



**HAL**  
open science

# Influence of water stress on susceptibility of red oak (*Quercus rubra*) to *Phytophthora cinnamomi*

Benoit Marçais, F. Dupuis, M. L. Desprez-Loustau

► **To cite this version:**

Benoit Marçais, F. Dupuis, M. L. Desprez-Loustau. Influence of water stress on susceptibility of red oak (*Quercus rubra*) to *Phytophthora cinnamomi*. *Forest Pathology*, 1993, 23 (5), pp.295-305. 10.1111/j.1439-0329.1993.tb00966.x . hal-02074181

**HAL Id: hal-02074181**

**<https://hal.science/hal-02074181>**

Submitted on 20 Mar 2019

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

European journal of Forest Pathology  
1993, 23(5): 295:305  
Doi : 10.1111/j.1439-0329.1993.tb00966.x

## Influence of water stress on susceptibility of red oak (*Quercus rubra* L.) to *Phytophthora cinnamomi* Rands

---

By B. Marçais<sup>1</sup>, F. Dupuis<sup>2</sup>, M.L. Desprez-Loustau<sup>2</sup>

<sup>1</sup> Laboratoire de pathologie forestière, INRA, 54280 Champenoux, France. Tel: 83 39 40 41.  
Fax: 83 39 40 69.

<sup>2</sup> Station de Pathologie végétale INRA, 71 Av. Ed. Bouleaux, B.P. 81, 33883 Villenave d'Ornon Cedex, France.  
Tel: 56 84 32 10. Fax: 56 84 32 22.

### Abstract

Influence of water status of oak trees (*Quercus rubra* L.) on the development of *Phytophthora cinnamomi* lesions was studied. On agar media or excised inner bark, growth of *P. cinnamomi* was reduced by low water potentials. In contrast, on young saplings or mature oak trees the development of *P. cinnamomi* lesions was not affected during a period of water stress. But after the end of the water stress treatment, susceptibility of the young saplings to *P. cinnamomi* increased.

**Key words:** *Phytophthora cinnamomi*, *Quercus rubra*, water stress

### 1 Introduction

*Phytophthora cinnamomi* Rands causes the ink disease on northern red oak, *Quercus rubra* L. Dieback of the affected trees has not been reported (ROBIN *et al.*, 1992), but the pathogen induces a cortical canker on the lower part of the trunk, reducing the value of the timber. The disease can be very severe in the southwest of France (Basque region) with 30 to 60 % of the trees in some stands having a trunk canker. The collar and the stem of northern red oaks are susceptible to *P. cinnamomi* though the tree limits rather well the tangential spread of the fungus. Roots, however, especially those of small diameter (1-5 cm), are much more resistant, which explains the lack of dieback of affected trees (MARÇAIS, 1992).

Data on ink disease distribution in the northern red oak forest of southwest France are still incomplete, but, results suggest that the disease is prevalent on dry or waterlogged sites (MARÇAIS, 1992; PILARD-LANDEAU, 1984). For example, in the forest of Mixe-Bidache (Pyrénées Atlantiques), affected trees were more common on tophills and on slopes facing south (MARÇAIS, 1992). As oaks growing on waterlogged sites are prone to water stress during drought (BECKER *et al.*, 1982), this suggests that water shortage could enhance the susceptibility of oak trees to *P. cinnamomi*. Predisposition of plants to diseases by water stress has been reported by many authors (BLAKER and MAC DONALD, 1981; DESPREZ-LOUSTAU and DESSUREAULT, 1988; DUNIWAY, 1983 and 1977; RISTAINO and DUNIWAY, 1989; SCHOENEWEISS, 1981). However, Pythiaceae fungal growth has been shown to be inhibited by low water potentials (DUNIWAY, 1983; LUND and GRIFFIN, 1981; SULISTYOWATI and KEANE, 1992). This was shown to have important consequences on the *P. cinnamomi* induced dieback of *Eucalyptus marginata* in Australia: on dry sites, growth of the pathogen in host cortical tissues was reduced during summer, due to the low water potential of the tree tissues (TIPPETT *et al.*, 1987). Therefore, in order to describe the effect of a water shortage on the ink disease, we studied the consequences of water stress both on host resistance and on pathogen growth. Stem susceptibility to *P. cinnamomi* was investigated because the principal symptom of the disease is a trunk canker.

## 2 Materials and methods

### 2.1 Effect of osmotic potential of agar media on growth of *P. cinnamomi*

The water potential of the growth media was adjusted by addition of solutes to water agar (20 gL<sup>-1</sup>). Solutes used were CaCl<sub>2</sub>, KCl or mannitol at 2.1, 4.1, 6.2, 8.2, 10.3 or 12.3 osmoles per liter or P.E.G.600. at 20, 40, 80, 120, 160 or 200 gL<sup>-1</sup>. In order to obtain media with water potential between 0 and -3 MPa, concentrations of the three first solutes were calculated according to the formula:  $P = R \times T \times O$ , where P is the water potential, in MPa, T the temperature, in K, O the osmolarity and R the constant 8.32 10<sup>-3</sup> L(MPa)K<sup>-1</sup>Mol<sup>-1</sup>. The media osmotic potentials were checked a day before use with a psychrometer. The radial growth of *P. cinnamomi* at 25°C (isolate 342, from *Q. rubra*, France) was determined three days after media inoculation, three replicates per osmotic potential x chemical combination being used.

