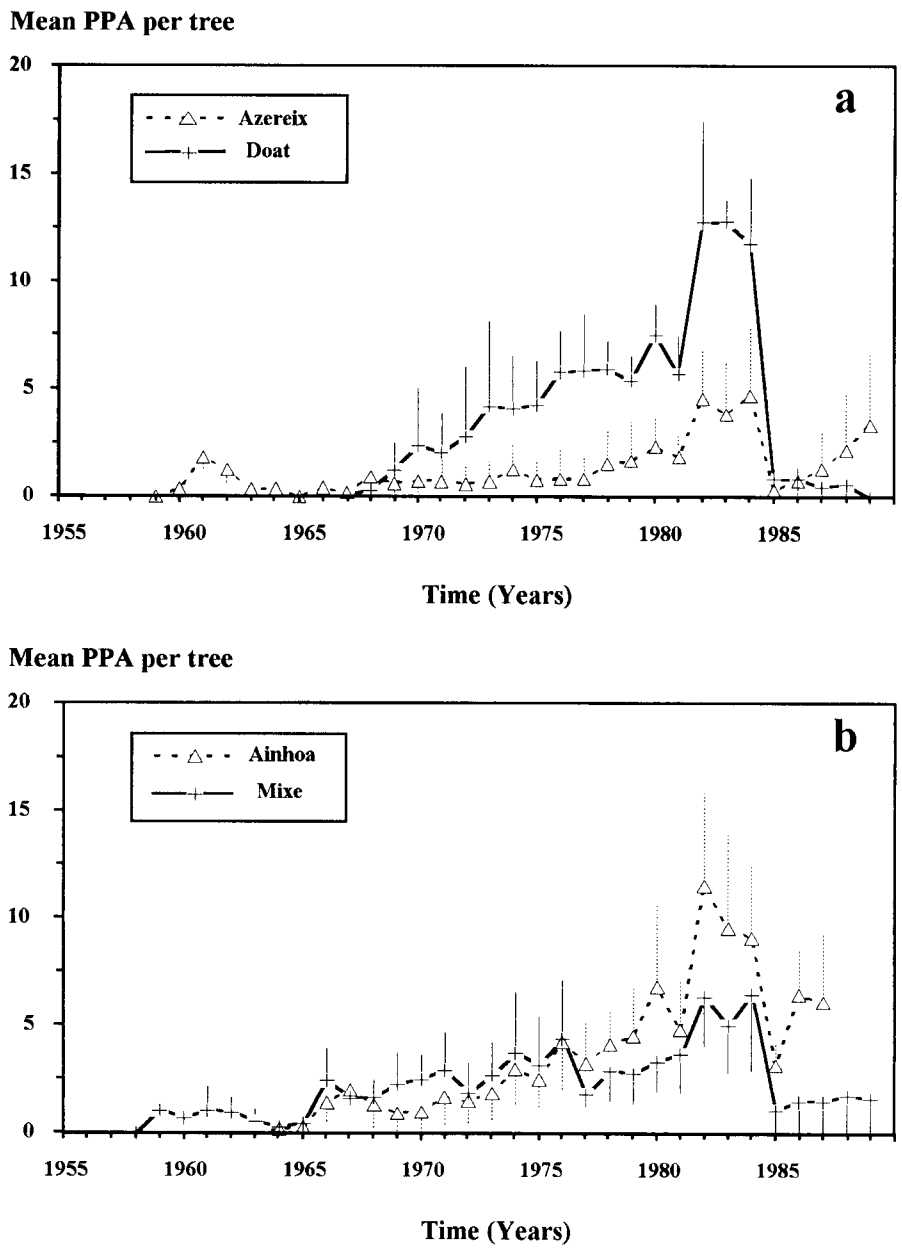

Fig 4. Evolution of the ink disease on the studied *Quercus rubra* plots: mean annual percentage of perimeter attacked *(PPA)* per tree in each plot from 1958 to 1989. (**a**) Eastern plots; (**b**) western plots. The bars represent standard errors.

of the trunk compared with the northeast side (fig 5). For each of the five trees, the *t*-test indicated a significant difference at the 5% level between the *PPA* of the two trunk sides (*t* of 2.4, 3.0, 4.1, 2.3, 2.4; *df* of 9).

