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Beech decline in Central Europe driven by the interaction between *Phytophthora* infections and climatic extremes

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Summary

During the past decade, and in particular after the wet year 2002 and the dry year 2003, an increasing number of trees and stands of European beech (*Fagus sylvatica* L.) in Bavaria were showing symptoms typical for *Phytophthora* diseases: increased transparency and crown dieback, small-sized and often yellowish foliage, root and collar rot and aerial bleeding cankers up to stem heights of >20 m. Between 2003 and 2007 134 mature beech stands on a broad range of geological substrates were surveyed, and collar rot and aerial bleeding cankers were found in 116 (86.6%) stands. In most stands the majority of beech trees were declining and scattered or clustered mortality occurred. Bark and soil samples were taken from 314 trees in 112 stands, and 11 *Phytophthora* species were recovered from 253 trees (80.6%) in 104 stands (92.9%). The most frequent species were *P. citricola*, *P. cambivora* and *P. cactorum*. Primary *Phytophthora* lesions were soon infected by a series of secondary bark pathogens, including *Nectria coccinea*, and wood decay fungi. In addition, infected trees were often attacked by several bark and wood boring insects leading to rapid mortality. Bark necroses were examined for their probable age in order to determine whether the onset of the current *Phytophthora* epidemic was correlated to rainfall rates recorded at 22 Bavarian forest ecosystem monitoring stations. A small-scale survey in nine Bavarian nurseries demonstrated regular infestations of all beech fields with the same range of *Phytophthora* species. The results indicate that (1) *Phytophthora* species are regularly associated with beech decline and may also be involved in the complex of 'Beech Bark Disease', (2) excessive rainfalls and droughts are triggering the disease, and (3) widespread *Phytophthora* infestations of nursery stock might endanger current and future silvicultural projects aiming on the replacement of non-natural conifer stands by beech dominated mixed stands.

1 Introduction

Due to its high shade tolerance and growth capacity, and its wide climatic and geological amplitude (e.g. atlantic to continental climate, colline to montanous zone, moderately dry to periodically wet soils with pH ranging from <3 to >7) European beech (*Fagus sylvatica* L.) is the most competitive tree species in Western and Central Europe and in mountain areas of Eastern and Southern Europe, and would naturally dominate far more than 50% of the forests (Ellenberg 1986; Walentowski et al. 2004; Ammer et al. 2005; Kölling et al. 2005; Felbermeier and Mosandl 2006). Consequently, in new silvicultural concepts aiming on the replacement of non-natural pure conifer stands by mixed forests, beech is the most important tree species to stabilise the ecosystems against predicted risks of climate change (Ammer et al. 2005; Kölling et al. 2005; Fritz 2006).

Apart from the complex 'Beech Bark Disease' (BBD), *F. sylvatica* was traditionally considered being non-problematic with regard to its susceptibility to pathogens and insects (Butin 1996; Felbermeier and Mosandl 2006). However, during the past decade, and in particular after the wet spring and autumn of 2002 and the extreme drought of 2003, an increasing number of trees and stands of European beech in Central Europe are declining,

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and show symptoms typical for *Phytophthora* diseases: small-sized, sparse and often yellowish foliage, crown dieback, root and collar rot, and aerial bleeding cankers up to stem heights of >20 m (Jung et al. 2005). In the Forest Condition Monitoring of 2006 beech was the most severely damaged tree species in Bavaria, Southern Germany with 46.9% of the trees showing crown transparency >25% (Anonymous 2006a). The susceptibility of *F. sylvatica* to *Phytophthora* species is known since 1930's thorough studies of the root and collar rot epidemic caused by *P. cambivora* and *P. syringae* in United Kingdom beech forests (Day 1938, 1939). The next reports came from Bavaria, southern Germany, where the occurrence of *P. cambivora*, *P. citricola* and other *Phytophthora* spp. in beech stands was first recorded by Jung and Blaschke (1996). Since the late 1990's a severe dieback of whole beech stands due to root and collar rot damages caused by *P. cambivora* and *P. pseudosyringae* occured on both periodically waterlogged and base-rich sites in north-western Germany (Hartmann and Blank 1998; Hartmann et al. 2006).

In the last 5 years, beech root and collar rot have been reported from the United Kingdom to Romania and from southern Sweden to southern Italy, and various *Phytophthora* species were recovered from symptomatic trees (Balci and Halmschlager 2003b; Motta et al. 2003; Cech and Jung 2005; Jung et al. 2005; Belisario et al. 2006; Diana et al. 2006; Brown and Brasier 2007; Denman et al. 2007; Munda et al. 2007; Schmitz et al. 2007). Consequently, the involvement of *Phytophthora* infections in beech decline was suggested (Jung et al. 2005; Schmitz et al. 2007).

The objectives of this study were (i) to investigate a representative number of beech stands on a wide range of site conditions for the occurrence of *Phytophthora*-related disease symptoms and the identification of the involved *Phytophthora* species, (ii) to describe the symptoms caused by *Phytophthora* spp. on beech, (iii) to evaluate climatic factors that triggered the onset of the current epidemic on beech, and (iv) assess the risk of disease spread via infested nursery stock.

2 Materials and methods

2.1 Study sites and field surveys

Between July 2003 and October 2007, 104 forest and 30 amenity beech stands on a wide range of typical beech sites in Bavaria were examined for the presence of crown damages and typical *Phytophthora* symptoms in the root systems and at the stems. Secondary bark pathogens and wood rot fungi were also noted. In all stands beech was the dominant tree species. Criteria for stand selection were disease records by forest and park authorities (31 stands) and high level of crown damage on permanent plots of the Bavarian State Forestry (seven stands). However, the majority of stands (96) were selected randomly. With 112 out of 134 stands, the geographical focus of the survey was in southern Bavaria in the Bavarian Alps and the large moraine belt and the tertiary hills between the Alps and the Danube river where beech stands are a major component of the forest coverage.

In 112 of the 134 stands samples were taken from a total of 314 mature beech trees, and isolations for *Phytophthora* spp. carried out. Collar rot tissue was sampled from 126 trees in 65 stands while aerial bark cankers between 2 to 15 m above the ground were sampled from 40 trees in 34 stands. In total necrotic bark was sampled from 166 trees in 85 stands while soil samples were taken from 170 declining trees in 58 stands. From 22 trees both soil and bark samples were taken. In two stands several naturally grown 1–5 years old beech saplings with disease symptoms were harvested, and isolations from necrotic root and collar tissue made.

2.2 Sampling and isolation procedures, and species identification

Bark samples including the cambium were taken from the upper 20 cm of the lesions, placed in distilled water, and transported to the lab in cool boxes. Over 1–3 days the water was replaced four times per day in order to remove excess polyphenols. In the case of active lesions with an orange-brown, flamed appearance of the inner bark 20–50 small pieces (c.8 × 3 × 3 mm) were cut from different parts and depths of the lesion, blotted on filter paper, and plated onto selective PARPNH agar (Jung et al. 1996, 2000; Jung and Blaschke 2004). With inactive, dark brown lesions pieces of tissue were shredded, flooded in distilled water, and baited with oak and beech leaflets (see below). The water was replaced daily in order to remove excess polyphenols and decrease bacterial populations.