### 2.2 Inner bark relative water content (RWC)

The inner bark RWC was determined on bark samples according to TIPPETT *et al.* (1987). The relation between this parameter and the predawn leaf water potential (PLWP) was investigated at Pierroton near Bordeaux on 20 to 40-year-old *Q. rubra* trees during the summer of 1990. PLWP was measured with a pressure chamber (SCHOLANDER *et al.*, 1964) on leaves sampled on low small branches inserted directly on the trunk at 1-3 m from soil level (3 leaves per tree). Both parameters were determined on three different dates (June 22, July 24 and August 29), for seven trees and were replicated three times.

### 2.3 *P. cinnamomi* growth on excised inner bark

A test was performed to estimate the susceptibility of adult *Q. rubra* to *P. cinnamomi* under controlled environmental conditions (SCEC). Blocks (2.5 cm x 7.5 cm) were cut from the inner bark of the tree to be tested, including all tissues external to the cambium. These blocks were stored at 5°C, soaked the day after sampling in tap water for one hour and put in a chamber maintained at 100% relative humidity and 25°C. The cambium side (inner face) was injured with a cork-borer and inoculated with an agar disk from the edge of a 3 days old *P. cinnamomi* culture (isolate 342). The length of discoloured phloem on the inner face of the block was measured on the third day.

This technique was also used to investigate the influence of secondary phloem water content on *P. cinnamomi* growth. Inner bark blocks with various RWC were obtained by controlling the relative humidity of the chamber with NaCl solutions of 0, 3.5, 17, 50, 88 and 117 gL<sup>-1</sup>. For this experiment, the pieces of phloem were sampled in September 1990, on a mature *Q. rubra*, at Pierroton and dead bark was removed. The trunk diameter at breast height was of 30 cm; bark thickness was of 0.5 to 0.6 cm. the blocks were not soaked in water before the trial. In each chamber, seven bark blocks, four of which were inoculated as described above with isolate 342 of *P. cinnamomi*, were left for equilibration at 25°C. After three days, the blocks were weighed, the lesion length on inoculated blocks was recorded and they were all replaced in the chamber at 25°C for a further three days. At that time, lesion length on inoculated blocks and fresh, saturated and dry weights of all blocks were measured. Bark block RWC and *P. cinnamomi* growth rate were calculated between the third and sixth day following inoculation. This experiment was repeated in June 1992, using the same tree from Pierroton but a different isolate of *P. cinnamomi* (isolate 9 from *Q. rubra*, France). The six chambers had NaCl solutions of 0, 3.5, 17, 50, 70, and 88 gL<sup>-1</sup>. Bark block RWC and lesion length rate were determined on the third and the fourth day following inoculation.

### 2.4 Stress treatment of young trees and inoculation with *P. cinnamomi*

In July 1990, 54 two-year-old *Q. rubra* saplings, provenance 'Doat' (Gers, France), growing in a half sand, half peat potting medium, were placed in a growth chamber at 25°C with a day period of 12 h. Six groups of nine saplings each were submitted to increasing levels of water stress. Water was withheld for five of the groups. During the stress treatment, PLWP was determined with a pressure chamber (SCHOLANDER *et al.*, 1964) and pots were weighed twice a week. For each group limited watering was resumed when the average PLWP reached a given level, which varied from -0.3 to -1.8 MPa. The amount of water provided twice a week to each sapling was then calculated to keep a constant pot weight. A month after the beginning of the experiment, normal watering was resumed.

Plants of the control group were fully watered twice a week throughout the experiment. Saplings were inoculated one week after the beginning of the experiment. The stem was injured with a scalpel and an agar disk from the edge of a *P. cinnamomi* culture (isolate 9) was placed on the wound. The inoculation site was wrapped with plastic ribbon. The necrotic lesion that subsequently developed was measured externally weekly during the water stress treatment and, again one and twelve months after rewatering all the plants.

A second experiment was performed in June 1992 with 20 four-year-old *Q. rubra* of the same provenance. They were randomized in two equal groups, one control and the other to be submitted to a stress treatment of about one month, and were placed in a growth chamber at 20°C with a day period of 12h. For all saplings, PLWP was determined twice a week during the 15 last days of the treatment. Control saplings were watered twice a week whereas stressed saplings were watered once after two weeks and, again, when their PLWP reached -1.2 MPa. They all received normal watering after. Using the same techniques as previously described, saplings were inoculated with isolate 9 of *P. cinnamomi* at the beginning of the experiment and the developing lesion was measured at the end of the stress treatment and again 30 and 45 days after.

**Table 1. Description of plots where *Quercus rubra* trees were inoculated with *Phytophthora cinnamomi* (Basque region, summer 1990)**

| Plot                       | Site type <sup>2</sup> | Topography     | Age | Percentage infection <sup>3</sup> |
|----------------------------|------------------------|----------------|-----|-----------------------------------|
| Ainhoa (Ai1 <sup>1</sup> ) | 2.1                    | slope          | 31  | 30                                |
| Ainhoa (Ai2)               | 2.3                    | flat           | 64  | 18.3                              |
| Sare (Sa)                  | 3.1                    | slope          | 60  | 28.4                              |
| St. Pée (Stp)              | 2.3                    | bottom + slope | 38  | 17.5                              |

<sup>1</sup> Name of the plots used in figures.  
<sup>2</sup> According to B. PILARD-LANDEAU (1984). 3.1 sites are drier than 2.3 sites. 2.1 sites have steeper slopes than 2.3 sites.  
<sup>3</sup> Percentage of trees with trunk canker within each plot (sample size = 100).

