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Phytophthora root and collar rot of alders in Bavaria: distribution, modes of spread and possible management strategies

T. Jung*† and M. Blaschke

Bavarian State Institute of Forestry (LWF), Section Forest Ecology and Forest Protection, Am Hochanger 11, D-85354 Freising, Germany

A survey of symptoms of phytophthora root and collar rot of common (*Alnus glutinosa*) and grey alder (*A. incana*) in riparian and forest stands in Bavaria was conducted by the Bavarian State Forestry and river authorities. Symptoms were seen in 1041 out of 3247 forest alder stands. The majority of the affected stands (80·9%) were less than 21 years old; 46% of these young stands were growing on nonflooded sites and 92% had been planted. The riparian survey showed that symptoms were widespread along more than 50% of the river systems. Along some rivers the disease incidence exceeded 50%. The 'alder *Phytophthora*' was recovered from 166 of 185 riparian and forest alder stands with symptoms. In 58 of the 60 rivers and streams investigated in detail, the source of inoculum was traced back to infested young alder plantations growing on the river banks or on forest sites that drain into the rivers. Once introduced to a river system, the 'alder *Phytophthora*' infects alders downstream. Baiting tests showed that the 'alder *Phytophthora*' was present in rootstocks of alders from three out of four nurseries which regularly bought in alder plants for re-sale, but not in rootstocks from four nurseries that grew their own alders from seed. In addition, the infected nurseries used water from infested water courses for irrigation. The Bavarian State Ministry for Agriculture and Forestry has developed a code of practice for producing healthy alder plants in forest nurseries. This includes a 3-year fallow period between bare-rooted alder crops because of poor survival of the 'alder *Phytophthora*' in soil.

Keywords: *Alnus*, nursery, pathway, *Phytophthora*, plantation, riparian

Introduction

The genus *Alnus* is represented in Europe by four species, most of them characterized by their ability to rapidly colonize abandoned or bare land and tolerate high groundwater tables and periodic flooding (Gibbs *et al*., 2003). A common feature of the genus is its ability to ameliorate soil due to a root symbiosis with actinomycetes (*Franckia*) which are able to fix atmospheric nitrogen.

Alnus glutinosa (common alder) is the most widespread species of alder occurring across Europe from sea level to 1800 m. It grows on wet and clay soils, colonizing riverbanks or swampy areas. It has high conservation value, and is widely used in reforestation for consolidating riverbanks and stabilizing slopes. It produces valuable timber. *Alnus incana* (grey alder) is a central to eastern European species; in the south it grows mainly in mountain areas. As it is a root sprout pioneer that tolerates both dry conditions and flooding, *A. incana* is very important for improving the stability of slopes and riverbanks. Green alder (*A. viridis*) is a common shrub in the Alps, colonizing steep clayey slopes and the banks of mountain streams. *Alnus cordata* (Italian alder) is endemic to southern Italy, growing in nonriparian pure and mixed forests in the Apennine mountains and in plantations.

In 1993, a previously unknown lethal disease of *A. glutinosa* was recorded in southern Britain. It occurred mainly along riverbanks, but also in orchard shelter belts and woodland plantations (Gibbs, 1995). In the following years, the disease was also found on *A. incana* and *A. cordata*, and in Germany, France, Ireland, Sweden, the Netherlands, Belgium, Austria, Hungary, Estonia, Lithuania and Italy (Hartmann, 1995; Mathieu, 1996; Cech, 1997; Werres, 1998; Schmidt *et al*., 1998; Gibbs *et al*., 1999, 2003; Olsson, 1999; Jung *et al*., 2000b; Streito & Gibbs, 2000; Szabó *et al*., 2000; Werres *et al*., 2001; Santini *et al*., 2001, 2003; Streito *et al*., 2002a; Brasier & Jung, 2003; Nagy *et al*., 2003). Affected trees showed symptoms typical of phytophthora root and collar rot: abnormally small, sparse and often yellowish foliage, a dieback of the crown, early and often excessive fructification

*To whom correspondence should be addressed.

†E-mail: jun@lwf.uni-muenchen.de

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with unusually small cones, tongue-shaped necroses of the inner bark and the cambium which extended up to 3 m from the stem base with tarry or rusty spots on the surface of the bark (Gibbs *et al*., 1999, 2003; Jung & Blaschke, 2001). The causal organism was an interspecific hybrid of *P. cambivora* and an unknown *Phytophthora* related to *P. fragariae* (Brasier *et al*., 1995, 1999; Brasier, 2003). This 'alder *Phytophthora*' is morphologically similar to *P. cambivora*, but can be distinguished by its homothallism, high level of zygotic abortion, distorted oogonia and lower cardinal temperatures for growth. Several variants are known which differ in their chromosome numbers, oogonial and antheridial morphology, cultural stability and colony morphology. The viability of oospores differs significantly between the variants, and germination has never been observed (Delcan & Brasier, 2001).

In pathogenicity tests, both the standard form and the Dutch variant were highly aggressive pathogens of common alder, whereas the Swedish, German and UK variants and *P. cambivora* were only weakly aggressive (Brasier & Kirk, 2001). The standard form, the Dutch and the Swedish variants were nonpathogenic to a series of other tree species, indicating that the alder *Phytophthora* variants are relatively host-specific (Brasier & Kirk, 2001; Santini *et al*., 2003).

In Bavaria, many alder plantations have been established since the early 1980s. This is a result of governmental and EU subsidies that encourage the afforestation of former agricultural land, the replacement of spruce stands on wet forest sites following devastating storm damage in January 1990, and stabilization of steep slopes with degraded forest stands and banks of white-water rivers in the Alps.

Results of a 1-year study indicated that the phytophthora disease of alders was widespread in Bavaria in both riparian ecosystems and forest plantations (Jung *et al*., 2000b). Therefore, the project was extended for another 3·5 years in order to assess the distribution of the disease in detail, to investigate modes of disease spread and to develop a management plan for the disease.