For soil samples three to five soil-root-monoliths (size about 20 × 30 × 30 cm) were taken around each tree in a distance of 50–150 cm from the stem base, and aliquots of rhizosphere soil from all monoliths were bulked (about 1 l). Isolations were carried out in the lab at 16–20°C using 2–7 day-old leaflets of *Quercus robur* and *F. sylvatica* seedlings as baits floated over flooded soil (Jung et al. 1996, 1999, 2000). Infected brownish leaflets which usually appeared after 3–7 days were controlled for presence of *Phytophthora* sporangia using a light microscope. Positive leaflets were blotted dry, cut into small segments and plated onto selective PARPNH-agar. Petri dishes were incubated at 20°C in the dark, and examined daily under the stereomicroscope for *Phytophthora* –like hyphae. *Phytophthora* isolates were transferred onto carrot-juice-agar.

Isolates were identified by comparing colony growth patterns, morphological features of sporangia, oogonia, antheridia, chlamydospores and hyphal swellings, and cardinal temperatures of growth with known isolates and species descriptions in literature (Waterhouse 1963; Waterhouse and Waterston 1964, 1966a,b,c; Kröber 1985; Stamps et al. 1990; Erwin and Ribeiro 1996; Jung et al. 1999, 2002, 2003b). Heterothallic species were crossed with tester strains of known mating types from the Centraalbureau voor Schimmelcultures, Utrecht, Netherlands. Sporangia were observed on discs (15 mm diam), cut from the growing edge of a 5–7-day-old culture grown on V8A at 20°C in the dark, and flooded with non-sterile soil extract water (Jung et al. 1996).

When classical identification was ambiguous, ITS-rDNA sequences were generated according to Cooke et al. (2000) and compared with sequences of *Phytophthora* species published at GenBank.

2.3 Nursery surveys

Twelve beech fields in nine forest nurseries in Bavaria were surveyed between 2001 and 2007. In each field 20–40 beech plants were harvested together with adhering soil. In two nurseries patch dieback was widespread and seedlings with root and collar rot were sampled. In the other nurseries root symptoms and mortality were rare so that predominantly non-symptomatic plants were randomly selected. In the lab the plants were put in plastic buckets, flooded and baited with oak and beech leaflets at 16–20° as described above.

2.4 Association of the damages with climatic factors

Data on the mean monthly precipitations of the years 2002–2004 at 22 Bavarian forest ecosystem monitoring stations were gathered from the Bavarian State Institute of Forestry (LWF) in Freising, and expressed as deviations from the 30-years mean values of Bavaria (0 line). Bark necroses on beech were examined for their probable age, and a comparison between rainfall and lesion age was made to determine whether the onset of the current *Phytophthora* epidemic of beech was triggered by rainfall patterns. Lesion age was assessed according to the following classification: active lesions are characterised by an orange-brown and watersoaked appearance of the inner bark, while lesions from the previous year have a dark-brown and dry inner bark; in addition the latter are confined by bark cracks and most often by beginning formation of callussing tissues. In two-years old lesions the bark is loose but still attached while in older lesions the necrotic bark has been shed.

3 Results

3.1 Distribution of disease symptoms

In accordance to the results of the Bavarian Forest Condition Monitoring (Anonymous 2006a) in 129 of the 134 stands a majority of beech trees showed high crown transparency levels (>25%) and severe deteriorations of the crown structure, indicative for both acute and chronic problems in the fine root system. As a typical shade tree European beech is normally characterised by a fan-like and expanded arrangement of lateral branches and twigs and a very dense crown (Felbermeier and Mosandl 2006). However, due to a long-term stunted growth of shoots the lateral twigs were clustered around the major branches and at the ends of branches leading to brush-like and claw-like structures. Moreover, excessive losses of lateral twigs and small branches occurred in most trees, altogether increasing crown transparency significantly (Figs 1 and 2). Severely damaged crowns often showed abundant fructification (Fig. 2). The final phase of the disease was characterised by

Fig. 1. Upper crown of a mature declining beech in summertime with high transparency and brush- and claw-like clusters of foliage due to long-term stunted growth of shoots and excessive losses of lateral twigs.

Fig. 2. Upper crown of a mature declining beech in wintertime with high transparancy and severe deterioration of crown structure, *i.e.* stunted growth of shoots and excessive losses and dieback of lateral twigs; note the excessive fructification.

a dieback of branches and parts of the crown often accompanied by yellowing of leaves. Mortality of individual trees or groups of trees could be found in most stands. In 99 (73.9%) of the 134 surveyed stands (23 amenity tree stands and 76 forest stands), collar rot symptoms were present. They were characterised by orange-brown tongue-shaped necroses of the inner bark and the cambium, and tarry or rusty spots on the surface of the bark that usually extended 1–2 m from the stem base (Fig. 3), but in some cases could reach up to 7 m. Furthermore, in 48 stands (35.8%; 10 amenity stands and 38 forest stands) aerial bleeding cankers up to 21 m stem height were also found (Fig. 4). These cankers had no particular orientation, and were often located above collar rots and below branch forks. The affected trees were often suffering from multiple cankers that tended to be lined up along the stem and following the fibre course. In most stands collar rots and cankers had a scattered distribution. However, in nine amenity and nine forest stands 25–50% of trees were affected by collar rots and aerial cankers. These stands were growing on heavy loam or clay soils derived from moraines (six stands on stagno-gleyic luvisols and gleysols), alluvial sediments (four stands on calcaric fluvisols), gypsum (three stands on cambisols), claystones and flysch (each one stand on stagnic gleysol), loess (one stand on stagno-gleyic luvisol) and limestone (one stand on calcaric cambisol). In purple-leaved beech varieties (*Fagus sylvatica* 'purpurea' and 'atropunicea') a pink discoloration was common in cambium and xylem near and underneath bark lesions caused by either *P. cambivora* or *P. citricola*. In 58 beech stands rhizosphere soil samples were taken, and in 46 stands (79.3%) extensive fine root losses (Fig. 5), dieback of tap roots and necrotic lesions on suberised roots (Fig. 6) were found. Exceptions were the eight stands without detection of

Fig. 3. Severe collar rot symptoms caused by *P. cambivora* on a mature beech growing in a mixed forest in the Bavarian Alps.

Phytophthora spp. and four stands on acid and sandy sites where *Phytophthora* spp. were recovered from above-ground bark lesions but not from rhizosphere soil below the lesions.

In 26 stands groups of trees or parts of the stands were affected by storm damages. Studies of the deeper root system of recently wind-thrown beech trees showed extensive losses of fine roots and necrotic lesions and dieback on coarser roots.