## 2.5 Tree susceptibility and water status in forest conditions

Four plots were chosen near Bayonne (Table 1), representing the different hydric states of vegetation sites in the area (PILARD-LANDEAU, 1984). They were all located in pure planted forests of northern red oak. Fifteen *Q. rubra* per site, with a diameter at breast height of 20 to 50 cm were selected. The bark thickness ranged from 0.4 to 0.8 cm. Bark was injured to the cambium with a cork-borer and inoculated with an agar disk from the edge of a 3 days old *P. cinnamomi* culture (isolate 342). This was done in 1990 on two dates: i.e. the 15<sup>th</sup> May at Ainhoa 1 (Ai1), Sare (Sa) and St Pée (Stp) sites, and the 30<sup>th</sup> of May at Ainhoa 2 (Ai2) site. The inoculation site was covered with sterilised wet cotton wool and aluminium paper and then wrapped with a plastic film fastened with glue. Lesions developing on the trunks above the inoculation point were measured on June 14, July 3, July 20, August 25 and September 19 with a non destructive method adapted from TIPPETT and BARCLAY (1987), using a Plant Impedance Ratio Meter (PIRM, Biosensor, Melbourne, Australia). At the time of the last measurement, all tissues were removed down to the cambium to record the length of discolored secondary phloem. Two inner bark blocks per tree were sampled at the time of inoculation, during each subsequent visit except the last one and on August 16 to determined their RWC and their SCEC, as described in the paragraph 2.2 and 2.3.

## 2.6 Statistical analysis

The normality of the data distribution was checked with the Shapiro-Wilks test (SAS INC., 1988). When the distribution was not normal, which was the case for lesion length data on young stressed saplings, Kruskal-Wallis test was used (SNEDECOR and COCHERAN, 1957). Repeated measures analysis of variance (SAS INC., 1988) was performed to compare the bark RWC in the field experiment. Student t-

test (SAS INC., 1988) was used when 2 treatments were compared. All the statistical tests were performed at the 0.05 level of significance.

### 3 Results

#### 3.1 Relationship between inner bark RWC and PLWP of suckers

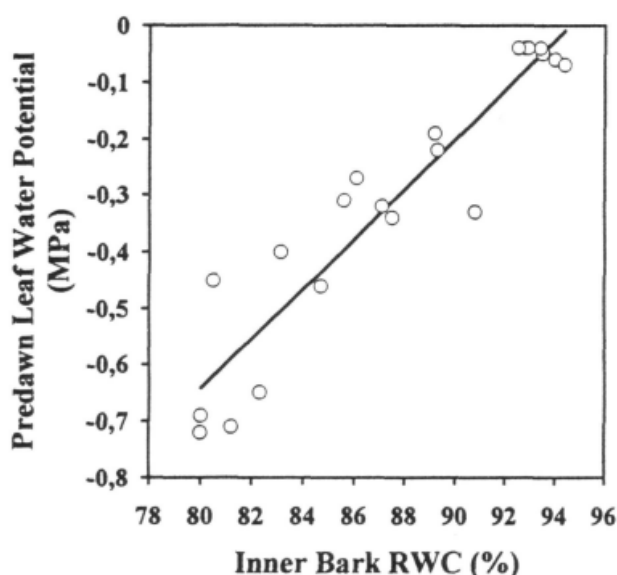
During the summer of 1990, inner bark relative water content (RWC) and predawn leaf water potential (PLWP) of the studied oaks were significantly correlated ( $r = 0.94$ ,  $df = 19$ ). There was little variation for both measured parameters within samples taken from a single tree on the same day. A linear relationship between these two parameters was defined by the following equation (Fig. 1):

$$PLWP = 0.044 (\pm 0.004) \times RWC - 4.16 (\pm 0.32) \quad r^2 = 0.883 \quad [1]$$

#### 3.2 Influence of water potential on *P. cinnamomi* growth under laboratory conditions

On agar media, daily radial growth of *P. cinnamomi* was linearly correlated with water potential and there was no apparent difference between the four media (Fig. 2a). When results were pooled, the Pearson correlation coefficient was 0.905 ( $df = 22$ ).

