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Original article

Can *Phytophthora quercina* have a negative impact on mature pedunculate oaks under field conditions?

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Abstract – Ten oak stands in southern Sweden were investigated to evaluate the impact of the root pathogen *Phytophthora quercina* on mature oaks under field conditions. *Phytophthora quercina* was present in five of the stands, while the other five stands were used as controls to verify the effect of the pathogen. In each stand, a healthy, a moderately declining and a severely declining tree were sampled. Fine-root length and nutrient status of each tree were analyzed, and the chemistry of the soil surrounding each tree was determined. The results showed that *P. quercina* can cause substantial reductions in the fine-root length of mature trees under natural conditions. The impact of the pathogen varied depending on tree vitality and season, being most pronounced for declining trees after an unusually dry summer. Despite the significant reduction in live fine-root length of declining trees in *Phytophthora*-infested stands, no consistent effects were found on the nutrient status of trees. Based on the significant impact of the pathogen on the fine-root systems of declining trees, we suggest that *P. quercina* contribute to oak decline in southern Sweden at the sites where it is present. No explanation is currently available for the decline of trees in non-infested stands, but the lack of symptoms of root damage indicate, together with the extensive root growth of declining trees, that root pathogens are not involved in the decline at these sites.

***Quercus robur* / *Phytophthora quercina* / root vitality / soil chemistry / nutrient status**

Résumé – *Phtytophthora quercina* peut-il avoir un effet négatif sur les chênes pédonculés adultes en conditions de terrain ? Dix peuplements de chêne du sud de la Suède ont été examinés pour évaluer l'impact du pathogène racinaire *Phytophthora quercina* sur des chênes adultes en conditions de terrain. *P. quercina* était présent dans cinq peuplements, les cinq autres furent utilisés comme témoin des effets du pathogène. Dans chaque peuplement, un arbre sain, un arbre modérément dépérissant et un arbre très dépérissant ont été échantillonnés. La longueur des fines racines et le statut minéral de chaque arbre, ainsi que les caractéristiques chimiques du sol alentour ont été déterminés. Les résultats ont montré que *P. quercina* peut causer des réductions substantielles de la longueur des fines racines des arbres adultes dans les conditions de terrain. L'impact du pathogène varie selon la vitalité de l'arbre et la saison, avec des effets plus prononcés après un été particulièrement sec pour les arbres dépérissants. Malgré la réduction significative de la longueur des fines racines chez les arbres dépérissants dans les peuplements infectés par *P. quercina*, aucun réel effet n'a été trouvé sur le statut minéral des arbres. En nous appuyant sur l'impact significatif au niveau des fines racines, nous suggérons que *P. quercina* contribue au déclin des chênes dans le sud de la Suède.

***Quercus robur* / *Phytophthora quercina* / vitalité des racines / caractères chimiques du sol / statut minéral**

1. INTRODUCTION

Phytophthora is a genus of fungus-like microorganisms that belongs to the phylum Oomycota in the kingdom Chromista. Species of *Phytophthora* cause a variety of diseases in many different types of plants, ranging from seedlings of annual crops to mature forest trees. Most species cause root rot, damping off of seedlings, and rot of lower stems and tubers. Others cause rot or blight of buds, fruits or foliage [16]. Among the species causing severe diseases in forest ecosystems, *P. cinnamomi* in Jarrah ecosystems (*Eucalyptus marginata*) in Australia, *P. lateralis* on Port-Orford-Cedar in North America and the hybrid *Phytophthora* on *Alnus* spp. in Europe are probably the most well-known [10, 18, 46].

During the past decade, several different *Phytophthora* species have also been suggested to be involved in the decline of oak [8, 9, 24, 27]. In central, western and southern Europe, a diverse population of *Phytophthoras* have been found in the oak forests [5, 9, 25, 27, 28, 43, 53], and several of these have been demonstrated to cause extensive root rot and stem damage of oak seedlings grown in glasshouses [25, 26, 28–30, 33, 42, 44]. In addition, significant correlations have been found between the presence of *P. quercina*, an oak-specific fine-root pathogen, and other *Phytophthora* species in the rhizosphere soil and crown defoliation of mature oaks in Germany, Italy, Austria and Turkey [5, 6, 27, 53]. It is assumed that these correlations are the result of an impeded water and nutrient uptake as a consequence of root damage caused by the pathogens. However, *Phytophthora* species are highly sensitive to environmental conditions, such as water availability [16], temperature [16] and soil chemistry [12, 14, 16, 38, 45, 54]. In addition, various environmental factors may also affect the susceptibility of the trees to infection [19, 34]. It is thus uncertain whether the impact of *P. quercina* observed in short-term experiments with potted oak seedlings will be the same on

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Table I. Some site and stand characteristics of the ten oak stands included in the study. All stands have mesic soil moisture.

Block	Stand	Geographical position	Presence of *P. quercina*	Age (y)	Forest type[1]	Geological substrate	Soil texture	pH($BaCl_2$)[2]
1	1	616249/137250	Yes	95	F	Moraine	Loam	3.74
	2	620875/138625	No	110	F	Moraine	Loam	3.75
2	3	623125/139875	Yes	65	D	Sediment	Clay	3.80
	4	622875/139875	No	100	Q	Sediment	Clay	3.36
3	5	621379/134622	Yes	75	Q	Moraine	Loam	3.91
	6	615874/133126	No	80	Q	Sediment	Clayey loam	3.54
4	7	623129/140623	Yes	90	F	Moraine	Silt	3.96
	8	620876/134625	No	90	F	Moraine	Silt	3.78
5	9	623377/145876	Yes	100	F	Sediment	Loam	3.91
	10	624293/144317	No	73	F, D	Moraine	Loam	3.81

[1] Q = pure *Q. robur* stand, F = mixture with *Fagus sylvatica*; D = mixture with other deciduous species.
[2] Median values for the organic layer and the upper 30 cm of mineral soil.

mature oaks under natural growth conditions. Hitherto, only one study has examined the quantitative effect of *Phytophthora* species on the root systems of mature oaks in forests and tried to relate the root damages to the crown symptoms (i.e. [27]). Furthermore, no data on water relations and mineral nutrition is available for infected oaks under field conditions. The knowledge about the effects of *Phytophthoras* on mature oaks under natural conditions is therefore still limited.

Similar to the situation in Southern and Central Europe, oaks in Sweden (particularly *Quercus robur*) have shown dramatic deterioration in health during recent decades [48]. The reasons for the decline are unclear. Recently, three different species of *Phytophthora* were recovered from 11 out of 32 oak stands in the southernmost part of the country [20]. The most frequently recovered species was *P. quercina*. *Phytophthora quercina* was found to cause root infection in oak seedlings, in artificial soil mixtures as well as in acid forest soils, with subsequent necrosis and die-back of the root systems [21, 22]. A weak association was also found between the occurrence of *P. quercina* and the vitality of mature oak stands [23].

