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Winter survival of *Phytophthora alni* subsp. *alni* in aerial tissues of black alder

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ABSTRACT: The winter survival of the invasive pathogen *Phytophthora alni* subsp. *alni* in black alder stems was studied in the bankside alder stand of the Moravská Dyje River in southern Bohemia after two very different winter seasons: cold in 2008/2009, with the average temperature of –1.96°C, and extremely mild in 2006/2007, with the average temperature of 2.54°C. The difference in these two winters resembles the expected potential climate change in Central Europe in this century. After the cold winter of 2008/2009, the pathogen survived in only 13.91% of the samples, with the average survival rate of 2.70%. The pathogen survived the mild winter much better and was successfully isolated from 86.09% of the samples, with the average survival rate of 25.52%. Moreover, the total thickness of the covering tissues (outer + inner bark) and exposure to the most heated southwestern quadrant of stem girth positively affected the pathogen survival. Winter freezing seems to be an important environmental factor regulating the pathogen survival in alder stems and disease severity.

Keywords: *Phytophthora alni*; winter survival; black alder; temperature; *Phytophthora* alder disease

A new *Phytophthora* disease of black alder has been spreading across Europe since the early 1980's (Gibbs et al. 2003). This cause of lethal root and collar rot disease, formerly known as alder-*Phytophthora* and more recently named *Phytophthora alni* (Brasier et al. 2004), affects three European *Alnus* species: the black, grey and Italian alders (Jung, Blaschke 2006). The pathogen is distributed throughout Western, Northern, Central and Southern Europe and causes significant losses of trees in some European countries (Gibbs et al. 1999; Streito et al. 2002; Jung, Blaschke 2004) as it spreads eastward. *Phytophthora alni* was first isolated in the Czech Republic in 2001 (Cerny et al. 2008). The proportion of diseased or dead trees has gradually increased in permanent plots investigated by several researchers (Streito et al. 2002; Webber et al. 2004; Jung, Blaschke 2006; Schumacher 2006), and the disease has become epidemic in some areas (Streito et al. 2002; Jung, Blaschke 2006; Schumacher 2006). The species consists of three subspecies, with *P. alni* subsp. *alni* found to be the most frequent and pathogenic among them (Brasier, Kirk 2001; Brasier 2003). The current death of alders along European rivers damages riparian ecosystems, destabilises riverbanks and affects the shelter of fish, birds and other wildlife. Moreover, *P. alni* represents a significant threat to the natural environment (Brasier 2008). Important economic losses in forestry can also be expected after the infestation of *P. alni* in nursery stock and its distribution in forest plantations.

Climate change is likely to have a profound impact on plant-pathogen interactions (Jeger, Pautasso

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2008), and numerous researchers have focused on this topic (e.g. Anderson et al. 2004; Bergot et al. 2004; Garrett et al. 2006; Desprez-Loustau et al. 2007; Chakraborty et al. 2008; Evans et al. 2008; La Porta et al. 2008; Pautasso et al. 2010). Several fungal diseases in trees can become more devastating because of the following factors:

(i) abiotic stresses, such as drought and flooding, are known to predispose trees to several pathogens;
(ii) temperature and moisture affect the pathogen sporulation and dispersal, and changes in climatic conditions are likely to favour certain pathogens;
(iii) the migration of pathogens triggered by climatic change may increase disease incidence or geographical range when the pathogens encounter new hosts and/or new potential vectors;
(iv) new threats may appear either because of a change in the tree species composition or because of invasive species (La Porta et al. 2008).

The impact of many diseases is likely to increase with a temperature rise in the winter, resulting in more successful pathogen survival (Coakley, Scherm 1996; Bergot et al. 2004). In this century, the winter temperature can reach from 3.0°C to 4.0°C in Central and Eastern Europe; the average winter temperature can exceed 0°C, and the change in climate can specifically concern the lowest winter minimum temperatures (IPCC 2007). Recent models predict an increase in the distribution and local impact of a range of forest pathogens, including *P. cinnamomi* (Desprez-Loustau et al. 2007). Winter survival is a dominant cue for the development of ink disease caused by this pathogen in oak in Europe (Brasier, Scott 1994; Marçais et al. 1996; Bergot et al. 2004). Therefore, we predict that winter temperatures will play a key role in the survival of other invasive *Phytophthora* spp. in Europe, including *P. alni*.