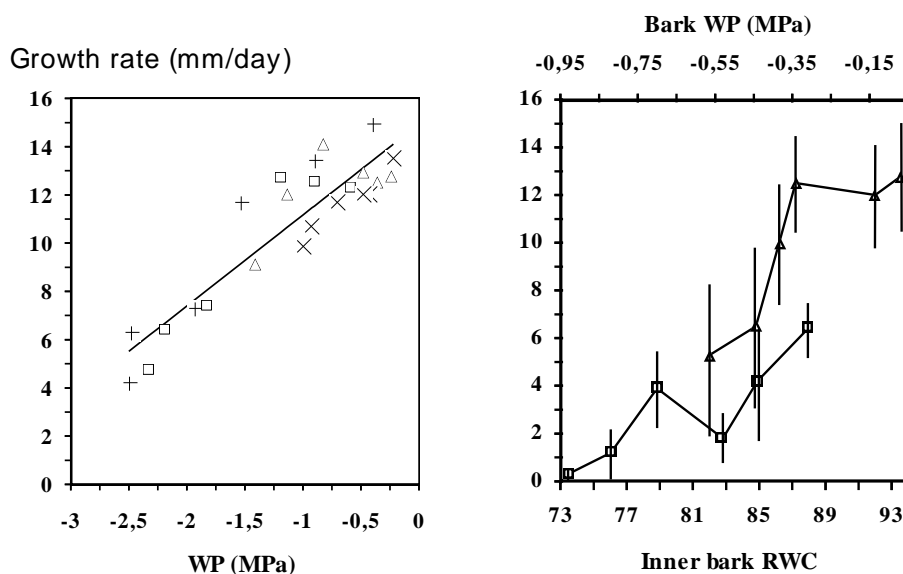
In the chambers containing NaCl, the RWC of bark blocks were close to equilibrium after the third day: during the September 1990 experiment, mean variation in RWC between the third and the sixth day was 4.7 %. There was a significant difference between the mean RWC of inoculated and non-inoculated bark blocks during the June 1992 experiment ( $t = 4.618$ ,  $df = 4$ ), but not in the September 1990 experiment ( $t = 0.894$ ,  $df = 4$ ). Therefore, for each chamber, mean RWC between the third and fourth or sixth day of non-inoculated bark blocks was compared with the growth rate of *P. cinnamomi* on inoculated blocks. The water potential of the bark blocks was calculated according to the relation defined by equation [1]. The bark blocks were dryer during the first experiment compared to the second but, in both cases, the growth rate of *P. cinnamomi* decreased with the block RWC (Fig. 2b). During the June 1992 experiment, the fungal growth rate on the excised bark was about half at a RWC of 82 % compared to the range of 87 to 95 %.



**Fig. 1.** Relation between inner bark relative water content (RWC) and predawn leaf water potential (PLWP) on *Quercus rubra*.  $PLWP = 0.044 \times RWC - 4.16 \quad r^2 = 0.883$

### 3.3 Susceptibility of young stressed plants

Except for the fully watered and the most stressed treatments, the different watering regimes led to very heterogeneous results. Therefore, *a posteriori*, plants were separated into three groups, according to their PLWP throughout the last three weeks of the water stress. The 19 saplings of group 1 had a PLWP which remained higher than -0.4 MPa; The 16 saplings of group 2 experienced PLWP between -0.4 and -1.2 MPa; and the 19 saplings of group 3, a PLWP of less than -1.2 MPa. There were no significant differences in lesion length between saplings within the three groups during the stress period (Fig. 3). However, after rewatering, *P. cinnamomi* continued growing in the secondary phloem of many saplings in groups 2 and 3, but few in group 1 (Fig. 3). Following the end of the stress treatment, significant differences in the increase of lesion length between groups 1, 2 and 3 were found ( $H = 13.63$ ,  $df = 2$ , probability of less than 0.01). Group 2 and 3 had an increase between the 24<sup>th</sup> and the 57<sup>th</sup> day significantly greater than group 1. There was no increase in lesion length for any of the groups following the elapse of a 2 month period after inoculation.



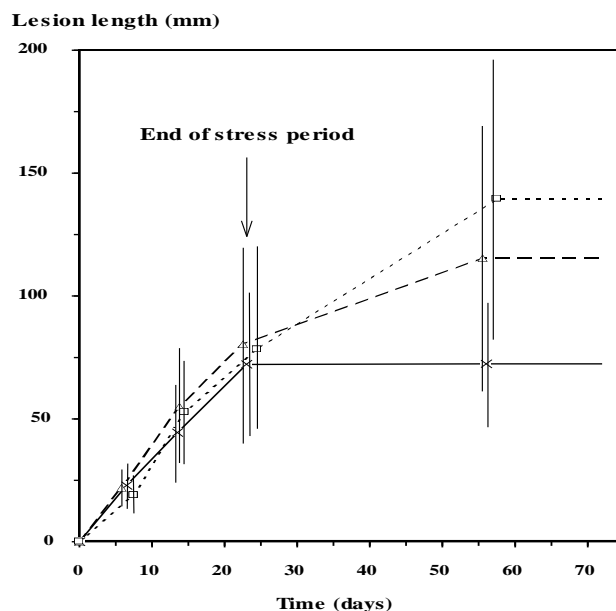
**Fig. 2.** Relation between growth rate of *Phytophthora cinnamomi* and water status of the media. a. On agar media. (X): mannitol; (Δ): P.E.G.600; (□): CaCl<sub>2</sub>; (+): KCl. Linear regression with pooled data from the four media:  $RG = 3.8 \times WP + 14.9$   $r^2 = 0.819$   
 b. On inner bark blocks of *Quercus rubra*. (□): experiment 1 (September 1990); (Δ): experiment 2 (June 1992). Vertical bars represent standard errors. Water status is expressed as relative water content (RWC) and water potential (WP). These two parameters are linked by the following equation:  $WP = 0.044 \times RWC - 4.16$ .

