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Combined effects of drought stress and *Armillaria* infection on tree mortality in Norway spruce plantations

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ABSTRACT

For the past two decades in the Czech Republic, Norway spruce (*Picea abies*) trees have been weakened by drought and subsequent attack by *Armillaria* root disease and bark beetles (*Ips typographus, I. duplicatus*, and *Pityogenes chalcographus*). We determined whether thinning of trees decreased mortality at 40 forest locations in the Czech Republic. The majority of the locations experienced long-term drought stress and very low groundwater levels. We also identified the species of *Armillaria* associated with the spruce decline and determined the reliability of visual detection of *Armillaria* infection.

The mortality of trees at the 40 locations increased nearly linearly during the 5 years of the study. Sites were established in 2012, thinned or not thinned in October 2012, and were assessed in September and October in each year from 2012 to 2016. Thinning, with an intervention intensity of 30–40%, did not alter tree mortality at the locations. The proportion of dead trees was significantly greater in older than in younger stands in the last 3 years of the study.

Among the trees that were suspected of being attacked by *Armillaria* based on visual inspection by foresters, 53% were confirmed (supported by statistical significance) to be infected by *Armillaria* spp. after morphological and genetic assessment. Among the trees with confirmed infections, 56% were infected by *Armillaria ostoyae*, 32% were infected by *A. cepistipes*, and 1% were infected by *A. gallica* (the rest could not be identified). Resinosis was positively associated with the occurrence of *A. ostoyae*. This species was more common on loamy flat locations, whereas *A. cepistipes* was more common on stony, sloped locations. The occurrence of *Armillaria* was negatively associated with increasing pH.

Although our results indicate that spruce decline is strongly associated with the presence of *Armillaria* and that visual detection of *Armillaria* is reliable, management options for reducing *Armillaria* infection and damage appear to be highly limited. Forest managers should begin preparing to convert stands of Norway spruce to stands of other tree species that are better adapted to the local conditions and that are less susceptible to attack by *Armillaria* species.

1. Introduction

Forest management has significantly changed during the last two decades. Land-use change (i.e., the shift from semi-natural forests to intensively managed plantations) together with global climate change (i.e., increasing temperatures and decreasing precipitation) have often led to forest decline, and many tree species have experienced dieback worldwide (Allen et al., 2010). It is often difficult to determine whether changes in land-use or climate or their interaction has been most responsible for forest decline. The cause of contemporary forest decline has been the focus of many studies (e.g., Gonthier et al., 2010; Sinclair, 1965; White, 1986; Mueller-Dombois, 1987; Manion, 1991; Auclair et al., 1992; Houston, 1992; McEwan et al., 2011; Millar and Stephenson, 2015; Pautasso et al., 2012; Rehfuess, 1985). Decline often involves a complicated interaction between abiotic and biotic factors that limit tree growth, reduce foliage quality, and weaken root systems. These interactions can kill individual trees and entire stands (Garcia, 2009; Van Mantgem et al., 2009).

Another factor contributing to forest decline is disease (Lilja et al., 2006; McKinney et al., 2014; Mitchell et al., 2014; Kuzmin and

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Kuzmina, 2015; Černý et al., 2016). Pathogens often cause disease on particular tree species that serve as hosts (Haavik et al., 2015), and pathogens are currently contributing to the decline of Norway spruce (*Picea abies* (L.) H. Karst.) in Europe (Gonthier et al., 2010; Pautasso et al., 2012; Rehfuess, 1985).

Pure spruce forests are now common throughout Central Europe (Spiecker, 2000). Stands of Norway spruce account for 51% of the forested area in the Czech Republic, and most of this forested area is represented by commercial plantations (MZe, 2014). Norway spruce is not native to many areas of Central Europe, and the decline of the plantations in the region has been attributed to inappropriate abiotic and geographic conditions (Holuša, 2004). When allochthonous trees like Norway spruce in Central Europe are exposed to low-nutrient conditions (Kulhavý and Klimo, 1998) and intensive mechanical damage (resulting from game), they become highly vulnerable to extreme weather events (frost, rapid drops in temperature, and drought) and to pathogen attack (Holuša, 2004; Šrámek et al., 2008).