Winter temperatures can be a crucial factor affecting the survival and impact of *P. alni* subsp. *alni* (PAA) for several reasons. First, chlamydospores, as potential resting structures, are not observed in this organism (Brasier et al. 2004). Second, a high proportion of oospores as putative survival structures are either fully aborted or thin-walled, and normally developed oospores usually have low viability (Brasier et al. 2004). Delcán and Brasier (2001) observed no oospore germination in this organism, and they connected this finding with known meiotic irregularities in this hybrid. This finding suggests that oospores cannot act as survival structures (Jung, Blaschke 2004). Third, the poor survivability of this organism in the soil and rhizosphere (partially due to poor competitive ability) has been documented several times (e.g. Delcán, Brasier 2001; Jung, Blaschke 2004). Fourth, the sensitivity of the pathogen to frost can be expected on the basis of field observations and laboratory experiments performed by Schumacher et al. (2006) and Černý et al. (2012). Thus, it is important in forestry, landscape and water management to understand the potential reaction of a pathogen to an increase in winter temperature and its resulting impact and distribution.

The aims of this study are as follows:

(i) to determine if the winter survival of PAA in bark tissues is different after cold and mild winters;
(ii) to find out if the presence of the pathogen is dependent on the thickness of the covering tissue (outer + inner bark);
(iii) to determine whether the exposure of stems to heat caused by sunlight has any effect on the pathogen.

Furthermore, we discuss the spread and distribution of the pathogen in Europe based on known field data. The mathematical prediction of its ultimate area is still difficult because of the current invasion and poor autecological knowledge, which is a limiting factor in the use of statistical modelling to predict species distribution (Austin 2002).

MATERIAL AND METHODS

Study site

The study site is situated in the Jindřichův Hradec district (Southern Bohemia, Czech Republic) and belongs to the humid region of the warm temperature zone (Cfb) according to Köppen's climatic classification and to moderately warm climatic region 7 (MW7) according to Quitt's classification (Tolasz et al. 2007). Long-term (1961–2000) measurements have shown that the climatic conditions in this area are characterised by a winter air temperature ranging from –2°C to –1°C, an average annual number of ice days ranging from 40 to 50 and an average seasonal number of days with snow cover ranging between 40 and 50 (Tolasz et al. 2007).

The alder stand (centred at 49°06'33.40"N; 15°26'46.57'E; 468 m a.s.l.) is approximately 600 m long and is located along both banks of the Moravska Dyje River along a distance of 26.8–27.4 km in a highly meandering stream bed ca 3 km from the city of Dačice and 17 km from the Austrian bor-

der. The Moravska Dyje River is 4–10 m wide at the location and meanders southwards through meadows in an alluvial plain. The average flow rate is 2.63 $m^3 \cdot s^{-1}$ at the water measuring station in Janov, the Czech Hydrometeorological Institute (CHMI), ca 10 km to the south of the studied site.

The species composition of the tree and shrub layer in the stand was determined along with the frequency of particular species. The health status of the alders and the frequency of *Phytophthora* alder disease were also determined. Diseased trees were considered those showing the presence of characteristic symptoms of the disease, including bleeding canker on the main roots, buttresses, collars or stems and characteristic flame-shaped lesions on the collars and stems and/or withered crowns with reduced foliage (> 25%).

Climatological data

The climatological data (average, minimum and maximum temperatures and height of snow cover) were provided by the CHMI and were acquired at the climatological station of Kostelní Myslová (49°09'N; 15°26'E), located ca 4.5 km to the north of the studied site. For comparison, we used the data measured through both winter periods (from 22nd December to 20th March in 2006/07 and 2008/09). In the analysis, we used the provided data (average, minimum and maximum temperatures and height of snow cover) and certain characteristics that were calculated from the data:

(i) the number of frost days (days when the daily minimum temperature 2 m above ground was below 0°C);
(ii) the number of ice days (days when the daily maximum temperature was less than 0°C);
(iii) the number of days with unbroken snow cover (the grounds of the station and the immediate vicinity were at least half covered by a snow layer with 1 cm in depth at least).