During the summer 1992 experiment, PLWP of the fully watered saplings was never lower than -0.4 MPa whereas that of all stressed saplings became lower than -1.2 MPa between the 28<sup>th</sup> and 37<sup>th</sup> day following inoculation. Again, there was no significant difference in lesion length between the stressed and control saplings at the end of the water stress treatment ( $H = 1.29$ ,  $df = 1$ , probability over 0.25) but, within the 30 days following rewatering, lesion increase was significantly higher on the stressed saplings than on the control saplings ( $H = 8.02$ ,  $df = 1$ , probability of less than 0.01). Between the 30<sup>th</sup> and the 45<sup>th</sup> day following rewatering, there was no increase in lesion length for any of the saplings of either treatment.

During 1990, the southwest of France experienced a severe drought. Following rainfall events at the end of June, a dry period ensued during which tree inner bark RWC reached low levels for some of the plots (Fig. 4). There appeared to be significant differences in inner bark RWC between the four plots (Table 2, Fig. 4). The Sare plot was the driest for almost all the sampling dates while the Ainhoa 2 plot



remained relatively wet during July and August. The increase in lesion length did not appear to be related to plot water status: trees of the plots of Ainhoa 1, Ainhoa 2 and Sare exhibited similar susceptibility to *P. cinnamomi* whereas trees of the St Pée plot were more resistant (Fig. 4 and 5). Furthermore, between the 20<sup>th</sup> of July and the 25<sup>th</sup> of August, there was no significant correlation between mean inner bark RWC and lesion increase ( $r = -0.128$ ,  $df = 58$ ).



**Fig. 3.** Lesion length evolution on stressed *Quercus rubra* saplings inoculated with *Phytophthora cinnamomi* in a growth cabinet during summer 1990. (-x-): Class 1 (predawn leaf water potential (PLWP) higher than -0.4 MPa). (-Δ-): Class 2 (PLWP between -0.4 and -1.2 MPa). (--□-): Class 3 (PLWP lower than -1.2 MPa). Standard deviations are given for group means because distributions of the data are not normal.

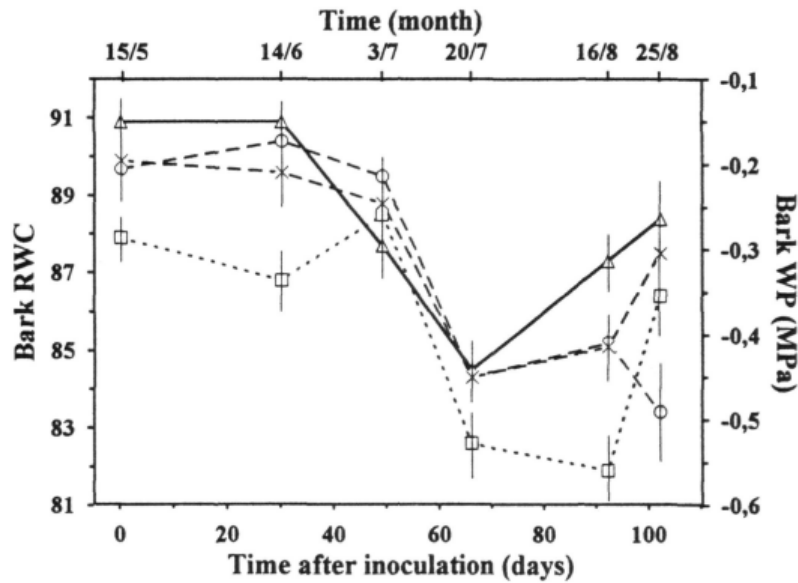
### 3.4 Field study

There was no significant difference between the lesion length measured with the PIRM and the length of discolored tissues recorded after bark removal ( $t = 0.65$ ,  $df = 58$ ).

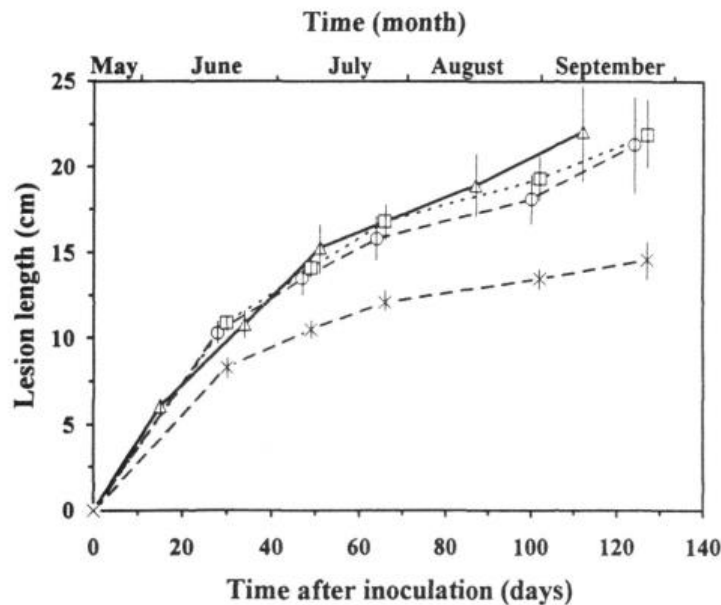
**Table 2.** Comparison of inner bark RWC of *Quercus rubra* at four sites in the Basque country during 1990 summer.

| Source       | df  | MS     | F     | P>F   | Adj. P>F |       |
|--------------|-----|--------|-------|-------|----------|-------|
|              |     |        |       |       | G-G      | H-F   |
| Sites        | 3   | 136.92 | 6.31  | 0.001 |          |       |
| error        | 55  | 21.69  |       |       |          |       |
| Time         | 5   | 324.70 | 58.02 | 0.001 | 0.001    | 0.001 |
| Time x Sites | 15  | 26.26  | 4.69  | 0.001 | 0.001    | 0.001 |
| error        | 275 | 5.60   |       |       |          |       |

General linear models (GLM procedure) of SAS (SAS INSTITUTE 1988) was used for this repeated measures analysis of variance. Adj. P>F are probabilities associated with Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted F-tests. MS, mean square.



