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The effects of flooding and *Phytophthora alni* infection on black alder

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ABSTRACT: The influences of long-term flooding and *Phytophthora alni* subsp. *alni* infection on the growth and development of 4-year-old *Alnus glutinosa* (black alder) saplings were investigated. The black alder saplings were divided into four groups and then subjected to combinations of both factors – flooded and inoculated with pathogen, flooded non-inoculated, non-flooded inoculated, and control. The biomass of the living roots and actinorrhizae, increase in stem length, length of leaves, rate of chlorotic foliage, amount of foliage biomass and length of stem necrosis were assessed after seven weeks. Both factors, flooding and *P. alni* infection significantly affected the black alder. In addition, a significant effect of interaction was observed. The inoculated flooded group had a substantially lower biomass weight of living roots, actinorrhiza and leaves than the other groups. The necroses caused by the pathogen in the flooded group were more extensive than those in the non-flooded one. These findings demonstrate that the simultaneous incidence of stress caused by flooding and *P. alni* infection is highly dangerous for black alder.

Keywords: alder decline; *Alnus glutinosa*; flooding; *Phytophthora alni*

In August 2002, the west part of the Czech Republic was afflicted with flooding that exerted stress on hundreds of kilometres of riparian alder stands in several catchments, especially in western, middle and southern Bohemia. The flooding or total water saturation of soil lasted for several weeks or months in many of the affected areas. In the years following the floods, the extended alder population appeared to decline in many of the affected riparian stands, which had been healthy prior to the floods (Strnadová et al. 2006). Therefore, it was likely that this decline was connected to the flooding that occurred in 2002 (Vyhlídková et al. 2005) because the increased water level and flooding could damage the alders and induce morphological changes as seen by McVean (1956). The dangerous pathogen of alders *Phytophthora alni* has been spreading rapidly in alder stands, particularly in the western part of the Czech Republic in recent years, and has leading to significant losses in highly affected stands (Cerny et al. 2008). We felt it important to distinguish which of these factors was the real cause of the decline. Extensive field studies have taken place over the last few years (2003–2009) in the Czech Republic. While they are still in progress, one preliminary study on this topic has been published so far (Strnadová et al. 2006). This study showed that both factors could contribute to the alder decline in the investigated stands because the incidence of *P. alni* symptoms as well as an increased water level and extent of flooded area in August 2002 (Strnadová et al. 2006) were significantly correlated with the damage to alder stands.

Ground water table fluctuation and long-term waterlogging could be primary abiotic causes of damage to several tree species (Kozlowski 1997). Flooding

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alters the soil structure, depletes oxygen and leads to the accumulation of carbon dioxide. This, in turn, induces anaerobic conditions, which inhibit growth and lead to the decay of the root system (Kozlowski 1997). The changes in several tree species in response to flooding were summarized by Kozlowski (1997), in black alders by McVean (1956) and in speckled alders by Ohmann et al. (1990). Black alders subjected to flooding produced a considerable amount of adventitious roots and hypetrophied lenticels, and created new roots near the soil surface. The flooding led to a decrease in the number of nodules in deeper layers, the death of deep roots, stunting growth, the death of some branches and, in some cases, the death of alder seedlings or trees (McVean 1956).

The mechanism by which flooding induced the current decline in black alders in the Czech Republic was described by Vyhlídková et al. (2005), who stated that the alder decline along the Lužnice River (southern Bohemia) was induced by the mechanical effects of flooding, depletion of soil oxygen and invasion by microorganisms of the weakened alders (polyetiologic decline). The preliminary outcomes of a multidimensional analysis showed that floods could play an important role in the decline of alders along the Lomnice River in southern Bohemia (Strnadová et al. 2006).

The pathogen that had a key role in the decline of the black alder, *Phytophthora alni*, was first isolated in northwest Bohemia in the Czech Republic in 2001. Since then, the pathogen has been isolated from about 60 alder stands and continues to spread rapidly, particularly in the western part of the Czech Republic (Cerny et al. 2008). The disease has also been found in several river systems, some of which are connected to watercourses in eastern Bavaria (Jung, Blaschke 2004) and northern Austria (Cech 2001).