The objective of this study was thus to determine the impact of *P. quercina* on root systems of mature oaks under field conditions. We also wanted to evaluate if the root damage was related to the crown defoliation and mineral nutrition of the trees, and thereby elucidate whether this pathogen may contribute to oak decline in southern Sweden. Since acidification-induced nutrient imbalances of trees have been discussed as a cause for tree decline in Sweden, and the asexual as well as sexual reproduction of *Phytophthora* species are known to be influenced by soil chemistry [12,14,16,38,54], we also wanted to investigate if the root damage caused by *P. quercina* was related to the chemical conditions in the soil surrounding the tree. A field study, comparing the root systems, the tree nutrient status and the soil chemistry between healthy, moderately declining and severely declining oak trees in five stands with *P. quercina* was thus conducted. To verify that the possible differences obtained between healthy, moderately declining and severely declining trees were due to *P. quercina* and not a general phenomenon occurring in all oak stands as a consequence of the strongly reduced photosynthetic capacity of declining trees, a split-plot design was used. Each of the five infested stands was thus paired with a non-infested stand with similar stand characteristics. For further information on the pairing of stands, see Materials and Methods.

The following hypotheses were tested.
(i) Healthy trees have a greater fine-root vitality, measured as live fine-root length per unit soil volume, than declining trees. This applies to stands with, as well as without, *P. quercina*.
(ii) The live fine-root length per unit soil volume is lower for trees growing in stands with *P. quercina* than for trees growing in stands without the pathogen.
(iii) Due to their greater fine-root vitality, healthy trees have a better nutrient status than declining trees, irrespective of whether *P. quercina* is present or not.
(iv) Soil around healthy trees has higher pH and base saturation than soil around declining trees. This applies to stands with, as well as without, *P. quercina*.

2. MATERIALS AND METHODS

2.1. Experimental design and study sites

Soil, roots and leaves in ten *Q. robur* stands in the southern part of Sweden (latitude 55.3°–56.1°) were sampled to determine the occurrence of *Phytophthora* species, length and vitality of roots, and the chemical status of soil, leaves and fine roots. Five of these stands had previously been found to host the root pathogen *P. quercina* [20]. To verify that the possible differences obtained between trees of differing vitality were due to *P. quercina* and not a general phenomenon occurring in all oak stands, a split-plot design was used. Each of the five infested stands was thus paired with a non-infested stand with similar stand characteristics. The pairing of stands was primarily based on soil texture, soil chemistry and geographical location of the stands, but geological substrate, stand age and forest type were also taken into consideration. Out of 50 non-infested stands investigated within the geographical area, the five stands that most closely resembled the infested stands were chosen. Some of the stand characteristics used to pair the investigated stands are presented in Table I. The mean annual temperature and mean annual precipitation in the area studied ranged from 7.1 to 8.7 °C and from 607 to 780 mm, respectively, between 1991 and 2001 [47].

In each of the stands, three dominant or co-dominant trees, belonging to different crown defoliation classes, were chosen for sampling: a healthy tree (crown defoliation 0–10%), a moderately declining tree (crown defoliation 25–40%) and a severely declining tree (crown defoliation > 50%). Data on crown defoliation was available from 1988, 1993 and 1999 to ensure consistent trends in the defoliation of each tree. The chosen trees within a stand had the same topographical position and were situated within 50 m from each other.

2.2. Isolation of *Phytophthora* species

To verify the presence of *P. quercina* in the five stands from which it was previously recovered, as well as its absence from the other five stands, soil was sampled from the rhizosphere of each tree on three different occasions during a 12-month period (June 2002, August 2002 and March 2003). On each sampling occasion, rhizosphere soil from the organic layer and from a depth of 0–30 cm in the mineral soil was taken from two monoliths close to each tree, at a distance of 80–110 cm from the stem base. Aliquots of rhizosphere soil from the two monoliths were bulked, and subsamples were used for isolation tests. *Phytophthora* species were isolated using the soil baiting method described by Jung et al. [25, 27].

In addition, small samples of fine roots were taken from each tree at each sampling occasion, in order to perform isolation tests of *Phytophthora* species. For each tree, approximately 50 pieces of thoroughly washed fine roots were cut longitudinally and plated onto selective PARPNH agar (100 mL L^{-1} vegetable juice produced by Granini, Eckes-Granini, France and 20 g L^{-1} agar amended with 3 g L^{-1} $CaCO_3$, 10 mg L^{-1} pimaricin, 200 mg L^{-1} ampicillin, 10 mg L^{-1} rifampicin, 25 mg L^{-1} pentachloronitrobenzene, 62 mg L^{-1} nystatin and 50 mg L^{-1} hymexazol). The plated fine-root pieces had a length of 4–5 cm and included necrotic root segment as well as healthy looking tissue in close connection to the diseased tissue (i.e. within 2 cm).

2.3. Root vitality and symptoms of infection

Since *Phytophthora* diseases are strongly influenced by the prevailing climatic conditions, sampling of the root system of trees was performed on three different occasions during a 12-month period. Roots from each tree were sampled on the same occasions as the soil for isolation of *Phytophthora*: June 2002, August 2002 and March 2003. On each sampling occasion, two soil monoliths measuring 20 × 30 cm and down to a depth of 30 cm in the mineral soil were removed at a distance of 80 to 110 cm from the stem base. The cardinal point of each monolith was noted so that no samples were removed from the same place as previous monoliths when sampling was repeated. The soil from each monolith was sieved through a 4 mm mesh to collect the roots present in the soil. The roots were placed in sealed plastic bags and stored at –18 °C until further processing.

The evening before washing, the roots were removed from the freezer and stored in a cold room (5 °C) to thaw. After washing, the roots were separated into dead or living based on general visible criteria, resilience, brittleness, bark integrity and colour of the stele. Live roots were defined as having an intact stele and cortex, being slightly elastic and white or brown in colour. Dead roots were defined as having fragmented bark, being inelastic and brittle, and being very dark in colour. In each root sample, length and width of 10 randomly selected lesions were measured (if 10 or more lesions were present). The roots were scanned, and root length and surface area were measured for different root diameter classes using the software WinRhizo Pro 5.0 (Regent Instruments, Québec, Canada). Roots were then sorted into different diameter classes, dried in a freeze-dryer (0–2 mm roots) or at 40 °C (> 2 mm roots) until constant weight, and weighed. In the results, only data on root length is presented since it is a more sensitive parameter than root biomass. Root length is also more closely related to the potential absorption of nutrients and water from soil [4]. The fine-root length constituted on average 88% of the total root length, and the results presented therefore mainly refer to differences and changes in this pool. Roots with a diameter of 0–2 mm are referred to as fine roots and roots with a diameter exceeding 2 mm as coarse roots.