The long-term (1960–2000) climatological data on the temperature and snow cover in the area were from the Climate Atlas of the Czech Republic (Tolasz et al. 2007).

Sampling

The first part of the fieldwork was performed after the mild winter in 2006/07. The next winter (2007/08) had nearly the same climatic course, so the investigation had to be postponed until the relatively cold winter of 2008/09 (see below). The sampling was performed the first week of spring in both years: the 21st–23rd of March in 2007 and the 23rd–25th of March in 2009.

First, the collars and stems of the alder trees (stem diameter at DBH ≥ 7 cm) were screened for the presence of exudates that had been produced in the bark cracks in the last vegetation period. The exudates characteristic of stem necrosis of *Phytophthora* alder disease were relatively durable and typically of tar appearance and consistency; they were glossy and vividly coloured in tone from rusty, red, purple, and wine to tarry and ink. The exudates above inactive lesions were dully coloured, as if smoked. When the vividly coloured exudates were found, the bark was carefully removed on several places beneath them (usually proximally located), and the margins of the lesions of subcortical tissues were identified. The fresh lesions were characterised by no marks of host-tissue decay and were honey and red to dark purple and had at least partially diffuse margins. Lesions that were coloured black and brown to buff with marks of decay and that were strictly bordered by callus formations beneath them were considered dead and were not sampled. The samples of conductive tissues (ca 100 cm^2) were stripped out with a sterilised wood chisel in the margins of active lesions (with parts of the adjacent healthy host tissues) usually 0.2–2.0 m above the ground level and put into sterile polyethylene bags. A total of 115 samples were taken in both years of the investigation. The samples were processed on the same day.

Phytophthora alni isolation protocol

Phytophthora alni was usually isolated by several different protocols (Brasier et al. 1995; Jung, Streito et al. 2002; Blaschke 2004). We did not use them, because the aim of our study was the prompt quantification of the survival rate. For instance, the main advantage of sampling and isolation method described in Jung and Blaschke (2004) was removal of polyphenols from the necrotic bark segments sampled by replacing water 4 times per day because excessive polyphenol secretion damaged *Phytophthora alni* a lot, but the disadvantage was the development of the pathogen in the sample preceding the isolation. Thus we decided for more appropriate and usable method as follows. We tested this method previously and obtained a lot of isolates of *P. alni* that yielded good results, but the samples had to be chosen precisely (Streito et al. 2002) and processed immediately.

The samples were washed under tap water and cleaned of bark remnants and subsequently processed under sterile conditions. Only the marginal part of the lesions, which was less than ca 1.0–1.5 cm from the line between the necrotised and healthy tissues (well visible along longitudinal cutting), was selected and then cut into small segments (ca 3 × 3 × 3 mm). The segments were surface-sterilised in 97% ethanol (3 s), washed in deionised water (5 s) and dried by sterile pulp. Twenty segments from each sample were placed at identical spacing on a Petri dish (9 cm diam.) with 20 ml of selective PARPNH media: pimaricin 10 ppm, ampicillin 200 ppm, rifampicin 10 ppm, pentachloronitrobenzene 25 ppm, nystatin 50 ppm, hymexazol 50 ppm, $CaCO_3$ 3 g, agar 20 g, V8-juice agar 100 ml and deionised water 900 ml (Jung et al. 1996). The plates were incubated at 20°C in the dark for 3 weeks. After 5–21 days, the plates were repeatedly examined for the presence of *P. alni* colonies, and the production of characteristic oogonia was verified under a binocular microscope. The number of segments bearing *P. alni* on each plate was registered.

The pathogen identity was confirmed by comparison of the rDNA sequence of the ITS region from the diseased-alder isolate with those deposited in GenBank, confirming its identity as PAA. The ITS sequence of the isolate (GenBank accession number EF194776) was closest to those of PAA isolates P669 and P818 deposited in GenBank under accession numbers AY689131 and AY689132 (Brasier et al. 2004; Cerny et al. 2008; Strnadová et al. 2010).