This paper describes the results of an extensive field survey of alders in both riparian and forest stands in Bavaria, and a small survey of forest nurseries to determine whether this disease is being spread on infected nursery stock. The ability of the 'alder *Phytophthora*' to survive in nurseries in the absence of a host was also investigated. Experimental work on modes of spread, infection and survival in the field is reported, as are the results of coppicing experiments to see whether this improves tree health.

Materials and methods

Field sampling and isolation procedures

The inner bark of active lesions was orange-brown and mottled. Old, inactive lesions were a uniform dark brown. Bark samples, including the cambium, were usually taken from the upper 20 cm of active lesions, placed in distilled water and transported to the laboratory in cool boxes. Over 2–5 days the water was replaced four times per day in order to remove excess polyphenols. 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, 2000a) (~150 pieces per tree in seven to eight Petri dishes). Some pieces of tissue from old inactive lesions were shredded, flooded with distilled water and baited with oak leaflets (as described below). The water was replaced daily in order to remove excess polyphenols and decrease bacterial populations.

Isolations from soil samples were carried out using 2- to 7-day-old leaflets of *Quercus robur* seedlings as baits floated over flooded soil (Jung, 1998; Jung *et al*., 1999, 2002). Infected brownish leaflets, which normally appeared after 3–7 days, 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 for *Phytophthora*-like hyphae.

Morphological and physiological characters and ITS DNA sequences of 216 isolates of the 'alder *Phytophthora*' were investigated in order to assign them to either the standard form or one of the variant types of the hybrid complex (Brasier *et al*., 1999; Brasier, 2003).

Field surveys

The distribution and extent of symptoms of phytophthora root and collar rot of alders in riparian and forest stands, i.e. bark lesions and crown symptoms, were surveyed between August 2001 and May 2002. This symptom survey was conducted by trained staff from local river and forest authorities. A disease leaflet was developed to facilitate the identification of disease symptoms in the field (Jung & Blaschke, 2001; http://www.lwf.bayern.de/lwfmerkblatt/phyto-aorg.pdf).

In order to validate this symptom survey, 300 forest alder stands, 200 of them recorded as healthy, were randomly selected and further investigated. The symptom survey of the river authorities was also validated, and most disease records along rivers and streams further investigated. Presence of *Phytophthora* spp. was confirmed by isolations from necrotic alder bark.

A map illustrating the distribution of disease symptoms along main rivers and streams in Bavaria was constructed using OCAD 5·05 software (Steinegger, Baar, Switzerland). The data of the forest survey were recorded and several analyses, e.g. age-class structure and site relations of diseased stands, carried out using Microsoft ACCESS 2000. A map showing the number of diseased forest stands per 12·5 km grid square was constructed using SoftCol 2·13 software (Gerhard Strauß, Biberach, Germany).

Distribution of the disease within catchments

As it is still not known how the pathogen was introduced into a river system, 60 rivers and streams throughout Bavaria were investigated for the probable primary source of inoculum. The water courses were surveyed for the most upstream diseased alders. Tributaries and forest stands in the catchments were surveyed for affected alder plantations. In addition, the catchments of 25 small streams where phytophthora root and collar rot of alders had not been recorded were surveyed for the presence of infested alder plantations. Using a contingency table combined with Fisher's exact test (program Prism 3 for Windows 95; GraphPad, San Diego, CA, USA), the relative risk of developing phytophthora root and collar rot symptoms was calculated for riparian alder stands with infested riparian or forest alder plantations in their catchment.

Nursery surveys

Alder fields were surveyed in three forest nurseries between January and March 2000 and in five additional forest nurseries between January and March 2001. In each nursery, 10–20 alder plants were selected at random and harvested together with adhering soil. The alder plants were potted in plastic buckets, flooded for 1 week and baited with oak leaflets in a glasshouse maintained at 16–20°C and 60% relative humidity (RH). Four weeks later, after a second flooding and baiting procedure, the root systems were harvested, washed and examined for root necrosis.

The survival time of the 'alder *Phytophthora*' in nursery soil in the absence of alders was determined at two nurseries, which were naturally infested in February 2000. One field was left unplanted for 2 years, while the other one was planted to spruce seedlings. In March 2002, 10 L soil samples from the upper 20 cm were randomly taken from the unplanted field, and 10 spruce seedlings were sampled at random from the spruce field. Both sets of samples were baited with oak leaflets.

Infection through unwounded bark

Pieces of necrotic bark from infected riparian alders were placed on the soil of 30 × 40 × 30 cm boxes containing 10–12, 3-year-old *A. glutinosa* seedlings. Controls received uninfected bark pieces. The boxes were incubated in a glasshouse at 18–20°C and 60% RH. A regime of 1-week flooding and 3 weeks of free drainage was applied for 6 months. After this time, the seedlings were assessed for the presence of disease symptoms, and reisolations from bark lesions were made onto PARPNH agar.

Infection courts in natural and planted trees

Alders with active, fresh lesions at the stem base were selected in both natural riparian stands and forest plantations, to determine the primary infection court. Root systems of these trees were partly or completely excavated and, if necessary, the outer bark of roots and the collar removed. Isolations from necrotic tissues were made to confirm the presence of the 'alder *Phytophthora*'.

Isolations from soil

Five alders with typical crown but absence of collar rot symptoms were harvested from two 5- to 6-year-old plantations together with their rhizosphere soil, and potted and baited with oak leaflets.

In order to test the ability of the pathogen to establish and survive in the soil, isolations were carried out in four riparian stands from rhizosphere soil and necrotic bark of three to five alders per stand.

Effect of coppicing on tree health

A coppice experiment was initiated in late winter 2001 in Bavaria. Three diseased plantations were chosen, two of them on nonflooded sites with different water relations and one on a periodically flooded site with absence of the disease upstream. In each stand, disease parameters such as necrosis length, proportion of girth at the collar with necrotic bark, and decline status of the crown (1 = healthy, 0 = declining, indicated by high transparency, stunted growth or even dieback) were recorded for at least 150 *A. glutinosa* trees before they were coppiced in February 2001. In June and August 2001, weeds were controlled mechanically. The number and vigour of the shoots per stool were recorded in July 2001 and 2002. Any correlation between the sprouting rate after coppicing and the prior proportion of necrotic stem girth at the collar and the prior vitality of the crowns was estimated using the nonparametric Spearman correlation (program Prism 3; Graph Pad).