2.4. Leaf chemistry

Leaves from the upper third of the south-facing side of each tree in stand 3–10 were removed with a hailstone shot-gun in August 2002. Approximately 40–45 leaves from each tree were used for chemical analysis. Before the analysis, leaf samples were dried at 40 °C to constant weight. Thereafter, the leaf stalks were removed and the leaves ground through a 1.5 mm mesh. Subsamples of leaves were digested in concentrated HNO_3. The concentrations of calcium (Ca), potassium (K), magnesium (Mg), sodium (Na), boron (B), aluminium (Al), iron (Fe), manganese (Mn), copper (Cu), zink (Zn), phosphorus (P) and sulphur (S) were determined using the inductively coupled plasma analyser (Perkin Elmer, Norwalk, USA). The concentration of nitrogen (N) was analysed using the Kjeldahl technique [3]. The ratios of Ca, K, Mg, B, Fe, Mn, Cu, Zn and P to N by weight were calculated.

2.5. Fine-root chemistry

Subsamples of fine-root material collected in August 2002 from 0–10 cm, 10–20 cm and 20–30 cm depth in the mineral soil were digested in concentrated HNO_3. The root samples from the organic layer were too small for chemical analysis. The concentrations of Ca, K, Mg, Na, B, Al, Fe, Mn, Cu, Zn, P and S were determined using the inductively coupled plasma analyser (Perkin Elmer, Norwalk, USA). The concentration of N was determined with an element analyser (VarioMax, Elementar Analysensysteme GmbH, Hanau, Germany). The ratios of Ca, K, Mg, B, Fe, Mn, Cu, Zn and P to N by weight were calculated. Forty subsamples of living fine-root tissue from the mineral soil were ashed to determine soil contamination. The average ash contents of the living fine roots were 3.0% (SD ± 0.9%, n = 14) at 0–10 cm depth, 3.4% (SD ± 0.6%, n = 13) at 10–20 cm depth and 3.6% (SD ± 1.0%, n = 13) at 20–30 cm depth, with an average for all fine-root samples of 3.3% (SD ± 0.8%, n = 40). Since the variation in ash content of fine roots within a soil layer was lower than 1%, and the variations between average values for each soil layer were low, pollution of adhering soil particles was considered to have negligible effect on the results of nutrient analyses and biomass estimates and no corrections were made to root data for soil contamination.

2.6. Soil chemistry

In addition to soil sampled for the isolation of *Phytophthora* species, soil from each tree was also sampled for chemical analysis.

This sampling was performed in August 2002. Samples were taken from five points, at approximately 1.0 m distance from the base of the stem, around each tree, using an auger with a diameter of 32 mm. The soil was separated into four different layers: organic layer and 0–10 cm, 10–20 cm and 20–30 cm of the mineral soil. Since the organic layer was generally very thin in these oak stands, soil for these samples was taken from an area measuring 10 × 10 cm close to each sampling point. The soil from each point was then bulked into one composite sample per layer per tree. Before chemical analysis, the organic soil was sieved through a 6 mm mesh and the mineral soil through a 2 mm mesh and all soil samples were dried at 40 °C to constant weight.

Twenty grams of soil were extracted in 100 mL 0.1 M $BaCl_2$ for 2 h [3]. Extraction took place at room temperature and the pH was then measured in the $BaCl_2$ filtrate. Aluminium concentration, as well as the concentrations of Ca, Mg, K, Na, Mn, Fe and B were determined with an inductively coupled plasma analyser (Perkin Elmer, Norwalk, USA). Concentrations of P, Cu and Zn were determined with the same inductively coupled plasma analyser after extraction of 20 g of soil with 100 mL acid EDTA solution (0.5 M ammonium acetate, 0.5 M acetic acid, 0.02 M EDTA) for 2 h. Carbon (C) concentrations were determined using an automatic carbon elementar analyzer (CR12, LECO Corporation, Michigan, USA), while the total nitrogen (N) was analysed using the Kjeldahl technique [3]. The results obtained from the chemical analyses were normalized to the dry matter content at 85 °C. The total exchangeable acidity, the cation exchange capacity and the base saturation were calculated.

2.7. Statistical analysis

When testing for differences between healthy, moderately declining and severely declining trees, and between infested and non-infested stands, split-plot ANOVA was used. If the interaction (marked with × in tables and figures) between treatment (= presence or absence of *P. quercina*) and tree vitality (= healthy, moderately declining or severely declining tree) was significant, stands with and without *P. quercina* were analysed separately. The Tukey test was used as a post hoc test when significant differences were found using ANOVA. Since the division into blocks was based on the factors mentioned above, the blocks differed in soil chemistry. Significant differences for blocks are therefore not given in the tables and figures. The significance of differences in live root length and in the proportion of dead root length between sampling occasions were tested with repeated measures ANOVA. The relation between live fine-root length and concentration of P in the soil and leaves was evaluated using the Pearson correlation. All statistical calculations, except the Pearson correlation, were performed using SuperAnova 1.11 and Statview 4.5 software (Abacus Concepts, Berkeley, USA). The Pearson correlation was performed using SPSS 10 for Macintosh (SPSS Inc., Illinois, USA).

3. RESULTS

3.1. Isolation of *Phytophthora* species

Phytophthora quercina was recovered from rhizosphere soil of healthy, moderately declining and severely declining trees in the five stands previously found to host this pathogen [20]. However, the frequency of isolation of *P. quercina* and the season of recovery varied between stands and trees. In June 2002, the pathogen was consistently recovered from soil in all stands. On the other sampling occasions, isolation success varied, but the pathogen was recovered from all sites and trees on at least one occasion of the three soil sampling occasions. *Phytophthora quercina* was also isolated from fine-root fragments with visible symptoms of disease and from healthy-looking tissue in close connection with the diseased tissue from all trees but the healthy one in stand 1. The pathogen was recovered only occasionally from fine roots sampled in June 2002, but more frequently in August 2002 and March 2003. *Phytophthora quercina* was not recovered from soil or roots of any tree in the five non-infested stands.

3.2. Root vitality and symptoms of infection

There was substantial die-back of non-suberized fine roots of severely declining trees in *Phytophthora*-infested stands. The die-back seemed to progress towards the mother roots. The suberized coarse roots of declining trees often had discoloured necrotic areas in close association with necrotic lateral roots, where one to several lesions had developed. The lesions varied in size, but were on average 2–5 mm in width and 10–15 mm in length. Some of the wounds were restricted to the outer cortical layer, while others extended into the vascular tissue. Necrotic areas and lesions also appeared on roots of healthy trees, but to a smaller extent than on declining trees. No corresponding patterns of necrosis and lesions in close connection with necrotic laterals were found on roots of trees growing in stands where *P. quercina* was not present.