During flooding, *P. alni* zoospores spread from naturally infected bark and infect other trees (Streito et al. 2002). It is known that natural infestations of alder trees by *P. alni* occur during floods (Jung, Blaschke 2004), and greater disease incidences have been described in areas that hold flood water for a long period of time (Gibbs et al. 1999, 2003; Streito et al. 2002; Jung, Blaschke 2004; Schumacher et al. 2006; Thoirain et al. 2007). Schumacher et al. (2006) found that flooding during the growing season causes the highest risk of infection. The anaerobic conditions in flooded soil could inhibit growth and lead to decay of the root system (Kozlowski 1997).

This study was conducted to determine whether *P. alni* had a greater affect on the alders that were stressed by flooding and to describe some of changes that occur in alders after being subjected to flooding, *P. alni* infection and a combination of both factors.

MATERIAL AND METHODS

Infection experiment

Four-year-old black alder plants (*Alnus glutinosa*) were used for the inoculation experiment. Eighty plants with well-developed actinorrhiza were potted in 18 × 18 × 18 cm plastic containers that were filled with sterile peat substrate (pH 5). Several months later, when the plants took root readily, they were randomly divided into four groups of 20 plants each. The first group of plants (the first treatment) was artificially infected with *P. alni* subsp. *alni* and then flooded up to the soil surface with filtered pond water without *Phytophthora* infection; this stable water level was maintained for the duration of the experiment. The second group (the second treatment) was flooded in the same manner as the first group but was not inoculated (non-inoculated). The third group (the third treatment) was inoculated but not flooded (non-flooded). The fourth group (the fourth treatment) was a control (non-flooded, non-inoculated). The experiment was conducted for seven weeks in May and June 2005 in a greenhouse. The temperature was maintained at 20–30°C in day/night temperature regime, and the air humidity was varied from 40 to 60%. The plants were controlled and watered with filtered pond water as needed to prevent the substrate from drying. The used pond water contained a relatively low oxygen concentration (< 4 $mg.l^{-1}$) to simulate the situation in flooded stands. It was filtered through the sand filter during the experiment. The catchment area of the tributary to the pond was free of disease caused by *P. alni*.

Phytophthora alni subsp. *alni* isolated from the bleeding canker of a black alder tree growing in a stand highly affected by the disease (Velký Pěčín, district Jindřichův Hradec, southern Bohemia, geographical coordinates 49°6'38"N and 15°26'49"E) was used for the inoculation. The microscopic and cultural characteristics of the isolate used here were identical to those of *P. alni* subsp. *alni* (Brasier et al. 2004). In addition, its colonies were uniform on carrot agar and V8 juice agar (Erwin, Ribeiro 1996) without any chimaeric zones. The optimal growth temperature was 24°C, and it produced oogonia that were moderately ornamented. The abortion of oogonia reached 50–70%. A comparison of the rDNA sequence of the ITS region of the isolate with

those deposited in GenBank confirmed its identity as *P. alni* subsp. *alni*. The ITS sequence of the isolate was closest to those of *P. alni* subsp. *alni* isolates P669 and P818 (Brasier et al. 2004) deposited in GenBank (accessed Nos AY689131 and AY689132).

A modified inoculation method was used to minimize the extent of mechanical injury (created by standard inoculation with mycelium on an agar plug) and to bring the actively parazitizing mycelium into the host stem. Young leaves of black alder seedlings cultivated in a greenhouse were used as the inoculation medium. Briefly, healthy leaves containing no marks of alteration, disease symptoms or signs of insect grazing and sucking were detached from the plants and rinzed in 95% ethanol (5 sec) and then sterile deionized water (15 sec). The leaves were then cultivated in sterile deionized water with segments of V8 agar that had been colonized by the *P. alni* isolate. After necroses developed, the presence of *P. alni* in the necrotized tissues was confirmed microscopically. The necrotized leaves were then cut into 5 × 5 mm segments and used for inoculation. To inoculate the plants, the stem bases (ca 2–3 cm above the collars) were wiped with a piece of pulp that had been rinsed in sterile water and surface sterilized with ethanol. Next, the surface tissues were vertically incised using a lancet, after which a segment of the leaf was inserted between the youngest wood and the external (outer) tissues of stem. The plants in the two infected treatments were inoculated with infected leaf segments; the plants in the two other groups were inoculated with healthy non-infected leaf segments. The cuts were then sealed with Parafilm. At the end of the experiment, the pathogen was reisolated from several cankers and confirmed to be *P. alni*. The experimental design was completely randomized.