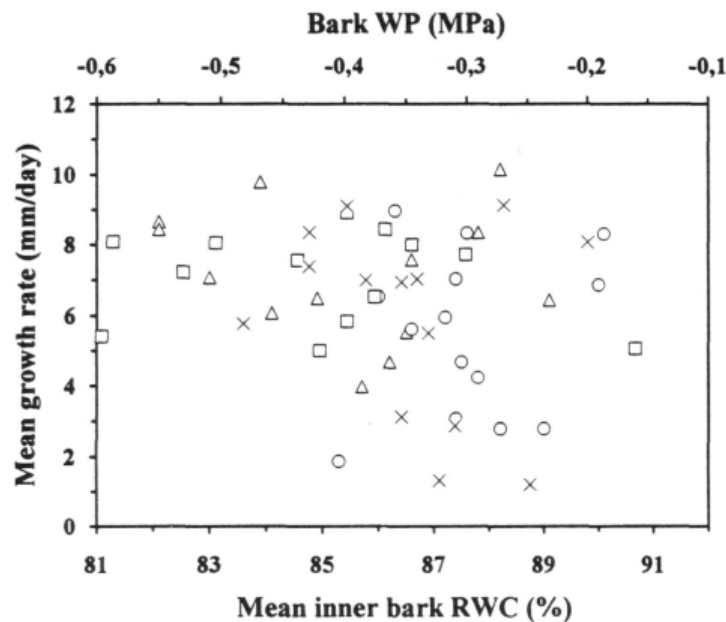
**Fig. 4.** Development of mean inner bark relative water content (RWC) of *Quercus rubra* at 4 sites in the Basque region in summer 1990. (-o-): Ai1; (-△-): Ai2; (-□-): Sa; (-x-): Stp. Water status is expressed as relative water content (RWC) and water potential (WP). These two parameters are linked by the following equation:  $WP = 0.044 \times RWC - 4.16$ . Inoculation date was May 15 (May 30 for Ai2). Vertical bars represent standard errors.



**Fig. 5.** Mean lesion length on *Quercus rubra* trunks after inoculation with *Phytophthora cinnamomi* at 4 sites in the Basque region in summer 1990. (-o-): Ai1; (-△-): Ai2; (-□-): Sa; (-x-): Stp. Vertical bars represent standard errors

During this period, from the 20<sup>th</sup> of July to the 25<sup>th</sup> of August, mean secondary phloem RWC in the forest was significantly negatively correlated with mean SCEC, though the correlation coefficient was low ( $r = -0.354$ ,  $df = 54$ ). Figure 6 shows that no tree with a low mean inner bark RWC had a low mean SCEC. In the period from the 15<sup>th</sup> of May to the 30<sup>th</sup> of July, when inner bark RWC was in the range of 85 to 94%, these two parameters were not correlated ( $r = 0.041$ ,  $df = 54$ ).





**Fig. 6.** Relationship between mean susceptibility to *Phytophthora cinnamomi* under controlled environmental conditions (SCEC) of excised bark blocks of *Quercus rubra* and mean inner bark relative water content (RWC) of tree in the forest throughout July and August 1990. (o): Ai1; ( $\Delta$ ): Ai2; ( $\square$ ): Sa; (x): Stp. Pearson correlation coefficient of -0.354, significant at 1%. Water status is expressed as relative water content (RWC) and water potential (WP) These two parameters are linked by the following equation:  $WP = 0.044 \times RWC - 4.16$ .

## 4 Discussion

Our results on the limiting effect of low water potentials on *P. cinnamomi* growth are in agreement with current literature (DUNIWAY, 1983, LUND and GRIFFIN, 1981). Inhibition of *P. cinnamomi* at a certain water potential was more pronounced in inner bark than on agar media. A water potential of -0.6 MPa greatly reduced the growth rate in excised inner bark, but had far less influence on agar media. This may be due to the fact that lesion size on the bark block reflects a balance between host resistance and pathogen growth. A similar growth reduction was demonstrated for *P. cinnamomi* in *E. marginata* secondary phloem and for *P. citrophthora* in different *Citrus* rootstocks secondary phloem: it decreased drastically for RWC ranging from 95 to 75 % (SULISTYOWATI and KEANE, 1992; TIPPETT *et al*, 1987). The difference in block RWC and in *P. cinnamomi* growth rate between the two experiments on excised inner bark (Fig. 2b) are probably due to the difference in the sampling period (June and September): red oak inner bark was shown to be dryer and less susceptible to *P. cinnamomi* in autumn than in spring (ROBIN, 1991).