There was no significant difference in live fine-root length or length of coarser roots between stands with and without *P. quercina* on any sampling occasion (Fig. 1, data for coarser roots is not shown). However, comparing the individual trees within each stand showed that live fine-root length of healthy trees in infested stands were significantly greater than live fine-root length of moderately declining (August 2002) and severely declining (August 2002 and March 2003) trees (Figs. 1a, 1c and 1e). In non-infested stands, on the other hand, there was no difference in live fine-root length between healthy and declining trees at any sampling occasion (Figs. 1a, 1c and 1e).

In stands with *P. quercina*, the proportion of dead fine roots (expressed in terms of fine-root length) was significantly higher in severely declining trees than in moderately declining trees (June 2002) and healthy trees (June 2002 and August 2002; Figs. 1b, 1d and 1f). In contrast, no differences in the proportion of dead fine roots were found between trees of differing vitality in stands where the pathogen was not present. Averaging the proportion of dead fine roots in relation to total roots (in terms of length) over the three sampling occasions showed that declining trees in *Phytophthora*-infested stands had a significantly higher proportion of dead fine roots than healthy trees, which is obvious when looking at the relative values for the trees (Fig. 2b). Despite the high proportion of dead fine roots in declining trees in *Phytophthora*-infested

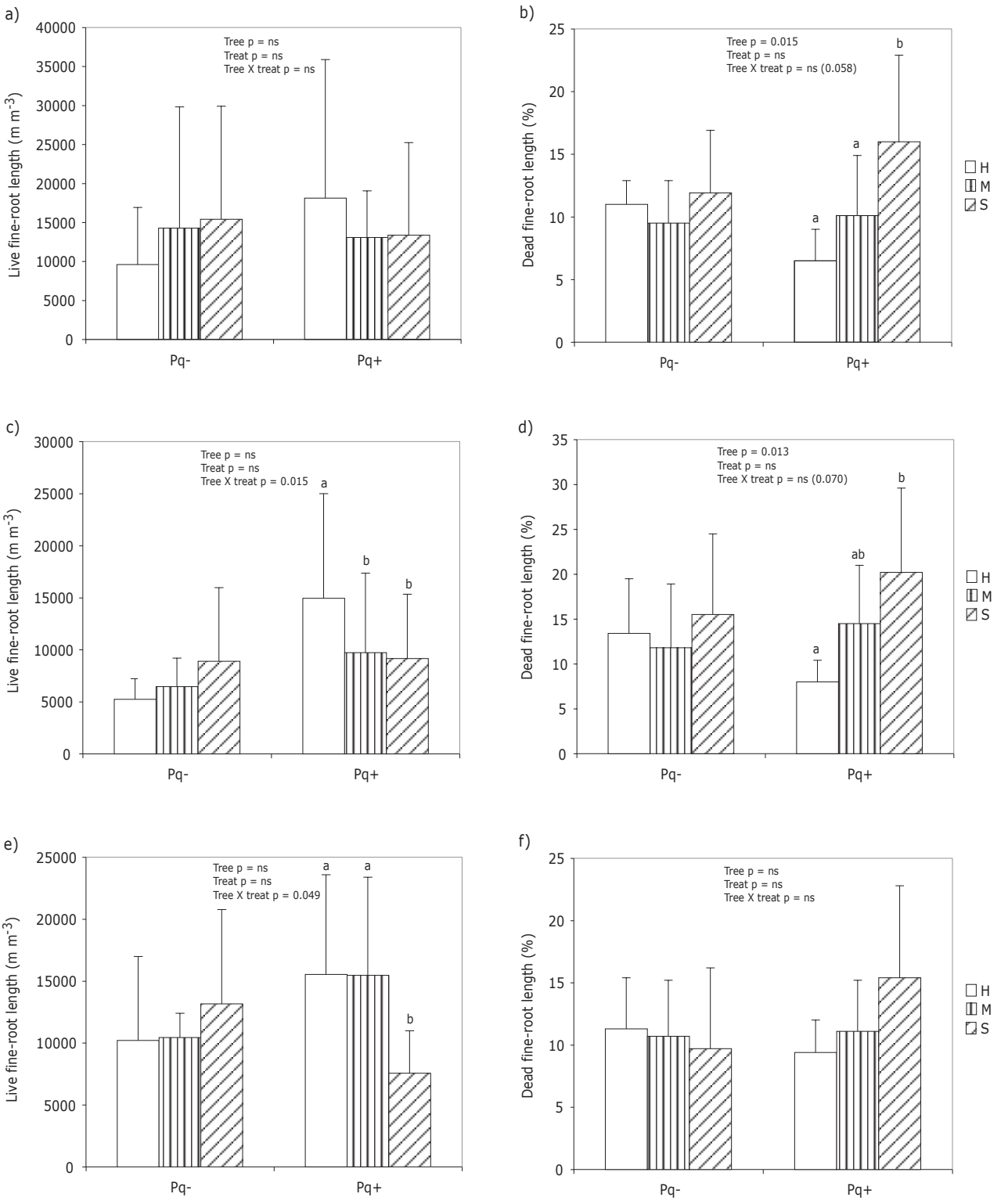

Figure 1. Live fine-root length (a, c, e) and the proportion of dead fine-root length in relation to total fine-root length (b, d, f) for healthy (H), moderately declining (M) and severely declining (S) trees on the three different sampling occasions (a, b = June 2002; c, d =August 2002; e, f = March 2003). Values given are mean + SD (n = 5). Pq– = stands where *P. quercina* is absent, Pq+ = stands where *P. quercina* is present. Statistics given are for split-plot ANOVA (Treat = treatment, Tree = tree vitality). When significant differences were found using ANOVA, lower-case letters denote statistical results of the post hoc test (Tukey); different letters indicate significant differences. The significance level is 5%.