Model validation

The lowest bark temperature computed by the model for the period 1960–1989 was about –13 °C. Bark temperatures were seldom lower than –10 °C. The longest period for which bark temperature of a tree remained below –10 °C throughout the winter was 28 h. Equation [4] was used out of the range in which it was established during only 1 day in all the plots (in 1985) for a mean daily temperature in the range of –8 to –13 °C. Equation [5] was also seldom used out of the range in which it was established: this occurred for 8 h in the Azereix plot and for 2 h in the Doat plot, both in 1985.

The model never predicted total elimination of *P cinnamomi* from the trunk cortical tissues ($I_s = I_n = 0$). This occurred only for the northern side of the trunk ($I_n = 0$; $I_s > 0.01$) in 1963 (Azereix and Mixe), in 1985 (Azereix and Doat) and in 1987 (Doat). Indeed, in the 1963 and 1985 annual growth ring of the Azereix trees (fig 5), in the 1985 and 1987 annual growth rings of the Doat trees and in the 1963 annual growth rings of the Mixe trees (results not shown), no traces of *P cinnamomi* lesion could be observed on the northeastern side of the trunk.

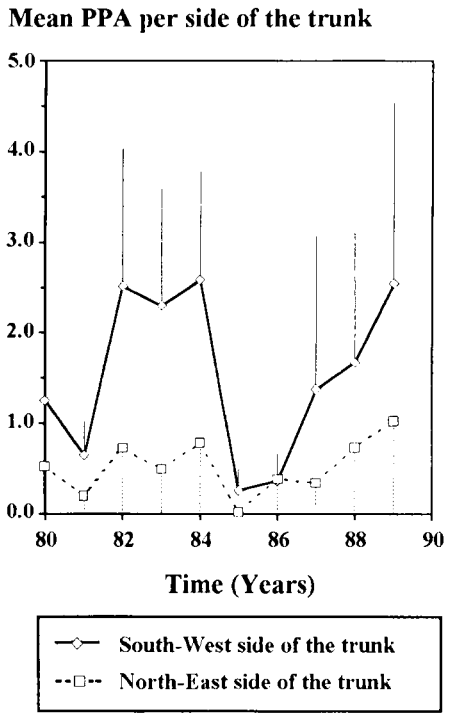

Fig 5. Evolution of the Mean *PPA* at Azereix on the southwest side of the trunks or on the northeast side (1980–1989). The bars represent standard errors.

The model outputs were significantly correlated with the annual evolution of the cankers (AE_i): the Pearson correlation coefficient was 0.45 between AE_i and I_s and 0.42 between AE_i and I_n ($df = 272$). The model computed low survival index ($I_s < 0.5$) in 1960, 1963 and 1985 for all the plots and in 1971, 1981, 1986 and 1987 for the plots of Azereix and Doat. The amount of lesions induced by *P cinnamomi* on the studied trees usually decreased in those years: AE_i were then very often negative and the percentage of 'healed' disks was high (table III, table IV). In particular, when the survival index for the southern side of the trunk (I_s) was lower than 0.1, AE_i was lower than –0.61 in 75% of the cases, and the percentage of 'healed' disks was over 50% in half of the cases (table III). When the model computed an I_s lower than 0.1, the survival index for the northern side of the trunk (I_n) was always 0. Yet, in 8–30% of the cases in which the model computed a low I_s (0.1 to 0.5), the cankers enlarged ($AE_i > 0$; table III). Those prediction errors of the model all corresponded to little developed cankers: when the model predicted an I_s between 0.1 and 0.5, the mean *PPA* was 5.3 ± 2.0 for the cases where AE_i was negative and 1.1 ± 0.6

Table III. Model validation: annual evolution of the canker on the trees studied (AE_i) for different levels of I_s, the *P cinnamomi* survival index for the south-facing trunk side (Ainhoa, Azereix, Doat, Mixe, 1968–1989).