Climate data

In the mild winter of 2006/2007, the average temperature was 2.54°C (average maximum temperature was 6.27°C; average minimum temperature was –0.52°C), while in the cold winter of 2008/09, the temperature reached –1.96°C (average maximum temperature was 0.57°C; average minimum temperature was –4.06°C). A *t*-test comparison showed that the differences in all three temperature values (average, minimum and maximum temperatures) of both winter seasons were highly significant ($P << 0.001$).

There were 51 frost days in the mild winter of 2006/07 and 71 frost days in the cold winter of 2008/09. A chi-squared goodness-of-fit test revealed that the difference in the number of frost days between the two seasons was not significant ($P = 0.070$). The number of ice days was the most important factor when the temperature of both winter seasons was considered. There were only 5 ice days in the mild winter of 2006/07 and a period with the temperature continuously below 0°C persisted for 4 days. In the cold winter of 2008/09, there were 37 ice days, and the longest period with a continuous temperature below 0°C lasted for 24 days. Unlike the number of frost days, a chi-squared goodness-of-fit test confirmed that the number of ice days was significantly different ($P << 0.001$).

The number of ice days in the mild winter was significantly different ($P << 0.001$) from the long-term average number of ice days (Tolasz et al. 2007). No difference between the number of ice days in the cold winter of 2008/09 and the long-term average number of ice days was found ($P = 0.528$).

The difference between both winter seasons can also be illustrated by the duration of unbroken snow cover, which lasted for 11 days in the winter of 2006/07 (the longest period with unbroken snow cover was 7 days) and 53 days in the winter of 2008/09 (the longest period with unbroken snow cover lasted for 31 days). A chi-squared goodness-of-fit test confirmed a statistically significant difference in this number ($P << 0.001$).

It should be stated that both winter seasons had important differences in the temperature course and the duration of snow cover. The winter of 2006/07 was extremely mild, while the winter of 2008/09 had a standard temperature course and corresponded to the long-term (1961–2000) climate characteristics of the area (Tolasz et al. 2007).

Data analysis

The data were digitised, and the percentage values of *P. alni* survival were transformed by arcsin transformation. The software package STATISTICA 7.0 (StatSoft, Inc., Tulsa, USA) was used for statistical analysis, and the *t*-test, chi-squared goodness-of-fit test, Mann-Whitney *U*-test and Generalised Linear Models were used at particular steps of analysis.

RESULTS

Studied alder stand

The tree stand (aged ca 40–60 years) was studied on both riverbanks. The tree stand was simple (one row of trees on each bank) and composed mainly of *Alnus glutinosa* (86%), *Fraxinus excelsior* (6%), *Salix fragilis* (4%) and individuals of other tree species. The species composition shows that *Alnenion*