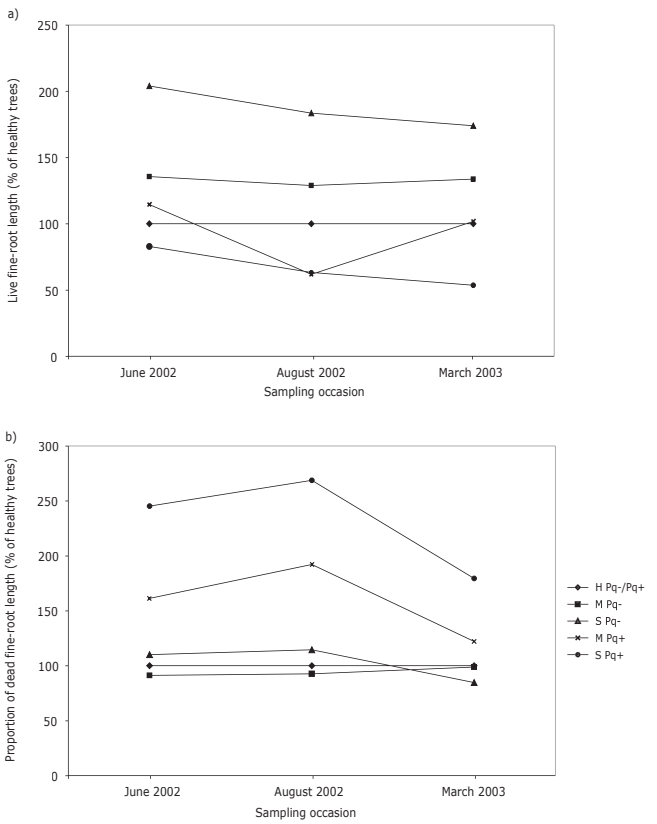

Figure 2. The variation in live fine-root length (a) and the proportion of dead fine roots (b) between sampling occasions for declining trees compared with healthy trees. The average values for the healthy trees in *Phytophthora*-infested (Pq+) and in non-infested stands (Pq–) are set at 100% (n = 5). H = healthy trees, M = moderately declining trees, S = severely declining trees, Pq– = stands where *P. quercina* is absent, Pq+ = stands where *P. quercina* is present. There were no significant differences between sampling occasions (repeated measures ANOVA).

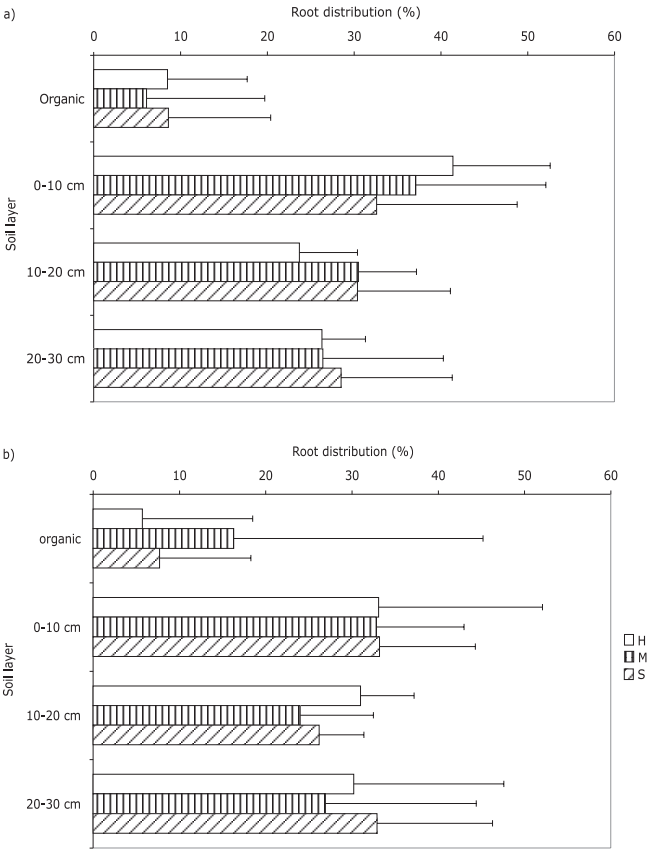

Figure 3. Distribution of fine roots in the organic layer and the upper 30 cm of mineral soil in August 2002 for stands with *P. quercina* (a) and stands without the pathogen (b). Values given are mean + SD (n = 5). H = healthy trees, M = moderately declining trees, S = severely declining trees. There were no significant differences between stands with and without *P. quercina* or between trees of differing vitality (split-plot ANOVA).

stands on some sampling occasions, there was no significant difference between stands with and without the pathogen (Figs. 1b, 1d and 1f). Coarse root length (diameter > 2 mm; data not shown), the average root diameter (data not shown), the proportion of fine-root length in relation to total root length (data not shown) and the specific fine-root length (cm length per g root; data not shown) did not differ significantly between trees or stands. There was no difference between trees or stands in the distribution of roots in the organic layer or the upper 30 cm of the mineral soil on any sampling occasion (represented by the sampling in August 2002, Fig. 3).

There were no significant differences in live fine-root length or the proportion of dead roots between sampling occasions (Figs. 1 and 2). However, there was a substantial decrease in live fine-root length, and an increase in the proportion of dead fine roots, for declining trees in *Phytophthora*-infested stands in August 2002 compared with June 2002. In March 2003, the moderately declining trees had recovered and showed similar live fine-root length to healthy trees, while severely declining trees still had considerably smaller live fine-root length. In non-infested stands, the variation between sampling occasions was smaller.

3.3. Leaf chemistry

The concentration of Cu was significantly higher in leaves of *Phytophthora*-infested trees than in non-infested trees (Tab. II). The concentration of N was significantly higher in leaves from healthy than in leaves from severely declining trees, and Zn was significantly higher in healthy and moderately declining trees than in severely declining ones (Tab. II). These differences were consistent for stands with and without the pathogen. With the exception of B/N, where healthy trees had significantly lower ratios than severely declining trees, there were no significant differences in the ratios of nutrients to N (Tab. II).

Table II. Nutrient concentration and ratios of nutrients to N (by weight) in leaves of *Q. robur*. Values given are mean ± SD (n = 4). Statistics are for split-plot ANOVA, and between trees, for the post hoc test (Tukey). Only significant differences are indicated in the table. H = healthy trees, M = moderately declining trees and S = severely declining trees.