Disease assessment

The increase in the length of the main stem and the vertical length of the necroses that developed on the stems were measured. Additionally, the rate of chlorotic foliage of each plant was evaluated on a scale of 1–5, according to the degree of chlorotization (1 = 0–10%, 2 = 11–25%, 3 = 26–50%, 4 = 51–75%, and 5 = 76–100%). Next, all of the living foliage attached to the plants was harvested, and the length of ten randomly selected leaves was measured. The root systems of all plants were then repeatedly gently washed and cleaned of the substrate; after, the living actinorrhizal nodes and living roots were separated from the dead biomass of the root systems. Finally, the biomass of the foliage, the living actinorrhizal nodes and the living roots were dried at 105°C and then weighed precisely.

All statistical analyses were performed using S-Plus 8.0.4 for Windows (Insightful Corporation, Seattle, WA, USA). The increase in stem length, the length of leaves and the biomass of the leaves, roots and actinorrhiza were analyzed using multidimensional analysis of covariance (2-way MANCOVA) with fixed effects (flooding and *Phytophthora alni* inoculation). The height of the plants at the beginning of the experiment was found to be an important independent factor potentially influencing some of the assessed values; it was used as the covariate. The effect of the factors plant height (covariate), flooding, *P. alni* and flooding × *P. alni* interaction on depending variables (increase in stem length, length of leaves and biomass of leaves, roots and actinorrhiza) were analyzed. The homogeneity of the variances was tested with the use of Levene's test. The length of stem necroses caused by *Phytophthora alni* subsp. *alni* in the flooding and non-flooding condition was

Table 1. The effect of long-term flooding and *Phytophthora alni* infection on the development of black alder saplings

Treatment per valid N	Length of necrosis (cm)	Root biomass (g)	Actinorrhiza biomass (g)	Height growth (cm)	Leaf length (cm)	Leaf biomass (g)	Chlorotic foliage
F-P-/20	0.00 ± 0.00^{a}	10.65 ± 0.78^{a}	0.61 ± 0.05^{a}	40.65 ± 2.55^{a}	9.12 ± 0.21^{a}	17.50 ± 0.85^{a}	0.00 ± 0.00^{a}
F-P+/19	10.62 ± 1.59^{b}	11.41 ± 0.81^{a}	0.55 ± 0.05^{a}	29.32 ± 2.66^{b}	8.17 ± 0.16^{b}	15.68 ± 1.02^{a}	0.89 ± 0.21^{b}
F+P-/20	0.00 ± 0.00^{a}	9.36 ± 0.66^{a}	0.55 ± 0.04^{a}	22.75 ± 2.03$^{b, c}$	7.89 ± 0.18^{b}	14.46 ± 0.70^{a}	2.75 ± 0.22^{c}
F+P+/20	17.86 ± 2.52^{c}	1.85 ± 0.60^{b}	0.09 ± 0.03^{b}	21.15 ± 2.34^{c}	7.51 ± 0.23^{b}	8.60 ± 1.11^{b}	3.25 ± 0.19^{c}

F-P- treatment: non-flooded and non-inoculated plants (control group); F-P+ treatment: non-flooded, inoculated plants; F+P- treatment: flooded, non-inoculated plants; F+P+ treatment: flooded and inoculated plants. Values (mean and standard error) followed by the same letter are not significantly different ($P > 0.05$). The degree of chlorotic foliage (8th column) rating on a scale 0–4 according to percentage (0 = 0–10%, 1 = 11–25%, 2 = 26–50%, 3 = 51–75%, 4 = 75–100%). All results are presented as means ± standard errors

analyzed with use of a unilateral *t*-test. The rate of chlorotic foliage was analyzed using a Kruskal-Wallis test followed by Tukey's post-hoc test for unequal n (Spjtvoll-Stoline test).