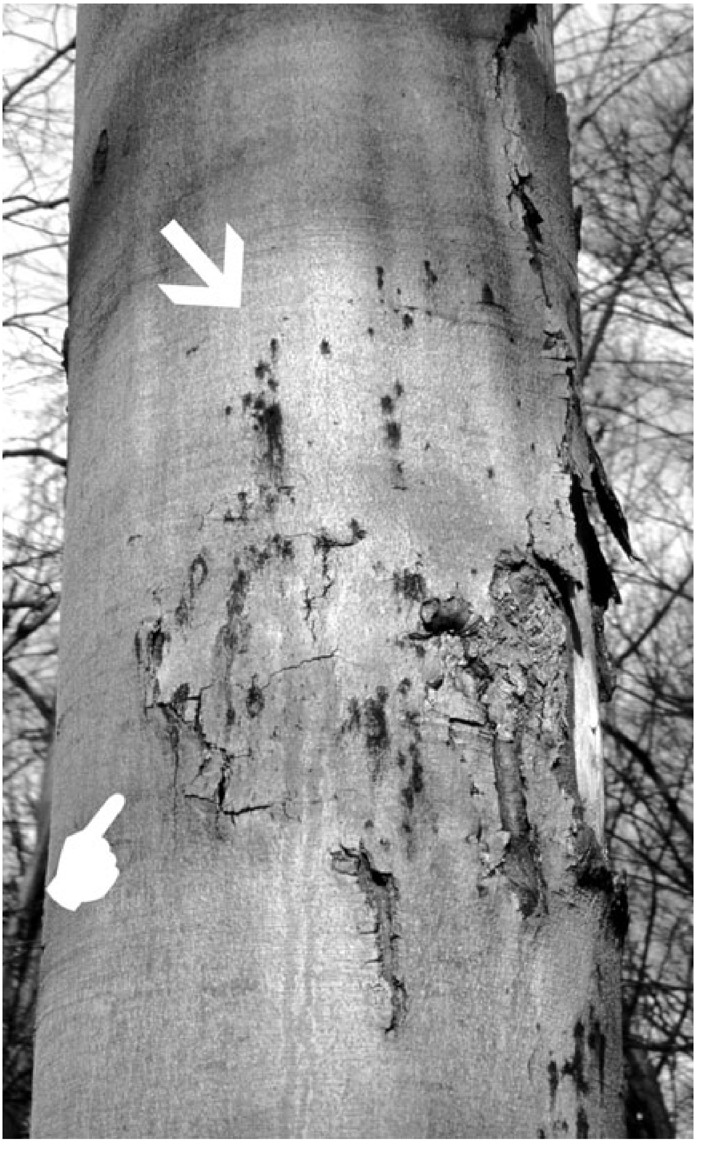

Fig. 4. Stem of mature declining beech tree in a mixed mountain forest in autumn 2004 with active (arrow) and inactive 1-year old (finger; cracking of bark) aerial bleeding cankers caused by *P. citricola*; bark with 2-years old necroses is already shed (right).

In mountain forests *Phytophthora* symptoms were usually more severe downslope of forest roads.

3.2 Distribution of *Phytophthora* species and association with disease symptoms

Bark samples were taken from 153 beech trees in 85 stands.

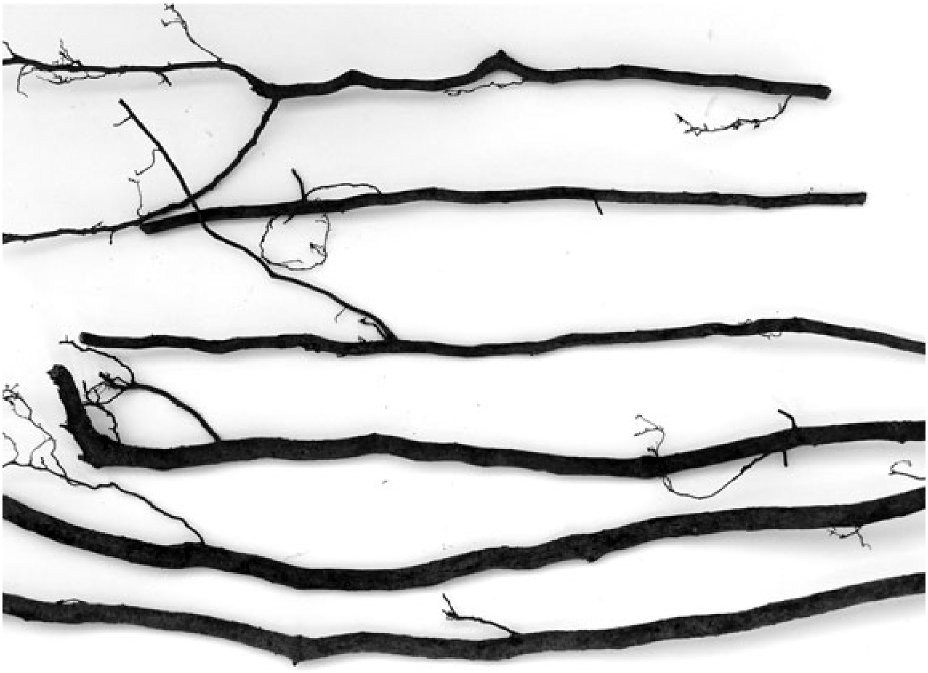

Fig. 5. Small woody roots (diam 2–5 mm) of a declining mature beech with severe losses of lateral roots and fine roots caused by *P. citricola* and *P. cactorum*.

From collar rot tissue, eight *Phytophthora* spp. were recovered from 117 trees (92.9%) in 64 stands (98.5%) (Table 1). The most important species were *P. cambivora* with 54 trees in 35 stands and *P. citricola* with 48 trees in 35 stands. *Phytophthora cactorum*, *P. gonapodyides* and *P. uliginosa* were only infrequently found.

From aerial bark cankers, five *Phytophthora* species could be isolated from 35 trees (87.5%) in 31 stands (91.2%) (Table 1). With 25 trees (62.5%) in 23 stands (67.6%) *P. citricola* was the most frequent causal agent of such cankers. *Phytophthora cambivora* and *P. gonapodyides* were each recovered from four trees in four stands, and *P. cactorum* from two trees in two stands. In one stand *P. citricola* and *P. gonapodyides*, and in two stands two different types of *P. citricola* (based on colony morphology and ITS sequence analysis) were isolated from the same cankers. From 13 beech trees bark samples were taken from both collar rots and aerial cankers. In all cases, the same *Phytophthora* species were recovered from both tissues.

In two stands *P. cambivora* and *P. pseudosyringae*, respectively, were also recovered from necrotic root and collar tissue of naturally grown 1–5 years old European beech saplings.

Soil samples were taken from the rhizosphere of 170 declining beech trees in 58 stands, and 123 samples (72.4%) in 47 stands (81%) yielded *Phytophthora* species (Table 1). The most frequent species recovered were *P. citricola* with 62 trees (36.5%) in 27 stands (46.6%), *P. cactorum* with 50 trees (29.4%) in 15 stands (25.9%) and *P. cambivora* with 24 trees (14.1%) in 13 stands (22.4%).

In four stands severely affected by storm damages isolation results demonstrated the presence of *P. cambivora* and *Pythium undulatum* in soil samples taken from the deeper root system of recently wind-thrown beech trees.