Tree vitality/element[1]	Stands with *P. quercina*			Stands without *P. quercina*		
	H	M	S	H	M	S
N	23.9 (± 2.3)	22.2 (± 1.8)	20.9 (± 1.4)	24.2 (± 4.0)	22.1 (± 3.2)	21.2 (± 5.8)
	Block × treatment, $p < 0.05$; tree vitality, $p < 0.05$; H vs. M, p = ns; H vs. S, $p < 0.05$; M vs. S, p = ns					
P	1.5 (± 0.1)	1.3 (± 0.3)	1.3 (± 0.2)	1.5 (± 0.3)	1.5 (± 0.3)	1.5 (± 0.4)
K	8.9 (± 1.2)	8.3 (± 1.2)	7.6 (± 0.8)	7.8 (± 1.1)	7.8 (± 0.9)	7.8 (± 1.4)
Ca	5.9 (± 1.7)	5.7 (± 0.6)	5.0 (± 1.1)	4.9 (± 1.3)	5.2 (± 0.5)	4.8 (± 0.7)
Mg	1.4 (± 0.4)	1.3 (± 0.4)	1.2 (± 0.3)	1.2 (± 0.4)	1.0 (± 0.3)	0.9 (± 0.2)
B	27.2 (± 8.7)	30.4 (± 15.4)	38.8 (± 16.6)	32.6 (± 7.0)	35.9 (± 19.8)	42.6 (± 18.9)
	Block × treatment, $p < 0.05$					
Cu	6.4 (± 1.3)	5.5 (± 1.3)	5.4 (± 0.9)	5.8 (± 1.3)	5.3 (± 0.8)	4.6 (± 0.7)
	Treatment, $p < 0.05$					
Zn	18.0 (± 2.9)	15.8 (± 2.0)	14.8 (± 1.5)	16.7 (± 3.9)	17.0 (± 2.6)	12.5 (± 2.3)
	Block × treatment, $p < 0.05$; tree vitality, $p < 0.05$; H vs. M, p = ns; H vs. S, $p < 0.05$; M vs. S, $p < 0.05$					
Ca/N	25.3 (± 9.9)	25.9 (± 3.9)	24.2 (± 6.2)	19.9 (± 3.1)	23.6 (± 2.2)	23.3 (± 4.3)
K/N	37.7 (± 6.9)	37.7 (± 6.0)	36.8 (± 6.6)	32.9 (± 7.0)	35.7 (± 5.5)	40.4 (± 18.2)
Mg/N	6.1 (± 2.0)	6.0 (± 1.8)	5.7 (± 0.9)	4.9 (± 1.5)	4.4 (± 1.4)	4.7 (± 1.8)
P/N	6.2 (± 1.1)	5.8 (± 1.2)	6.2 (± 1.4)	6.4 (± 1.3)	6.7 (± 1.2)	7.5 (± 3.3)
B/N	0.11 (± 0.04)	0.14 (± 0.07)	0.18 (± 0.08)	0.14 (± 0.04)	0.16 (± 0.08)	0.19 (± 0.05)
	Block × treatment, $p < 0.05$; tree vitality, $p < 0.05$; H vs. M, p = ns; H vs. S, $p < 0.05$; M vs. S, p = ns					
Cu/N	0.027 (± 0.004)	0.025 (± 0.004)	0.026 (± 0.004)	0.024 (± 0.004)	0.024(± 0.004)	0.023 (± 0.004)
Zn/N	0.08 (± 0.02)	0.07 (± 0.01)	0.07 (± 0.01)	0.07 (± 0.01)	0.08 (± 0.01)	0.06 (± 0.01)

[1] N, P, K, Ca, Mg (mg g^{-1}); B, Cu, Zn (μg g^{-1}); ratios are given in %.

3.4. Fine-root chemistry

Fine-root chemistry did not differ between stands with and without *P. quercina* (Tab. III). However, the concentration of Cu tended to be somewhat higher in fine roots of trees in stands with *P. quercina* than in stands without the pathogen. Furthermore, concentrations of Ca and Mg differed between trees (Tab. III). The variation in Ca was obvious at all sampling depths in the mineral soil, while Mg varied only in the upper two soil layers (data not shown).

3.5. Soil chemistry

There were few differences in soil chemistry between healthy and declining oaks throughout the different horizons, as represented by the soil chemical data at 20–30 cm depth in the mineral soil (Tab. IV). The only elements that tended to vary were N and Fe. Moderately declining trees had significantly higher concentrations of total N in the upper mineral soil layer (0–10 cm) than severely declining trees ($p <$ 0.05; data not shown). The concentration of exchangeable Fe showed a significant interaction between tree vitality and treatment in the organic layer ($p < 0.05$) and was significantly higher for moderately declining as compared to severely declining trees at 0–10 cm depth in the mineral soil ($p < 0.05$; data not shown). The concentration of P tended to differ between infested and non-infested stands, with significantly (organic layer: $p < 0.05$, Tab. V) or close to significantly (average values for the organic layer and the upper 30 cm of the mineral soil: $p = 0.079$, Tab. V) lower values in stands with *P. quercina*.

4. DISCUSSION

This study investigated the influence of *P. quercina* on mature oaks in southern Sweden. The results showed that healthy trees had a greater fine-root length per unit soil volume than declining trees in stands infested with *Phytophthora*. In non-infested stands, on the other hand, no significant differences in live fine-root length could be detected between trees of different vitality. The completely different patterns of root growth in infested compared with non-infested stands, together with the symptoms of pathogen infection on roots of trees in infested stands, indicate a significant negative impact of *P. quercina* on fine-root systems of mature oaks under field conditions, and support the previously detected association between presence of *P. quercina* in the rhizosphere and decline of oak stands in southern Sweden [23]. The association between root damage and severe defoliation of the tree crown may be a consequence of reduced C assimilation as a result of pathogen

Table III. Nutrient concentration in fine roots (0–2 mm) of *Q. robur*. Values given are mean ± SD for the mineral soil (0–30 cm depth; $n = 5$). Statistics are for split-plot ANOVA, and between trees, for the post hoc test (Tukey). Only significant differences are indicated in the table. H = healthy trees, M = moderately declining trees and S = severely declining trees.

Tree vitality/element[1]	Stands with *P. quercina*			Stands without *P. quercina*		
	H	M	S	H	M	S
N	8.5 (± 1.0)	8.4 (± 1.1)	8.5 (± 1.3)	8.6 (± 1.5)	8.6 (± 1.5)	8.0 (± 1.9)
	Block × treatment, $p < 0.05$					
P	0.4 (± 0.04)	0.5 (± 0.1)	0.4 (± 0.1)	0.5 (± 0.1)	0.5 (± 0.1)	0.5 (± 0.2)
	Block × treatment, $p < 0.05$					
Ca	3.7 (± 1.0)	3.1 (± 0.7)	4.0 (± 1.4)	2.7 (± 1.0)	2.4 (± 1.0)	3.5 (± 1.6)
	Block × treatment, $p < 0.05$; tree vitality, $p < 0.05$; H vs. M, p = ns; H vs. S, p = ns; M vs. S, $p < 0.05$					
K	2.4 (± 0.4)	2.3 (± 0.3)	2.4 (± 0.5)	2.0 (± 0.2)	1.8 (± 0.2)	1.7 (± 0.7)
	Block × treatment, $p < 0.05$					
Mg	1.0 (± 0.2)	0.9 (± 0.1)	0.8 (± 0.2)	1.0 (± 0.3)	0.9 (± 0.2)	0.9 (± 0.3)
	Block × treatment, $p < 0.05$; tree vitality, $p < 0.05$; H vs. M, p = ns; H vs. S, $p < 0.05$; M vs. S, p = ns					
B	20.0 (± 3.3)	17.2 (± 3.3)	16.1 (± 2.8)	17.7 (± 5.2)	15.6 (± 6.0)	22.0 (± 9.6)
Cu	9.2 (± 1.4)	9.2 (± 2.0)	8.9 (± 1.8)	7.7 (± 1.2)	7.6 (± 1.4)	8.2 (± 1.6)
	Block × treatment, $p < 0.05$					
Zn	43.3 (± 8.2)	45.4 (± 19.3)	47.6 (± 13.7)	30.8 (± 10.3)	32.6 (± 9.9)	45.4 (± 17.1)
	Block × treatment, $p < 0.05$					

[1] N, P, K, Ca, Mg (mg g^{-1}); B, Cu, Zn (μg g^{-1}).