RESULTS AND DISCUSSION

Confirmation of flooding and *P. alni* infection effects on black alder

The analysis of covariance confirmed that the both factors (flooding and *P. alni* infection) and their combination significantly influenced ($P < 0.05$) the characteristics of alder plants that were evaluated in this study. The assumptions of normality and homogeneity were fulfilled ($P > 0.05$).

Flooding had a significant effect ($P < 0.05$) on root and actinorrhiza biomass, height growth and foliar length and biomass. Flooding had the most important effect on root biomass ($F = 36.00$, $P < 0.001$).

The *Phytophthora alni* infection had a significant effect ($P < 0.05$) on root and actinorrhiza biomass and foliar length and biomass. Infection had the most prominent effect on actinorrhiza biomass ($F = 32.76$, $P < 0.001$).

The interaction of both factors (flooding and *P. alni*) significantly affected ($P < 0.05$) root and actinorrhiza biomass, height growth and foliar biomass, the most prominent effect was identified in reduced root biomass ($F = 35.08$, $P < 0.001$).

The effect of covariate (plant height) was identified ($P < 0.05$) in root and actinorrhiza biomass, stem increase and foliar biomass.

General differences in morphology among treatments

The plants subjected to flooding, artificial *P. alni* infection and the combination showed many morphological changes when compared to the control group. These differences include yellowing, the presence of small, sparse foliage in the crown, height growth, secondary stem base thickening, hypertrophy of lenticels on the stems, development of adventitious roots and necrosis development. In addition, the distribution and amount of root and actinorrhiza biomass differed between treatment plants and control plants.

The plants in the flooded treatment were characterized by the presence of yellowing, small and sparse foliage. The collars and basal portions of the stems were thickened, apparently as a result of the formation of a higher proportion of aerenchyma tissues. The lenticels on the collars, bases of stems and roots growing on the surface of the substrate were hypertrophied. A greater amount of adventitious roots on the collars were produced, and the root biomass was developed primarily near the soil surface. The actinorrhizal nodules were often found on the roots near the soil surface or on the collars. These symptoms resemble those that have been generally described for trees subjected to flooding (McVean 1956; Kozlowski 1997).

The infected treatment showed symptoms characteristic of bleeding cankers and black alder decline, including the presence of small, yellowing and sparse foliage and bleeding cankers on the stems and collars (Jung, Blaschke 2004). The rot of roots growing near the soil surface caused by the pathogen was noted in several cases. Adventitious roots developed on collars of many inoculated plants. All plants infected with *P. alni* showed symptoms characteristic of bleeding cankers and black alder decline, with the exception of one plant that did not develop any cankers. In that plant, bacterial colonization was observed at the inoculation point. It is possible that bacterial antagonism prevented infection by *P. alni*. The stem necroses varied in length considerably.

The symptoms of the combined treatment included factors found in both the flooded treatment and the infected treatment. These symptoms include the presence of yellowing, small and sparse foliage. Secondary thickening of the stem was observed on some plants, at least partially, in non-infested areas. The lenticels on the collars, bases of stems and roots growing on the soil surface of many plants were hypertrophied. Adventitious roots developed on the plants, although they were often killed by the pathogen invading from the necroses of the main stems. The biomass of the roots and actinorrhizal nodules was predominantly localized near the soil surface as a response to flooding. These surface roots, however, can be probably more easily colonized and killed by *P. alni* than the deeper ones, which is in agreement with observation of Jung and Blaschke (2004).

Differences among treatments in detail

When the development of *P. alni* infection in the flooded and non-flooded condition was compared, the length of the stem necroses in the flooded treatment was found to be 17.9 cm after seven weeks, which was significantly longer ($P < 0.05$) than that of the non-flooded treatment (10.6 cm). The length of necroses varied greatly in both treatments, however (Table 1). This variation is similar to those of other studies conducted on black alder saplings and excised logs (Brasier, Kirk 2001; Lonsdale 2003;

Schumacher et al. 2005 ; Clemenz et al. 2006). In the flooded treatment 17 plants were totally girdled after seven weeks, whereas in the nonflooded treatment only 8 plants. The non-inoculated treatments showed no sign of bleeding cankers.