Results

Recovery of *Phytophthora* species from necrotic alder bark

Over the 3 years of the experiment, the 'alder *Phytophthora*' was isolated from necrotic bark with isolation frequencies of < 30% during winter and > 80% in the other seasons. In all, 373 isolates were recovered from 104 riparian stands growing along 85 rivers and streams in all regions of Bavaria, from 13 alder carrs, swamps and reed belts of lakes, and from 50 forest plantations on nonflooded sites (Table 1). *Phytophthora citricola*, *P. gonapodyides* and *P. pseudosyringae* sp. nov. (Jung *et al.*, 2003) were also recovered. In some cases, typical rhizomorphs and mycelium of *Armillaria* sp. were found at a short distance

Table 1 Isolation results from necrotic bark of alders growing in riparian and forest stands in Bavaria

Stand types	No. of stands (rivers) sampled	No. of stands (rivers) with: ALN	CIT	GON	PSEU
Riparian stands	115 (89)	104 (85)	4 (4)	2 (2)	0
Alder carrs, swamps and reed belts of lakes	13	13	1	0	0
Forest plantations	58	50	1	0	2
Total	185	166	6	2	2

ALN, 'alder *Phytophthora*'; CIT, *P. citricola*; GON, *P. gonapodyides*; PSEU, *Phytophthora pseudosyringae* sp. nov. (Jung *et al.*, 2003).

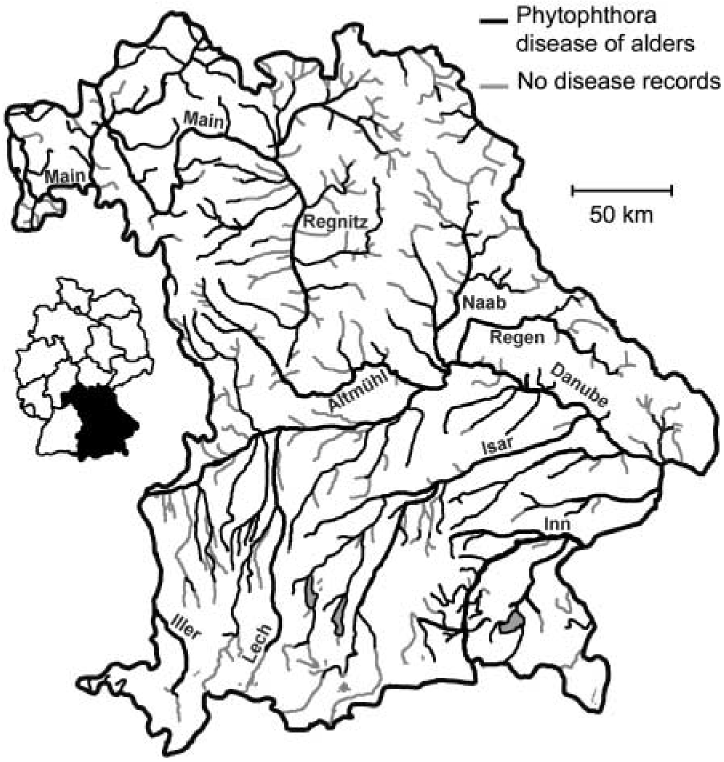

Figure 1 Distribution of phytophthora root and collar rot of alders along main rivers and streams in Bavaria. The small map on the left shows the location of Bavaria within Germany.

behind the active margins of the necroses from which the 'alder *Phytophthora*' was isolated.

Morphological and physiological characters and ITS-DNA sequences (Brasier *et al*., 1995, 1999; Brasier, 2003) showed that 62·5% of 216 investigated Bavarian 'alder *Phytophthora*' isolates belonged to the aggressive standard form; the remainder were variant types. Most (56%) of the latter belonged to the Swedish variant, but the German variant, several previously unknown unique types and putative backcross products with the parental species *P. cambivora* were also found (T. Jung, C. M. Brasier & S. A. Kirk, unpublished data). In some cases two different types were isolated from the same bark lesion. The Swedish and the German variant were usually isolated from laterally restricted and sometimes stripe canker-like necroses.

Field survey: riparian stands

The detailed symptom survey along rivers and streams in Bavaria was completed in November 2001. Most disease records from the main rivers came from river authorities, whereas small rivers and streams were surveyed by the State Forestry. The results show that the disease is present in riparian stands of *A. glutinosa* and *A. incana* growing along the majority of the main river systems representing more than 4500 river kilometres (Fig. 1). Since most of the main rivers and streams from which the disease was not recorded were not surveyed, the disease may be more prevalent. Affected alder stands were also found along hundreds of small streams and ditches. Along some rivers where disease records go back to the mid-1980s, disease incidence exceeded 50%. Isolations were attempted from necrotic alder bark from 115 riparian stands, and *Phytophthora* spp. were recovered from 110 stands (Table 1).

Disease incidences above 50% were found in alders growing in permanent contact with river water and in areas that retain flood water for a long period, i.e. flood plains, ox-bows and alder carrs. High incidence also occurred in areas subject to intermittent flooding, such as upstream of bridges with narrow apertures, and in alder stands growing on the banks and in the reed belts of lakes with infested tributaries, such as the Chiemsee, Simssee, Starnberger See and Ammersee.

There were also higher amounts of disease in *A. glutinosa* stands growing along lowland rivers as compared with *A. incana* stands growing along prealpine white-water rivers, but in mixed stands both species were equally affected.

There was no association of disease incidence with pH, nitrate or orthophosphate concentrations of river water (from < 1 to < 10 mg N L^{-1} and from $< 0{\cdot}02$ to $< 0{\cdot}4$ mg P L^{-1}).