Table IV. Concentration of chemical elements in stands with and without *P. quercina* at 20–30 cm depth in the mineral soil. Values given are mean ± SD, except for pH, where medians and ranges are given ($n = 5$ except for P where $n = 4$). There were no significant differences between *Phytophthora*-infested and non-infested stands or between trees of differing vitality. H = healthy trees, M = moderately declining trees and S = severely declining trees.

Tree vitality/ parameter[1]	Stands with *P. quercina*			Stands without *P. quercina*		
	H	M	S	H	M	S
pH	4.1 (3.9–4.3)	3.9 (3.7–4.3)	4.1 (3.9–4.3)	4.0 (3.7–4.3)	4.2 (3.4–4.3)	4.0 (3.6–4.3)
Al	168.8 (± 89.2)	176.5 (± 87.4)	111.2 (± 73.8)	166.2 (± 76.2)	174.4 (± 68.8)	156.9 (± 47.9)
Fe	4.6 (± 5.7)	7.4 (± 11.4)	1.7 (± 1.0)	11.8 (± 14.3)	15.9 (± 19.3)	11.3 (± 11.2)
Ca	57.3 (± 60.0)	50.5 (± 33.0)	67.5 (± 42.5)	42.4 (± 40.8)	44.5 (± 57.2)	70.3 (± 73.8)
K	42.0 (± 32.5)	31.6 (± 14.9)	29.9 (± 18.0)	23.2 (± 13.7)	24.4 (± 16.0)	23.5 (± 16.2)
Mg	16.2 (± 15.0)	11.4 (± 6.5)	9.5 (± 5.0)	8.1 (± 5.7)	10.1 (± 9.5)	11.2 (± 10.0)
N[2]	1.0 (± 0.4)	1.2 (± 0.4)	0.9 (± 0.4)	1.2 (± 0.7)	1.0 (± 0.7)	1.3 (± 0.7)
P	9.4 (± 8.2)	11.9 (± 7.2)	8.4 (± 7.3)	20.9 (± 21.8)	18.8 (± 17.6)	27.0 (± 19.4)
Total exchangeable acidity	21.1 (± 12.7)	21.2 (± 10.5)	16.0 (± 7.2)	19.9 (± 9.6)	21.3 (± 9.3)	19.0 (± 6.3)
Base saturation	19.0 (± 4.5)	17.2 (± 7.7)	23.0 (± 11.9)	13.6 (± 7.1)	13.3 (± 7.4)	18.3 (± 9.8)

[1] Al, Fe, Ca, K, Mg, P (μg g^{-1}); N (mg g^{-1}); total exchangeable acidity ($mmol_c$ kg^{-1}); base saturation (%).
[2] Values from one of the *Phytophthora*-infested stands deviated considerably from the rest of the N concentrations and this stand was therefore removed; values are therefore based on 4 stands.

infection. Maurel et al. [35–37] and Fleischmann et al. [17] demonstrated significantly reduced stomatal conductance and transpiration for seedlings of *Castanea sativa*, *Fagus sylvatica* and *Q. ilex* infected with various *Phytophthora* species. Similar results were also reported for *Persea americana* infected with *P. cinnamomi* [41]. However, the mechanism underlying the reduction in C assimilation and transpiration is unclear and further studies are needed before the link between root damage and overall tree vitality is fully understood. It also remains unclear why certain trees remain healthy despite close association with the pathogen while others succumb to infection. Soil chemical conditions have often been described to influence the development of disease [45], but in this study, no evidence was found that the soil chemical conditions govern the differences in disease expression of trees within a stand. However, it is possible that slight differences in several soil chemical factors together may create an additive effect that influences the reproduction and aggressiveness of the pathogen or the

Table V. Concentration of P in leaves and soil of each stand (mean for healthy, moderately declining and severely declining trees), and average values ± SD for stands with (Pq+) and without (Pq–) *P. quercina*. For stand 1 and 2, leaf concentrations of P are missing. For stand 9, concentration of P in the mineral soil is missing.

Block	Stand	Presence of *P. quercina*	Leaf P (mg g^{-1})	Soil P (µg g^{-1})				
				Organic	0–10 cm	10–20 cm	20–30 cm	Organic–30 cm
1	1	Yes	–	143.8	50.5	30.7	19.9	61.2
	2	No	–	149.1	47.0	25.4	15.0	59.1
2	3	Yes	1.4	131.8	25.0	16.8	22.7	49.1
	4	No	1.8	139.4	54.3	42.1	33.1	70.7
3	5	Yes	1.5	143.5	23.1	14.6	4.4	35.6
	6	No	1.5	218.6	118.2	97.6	47.0	120.3
4	7	Yes	1.0	98.1	17.2	9.9	5.9	32.8
	8	No	1.1	174.1	15.2	6.8	4.5	50.4
5	9	Yes	1.4	85.0	–	–	–	–
	10	No	1.5	289.2	19.4	6.8	4.0	75.4
		Pq+	1.3 (± 0.2)	118.7 (± 54.1)	28.9 (± 16.0)	18.0 (± 8.8)	13.2 (± 13.0)	44.6 (± 19.3)
		Pq–	1.5 (± 0.3)	199.8 (± 69.4)	50.8 (± 43.2)	37.8 (± 37.7)	21.9 (± 18.4)	77.6 (± 31.7)

susceptibility of the trees. The lack of symptoms of damage on roots of trees in non-infested stands indicate, together with the extensive root growth of declining trees in these stands, that root pathogens are not involved in the decline of trees at these sites. The reasons for the decline of oaks in these stands are still unknown.

The negative impact of *P. quercina* on the fine-root system is consistent with findings of Jung et al. [27], who compared root parameters of infested and non-infested mature trees over a number of stands in Germany. However, in contrast to their study, where trees in non-infested stands always had higher fine-root length and specific fine-root length than trees in infested stands, we found no significant difference in live fine-root length between trees growing in stands with *P. quercina* and those growing in stands without the pathogen. This is probably due to the lower concentrations of P in leaves and soil of infested stands as compared with non-infested stands (Tab. V). Phosphorus is a nutrient, which, together with N, S, K, Mg and Mn, is well-known to affect the allocation patterns of C in trees [15, 31, 34]. Shortage of P (and N) usually results in an increased allocation of C to the roots, thereby favouring root growth relative to shoot growth [15]. A high allocation of C to roots may result in a high capacity of trees to replace roots lost due to *Phytophthora* infection, and trees may thereby maintain a high amount of live fine roots despite the presence of *Phytophthora*. This explanation is supported by the strong correlations between, in particular, leaf P and live fine-root length, but also between soil P and live fine-root length (Fig. 4).