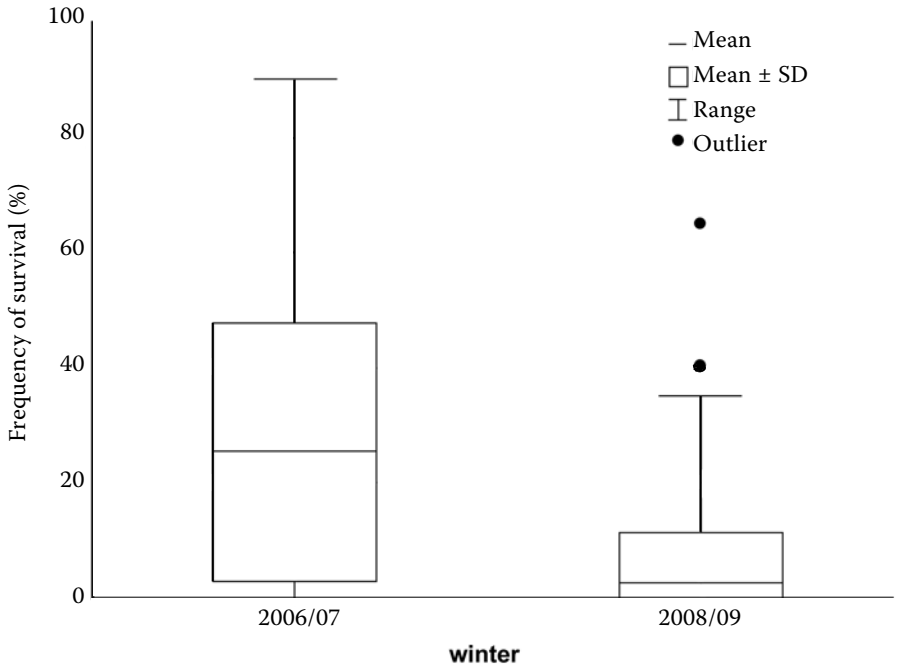

Fig. 1. The difference in *Phytophthora alni* survival in black alder stems after the mild winter in 2006/07 and the cold winter in 2008/09
SD – standard deviation, outlier – measured value > 3/2Q (interquartile range)

glutinoso-incanae Oberdorfer 1953 in mosaic with *Salicion triandrae* Müller et Görs 1958 was the indigenous plant community in the stand.

There were 292 mature black alders in the studied stand. Most of the alders – 241 (83%) trees – were apparently damaged by the pathogen. They showed characteristic symptoms of the disease: bleeding canker on the main roots, buttresses, collars or stems, characteristic flame-shaped lesions on the collars and stems or withered crowns with reduced foliage (> 25%). A large number of alders were damaged by the pathogen, and 37 had to be removed in 2009. Only 49 alders (17%) did not show any symptoms of *Phytophthora* disease in the summer of 2009.

Pathogen survival

After the mild winter of 2006/07, the pathogen was successfully isolated from 86.09% of the samples, and the average survival rate in the samples was 25.52% (SD = 22.36%). In the cold winter of 2008/09, the pathogen survived in only 13.91% of the samples, and the average survival rate was 2.70% (SD = 8.87%; Fig. 1). Despite the arcsin transformation, the data set from 2008/09 did not fulfil the assumptions of normality and homogeneity with regard to the extremely low pathogen survival during this winter. The Mann-Whitney *U*-test showed that the frequency of pathogen survival statistically differed between these two winters and that the survival after the mild winter of 2006/07 was substantially more successful than after the cold winter of 2008/09 ($P << 0.001$). The variability in the frequency of survival was extremely high (Fig. 1), which signalled that there were other factors that might influence the pathogen survival.

The analysis of site factors potentially responsible for survival was based on the data set from 2006/07 because the pathogen survival in 2008/09 was extremely low. A Generalised Linear Model was used for the analysis (the significance was $P < 0.01$, Table 1) and showed that the pathogen survival was significantly affected by the thickness of covering tissues ($P < 0.01$) and its orientation on the stem girth ($P < 0.05$). The pathogen conclusively survived more frequently in thicker covering tissues ($r = 0.301$; $P < 0.01$; Fig. 2), and its highest survival rate was found to be in the most heated southwestern quadrant of stem girth ($P < 0.05$). No influence of the sampling position (apex, side) in the stem lesion and height of the sampling position above the collar was found.

DISCUSSION

The two winter periods of our field research differed greatly in the temperature course. The difference between the average temperatures of the two winter periods was ca 4.51°C. The colder winter of 2008/09 had an average temperature of –1.96°C, which corresponded to the long-term climate characteristics of the respective climatic region in the Czech Republic (Tolasz et al. 2007). In contrast, the avg. temperature in the mild winter of 2006/07 reached 2.54°C and is in approximate accordance

Table 1. Overview of local factors affecting the survival of *P. alni* in black alder stems

	SS	df	MS	*F*	*P*
Intercept	1.934	1	1.934	23.896	< 0.001
Thickness of tissue	0.752	1	0.752	9.298	0.003
Exposure on stem	0.331	1	0.331	4.088	0.046
Error	9.064	112	0.081		

The GLM model of *P. alni* survival in alder stems after the mild winter of 2006/07. SS – sum of squares, df – degrees of freedom, MS – mean square, *F* – *F*-ratio, *P* – significance level

with the prediction of a temperature increase in this century (IPCC 2007). Moreover, both winter periods differed significantly in other characteristics, such as the number of frost days, and specifically ice days and days with snow cover. A decrease in the number of frost days will very likely be seen in the future (Meehl et al. 2004; Tebaldi et al. 2006; Planton et al. 2008). Similarly, simulations of climate change have shown that the lowest minimum winter temperatures increased more than the median minimum temperature, especially in Eastern, Central and Northern Europe (IPCC 2007). The comparison of the two winter periods (cold of 2008/09 and mild of 2006/07) corresponds well to the shift in winter climate in Central Europe that might occur in this century.