Field survey: forest stands

The local forest officers of the Bavarian State Forestry conducted a symptom survey of 3247 forest alder stands covering an area of 3664 ha; 74·3% of these stands were younger than 21 years. Most of these young stands were either replanted conifer stands that had been windthrown in January 1990, or plantations on former agricultural

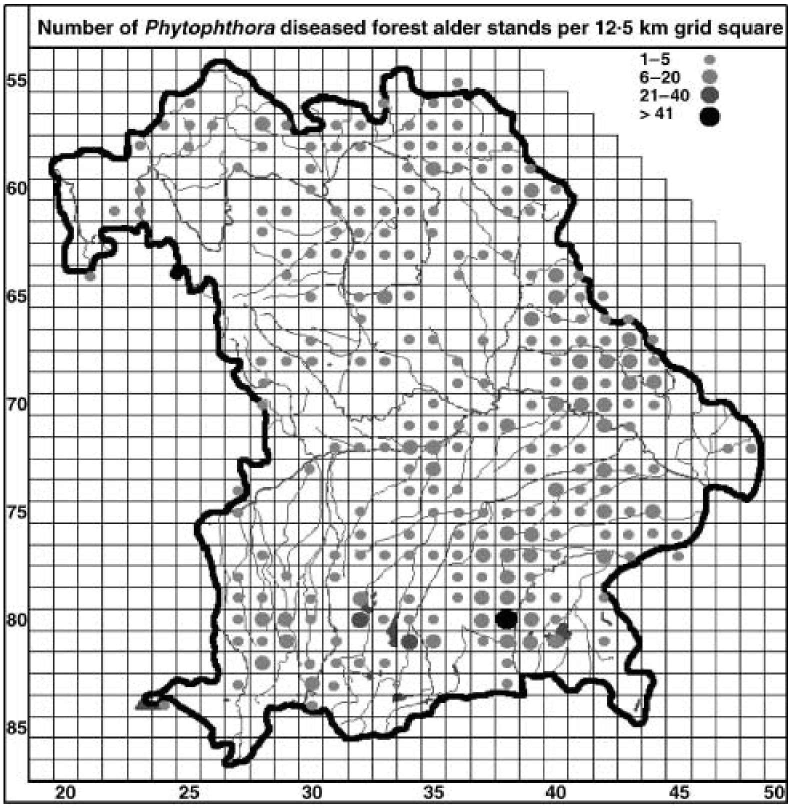

Figure 2 Distribution of forest alder stands suffering from phytophthora root and collar rot in Bavaria.

land. Symptoms of phytophthora root and collar rot of alders were recorded from 1041 stands (32·1%) covering 1655 ha (45·2%).

TJ undertook a validation of the symptom survey that had been conducted by field staff. This validation showed typical symptoms of phytophthora root and collar rot in 89 out of 100 stands that were recorded as diseased; however, 112 out of 200 stands that had been recorded as healthy also had trees with symptoms in them.

Symptoms were present in forest stands throughout Bavaria with the highest incidence in *A. glutinosa* stands in the prealpine moraine belt in southern Bavaria and the loess region flanking to the north of it (Fig. 2). *Phytophthora* spp. were recovered from the necrotic bark of alders in 53 out of 58 stands (Table 1).

The majority of disease-affected stands were 6–15 years old (Fig. 3a). The highest percentage of diseased stands was in the 16- to 20-year-old age class (41%) followed by the 6- to 15-year-old age class (36%). The stands with the highest proportion of affected trees, in some cases resulting in the death of the whole stand, were also in these age classes. Only 16% of the 1- to 5-year-old plantations showed collar rot symptoms.

In 455 of the 1041 diseased alder stands, only individual trees or small groups of trees were affected. Lower numbers of stands had a higher incidence of symptoms (Fig. 3b). The proportion of trees with symptoms was higher on wet or flooded sites, while on nonflooded sites collar rot symptoms usually appeared first on trees growing in wetter microsites. Of the 842 affected forest stands < 21 years old, 395 were growing on nonflooded sites, and the majority of them (91·5%) had been planted.

The occurrence of phytophthora root and collar rot in alder stands older than 20 years showed a strong association with flooding. The majority (121) of the 154 diseased mature stands occurred on the flood plains of rivers or streams. Eight of the 33 mature stands on nonflooded sites were receiving run-off water from infested young plantations located uphill. The other 25 mature stands with trees with symptoms on nonflooded sites were isolated from infested plantations, and the symptoms recorded by the local foresters were atypical of phytophthora root and collar rot. Further investigations of selected stands showed that the 'alder *Phytophthora*' could not be isolated and most of these stands were dying as a result of senescence or the deaths were associated with other pathogens (e.g. *Inonotus radiatus* and *Armillaria* sp.).

Distribution within catchments

No alder plantations with symptoms were found in the catchments of 25 streams with healthy riparian alder stands. However, in 58 of the 60 river systems with diseased riparian stands, there were affected plantations that had been established within the last 20 years on the river banks or on forest sites that drain into the rivers. Riparian alder stands were significantly more likely to develop phytophthora root and collar rot symptoms if infested alder plantations were present in their catchments (Table 2).