I_s *	*No of data*	AE_i **				*% of 'healed' disks* ***		
from		*1st quartil*	*Median*	*3rd quartil*	*% $AE_i > 0$*	*1st quartil*	*Median*	*3rd quartil*
0 to 0.1	15	–0.98	–0.91	–0.61	0	20	50	83
0.1 to 0.2	13	–0.69	–0.64	–0.43	8	0	20	40
0.2 to 0.3	0							
0.3 to 0.4	6	–0.40	–0.36	0.06	30	0	0	0
0.4 to 0.5	4							
0.5 to 0.6	8	–0.29	0.14	0.31	55	0	0	0
0.6 to 0.7	12							
0.7 to 0.8	34	–0.20	0.12	0.42	59	0	0	0
0.8 to 0.9	57	–0.05	0.30	0.50	72	0	0	0
0.9 to 1.0	123	–0.16	0.08	0.58	57	0	0	0

* *P cinnamomi* survival index, I_s, computed each year for all the trees (*I* for the south-facing trunk side); ** annual evolution of the trunk canker. Negative values of AE_i indicate that *P cinnamomi* has induced less lesion on the trunk in year *i* than in year *i* -1; *** a 'healed' disk is defined as a disk on which *P cinnamomi* induced lesions are present in the annual ring of the year *i* -1, but are no longer present in the annual ring of the year *i*.

for the cases where AE_i was positive. The increase in *PPA* occurred then only on the lower disk.

In contrast, when the model computed an I_S value higher than 0.5 (86% of the cases), cankers usually enlarged. The median for the AE_i were then between 0.1 and 0.3 and very few disks healed. In these cases, about 60% of the AE_i were positive.

I_n was a slightly less reliable index of cankers evolution than I_s: when model computed I_n lower than 0.1, *PPA* decreased (third quartil for AE_i of –0.43 and median for the percentage of 'healed' disks of 25%). However, when model predicted I_n higher than 0.1, cankers usually enlarged: then the medians for AE_i were all positive and the percentage of 'healed' disks was 0% in at least 75% of the cases (table IV). Nevertheless, I_n accurately predicted the evolution of the cankers at the northeastern side of the trunk at the Azereix plot between 1980 and 1989 (fig 6).

DISCUSSION

The development of the ink disease in red oaks appeared to be strongly influenced by climate: the evolution of *P cinnamomi* induced trunk cankers on trees located in four plots scattered throughout the area of the disease, far away from each other, exhibited very similar trends. This was particularly striking in 1982, when there was a sharp increase and in 1985 when there was a sharp decrease in disease (fig 4). The results of the model indicate that the severe

frosts which occurred during the winter of 1984–1985 is sufficient to explain the decrease in the *PPA* in 1985.

The model predictions usually fitted well to the observed evolution of the cankers. The frequency of years for which the model computes an I_s value lower than 0.1 and an I_n value equal to 0 should be a good indicator of the ability of *P cinnamomi* to overwinter in the trunk cortical tissues. Traces of *P cinnamomi* lesions were never present in the annual growth rings when the model computed a total elimination of the fungus from the oak trunk tissues during the winter. This occurred in 1963, 1985 and 1987 for the northern trunk side (I_n = 0). Moreover, amount of lesions induced by *P cinnamomi* on the studied trees usually decreased in the years for which the model computed poor survival of the pathogen, in particular when the I_s value was lower than 0.1 and the I_n value was equal to 0 (table III, table IV, fig 6). Years for which the model computed an I_s between 0.1 and 0.5 appeared generally unfavourable to canker extension. Nonetheless, canker of small size expanded in 8–30% of cases in these years (table III). This might be explained by survival of *P cinnamomi* in root lesions below soil level during winter and recolonisation of the lower trunk during the growing season. During the period 1985–1987, the model predicted a lower survival of *P cinnamomi* in the cortical tissues for the trees of Doat than for the three others stands: the I_n computed was 0 in 1985 and 1987 for the Doat plot. It was never 0 for the trees of Ainhoa and Mixe, and for the trees of Azereix was 0 only in 1985. This is in agreement with the observed symptoms: the decrease of the *PPA* after 1984 was more dramatic in Doat than in the other stands.