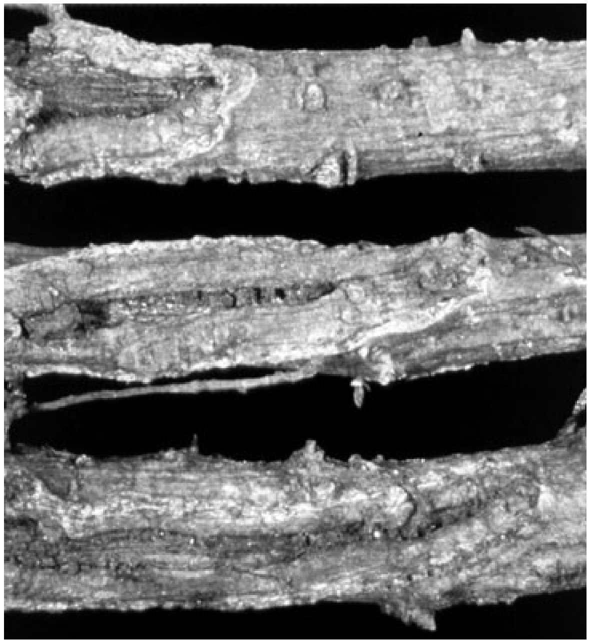

Fig. 6. Woody roots (diam ca 5 cm) of a declining mature beech with callussing open lesions caused by *P. cambivora*.

Table 1. **Recovery of *Phytophthora* species from infected bark tissue and rhizosphere soil samples of declining mature beech trees in Bavaria.**

Sample type	No. of stands/trees	Infected stands/trees	No. and proportion of stands/trees with CAM	CIT	CAC	GON	SYR	*P.* spp.
Collar rots								
Stands	65	64 (98.5)	35 (53.8)	35 (53.8)	7 (10.8)	3 (4.6)		4 (6.2)[2]
Trees	126[1]	117 (92.9)	54 (42.9)	48 (38.1)	10 (7.9)	3 (2.4)		4 (3.2)
Aerial cankers								
Stands	34	31 (91.2)	4 (11.8)	23 (67.6)	2 (5.9)	4 (11.8)		2 (5.9)[3]
Trees	40[1]	35 (87.5)	4 (10.0)	25 (62.5)	2 (5.0)	4 (10.0)		3 (7.5)
Soil								
Stands	58	47 (81.0)	13 (22.4)	27 (46.6)	15 (25.9)	5 (8.6)	6 (10.3)	5 (8.6)[4]
Trees	170	123 (72.4)	24 (14.1)	62 (36.5)	50 (29.4)	7 (4.1)	17 (10.0)	5 (2.9)
All samples								
Stands	112	104 (92.9)	43 (38.4)	70 (62.5)	21 (18.8)	10 (8.9)	6 (5.4)	3 (2.7)
Trees	314	253 (80.6)	74 (23.6)	127 (40.5)	62 (19.8)	13 (4.1)	17 (5.4)	4 (1.0)

Values in parentheses are expressed as percentages.
CAM, *P. cambivora*; CIT, *P. citricola*; CAC, *P. cactorum*; GON, *P. gonapodyides*; SYR, *P. syringae*.
[1]From 13 trees bark samples were taken from both collar rots and aerial cankers, from 9 trees both soil and bark samples were taken.
[2]*P. uliginosa*, *P. citricola* type 2 and unknown *Phytophthora* sp.
[3]*P. citricola* type 2 (undescribed *Phytophthora* species close to *P. citricola* based on ITS sequence analysis).
[4]*P. pseudosyringae*, *P. psychrophila*, *Phytophthora* taxon 'Pg chlamydo'.

Table 2. **Distribution of *Phytophthora* species in declining mature beech stands in Bavaria with regard to different geological substrates.**

Geological substrate	No. of stands (trees)	Infected stands (trees)	No. of stands (trees) with CAM	CIT	CAC	GON	PSEU	SYR	*P.* spp.
Limestone	23 (57)	21 (38)	5 (7)	17 (26)	3 (3)	2 (2)			
Flysch	6 (16)	5 (11)	3 (4)	5 (7)					
Granite	2 (2)	2 (2)				1 (1)	1 (1)		
Conglomerate	1 (1)	1 (1)		1 (1)					
Moraine sediments									
Young	20 (51)	20 (45)	12 (15)	12 (24)	2 (2)	3 (4)	1 (1)	1 (1)	3 (4)
Old	4 (12)	4 (9)	4 (8)	1 (2)			1 (1)		
Moraine gravels	10 (31)	10 (28)	1 (1)	8 (14)	3 (10)	3 (4)		2 (3)	
Alluvial deposits	10 (51)	10 (51)		11 (28)	7 (36)			3 (13)	2 (3)
Tertiary deposits	20 (44)	15 (35)	5 (16)	9 (16)	5 (10)	1 (2)			
Loess	2 (7)	2 (3)	1 (1)	2 (2)					
Claystone	3 (9)	3 (8)	3 (7)	1 (2)					
Gypsum	4 (16)	4 (13)	3 (9)	1 (3)	1 (1)				1 (1)
Mylonite	1 (2)	1 (1)	1 (1)						
Sandstone	6 (15)	6 (8)	5 (5)	2 (2)					1 (1)
Total									
Stands	112	104 (92.9%)	43 (38.4%)	70 (62.5%)	21 (18.8%)	10 (8.9%)	3 (2.7%)	6 (5.4%)	7 (6.3%)
Trees	314	253 (80.6%)	74 (23.6%)	127 (40.5%)	62 (19.8%)	13 (4.1%)	4 (1.0%)	17 (5.4%)	9 (2.9%)

CAM, *P. cambivora*; CIT, *P. citricola*; CAC, *P. cactorum*; GON, *P. gonapodyides*; PSEU, *P. pseudosyringae*; SYR, *P. syringae*; *P.* spp., *P. psychrophila*, *Phytophthora* taxon 'Pg chlamydo', *P. uliginosa* and unknown *Phytophthora* spp.

In total 349 isolates of 11 different *Phytophthora* species were recovered from symptomatic bark tissues or rhizosphere soil of 253 out of 314 beech trees (80.6%) in 104 of the 112 sampled stands (92.9%) (Table 2, Fig. 7). With 127 trees (40.5%) in 70 stands (62.5%) *P. citricola* was the most frequent species followed by *P. cambivora* with 74 trees (23.6%) in 43 stands (38.4%), and *P. cactorum* with 62 trees (19.8%) in 21 stands (18.8%). *Phytophthora gonapodyoides*, *P. syringae*, *P. pseudosyringae*, *P. psychrophila*, *P. uliginosa* and three yet undescribed *Phytophthora* taxa were rarely recovered. In 19 stands (17%) both *P. citricola* and *P. cambivora*, and in 12 stands (10.7%) both *P. citricola* and *P. cactorum* were present.