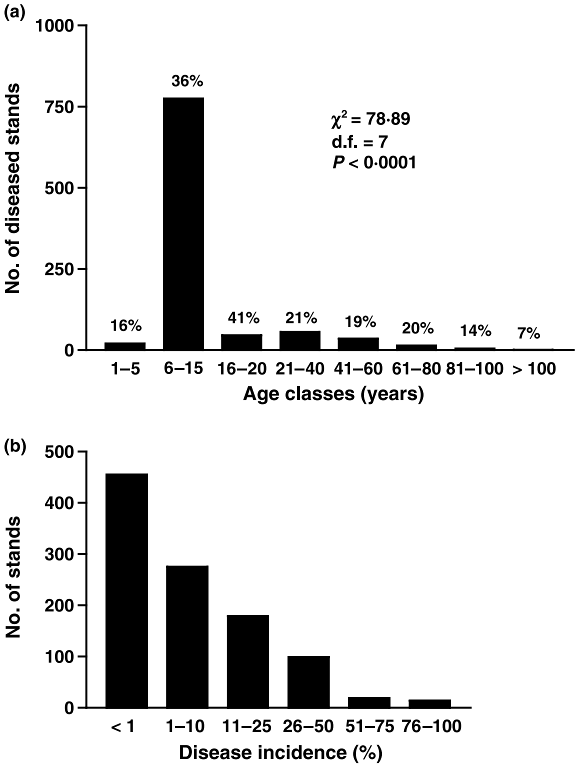

Figure 3 Forest alder stands with phytophthora root and collar rot in Bavaria. (a) Number and percentage of diseased stands in different age classes; (b) number of stands < 21 years old in different disease incidence classes.

Table 2 Contingency table: occurrence of infested plantation in catchment area/phytophthora root and collar rot of riparian alders

Infested plantation in catchment area	Number of rivers with diseased alders	Number of rivers with healthy alders	Total
Present	58	0	58
Absent	2	25	27
Total	60	25	85

Relative risk = 13·5; 95% confidence interval, 3·556–51·24; Fisher's exact test, $P < 0{\cdot}0001$.

In the forest district 'Rotter Forst' near Rosenheim, 73 alder plantations were planted on wet gley soils in the early 1990s after storm damage. Although the alder plants came from several nurseries, typical disease symptoms were found in all plantations, in 14 mature stands that receive drainage water from these plantations, and along most drainage ditches and brooks. Several variants of the 'alder *Phytophthora*' were recovered from 14 plantations and two mature stands, from naturally regenerated alders growing in these plantations, and from riparian alders growing along drainage ditches, brooks and rivers inside and outside of the forest.

Via their tributaries, most of the large Bavarian rivers, e.g. the Danube, Main, Lech, Isar and Inn (Fig. 1), are receiving run-off water from more than 100 infested alder plantations.

In the two *Phytophthora*-infested rivers without affected plantations in their catchment, diseased natural alder stands were found downstream and on the banks of the raceways of commercial fish farms. No alders with root and collar rot were present upstream.

Nursery surveys

The 'alder *Phytophthora*' was baited from rootstocks of alder plants from three out of four Bavarian nurseries which regularly bought alder plants from intensive, large-scale commercial nurseries for re-sale, but not from rootstocks from four nurseries that grew their own alder plants from seeds (Table 3). At least two of the three disease-affected nurseries used irrigation water taken from rivers with diseased alder stands upstream from the point of extraction.

All alder plants from these nurseries appeared healthy and had no visible lesions on their roots and collars when coming from the nurseries. However, on many plants, 2 weeks after the second flooding period, the 'alder *Phytophthora*' was isolated from necrotic fine roots and bark lesions on suberized roots.

Other *Phytophthora* species that were baited from the flooded root stocks included *P. cambivora*, *P. cactorum*, *P. citricola*, *P. gonapodyides*, *P. megasperma* and *P. quercina* (Table 3). From several individual alder plants, the 'alder *Phytophthora*', *P. cambivora* and three other *Phytophthora* species were recovered.

At two nurseries, former alder fields that were naturally infested by the 'alder *Phytophthora*' in February 2000 and either left unplanted or planted to spruce and beech, were re-investigated in March 2002. However, the pathogen was not recovered from either field (Table 3).

The spruce plants showed patchy dieback and chlorosis, and about 50% of the beech plants were already dead and the remaining living plants had extensive root rot. Baiting tests from rhizosphere soil as well as direct isolations from necrotic roots revealed various *Phytophthora* species, including *P. cambivora* and *P. citricola* (Table 3).

Infection courts

Detailed morphological investigations of the root system and the collar of many infected alder plants, old growth and coppice shoots from young plantations and of riparian natural alders with fresh lesions revealed different locations of the infection courts. In riparian, naturally regenerated alders the infection usually started from lenticels or unsuberized adventitious roots produced at the collar or, less frequently, at the surface of exposed large roots, and extended towards the root collar. The distal part of the root system was healthy. In some cases, isolated bark lesions which yielded the 'alder *Phytophthora*' were found 50–100 cm above ground level, indicating infection during flooding.

In young, planted alders on nonriparian sites, at least a part of the root system beyond the collar rot was usually dead and often individual tap roots could be identified

Table 3 Isolation results from nursery-grown plants in Bavaria

Nursery no.	Tree species[a]	*Phytophthora* species[b] ALN	ALN × CAM	CAM	MEG	CAC	CIT	GON	QUE	CHLA
Nurseries buying in alder plants for re-sale										
1	GLU	X[c]	–	–	–	–	–	–	–	–
2	GLU	–	X	X	X	–	X	X	–	X
	INC	X[d]	–	X	–	–	X	X	–	X
	VIR	–	–	X	–	–	X	–	–	–
3	GLU	–	–	–	X	–	X	X	–	X
4	GLU	X[c]	–	X	–	–	–	X	–	X
Nurseries growing alder plants from seeds										
5	GLU	–	–	–	X	X	X	–	–	–
6	GLU	–	–	–	–	–	–	–	X	–
7	GLU	–	–	X	X	X	X	–	–	–
8	GLU	–	–	–	–	X	X	–	–	–
Nursery fields that were stocked with alder plants and infested by the 'alder Phytophthora' in 2000 tested again in 2002										
1	Unstocked	–	–	–	–	–	–	–	–	–
2	PIC	–	–	X	X	–	X	X	–	–
	FAG			X			X	X		

[a]GLU, *Alnus glutinosa*; INC, *A. incana*; VIR, *A. viridis*; PIC, *Picea abies*; FAG, *Fagus sylvatica*.
[b]ALN, 'alder *Phytophthora*'; ALD × CAM, putative backcrosses between ALN and *P. cambivora* (according to ITS data); CAM, *P. cambivora*; MEG, *P. megasperma*; CAC, *P. cactorum*; CIT, *P. citricola*; GON, *P. gonapodyides*; QUE, *P. quercina*; CHLA, 'P. taxon Pgchlamydo', an as yet undescribed chlamydospore-forming species close to *P. gonapodyides* (Brasier & Jung; 2003). X, isolated; –, not isolated.
[c]Standard form.
[d]Standard form and Swedish variant.

through which the 'alder *Phytophthora*' invaded the collar. However, old growth and shoots of coppiced alder stools growing in these plantations, as well as some of the planted alders, were infected at the collar.