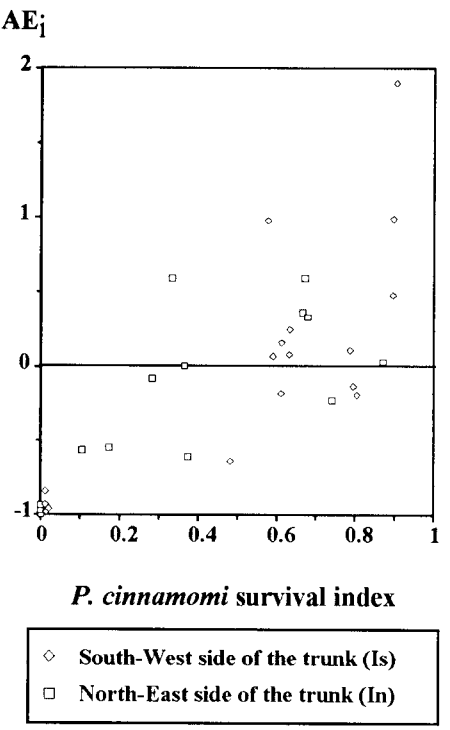

Fig 6. Relationship between the annual evolution of the canker, AE_i (on trunk side toward northeast or toward southwest), and the *P cinnamomi* survival index for the trunk side toward south or toward north (I_s or I_n).

As predicted by the model, a smaller canker development on the northern side of the trunk compared to the southern side was observed at Azereix (fig 5).

Although ink disease was not reported for any eastern red oak stands before 1984, our study shows that it has been present at least since 1959 in Azereix and 1967 in Doat. Evidently, the disease has not spread in the last 25 years (fig 1), despite a wider distribution of both the host and the pathogen (Grente, 1961; Vegh and Bourgeois, 1975). At present, very few trees with a trunk canker can be found to the east of Tarbes (Levy, 1992; fig 1). The results are therefore consistent with the hypothesis that extension of the ink disease to new areas might be limited by meteorological variables (Delatour, 1986). Our results give further support to the hypothesis that winter frost is the meteorological variable limiting the distribution of the disease. The most

Table IV. Model validation: annual evolution of the canker on the trees studied (AE_i) for different levels of I_n, the *P cinnamomi* survival index for the south-facing trunk side (Ainhoa, Azereix, Doat, Mixe, 1968–1989).

I_n * from	No of data	AE_i ** 1st quartil	Median	3rd quartil	% $AE_i > 0$	% of 'healed' disks *** 1st quartil	Median	3rd quartil
0 to 0.1	29	–0.91	–0.69	–0.43	4	0	25	60
0.1 to 0.2	5	–0.35	–0.16	0.15	43	0	0	0
0.2 to 0.3	9							
0.3 to 0.4	11	–0.28	0.12	0.27	47	0	0	0
0.4 to 0.5	6							
0.5 to 0.6	13	–0.20	0.15	0.67	62	0	0	0
0.6 to 0.7	21	–0.19	0.13	0.29	67	0	0	0
0.7 to 0.8	27	–0.01	0.31	0.71	74	0	0	0
0.8 to 0.9	44	–0.18	0.06	0.45	55	0	0	0
0.9 to 1.0	107	–0.16	0.13	0.64	60	0	0	0

* *P cinnamomi* survival index, I_n, computed each year for all the trees (*I* for the south-facing trunk side); ** annual evolution of the trunk canker. Negative values of AE_i indicate that *P cinnamomi* has induced less lesion on the trunk in year *i* than in year *i*-1; *** a 'healed' disk is defined as a disk on which *P cinnamomi* induced lesions are present in the annual ring of the year *i*-1, but are no longer anymore present in the annual ring of the year *i*.

severely infected stands can be found in the Basque area (Biarritz) where the winters are very mild (Choisnel et al, 1987), with more infected trees per stand and cankers on the trunks higher than elsewhere in the southwest of France (Levy, personal communication). Moreover, in Azereix, the plot with the coldest winter, the development of the trunk cankers remained limited (fig 4) and the ink disease may be more restricted to the roots. The model developed accurately predicted the evolution of the cankers on the studied trees. However, during the study period (1960–1989), there were few years in which frost was severe enough to eliminate *P cinnamomi* from trunk cortical tissues. As a result, there was insufficient data to fully test the model. Therefore, it requires further validation concerning the relationship between *P cinnamomi* survival in trunk tissues and the frequency of lesion reinitiation after the winter. Ultimately, the model should allow good prediction of the area in which a poor overwintering of *P cinnamomi* in the trunk tissues will strongly limit the development of the ink disease on red oaks.

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