Nevertheless, values of inner bark RWC in the range of 80 to 85% greatly reduced daily growth of *P. cinnamomi* in excised secondary phloem of *Q. rubra* (Fig. 2b). Such values of inner bark RWC were commonly measured on oak during the summer of 1990 in the Basque region (Fig. 4). Daily variations of the inner bark RWC of oak trees did not exceed 2 % (Unpublished results). But, neither mature standing oak trees in the forest, nor young saplings in the growth chamber showed limitation of *P. cinnamomi* growth at low tissue water potentials (Fig. 3, Fig. 5). In contrast to this, *P. cinnamomi* growth was limited on *E. marginata* at low bark water potential (SMITH and MARKS, 1983; TIPPETT *et al*, 1987). For the field study, this may possibly be explained by the influence of factors not taken into account as illustrated, for example, by the lower susceptibility observed in trees at the St Pée site.

However this could also be explained by a lowered resistance of the oak trees to *P. cinnamomi* under stress conditions. This was demonstrated on young *Q. rubra* saplings by monitoring lesion extension

after the end of the water stress treatment, under conditions where secondary phloem RWC was no longer limiting for *P. cinnamomi* growth (Fig. 3). During the stress treatment, saplings underwent successive water stress periods followed by short periods of partial recovery after the limited watering. It can be hypothesized that *P. cinnamomi* growth was slower in stress saplings than in control saplings during the stress periods, when secondary phloem water potential was low, but faster during the periods of partial recovery. This could explain the lack of overall difference in lesion extension between stressed and control saplings. Moreover, during the field study, the results obtained on excised inner bark blocks (Fig. 6) suggest that the oak trees which experienced the lower secondary phloem RWC during the summer could have had a lowered resistance to *P. cinnamomi*. Bark blocks were sampled and inoculated after resaturation, under hydric conditions which were optimal for the pathogen growth.

The two phenomena, limitation of *P. cinnamomi* growth and reduction of oak resistance occurred within the same range of inner bark RWC, i.e. at 80 to 89 % (water potential of -0.85 to -0.25 MPa respectively, Fig. 2, Fig. 3 and Fig. 6). The balance between host resistance and pathogen growth remained unchanged during the water stress.

This could explain why several authors found no post-inoculation water stress effect on *Phytophthora* induced diseases while a pre-inoculation water stress did increase disease severity (DUNIWAY, 1977; RISTAINO and DUNIWAY, 1989). KACKLEY *et al.* (1990) also explained their results as a combined effect of drought stress both upon the host and the pathogen.

The reason for lowered resistance of *Q. rubra* during and after water stress is unknown. Results from the experiments on young oaks suggest that occurrence of defense mechanisms may be delayed by water stress: on well watered saplings, *P. cinnamomi* induced lesions were confined within the month following inoculation whereas on stressed saplings, they were confined within the month following the end of the water stress treatment (Fig. 3). Some host-defense mechanisms such as necrophylactic periderm formation may be inhibited at low water potential (BIGGS and CLINE, 1986; PURITCH and MULLICK, 1975).

In the present study, we described the immediate influence of water stress on infection by *P. cinnamomi*. The results obtained with the young saplings (Fig. 3) suggest that the severity of the ink disease may be enhanced by water shortages on dry sites, especially if successions of drought and rainy periods are frequent. The effect of water shortages on the development of the ink disease of *Q. rubra* needs to be investigated over a period of several years.

## Acknowledgement

We sincerely thank C. VAN MEER and H. RIVIÈRE for their technical assistance and C. DELATOUR for reviewing the manuscript.

## References

- BECKER, M.; LEVY, G., 1982: Le dépérissement du chêne en forêt de tronçais; les causes écologiques. *Ann. Sci. Forest.* **39**:439-444.
- BIGGS, A.R.; CLINE, R.A., 1986: Influence of irrigation on wound response in peach bark. *Can. J. Bot.* **8**:405-408.
- BLAKER, N.S.; MAC DONALD, J.D., 1981: Predisposing effects of soil moisture extremes on the susceptibility of rhododendron to *Phytophthora* root and crown rot. *Phytopathology* **71**:831-834
- DESPREZ-LOUSTAU, M.L.; DESSUREAULT, M., 1988: Influence de stress contrôlés sur la sensibilité du bouleau jaune au chancre godronien causé par *Godronia cassandrae* Peck. f.sp. *betulicola* Groves. *Can. J. For. Res.* **18**:121-127.
- DUNIWAY, J.M., 1977: Predisposing effect of water stress on the severity of *Phytophthora* root rot on safflower. *Phytopathology* **67**:884-889.
- DUNIWAY, J.M., 1983: Role of physical factors in the development of *Phytophthora* diseases. Page 175-187 in: *Phytophthora. its biology, taxonomy, ecology and pathology*. ERWIN, D.C.; BARTNICKI-GARCIA, S.; TSAO, P.H., eds. American Phytopathological Society, St. Paul, MN. 392 pp.
- KACKLEY, J.P.; GRYBAUSKAS, A.P.; HILL, R.L.; DERNOEDEN, P.H., 1990: Influence of temperature-soil water status interactions on the development of summer patch in *Poa* spp. *Phytopathology* **80**:650:655.
- LUND, E.J.; GRIFFIN, D.M., 1981: Effect of water potential on fungal growth and turgor. *Trans. Br. Mycol. Soc.* **76**:33-40.