Direct spread of zoospores from infected alder bark and infection of the bark of the collar or bare roots of other alders were demonstrated by a pathogenicity test where small pieces of necrotic bark from infected riparian alders were placed on the soil of boxes containing 3-year-old *A. glutinosa* seedlings. After 6 months, infected and dead alders with collar rot and isolated bark lesions above the collar were present in all infested boxes, and the pathogen was recovered from all of them. The infected alders were smaller than the control plants and showed chlorotic and dwarfed foliage. Sporangia were observed on flooded necrotic bark pieces from which *Phytophthora* was baited.

Isolations from soil

Five alders with typical crown symptoms, but no collar rot were harvested from two 5- to 6-year-old plantations. The 'alder *Phytophthora*' was isolated from the rhizosphere of four trees, and *P. gonapodyides* was recovered from two alders.

In all four stands, the isolation tests from necrotic bark always yielded the standard form of the 'alder *Phytophthora*', whereas the baiting tests with the soil samples showed a different picture. *Phytophthora citricola* was isolated from 14 soil samples in three stands, whereas only three soil samples from two stands yielded the 'alder *Phytophthora*' (Table 4). In one stand, *P. cactorum* was isolated, while *P. gonapodyides* was isolated from another.

Effect of coppicing on tree health

The two plantations near Wolfratshausen were established in 1995 with the same nursery stock. One plantation was on a wet site with a periodically high water table at the bottom of a hill, and the other was on a moist site on an upper slope. Six years after planting, the proportion of diseased and dead alders was twice as high at the wet site (Table 5). There was a highly significant negative correlation between the proportion of necrotic stem girth and crown health on all sites (Table 5), even though about 30% of alders with > 50% necrotic stem girth still had healthy-looking crowns (Table 6).

In the plantation on the moist site with the lowest disease incidence before coppicing, 72·9% of the alders showed live re-growth 3 months after coppicing. Sprouting rates in the plantations on the wet site with high disease incidence and mortality rate and on the riparian site with high mortality rate before coppicing were much lower (30·6 and 28·3%, respectively) (Table 5).

In all three plantations, wilting and mortality of shoots during hot periods in summer 2001 and re-infections of shoots from the root system further decreased the proportion of stools with living sprouts until summer 2002 (Table 5).

The sprouting rate in all three forest plantations was negatively correlated with the proportion of necrotic stem

Table 4 Comparison of *Phytophthora* populations in necrotic bark and rhizosphere soil of common alders in four riparian stands

River	No. of alders	No. of alders with:[a] ALN Bark	ALN Soil	CIT Bark	CIT Soil	CAC Bark	CAC Soil	GON Bark	GON Soil
Glonn[b]	3	3	1	0	0	0	0	0	0
Große Vils[b]	5	5	0	0	5	0	0	0	0
Zillhamer Ache[c]	5	5	2	0	4	0	0	0	3
Abens[d]	5	5	0	0	5	0	3	0	0
Total	18	18	3	0	14	0	3	0	3

[a]ALN, 'alder *Phytophthora*'; CIT, *P. citricola*; CAC, *P. cactorum*; GON, *P. gonapodyides*.
[b]Natural stand.
[c]Planting on stream banks.
[d]Forest plantation.

Table 5 Association of site conditions with disease incidence of *Alnus glutinosa* trees growing in plantations infested with the 'alder *Phytophthora*', and sprouting rate 5 and 17 months after coppicing. Nonflooded plantations A1 and A2 were growing at the moderately moist top (A1) and at the wet bottom of a hill (A2); plantation B was growing on a riparian site

Plantation no.	No. of alders	Diseased (dead) alders with collar rot symptoms (%) before coppicing	Spearman correlation r_S between proportion of necrotic stem girth and vigour of the crown	Stools (%) with living sprouts after coppicing 2001	Stools (%) with living sprouts after coppicing 2002	Spearman correlation r_S between sprouting rate and: Proportion of necrotic stem girth	Spearman correlation r_S between sprouting rate and: Vigour of the crown
A1[a]	150	31·3 (6·7)	–0·2759 (P = 0·0010)	72·9	57·1	–0·5248 (P < 0·0001)	0.1849 (P = 0·0305)
A2[a]	257	52·1 (23·7)	–0·5744 (P < 0·0001)	30·6	24·0	–0·4463 (P < 0·0001)	0·2769 (P < 0·0001)
B[b]	699[c]	26·5 (34·8)	–0·6553 (P < 0·0001)	28·3	25·4	–0·4179 (P < 0·0001)	0·1655 (P = 0·0371)

[a]Plantation near Wolfratshausen established in 1995 with planting stock from nursery 2 (Table 3).
[b]Plantation near Mainburg established in 1988 with planting stock from nursery 4 (Table 3).
[c]Only 159 alders were coppiced.

Table 6 Effect of the proportion of necrotic stem girth on crown health of 8- to 15-year-old *Alnus glutinosa* trees growing in plantations A1, A2 and B (see Table 5 for details) infested with the 'alder *Phytophthora*', and sprouting rate 5 months after coppicing

Proportion of stem girth with necrotic bark (%)	No. of alders	Proportion of alders with healthy crowns (%)	Sprouting rate (%)
100	15	0	0
76–99	93	29·0	11·8
51–75	81	34·6	19·8
26–50	57	57·9	36·8
11–25	35	65·7	46·2
0–10	38	76·3	50
0	197	84·3	74·6
Total/average	516	49·7	34·2

girth at the collar (Table 5). There was a weaker positive correlation with crown health (Table 5). Many trees with healthy crowns and no symptoms of collar rot did not re-grow after coppicing (Table 6).