We found important differences in the PAA survival rate in the tree trunks of black alder between the two winter periods. During the mild winter, the pathogen survived more successfully. Moreover, we found that the pathogen survival rate depended on the total thickness of covering tissues (outer + inner bark) and exposure to the most heated southwestern quadrant in the stem girth.

The low pathogen survival in the aerial tissues in the cold winter (the pathogen survived in 13.91% of the samples with a total survival rate of 2.70%) generally corresponded to our hypothesis based on the absence of potential survival structures in PAA, its low competitiveness and its sensitivity to frost (e.g. Delcán, Brasier 2001; Brasier et al. 2004; Jung, Blaschke 2004; Schumacher et al. 2006; Černý et al. 2012). The laboratory experiment (Černý et al. 2012) provided a proof of the pathogen's sensitivity to heavy frost because its viability quickly decreased during incubation at –10°C (a temperature that regularly occurred during the winter of 2008/09). We also presume, in accordance with Bergot et al. (2004), that winter survival is likely to be more critical when the patho-

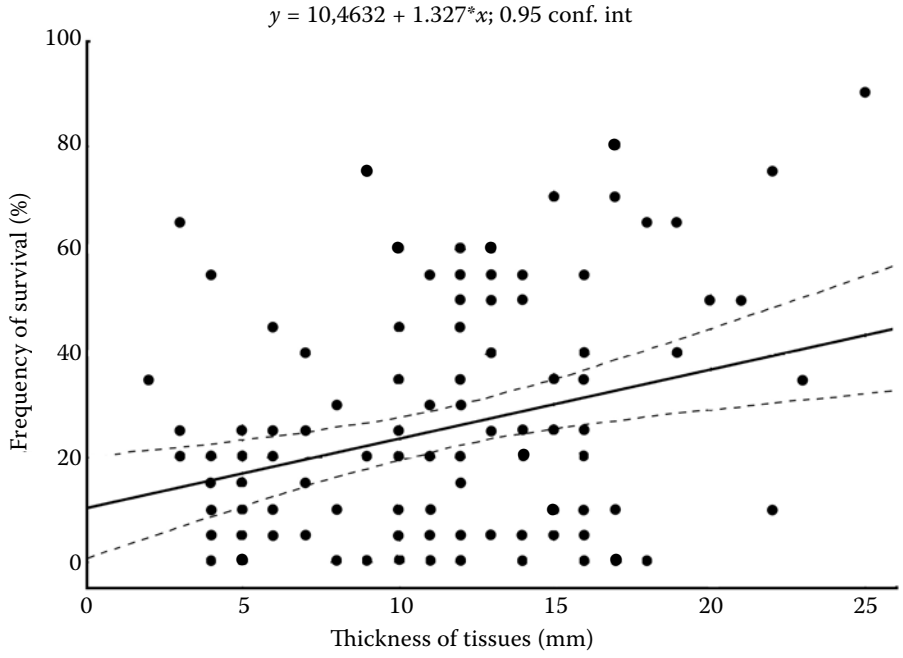

Fig. 2. Dependence of *P. alni* survival in black alder stems on the thickness of covering tissues
regression of the frequency of *P. alni* survival after the mild winter of 2006/07 to the thickness of covering tissues (inner + outer bark) of black alder stems, Y – regression equation. 0.95 conf. int. – confidence interval