3.3 Site relations

Phytophthora species were recovered from stands on a wide range of geological substrates, *i.e.* limestone, flysch, moraine gravels and sediments, conglomerates, alluvial deposits, tertiary deposits, loess, gypsum, claystone, granite, mylonite and sandstone (Table 2). Soil types (FAO classification) included rendzinas, orthic and stagno-gleyic luvisols, eutric, calcaric, dystric, vertic and podzolic cambisols, podzols, stagnic gleysols, gleysols and fluvisols. The infested soils were characterised by gritty-loamy, sandy-loamy, loamy, silty or clayey soil texture and a mean soil-pH ($CaCl_2$) between 3.3 and 7.0. Based on observations dieback and mortality were more severe on base-rich sites and on sites with periodically fluctuating water tables (gleysols and stagno-gleyic luvisols).

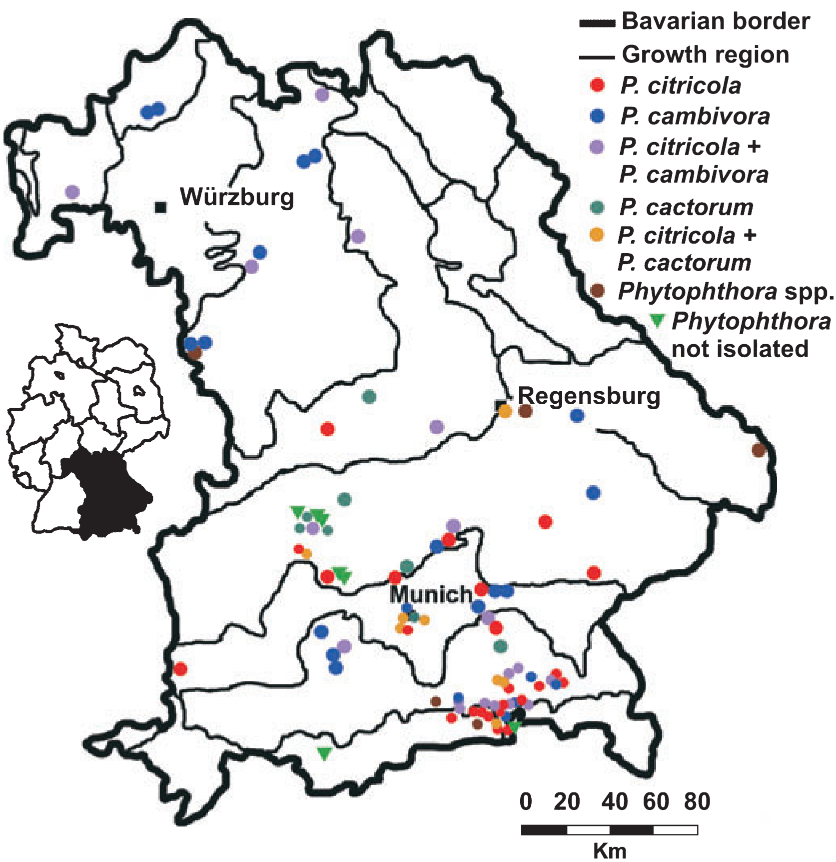

Fig. 7. Distribution of *Phytophthora* species in mature beech stands in Bavaria. The small map on the left shows the location of Bavaria within Germany.

The population of soil-borne *Phytophthora* species varied markedly depending on the site conditions. Despite of a general overlapping of their distribution *P. cambivora* and *P. citricola* showed different site preferences. The main distribution of *P. cambivora* was on sites with a low pH (3.5–5.5 in $CaCl_2$) and loamy to clayey texture of the soils which were derived from flysch, moraine and tertiary sediments, loess, gypsum, claystones and sandstones. In contrast, most records of *P. citricola* came from sites with less compacted soils, rich in base cations with a high pH (4.5–7.2 in $CaCl_2$). These soils were mainly derived from limestone, base-rich moraine sediments and gravels from the last ice age, alluvial deposits, flysch and loess (Table 2). The distribution of the three most important *Phytophthora* species in forest and urban amenity stands also showed interesting differences. While *P. citricola* was widespread on both forest (49 stands) and urban sites (21 stands), the main distribution of *P. cactorum* was on urban sites (13 out of 21 stands). In contrast, *P. cambivora* was almost exclusively found on forest sites (40 out of 43 stands).

The vertical limits of *Phytophthora* distribution were 1100 m a.s.l. (*P. pseudosyringae*), 870 m a.s.l. (*P. citricola*), 800 m a.s.l. (*P. gonapodyides*), 750 m a.s.l. (*P. cambivora*), and 600 m a.s.l. (*P. cactorum*).

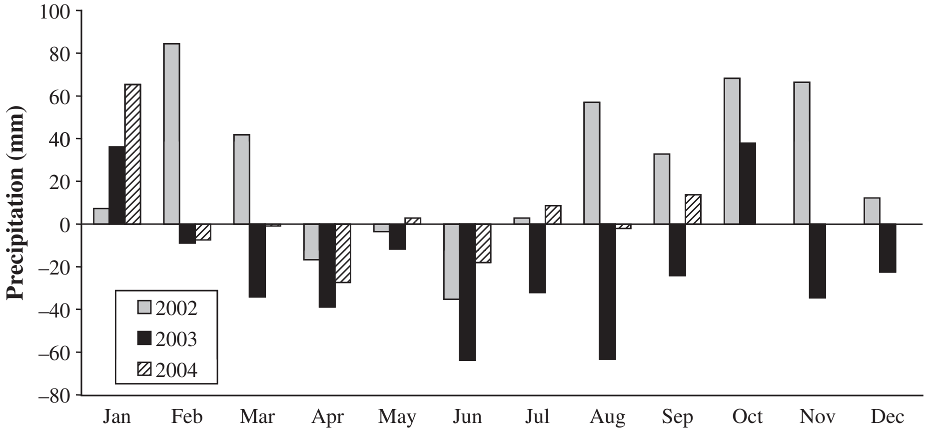

Fig. 8. Mean monthly precipitations of the years 2002–2004 at 22 Bavarian forest ecosystem monitoring stations expressed as deviations from the 30-years mean values of Bavaria (0 line) (graphic by Stephan Raspe, Bavarian State Institute of Forestry LWF).

Table 3. ***Phytophthora*** **infestation of beech plants in forest nurseries in Bavaria.**

		Phytophthora – species							
	Year	CAM	CIT	CAC	GON	MEG	QUE	PSEU	*P.* spp.
Nursery 1	2002	X	X		X	X			
Nursery 2[1]	2003	X							X
	2003	X		X					
Nursery 3[1]	2002	X							
	2003		X	X					
Nursery 4[1]	2003		X	X	X				
	2003			X			X		
Nursery 5	2001		X	X				X	
Nursery 6	2004	X	X	X		X			
Nursery 7	2001			X					
Nursery 8	2005		X	X					
Nursery 9	2007	X							
Infested nurseries (%)		56	67	78	11	11	11	11	11

CAM, *P. cambivora*; CIT, *P. citricola*; CAC, *P. cactorum*; GON, *P. gonapodyides*; MEG, *P. megasperma*; QUE, *P. quercina*; PSEU, *P. pseudosyringae*; *P.* spp., unknown heterothallic *Phytophthora* species.
[1]Two different fields investigated.