- MARÇAIS, B., 1992: Influence de facteurs de l'environnement sur le développement de l'encre du chêne rouge (*Quercus rubra* L.), maladie provoquée par *Phytophthora cinnamomi* Rands. Thèse de doctorat. Université de Nancy 1. 104p.
- PILARD-LANDEAU, B., 1984: Le chêne rouge d'Amérique : station, production et sylviculture dans le sud-ouest. Mémoire de 3<sup>e</sup> année E.N.I.T.E.F. 540 pp.
- PURITCH, G.S.; MULLICK, D.B., 1975: Effect of water stress on the rate of non-suberized impervious tissue formation following wounding in *Abies grandis*. *Jour. of Exp. Bot.* **26**:903-910.
- RISTAINO, J.B.; DUNIWAY, J.M., 1989: Effect of preinoculation and postinoculation water stress on the severity of *Phytophthora* root rot on processing tomatoes. *Plant Disease* **73**:349-352.
- ROBIN, C., 1991: La maladie de l'encre du chêne rouge *Quercus rubra* L. causée par *Phytophthora cinnamomi* Rands : perspectives pour l'amélioration génétique de la résistance. Thèse de doctorat. Université de Bordeaux 2. 140p.
- ROBIN, C.; DESPREZ-LOUSTAU, M.L.; DELATOUR, C., 1992: Factors influencing growth of trunk cankers of *Phytophthora cinnamomi* in *Quercus rubra*. *Can. J. For. Res.* **22**:367-374.
- SAS INSTITUTE INC., 1988: Sas/Stat guide for personal computers, version 6.03 edition. SAS Institute Inc., Cary, NC.
- SCHOLANDER, P.F.; HAMMEL, H.T.; HEMMINGSEN, E.A.; BRADSTREET, E.D., 1964: Hydrostatic pressure and osmotic potential in leaves of mangroves and some other plants. *Proc. Nat. Acad. Sci. USA* **52**:119-125.
- SCHOENEWEISS, D.F., 1981: The role of environmental stress in diseases of woody plants. *Plant Disease* **65**:308-314.
- SMITH, I.W.; MARKS G.C., 1986: Effect of moisture stress in *Eucalyptus sieberi* on growth of lesions caused by *Phytophthora cinnamomi*. *Aust. For. Res.* **16**:273-279.
- SNEDECOR, G.W.; COCHRAN, W.G., 1957: Stastical methods. 6<sup>th</sup> edition. The Iowa State University Press, Ames, Iowa, USA.
- SULISTYOWATI, L.; KEANE, P.J., 1992: Effect of soil salinity and water content on stem rot caused by *Phytophthora citrophthora* and the accumulation of phytoalexin in *Citrus* rootstocks. *Phytopathology* **82**:771:777.
- TIPPETT, J.T.; BARCLAY, J.L., 1987: Detection of bark lesions caused by *Phytophthora cinnamomi* in *Eucalyptus marginata* with the impedance ratio meter and the Shigometer. *Can. J. For. Res.* **17**:1228-1233.
- TIPPETT, J.T.; CROMBIE, D.S.; HILL, T.C., 1987: Effect of phloem water relations on the growth of *Phytophthora cinnamomi* in *Eucalyptus marginata*. *Phytopathology* **77**:246-250.

## Summary

*Phytophthora cinnamomi* Rands causes ink disease on *Quercus rubra* L. The main symptom is a cortical canker on the trunk. The influence of water supply on oak susceptibility to this pathogen was studied. On excised inner bark, *P. cinnamomi* growth was greatly reduced at a water potential of -0.5 to -1 MPa, which are in the range of those found in water-stressed trees. Such water potentials have only a small influence on fungal growth rate on agar media. In contrast, on young saplings or on mature oak trees, the development of *P. cinnamomi* induced lesions was not affected during water stress. Results suggest that susceptibility of the oak cortical tissues was increased by water stress. In particular, after rewatering, when host tissues return to high water potential, young oaks subjected to a water stress treatment showed higher susceptibility to *P. cinnamomi* than control oaks.

## Resumé

*Phytophthora cinnamomi* Rands est responsable de la maladie de l'encre du chêne rouge (*Quercus rubra* L.), dont le principal symptôme est un chancre cortical sur tronc. Nous avons étudié l'influence de l'alimentation en eau des chênes sur leur sensibilité à ce parasite. Sur écorce excisée, la croissance de *P. cinnamomi* est fortement limitée par des potentiels de l'eau de -0.5 à -1 MPa, de l'ordre de ceux rencontrés sur arbre en stress hydrique. De tels potentiels de l'eau ont un faible impact sur la croissance du champignon sur milieu gélosé. Par contre, sur plante entière, jeunes plants ou chênes de 40-60 ans, le développement des lésions induites par *P. cinnamomi* n'est pas affecté durant un stress hydrique. Les résultats suggèrent que la sensibilité des tissus corticaux du chêne est augmentée par le stress hydrique. En particulier, après réarrosage, quand les tissus de l'hôte reviennent à des potentiels de l'eau élevés, les jeunes plants ayant subi le traitement de stress se montrent plus sensibles à *P. cinnamomi* que les témoins.