Discussion

The objectives of this study were to show the distribution of phytophthora root and collar rot of alders in riparian and forest stands in Bavaria and to investigate modes of spread and survival of the 'alder *Phytophthora*' in order to develop management strategies.

The extensive symptom survey and detailed investigations of selected stands across Bavaria demonstrated that the disease is widespread along most of the main rivers and streams and hundreds of brooks and drainage ditches, with disease incidences above 50% along water courses with a long disease history. These data on the distribution and the severity of the disease in riparian ecosystems in Bavaria are comparable with those in north-eastern France (Streito *et al*., 2002a), and exceed the situation in the UK (Gibbs *et al*., 1999, 2003) where the disease was first described. The finding of highest disease incidences in alders growing in permanent contact with river water and in areas that hold flood water for a long period, i.e. flood plains, ox-bows, alder carrs and reed zones of lakes with infested tributaries, is in accordance with results from France, the UK, the Netherlands and Austria (Gibbs *et al*., 1999, 2003; Cech, 2001; Streito *et al*., 2002a).

Sporadic reports of phytophthora root and collar rot of alders from plantations on nonflooded sites in the UK, France, and Italy (Gibbs, 1995; Santini *et al*., 2001; Streito *et al*., 2002a) were confirmed and surpassed by the results of this survey in 3247 forest alder stands in Bavaria. Disease symptoms were recorded in more than 1000 stands. The validation in this study indicates that this number may be an underestimate, because 56% of 200 stands reported as healthy contained disease-affected trees, while there were about 10% false-positives.

Mature alder stands with phytophthora root and collar rot were found exclusively on sites that were either seasonally flooded by infested water courses or receiving drainage water from infested young alder plantations. The majority (85%) of the diseased forest stands were less than 21 years old. Since almost half of them were growing on nonflooded sites, and more than 90% of these had been planted, an introduction of the 'alder *Phytophthora*' with infested nursery stock is most likely. The oldest affected alder plantation on a nonflooded forest site without any possibility of receiving drainage water from younger infested plantations was established in 1982. This supports Gibbs *et al*. (2003), who suggested that the phytophthora disease of alders is unlikely to have occurred before the 1980s.

The detailed investigation of 60 rivers and streams with diseased alder stands, and a survey of the catchments of 25 small streams without affected alder stands also supported the hypothesis that diseased planting stock might be a major means of long-distance disease spread. In 58 of the 60 infested rivers, the source of inoculum could be traced to infested plantations on river banks or in forests that drain into the rivers, whereas no infested plantations were present in the catchments of the uninfested streams. Alder stands are usually established on permanently or seasonally waterlogged sites, where water floods after periods of heavy rain or snowmelt. As a consequence, zoospores of the pathogen may spread from infected planted alders to old trees and naturally regenerating alders in these stands, as well as downhill and along drainage ditches. Detailed investigations on the spatial patterns of the disease in the forest district 'Rotter Forst' with 73 infested alder plantations established on wet gley soils in the early 1990s supported this conclusion.

The ability of the 'alder *Phytophthora*' to spread during flooding by zoospores from naturally infected bark and infect through unwounded bark was demonstrated by a pathogenicity test and by Streito *et al*. (2002b) using alder shoots as baits *in situ*. Morphological investigations of possible infection courts in both young planted and mature riparian alders supported this experimental work. The primary infection courts were adventitious roots or lenticels in naturally regenerated alders on flooded sites, while in young planted alders on nonflooded sites, invasion was usually from an infected root system to the root collar.

In the two infested rivers without diseased plantations in their catchments, the disease was found only downstream of fish farms. As young fish are transported in river water from hatcheries, it is possible that the pathogen was inadvertently introduced when these fish farms were stocked.

The presence of the 'alder *Phytophthora*' in nursery stock was shown by a small-scale forest nursery survey. It was recovered from rootstocks of symptomless alders from three out of four Bavarian nurseries which bought in alders from intensive, large-scale commercial nurseries for re-sale. In contrast, the 'alder *Phytophthora*' was not present in rootstocks from four nurseries that grew their own alder plants from seed. All plantations established with alder plants from those nurseries were still healthy, while there was a high incidence of disease in plantations established with plants from infested nurseries. In Italy, the disease and the pathogen were found in both a young plantation of *A. cordata* and the *A. cordata* field of the nursery where the plants were grown (Santini *et al*., 2003). These results emphasize how harmful pathogens can be spread between nurseries through the pyramid sales of nursery stock. Another way that nurseries could have become infested is from irrigation water taken from rivers contaminated by diseased alder stands upstream. This latter mode of introduction was also suggested for an infested nursery in western England (Gibbs *et al*., 2003).

The demonstrated occurrence of multiple *Phytophthora* species in the rhizosphere of individual nursery plants enhances the probability of evolution and emergence of new *Phytophthora* species, and new tree diseases (Brasier & Jung, 2003). This might already have happened in the case of the hybrid forms, as indicated by the finding of the standard form and the Swedish variant of the 'alder *Phytophthora*', *P. cambivora* and putative backcross products between *P. cambivora* and the 'alder *Phytophthora*' in one of the nurseries.

Various other *Phytophthora* species were also baited from the flooded alder plants, among them *P. cambivora*, *P. cactorum*, *P. citricola*, *P. megasperma* and *P. quercina*. Since these species are known as serious pathogens of several mainly broad-leaved tree species, e.g. beech, horse and sweet chestnut, maples and oaks (Brasier & Strouts, 1976; Hartmann & Blank, 1998; Jung *et al*., 1999, 2003; Vettraino *et al*., 2001), these results have serious implications for the future establishment of forest stands with nursery stock in general. The findings of patchy dieback and chlorosis of spruce seedlings and high mortality of beech seedlings on former alder fields due to an extensive root rot caused by *P. cambivora* and *P. citricola* support this view.