3.4 Chronology of primary and secondary damages, and association with climatic factors

In most stands, old lesions and fresh lesions were present. However, the majority of the *Phytophthora*-induced bark necroses could be dated back to the year 2002 (Fig. 4) which was characterised by extremely high precipitations in spring, late summer and autumn, often in form of heavy rain (Fig. 8 and Anonymous 2002, 2003). In spring 2003, *Phytophthora* spp. were breaking out from the margins of many 2002 lesions and spreading in the bark during the extremely dry summer and autumn of this year (Fig. 8 and Anonymous 2003). In 2004 and 2005 re-growth was observed from the margins of many necroses of the preceding year, while 1- and 2-year-old parts of these necroses were usually already covered by fruiting bodies of a series of secondary parasitic fungi; 3-year-old parts of these necroses were beginning to shed (Fig. 4). In all 47 stands with aerial *Phytophthora* cankers *Nectria coccinea* or its anamorph *Cylindrocarpon candidum* were regularly found as secondary invaders of dead bark. Other secondary invaders of aerial cankers were *Oudemansiella mucida*, and more rarely *Inonotus nodulosus*, *Polyporus squamosus*, *Fomes fomentarius* and *Phlebia radiata*. *Phytophthora* collar rot lesions were usually invaded by the wood-rotting fungi *Ustulina deusta* (38 stands) and *Armillaria mellea* s.l. (29 stands). *Nectria coccinea* and *C. candidum*, *Armillaria* sp. and *U. deusta* were often found 1–2 cm behind an active *Phytophthora* lesion front. Furthermore, in 2004 and 2005 predisposed trees in many stands were attacked by secondary bark beetles, in particular *Taphrorychus bicolor* and *Trypodendron domesticum*. Interestingly, *T. bicolor* was often found using *Phytophthora* infected bark for establishment of breeding galleries. In 2006 and 2007 fresh bark beetle attacks were only rarely found.

3.5 Infestation of nursery fields

The small-scale nursery survey demonstrated regular *Phytophthora* infestations of all 12 beech fields in nine forest nurseries in Bavaria. In total eight *Phytophthora* species were recovered. The most widespread were *P. cactorum* (eight fields in seven nurseries) followed by *P. citricola* (six nurseries) and *P. cambivora* (six fields in five nurseries) (Table 3). In nine fields more than one *Phytophthora* species were found; two fields were infested with four different species. In most fields root symptoms and scattered or patchy dieback and mortality of beech plants were visible, often concentrated in and around slight depressions. In two fields about 50% of the beech plants were already dead and the surviving plants had extensive root rot.

4 Discussion

4.1 Involvement of *Phytophthora* spp. in beech decline, site relations and interactions with climatic factors

This study demonstrated the occurrence of soil-borne *Phytophthora* species and typical disease symptoms at root, stem and crown level in most of the 134 beech stands investigated in Bavaria. *Phytophthora* infested sites covered the whole range of typical beech sites with pH ($CaCl_2$) values between 3.3 and 7.0 and gritty-loamy, sandy-loamy, loamy, silty and clayey soil texture. Interestingly, many of the stands were growing on sites that hitherto were not believed to favour *Phytophthora* infections as the soils had either a very low pH (podzolic cambisols or podzols from sandstones, mylonite or granite) or a good vertical (rendzinas or sandy-loamy cambisols) or lateral drainage (steep slopes) thus preventing any waterlogging. Since the majority of the stands were randomly selected, a regular infestation of most beech stands in Bavaria can be suggested.

Phytophthora citricola and *P. cambivora* had the widest distribution and in pathogenicity tests have proven to be most aggressive to root systems and stem bark of beech. In soil infestation tests *P. citricola* and *P. cambivora* caused almost complete destruction of the fine root systems of young beech plants and 70 to 90% mortality within four months (Jung et al. 2003b), while *P. pseudosyringae* was markedly less aggressive (40% root rot, no mortality). Similar results were reported by Fleischmann et al. (2002). In underbark inoculation tests with logs of mature beech trees, *P. cambivora* and *P. citricola* caused bark necroses with a mean lesion size of 140 cm^2 within 5 weeks (Brasier and Jung 2003). Stem inoculation tests with young beech trees revealed similar results. Here, *P. gonapodyides* and *Py. undulatum* were also shown being pathogenic to beech (Jung and Blaschke 1996).

Phytophthora cambivora and *P. citricola* are also widespread in declining oak stands across Europe (Jung et al. 1996, 2000; Hansen and Delatour 1999; Vettraino et al. 2002; Balci and Halmschlager 2003a,b; Jönsson et al. 2005), and were shown to be pathogenic to root systems and bark of *Q. robur* (Jung et al. 1996, 1999, 2002, 2003a,b; Brasier and Jung 2003). Moreover, *P. cambivora* is the major cause of the devastating Ink Disease of sweet chestnut (*Castanea sativa*) in Southern Europe (Vettraino et al. 2001, 2005), while *P. cactorum* and *P. citricola* are involved in the widespread decline and mortality of horse chestnuts (*Aesculus hippocastanum*; Werres et al. 1995; Jung and Blaschke 1996; Brasier and Jung 2006; Webber et al. 2006) and several *Acer* and *Tilia* species (Brasier and Jung 2006; Jung unpublished results). The high susceptibilty of the most common broadleaved tree species from Europe to *P. cambivora, P. cactorum* and *P. citricola* obviously indicates a lack of adaptation, which suggests a relatively recent introduction to Europe of these globally distributed pathogens (Erwin and Ribeiro 1996; Waterhouse and Waterston 1966b,c). For *P. citricola*, which was first described in 1927 from Citrus trees in Taiwan, the recent widespread finding of isolates in symptomless broadleaved forests in Nepal (Vannini et al. 2007), supports the hypothesis of a non-European origin. Also *P. cambivora* is believed to be introduced in Europe, results of an isozyme study of a worldwide collection of *P. cambivora* isolates suggesting an Australian origin (Oudemans and Coffey 1991). In order to definitely clarify the invasive status of *P. cambivora*, *P. citricola* and *P. cactorum* in Europe, molecular studies of the genetic variability of a global collection of isolates using AFLPs (Brasier et al. 1999; Cooke et al. 2005), nuclear gene-specific primers and mitochondrial gene-specific primers (Ioos et al. 2006) are urgently required. This has already been done for the aggressive oak-specific fine root pathogen *P. quercina*. A molecular study of the genetic variability of a European collection of isolates using AFLP markers demonstrated that *P. quercina* is unlikely to be native to Europe, and that it might have been introduced on several occasions (Cooke et al. 2005). This hypothesis was recently supported by the widespread finding of *P. quercina* in oak forests of the eastern USA (Schwingle et al. 2007).