gen overwinters in the aerial system rather than in roots. The two other factors (thickness of covering tissues and exposure to the most heated quadrant of stem girth) seem to be less important in the pathogen survival, but are statistically well supported. The positive effect of the most heated quadrant on the pathogen survival agrees with the finding of Downing et al. (2008), who identified temperature as a factor playing an important role in its distribution. Our results are also in accordance with Marçais et al. (1996), who confirmed the effect of higher winter temperatures and orientation in the most heated side of the stem girth in *P. cinnamomi* survival in stems of red oak. In accordance with the modelling of *P. cinnamomi* behaviour as a result of climate change (Brasier, Scott 1994; Marçais et al. 1996; Brasier 1996; Bergot et al. 2004), we expect that warming will significantly enhance the impact of PAA in its locations.

Based on the experiments of Chandelier et al. (2006), it can also be predicted that the natural spread of the pathogen throughout Europe can be determined by low temperatures. Unfortunately, using mathematical prediction as a way to reveal the pathogen's potential distribution and specific response to climate change is still problematic because of its current invasion – the pathogen has not yet completely expanded into its potential range (Downing et al. 2008) – and because of the lack of autecological knowledge, which is a limiting factor in the use of statistical modelling to predict species distribution (Austin 2002). *P. alni* occurs regularly in areas with an incidence of cold continental winters, as shown in the findings in the northern part of its known area (e.g. Sweden, the Baltics and central Alaska); however, those findings belong mainly to *P. alni* subsp. *uniformis* – PAU (Brasier et al. 2004; Adams et al. 2010). It could be that the survivability of PAU is higher than that of PAA because of the high proportion of normally developed oospores in PAU (Brasier et al. 2004). It is likely that the importance of the motile stage of the pathogen (zoospores) in winter is low in regard to the absence of sporangial production at 8°C by PAA and PAU (Chandelier et al. 2006) and the low conductivity of river water in winter (e.g. Vega et al. 1998), which can reduce the survivability of free zoospores (Kong et al. 2012).

The explanation of the current unpredictable progress of PAA in Europe is difficult considering the absence of exhaustive knowledge of its autecology and disease epidemiology, although some results have been achieved (e.g. Gibbs et al. 1999; Delcán, Brasier 2001; Streito et al. 2002; Jung, Blaschke 2004; Schumacher et al. 2006; Thoirain et al. 2007; Downing et al. 2008; Marçais et al. 2009; Jung et al. 2009). The success of the pathogen partially results from its relative cold tolerance, confirmed by its lower cardinal temperatures and survival at 0°C (Brasier et al. 1995, 2004; Schumacher et al. 2006) and – 2.5°C (Černý et al. 2012). The anthropogenic spreading of the pathogen within the nursery stock (Jung, Blaschke 2004) is another possible reason. Undoubtedly, the success of the pathogen is also due to its effective natural spread and survival in river systems (cf. Gibbs et al. 1999; Streito et al. 2002; Jung, Blaschke 2004; Thoirain et al. 2007; etc.). It is possible that the existence of a suitable, widely accessible and easy-to-find refuge in alder roots and collars in the bank line allows the pathogen not only to grow and propagate directly in the transport medium but also to escape from the effect of winter frost in the aerial tissues and the competition of microorganisms in the roots in soil.

We conclude that the survival of PAA in the aerial tissues of black alder is highly dependent on the winter temperature, and its survival in these tissues during the winter that followed a standard climatic course in Central Europe was very limited. The pathogen population will likely respond to warming by a higher survival rate in aerial tissues, higher disease impact in its locations and, in accordance with findings of Chandelier et al. (2006), by higher production of inoculum. Winter freezing of the surface soil and necrotised aerial host tissues seems to be an important environmental factor regulating the pathogen survival and disease severity, especially in forests, nurseries and other plantations without available surface water (e.g. afforested agricultural land, shelterbelts, reclamations). However, the pathogen can likely escape both winter freezing and competition of soil microorganisms in alder roots in non-frozen water. Therefore, we suspect that the pathogen can successfully survive in areas with hard continental winters with severe frost and with limited snow cover, but the losses can be lower due to poor survivability in aerial host tissues. The disease severity can also be lower in colder areas due to decreased infection inoculum production in cold water (Chandelier et al. 2006).

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