In most European countries, only the standard form and/or one variant type of the 'alder *Phytophthora*' were found to be present (Brasier, 2003; Gibbs *et al*., 2003; Nagy *et al*., 2003; Santini *et al*., 2003). In contrast, in Bavaria, the standard form, the Swedish and German variants, putative backcross products with *P. cambivora*, and a series of unknown emerging variant types (T. Jung, C. M. Brasier & S. A. Kirk, unpublished data) were recovered from riparian and forest alder stands, suggesting that this area may be a 'hotspot' of evolutionary activity of this hybrid complex (Brasier & Jung, 2003).

Given all the results and observations reported here, it seems all too possible that the widespread distribution of infested alder plantations that drain into the river systems could account for the epidemic extent of phytophthora root and collar rot of riparian alders in Bavaria and the extremely high genetic variability of the 'alder *Phytophthora*' population. As far as is known, this is the first time that a widespread devastating phytophthora disease of trees has been shown to be most probably caused by the dissemination of infested nursery stock.

Oospores of the standard form and the known variants of the 'alder *Phytophthora*' have a low viability and are unable to germinate (Delcan & Brasier, 2001), suggesting that they may not act as survival structures. The almost exclusive isolation of *P. citricola* from rhizosphere soil of diseased alder trees from which the standard form of the 'alder *Phytophthora*' was isolated from all bark lesions demonstrates that survival of the latter species in soil under natural conditions is low. Also, in the Spreewald in eastern Germany, the 'alder *Phytophthora*' was not recovered from any soil samples (Schuhmacher, 2003).

Considering the apparent lack of a long-lived propagule (Delcan & Brasier, 2001) and the close specificity of the 'alder *Phytophthora*' to the genus *Alnus* (Brasier & Kirk, 2001; Santini *et al*., 2003), management concepts and control strategies which aim to diminish pathogen populations by depriving them of their only host species appear promising.

Possible management strategies

The further dissemination of inoculum with infested nursery stock would, *a priori*, undermine any management concept for the disease, and put an end to the silvicultural concept of pure *A. glutinosa* stands on wet forest sites. The lack of visible symptoms and the healthy appearance of the infested nursery-grown alder plants accentuates the inadequacy of visible controls and the urgent need for a molecular-based detection protocol and/or new conditions for the growth of alders in nurseries. Consequently, in the future, alders will be planted by the forest and river authorities only if the plant material is not infested by the 'alder *Phytophthora*'. Therefore, it is recommended that nurseries: (i) grow their alders in fields where no nursery plants have been grown for a certain length of time; (ii) grow their own alder plants from seed or buy alders for re-sale only from nurseries that grow their alders according to this code of good practice; (iii) do not use river or surface water for irrigation; (iv) do not grow any other nursery plants on the alder fields, in order to avoid passive introduction of the 'alder *Phytophthora*' with nonhost plants; (v) avoid the introduction of the pathogen from infested fields via soil particles.

The possible survival time of the pathogen in infested nursery soil is of particular interest to nursery owners. The inability to isolate it from naturally infested former alder fields of two nurseries that had either been left unplanted or planted by spruce and beech plants for 2 years indicates a rapid decrease of 'alder *Phytophthora*' populations in the absence of alders. Therefore, a 3-year rotation between alders is recommended to ensure the extinction of pathogen populations from potentially infested fields. However, the dieback and chlorosis of spruce plants and the high mortality of beech plants caused by *P. cambivora* and *P. citricola* on these fields demonstrate that phytophthoras with wider host ranges have no problems establishing and surviving in nursery fields.

At present it is unclear whether the progressive process of collar infections and mortality of trees in infested plantations will eventually stop or inevitably lead to the collapse of affected stands. Since long-term data on the development of diseased forest stands are required for the silvicultural management, a series of 15 permanent plots were established in 2003 by the Bavarian State Forestry in stands of different ages and with different site conditions and disease incidence.

Coppice experiments in natural riparian alder stands in the UK showed high sprouting rates and low re-infections 4 years after coppicing (Gibbs, 2003). In contrast, the coppice experiments in three alder plantations in Bavaria resulted in markedly lower sprouting rates. Moreover, wilting of shoots during hot periods and re-infections of sprouts from the infected root system during the first 2 years further reduced the number of surviving stools. The main reason for the striking difference between the Bavarian and the UK results was most probably the different location of the infection court between riparian natural alders and alder plantations. In the latter, the 'alder *Phytophthora*' was introduced with the nursery stock, producing a high proportion of root damage before collar rot symptoms became visible. Therefore, before recommendations can be made, long-term data on disease progression in coppiced and noncoppiced forest plantations on different sites are required.

Compliance with the new conditions for growing alder plants in nurseries may be sufficient to allow the sustainable production of alder timber on nonflooded forest sites in the future. However, on riparian sites, newly planted, healthy alders could become infected from zoospores in flood water from infected alders upstream. Coppicing of infected trees and shoots may be a short-term control measure, but in the long term, a variety of resistant clones is needed in order to sustain riparian alder stands. Field and laboratory experiments in the UK with young plants from 15 European provenances have disproved the idea of resistance of *A. glutinosa* against the 'alder *Phytophthora*' at provenance level (Gibbs, 2003). However, healthy mature common alders were observed during this study, and also in other countries (e.g. Streito *et al*., 2002a), growing side by side with diseased and dead trees in riparian stands with high disease incidences and long disease histories. These trees either have walled-off lesions at the stem base or no lesions at all, and may possess natural resistance to the 'alder *Phytophthora*'. Consequently, a programme was started in 2001 in Bavaria to select and breed for resistant alders. The feasibility of such a selection breeding programme was recently demonstrated for *Eucalyptus marginata* and *P. cinnamomi* (Hüberli *et al*., 2003), and for *Chamaecyparis lawsoniana* and *P. lateralis* (Bower *et al*., 2000; Hansen *et al*., 2000; Sniezko & Hansen, 2000; Sniezko *et al*., 2003).

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