The amount of root and actinorrhiza biomass in the combined treatment was significantly lower than that of the other groups ($P < 0.001$). The amount of root and actinorrhiza biomass in the other treatments did not differ significantly (Table 1).

The rotten surface roots in the flooded inoculated treatment were killed in the consequence of extending stem necroses, because a majority of the killed surface roots were connected to the main necroses. It is possible that *P. alni* infected and destroyed some of the deep roots as well. However, we could not successfully isolate *P. alni* from the dead deep roots that were randomly obtained from the flooded treatment. We believe for several reasons that the pathogen does not play an important role in the rotting of the deep roots. The species has been rather infrequently (e.g. Jung, Blaschke 2004) or not at all (Schumacher et al. 2006) isolated from soil, rhizosphere or deep roots; we suppose that it can only weakly compete with other organisms in the natural soils. Jung and Blaschke (2004) found that in riparian, naturally infected and regenerated alders the infection usually starts at the collar or at the surface of exposed large roots and extends toward the root collar; the distal part of root system remains healthy. Moreover, in our experiment, flooded inoculated treatment was subjected to high acidity and anaerobic reducing conditions that probably created an unsuitable environment for the development of a substantial oomycetous infection on deep roots after a few days (Erwin, Ribeiro 1996; Schumacher et al. 2006). These results can indicate that the lower part of the root system dies as a result of hypoxia and that the surface roots are colonized and killed by *P. alni* as a consequence of extending stem necroses.

The stem length was reduced by 25 to 50% by both stress factors and by their combination ($P < 0.001$ in all cases). The stem length of the flooded treatment was not significantly different from that of the combined one (Table 1).

The length of the leaves was significantly reduced in the inoculated treatment ($P < 0.05$), flooded treatment ($P < 0.01$) and the combined treatment ($P < 0.001$) when compared to the control. The differences observed among these three treatments were not statistically significant (Table 1).

The foliar biomass of the combined treatment was reduced by approximately 50% when compared to the other treatments ($P < 0.001$). The differences in the foliar biomass observed among the other treatments were not statistically significant (Table 1).

The use of the Kruskal-Wallis test revealed a significant difference in the rate of chlorotic foliage among treatments. The post-hoc comparisons revealed that the control group differed significantly from the inoculated ($P < 0.01$), flooded and combined (both $P < 0.001$) treatments. The rate of chlorotic foliage was highest in the combined treatment (3.25 on a scale of 0 to 4); however, there was no significant difference observed between this treatment and the flooded one (Table 1). The flooding and subsequent hypoxia leads to the yellowing of foliage (Kozlowski 1997; Günthardt-Goerg, Vollenweider 2007). These significant differences in the rate of chlorotized foliage in the flooded treatments compared to the non-flooded ones indicate a role for hypoxia.

CONCLUSIONS

The majority of the assessed criteria in the experiment, including the amount of biomass of all investigated plant parts, was significantly reduced in the combined (flooded inoculated) treatment. These results are consistent with *P. alni* being more effective in the flooded treatment than in the non-flooded one. The plants affected by both factors were underdeveloped and declined quickly; some were dying by the end of the experiment.

The most important outcome of this study is the confirmation that *P. alni* causes more significant damage to alders that are stressed by flooding than to unstressed plants. Flooding clearly induces a decrease in host resistance (reduced uptake of nitrogen and other nutrients, investment to rebuilding of the root system, etc.) and accelerates the development of the disease caused by *P. alni*.

From an ecological point of view, alder stands with periodical or summer flooding and/or with a high water table can have a higher incidence of disease, as well as a more severe course of epidemics and higher losses of trees. This situation very probably occurred in great extent in the Vltava River catchment after the summer floods in 2002. The subsequent substantial stress persisted several months and contributed to the sudden onset of phytophthora alder decline in large affected areas in the Vltava River catchment.

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