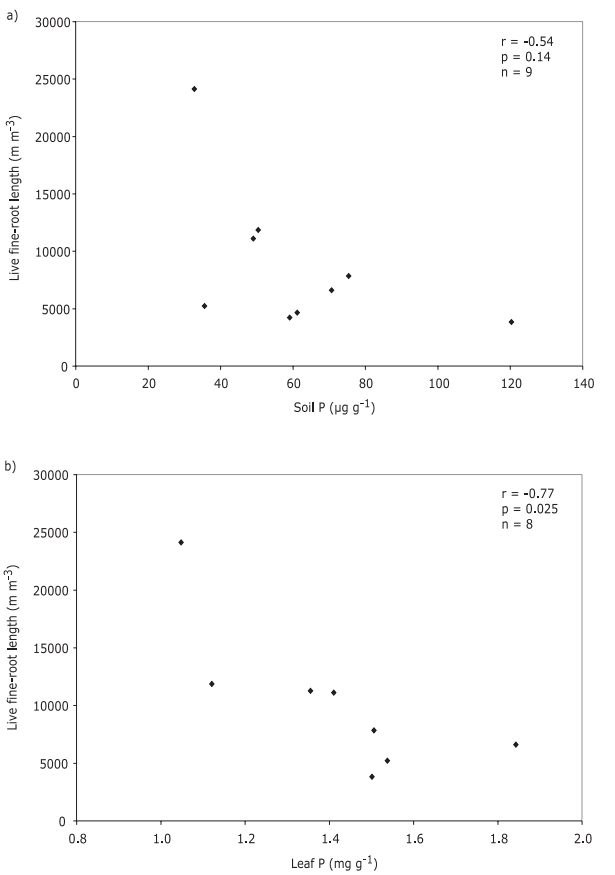

Figure 4. Live fine-root length in August 2002 in relation to soil P (a) and in relation to leaf P (b). The soil P is the average concentration for the organic layer and the upper 30 cm of the mineral soil. Statistics given are for the Pearson correlation.

The impact of the pathogen on the root system seemed to be dependent on the season, being most severe after an unusually dry summer (August 2002). This suggests an interaction between drought and *Phytophthora* attack, and is supported by previous investigations on oak seedlings, where Jung et al. [29] demonstrated that *P. quercina* caused higher amounts of root damage to *Q. robur* under conditions where drought and flooding were alternated than when moist soil conditions prevailed between flooding cycles. Severe drought may critically reduce the tolerance of the host to the pathogen through its influence on the photosynthetic rate of the plant [19]. Furthermore, *Phytophthora* species are generally regarded as weak competitors [50], and the infection of roots by *Phytophthora* zoospores may have been facilitated by the negative impact of drought

on the activity of the soil microbial community [40]. After the summer, the moderately declining trees seemed to restore the balance between root production and die-back of roots, resulting in a recovery of the root system as compared with healthy trees in March 2003. For severely defoliated trees, on the other hand, a recovery of the balance did not occur. This was probably due to the strongly reduced photosynthetic capacity of these trees.

Despite a significant reduction in the live fine-root length of declining trees in *Phytophthora*-infested stands, leaf concentrations of most nutrients did not differ much between healthy and declining trees. This is not surprising considering that the declining trees have a reduced crown and the fine-root system may thus be able to take up enough nutrients for the remaining crown. Nutrient deficiencies may therefore be difficult to detect, and alternative methods, such as root bioassays, may be necessary to evaluate the nutrient status of trees. In general, the concentrations of most nutrients were within what can be considered as the normal range for mature oak trees growing in forest soils [32, 51, 52]. The exception was the concentration of P and the ratio between P and N, which were somewhat low in most trees. The low concentration of P in leaves, the significant difference in the leaf concentration of N between healthy and severely declining trees in both infested and non-infested stands, and the patterns of root growth, suggest that N and P are the most critical nutrients for trees included in this study. As discussed above, a low availability of P and/or N may have important implications for the C allocation pattern in the trees [15, 31, 34], and thereby for the trees' ability to replace lost roots and defend themselves. That N seems to be a critical nutrient is somewhat surprising considering that the high deposition of N during recent decades has usually been considered to be part of the complex decline of forest trees [1, 2, 39]. However, several studies in Central Europe have dismissed excess N in soil and trees as a contributing factor in oak decline [7,49]. The number of stands sampled in this study was low and more extensive samplings, using alternative methods for detection of nutrient deficiencies, are required before conclusions can be drawn about the nutrient status of southern Swedish oak stands in general. Considering the high acidity of the soils and the small pools of base cations, the continued input of acidifying compounds is likely to eventually lead to nutrient deficiencies and decreased ecosystem stability.

It appears from our results that *P. quercina* has the ability to substantially reduce the live fine-root length of mature oaks under field conditions. However, why certain trees succumb to infection while others remain healthy is still unclear. Two factors that seemed to be of importance for the amount of root damage caused by *P. quercina* were the vitality of the trees and the prevailing climatic conditions. Apart from these factors, there are probably several other factors that may contribute in the development of the disease. Before we can understand the complex pattern of decline as a consequence of *Phytophthora* infection, we need to firmly address the issue of how the root damage caused by these pathogens are related to the symptoms of decline we can see in the crown of trees. In addition, we need to evaluate how various abiotic and biotic factors affect not only *Phytophthoras*, but also how they affect the C assimilation and allocation within trees. To understand these interactions, and to describe the disease development, conceptual methods may be useful.

Based on the significant negative impact of *P. quercina* on root systems of mature declining trees, we suggest that *P. quercina* contribute to southern Swedish oak decline. With reference to the hypotheses stated in the introduction we draw the following conclusions.

(i) Healthy trees in *Phytophthora*-infested stands had significantly greater root vitality (measured as live fine-root length per unit soil volume) than moderately declining (August 2002) and severely declining (August 2002 and March 2003) trees, indicating a significant impact of *P. quercina* on the root systems of declining trees. The effect of the pathogen seemed to depend on the climatic conditions, with the most pronounced effect on the root systems occurring after an unusually dry summer. In stands without *P. quercina*, there was no difference in live fine-root length per unit soil volume between trees of differing vitality, demonstrating that fine-root decay does not necessarily occur prior to noticeable above-ground symptoms in oaks.

(ii) The live fine-root length per unit soil volume was not lower for trees growing in stands infested with *P. quercina* than for trees growing in stands without the pathogen. This may be due to the lower availability of P in *Phytophthora*-infested stands, resulting in a high allocation of carbohydrates to root growth.

(iii) Despite the significant differences in live fine-root length between trees in *Phytophthora*-infested stands, there were few differences in leaf and root nutrient concentrations and the leaf concentrations of most nutrients seemed to be within what can be considered as the normal range for mature oaks in forests. However, healthy trees had significantly higher leaf concentrations of N than severely declining trees in infested as well as in non-infested stands and leaf concentrations of P were low in all trees.

(iv) Soil around healthy oaks did not have higher pH and base saturation than soil around declining oaks.

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