The severe deteriorations of the crown structure of beech trees observed in most stands of this study and at the Forest Condition Monitoring Plots of the Bavarian State Forestry (Anonymous 2003, 2004, 2006a) are the result of a long-term degeneration of the crowns, which is indicative for long-term problems in the root system. Considering the high aggressiveness of *Phytophthora* species to roots and bark of beech, their regular association with declining beech trees as shown by this study and by investigations in north-western Germany and Belgium (Hartmann and Blank 1998; Hartmann et al. 2006; Schmitz et al. 2007), and the similarity of root and crown symptoms of declining beech and oak trees, it seems likely that *Phytophthora* species are strongly involved in the widespread chronic decline of beech as was shown for European oak decline (Brasier et al. 1993; Jung et al. 1996, 2000, 2003a; Gallego et al. 1999; Vettraino et al. 2002; Balci and Halmschlager 2003a,b; Jönsson et al. 2005). Likewise, an interaction between a progressive destruction of beech fine root systems with increasing age and decreasing regeneration capacity, climatic extremes, in particular heavy rain and droughts, site conditions, and secondary fungi and insect pests is suggested. In addition, on many sites several *Phytophthora* species, *i.e. P. cambivora, P. citricola, P. cactorum* and *P. gonapodyides* caused collar rot and aerial bark cankers in beech trees, leading to a rapid dieback of the trees. Moreover, these primary necroses are usually invaded by a series of secondary bark pathogens and wood rotting fungi, exacerbating the damages and predisposing the trees to storm damages. However, detailed studies on the fine root status of declining and healthy beech trees on a wide range of site conditions, and on the correlation between root and crown condition as done for European oak decline (Jung et al. 2000; Vettraino et al. 2002; Balci and Halmschlager 2003a) are required before final conclusions on the involvement of *Phytophthora* species in beech decline can be drawn.

In contrast to the slow and chronic decline of the preceding decade, beech stands across Bavaria experienced a sudden and strong increase of crown damages and mortality levels in 2003 and 2004 (Anonymous 2003, 2004). The sudden dieback coupled with the presence of *Phytophthora* collar rots and aerial cankers in supposedly non-conducive soils/sites, raises the question of the triggering factors. Since in most stands the majority of the *Phytophthora*-induced bark lesions could be dated back to the extremely wet year 2002, and extensive fine root losses were observed in most of the sampled stands the following hypothesis seems feasible: the extremely high precipitations in spring, late summer and autumn 2002 (Fig. 8) led to prolonged favourable conditions for the continuous production and spread of *Phytophthora* zoospores even on well-drained soils. As a consequence, multicyclic fine root infections (Erwin and Ribeiro 1996) in the wet soils caused an extensive destruction of the fine root systems of beech trees. Moreover, due to the low tolerance of beech to waterlogging (Ellenberg 1986; Kölling et al. 2005; Felbermeier and Mosandl 2006) and the high inoculum pressure *Phytophthora* species were able to invade suberised root and stem bark of mature trees on many sites. In 2003, the weakened and predisposed beech stands were faced with the strongest drought of the past 100 years (Fig. 8; Anonymous 2003, 2004). As a consequence, the necessary regeneration of the reduced fine root capacities was inhibited, and beech trees in most stands were suffering from extreme drought stress leading to premature leaf fall (Anonymous 2003), predisposing the trees to attacks by secondary fungi and bark beetles, and resulting in severe crown dieback and increased mortality levels.

The feasibility of this hypothesis is also supported by the observation made in this study and in the Forest Condition Monitoring (Anonymous 2003, 2004) that in stands with a high disease incidence of beech other hardwood species with higher tolerance to *Phytophthora* spp., *i.e.* Common ash (*Fraxinus excelsior* L.), and hornbeam (*Carpinus betulus* L.), were much less affected by the 2003 drought.

Interactions between *Phytophthora* infections, floodings and droughts are well known and generally accepted as triggers of epidemics (Duniway 1977, 1983; Brasier et al. 1993; Erwin and Ribeiro 1996; Brasier and Jung 2003; Jung et al. 2003a; Jung and Blaschke 2004). For oak decline in Central Europe and parts of Western and Northern Europe Jung et al. (1996, 2000) suggested that the epidemic extent and its long duration are due to long-term changes of climatic conditions in the second half of the 20th century, *i.e.* a continuous increase of mean winter temperatures, a seasonal shift of precipitation from summer into wintertime, and a tendency to heavy rain (Schönwiese et al. 1994; Rapp and Schönwiese 1995; Hennegriff et al. 2006). For many regions of Central Europe and in particular southern Germany current models of climate change are predicting a further intensification of these climatic trends (Anonymous 2006b,c; Hennegriff et al. 2006). Therefore, a proliferation of *Phytophthora* damages may be expected, increasing the instability and vulnerability of forest ecosystems dominated by beech and other tree species susceptible to *Phytophthora*, *i.e.* oak, alder, maple, lime, fir and pine species. Recently, a model was developed showing that due to climate change the distribution and local impact of *P. cinnamomi* and a range of other forest pathogens, *i.e. Biscogniauxia mediterranea*, *Cryphonectria parasitica*, *Melampsora* spp., and *Sphaeropsis sapinea* will significantly increase in France at the end of the 21st century (Desprez-Loustau et al. 2007). For *P. cinnamomi* a significant extension of the pathogen' s activity and distribution in wide parts of Europe was already shown by the model of Brasier and Scott (1994).

The reason because beech decline was observed markedly later than oak decline even though beech is more susceptible to *Phytophthora* root and bark infections than *Q. robur* (Jung and Blaschke 1996; Brasier and Jung 2003; Jung et al. 2003b), can be explained by interactions with site factors and defoliating insects. The main distribution of *Q. robur* is on sites that are prone to *Phytophthora* infections, *i.e.* riparian sites and sites with heavy soils and high or fluctuating water tables. In contrast, beech is less tolerant to heavy soils and high water tables and largely avoids these sites. Therefore, it is not surprising that *Phytophthora* forest damage started in oak stands on *Phythophthora*-conducive sites despite of the lower susceptibility of the dominant tree species. Furthermore, oak decline is a complex phenomenon. Results of several studies have clearly shown that dieback of oak stands requires the interaction of fine root losses by *Phytophthora*, insect defoliations and climatic extremes (Jung et al. 2000; Hartmann and Blank 2002; Thomas et al. 2002). Oaks are highly susceptible to various defoliating caterpillars and gradations and total stand defoliations occur periodically (Hartmann and Blank 1992, 2002; Thomas et al. 2002) while severe defoliations of beech stands are extremely rare (Kölling et al. 2005).

During the last five years root and collar rot of beech has been found in most parts of Europe and the eastern USA, and several *Phytophthora* species were recovered from symptomatic beech trees in Austria (*P. cambivora*, Cech and Jung 2005; *P. citricola* and *P. cactorum* Jung and Cech, unpublished), the Czech Republic (*P. citricola*, Jung and Jankowski, unpublished), Italy (*P. pseudosyringae*, Motta et al. 2003; Diana et al. 2006; *P. cactorum*, Jung, Vettraino and Vannini, unpublished; *P. cambivora*, Belisario et al. 2006), the Netherlands (*P. pseudosyringae*, Man In't Veld, pers. com.), Romania (*P. cambivora*, Jung and Chira, unpublished), Switzerland (*P. cactorum*, *P. citricola* and *P. syringae*, Jung, unpublished), Turkey (*P. cambivora*, Balci and Halmschlager 2003b), the United Kingdom (*P. cambivora*, *P. citricola*, *P. gonapodyides*, *P. ramorum* and *P. kernoviae* sp. nov., Brown and Brasier 2007; *P. pseudosyringae*, Denman et al. 2007), and the USA (*P. inflata,* Jung et al. 2005; Hudler et al. 2006). In north-western Germany *P. cambivora* and *P. pseudosyringae* are causing a widespread severe dieback of whole beech stands on both periodically waterlogged and base-rich sites (Hartmann and Blank 1998; Hartmann et al. 2006). Also, in Belgium, *P. cambivora* was recently recovered from bark cankers of beech trees in 19 out of 49 declining stands, and the involvement of *Phytophthora* infections in beech decline was also suggested (Schmitz et al. 2007). However, large-scale investigations on pathogen and disease distribution in these countries are required before general conclusions on the involvement of *Phytophthora* species in beech decline on a European scale can be drawn.

4.2 Aerial bark cankers and possible involvement of *Phytophthora* species in the complex of 'Beech Bark Disease'

In 40 stands, aerial bleeding cankers were found on mature beech trees that were similar to those described from 'Beech Bark Disease (BBD)'. In Europe, BBD is generally considered as a complex interaction of predisposing drought stress, subsequent colonisation of the bark by the scale insect *Cryptococcus fagisuga*, infection of the colonised bark by the weak parasite *Nectria coccinea* and, finally, invasion of the stem by wood decay fungi (Parker 1974; Lonsdale and Wainhouse 1987; Butin 1996). However, there has been much controversy over the relative importance of scale insects, *N. coccinea* and abiotic factors in disease development (Lonsdale and Wainhouse 1987). Surprisingly, in 31 of the 34 Bavarian stands where bleeding cankers had been examined in detail, *Phytophthora* species could be isolated from actively growing margins of the necroses. In most cases *N. coccinea* or its anamorph *C. candidum* were following the active lesion front at a distance of a few centimeters. In most stands no scale insects could be found. This is consistent with observations of Lonsdale (1980) who reported that most cases of BBD affecting mature stands in the United Kingdom occurred in the absence of significant scale populations. The data from the current study support the role played by *Phytophthora* species in the complex aetiology of BBD in Europe, maybe as the primary pathogen in mature stands. This may have been overseen in the past simply because specific methods for the detection of *Phytophthora* spp. were not used. This is supported by the finding of PAUCKE (1966) who observed increased incidences of BBD in Eastern German beech forests associated with increasing soil moisture, and by the observations of higher disease frequencies in depressions (WOOD and NIMMO 1962).

Three of the four *Phytophthora* species recovered from aerial cankers, *i.e. P. citricola, P. cambivora* and *P. gonapodyides*, are not able to produce caducous sporangia and thus the mechanism which enables these pathogens to reach 20 m stem height is unknown. Recently, however, BROWN and BRASIER (2007) demonstrated the presence of both airborne and soilborne *Phytophthora* species including *P. citricola, P. cambivora* and *P. gonapodyides* in non-symptomatic xylem tissue between isolated aerial cankers suggesting that *Phytophthora* species are able to spread within trees via xylem vessels. The occurrence of sequential multiple aerial cankers following the fibre course in many Bavarian stands strongly supports this hypothesis. However, it cannot be excluded that animal vectors may also be involved. In many stands of this study several species of snails, and in particular the vineyard snail (*Helix pomatia*), were frequently observed sucking at the exudates from *Phytophthora* cankers. Microscopical findings of typical oospores in fresh exudates from *P. citricola* cankers on beech in two Bavarian stands (data not shown) suggest that snails might act as vectors of *Phytophthora*. This is in accordance with results of EL-HAMALAWI and MENGE (1996) who found oospores and sporangia of *P. citricola* in the exudates from aerial cankers of avocado in Californian plantations, and proved experimentally that these structures are taken up by snails and transported up-stem where new cankers were formed. Moreover, the bark beetle *T. bicolor* was often observed to establish breeding galleries in fresh *Phytophthora* lesions on beech, and it seems feasible that this parasite is able to pass *Phytophthora* onto healthy trees while establishing sister broods. The feasibility of this pathway was shown for the sudden death of cocoa in Papua New Guinea caused by *Phytophthora palmivora* cankers (PRIOR 1986).

4.3 Infestation of nurseries

Fagus sylvatica is the most important tree species in new silvicultural concepts aiming on the replacement of non-natural pure conifer stands by mixed forests, in order to increase the ability of the ecosystems to withstand the threats by predicted climatic changes (AMMER et al. 2005; KÖLLING et al. 2005; FRITZ 2006). Hence, there is an increasing demand for nursery-grown beech plants, and the regular infestations with multiple *Phytophthora* species of beech fields in Bavarian nurseries are awkward. The majority of the beech fields were infested with the same *Phytophthora* species responsible for the widespread dieback of mature beech stands, *i.e. P. cactorum*, *P. cambivora* and *P. citricola*. These findings confirmed the results of surveys of nursery fields of beech and other tree species in northern Germany, and nursery fields of alder in Bavaria and eastern Germany (THEMANN et al. 2002; JUNG and BLASCHKE 2004; HARTMANN et al. 2006; SCHUMACHER et al. 2006). Also in Poland nursery fields of beech and other tree species were regularly found to be infested with several *Phytophthora* species (ORLIKOWSKI et al. 2004, 2006). The environmental risk of the presence of multiple *Phytophthora* species in most nursery fields is evident. The impact of a spread of *Phytophthora* species into beech forests via infested nursery stock was investigated by HARTMANN et al. (2006) in five afforestations on former agricultural land in northern Germany. Eight to 15 years after planting more than 70% of the beech trees were suffering from root and collar rot caused by *P. cambivora* and high mortality occurred. The devastating impact of a large-scale use of infested nursery stock on natural ecosystems was demonstrated by the root and collar rot epidemic of alders in Europe caused by *P. alni* and its subspecies (Gibbs et al. 2003; Jung and Blaschke 2004).

In conclusion, the results of this study demonstrate that (1) *Phytophthora* species are regularly associated with beech decline, (2) the succession of excessive rainfalls and droughts is triggering the disease, and (3) *Phytophthora* species may be involved in the complex of 'Beech Bark Disease'. The high susceptibility of the most competitive tree species of Central Europe to non-native, well-established *Phytophthora* species and the large-scale decline and dieback of beech stands are a serious threat to European forestry and arboriculture. The widespread *Phytophthora* infestations of nursery stock are likely to undermine any current and future silvicultural projects aiming on the replacement of pure conifer stands by beech dominated mixed stands. Therefore, management concepts for the production of non-infested nursery stock, the silvicultural treatment of declining mature beech stands and the control of the disease in the field are urgently required at a European scale.

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