The decline of Norway spruce plantations in the Czech Republic was first observed in the late 1990 s. In contrast to the decline of native mountainous spruce forests due to emissions (Balcar et al., 1994), the decline of trees in Norway spruce plantations was first manifested by the yellowing of leaves over large areas. This was followed by an increase in tree mortality around year 2000. The decline of Norway spruce involved 32 000 ha in the late 1990 s, and the affected area has been steadily increasing (Hlásny and Sitková, 2010).

Drought has been confirmed to be an important mortality factor for Norway spruce in the lowlands of the Czech Republic (Stanovský, 2002; Holuša et al., 2010); a dramatic decline in forest health was observed after the warm and dry period in 2003 (Holuša and Liška, 2002; Holuša et al., 2006). Trees weakened by drought were attacked by *Armillaria* root disease and were further weakened because their damaged root systems could not supply adequate water to the trees even when water was available. These weakened plantation trees were subsequently attacked by bark beetles (Holuša and Liška, 2002; Holuša et al., 2006; Hlásny and Sitková, 2010). The dominant species of bark beetles are *Ips typographus* (Linné 1758) and *Ips duplicatus* (Sahberg, 1836) in old spruce stands, and *Pityogenes chalcographus* (Linné 1767) in young stands. *Ips amitinus* (Eichhoff, 1871) has been found only occasionally (Holuša and Liška, 2002; Holuša et al., 2010, 2012).

Yellowing of leaves has been mainly detected in young stands (Slodičák and Novak, 2010). An increase in the infection of young stands by *Armillaria* spp. led forest managers to question whether trees should be thinned (Dušek et al., 2014; Jeniš, 2014). An important concern was whether the fresh stumps and logging scars caused by thinning or pruning can increase infection by *Armillaria* spp. and other pathogens (Robinson, 2003; Legrand et al., 2005).

Based on these decline problems of Norway spruce, we initiated a landscape-scale study in cooperation with forest managers. The study area included both moderate habitats (characterized by loamy soil and little or no slope) and extreme habitats (characterized by stony slopes) that differ in management (Čermák and Holuša, 2011).

The study had three objectives. First, by comparing natural mortality in plots that were thinned or not thinned, we tested the hypothesis that thinning increases natural mortality. Second, we determined whether mortality was affected by elevation and habitat type. Third, we determined the host vitality preferences of species in the genus *Armillaria*.

2. Materials and methods

2.1. Selection of study locations

The study was conducted at 40 locations in a hilly region with a surface of 100 × 50 km in the eastern Czech Republic (Table 1). Location altitude ranged from 280 to 680 m a.s.l. Mean annual air temperature was 9 °C, and annual precipitation was about 700 mm during the study.

A trend of increasing mean annual air temperature has been recorded in the study area over the past 50 years. Some years can be characterized as having above-average air temperatures from the 1990s and have experienced substantial spruce decline (Hlásny and Sitková, 2010). Periods of drought occurred in the study area in the 1990s (Holuša and Liška, 2002). A precipitation deficit of 200–250 mm compared to the long-term average was documented in the extremely dry year of 2003 (Hlásny and Sitková, 2010).

To assess drought risk for tree species in the study area, water balance maps for the years 2012–2014 was used. To accomplish this, the sum of precipitation was compared with evapotranspiration values (Šrámek et al., 2015). The calculation was performed for deep soil with available water capacity 170 mm in the deep of 1 m. The long-term stress was evaluated according to Braun et al. (2015) who found strong a relationship between mortality of spruce and the ratio of actual and potential evapotranspiration.

From 2012 to 2014, spruce trees in > 70% of the localities in the study area experienced long periods of drought stress (Šrámek et al., 2015). In the summer and autumn of 2015, the groundwater level and available water capacity were extremely low across the entire area (Daňhelka et al., 2015).

As reported by Šrámek et al. (2015), the long-term drought has resulted in strongly acidified soils with a median pH ($CaCl_2$) < 4 in the organic layer and in the upper 30 cm of the mineral layer. Exchangeable calcium is strongly deficient in the mineral layer to a depth of 50 cm, magnesium is deficient to a depth of 60 cm, and potassium is deficient to a depth of 10–40 cm. Total nitrogen content, on the other hand, is sufficient within the soil profile. Extractable contents of cadmium, lead, and zinc are above normal probably because of the high anthropogenic deposition in this industrial region.

The selected study locations were all > 1 ha and were dominated by Norway spruce trees that were < 50 years old. All stands had been artificially established with a uniform spacing and with a density of 3500–4500 trees/ha. The stands were regularly managed in accordance with models for managing Central European spruce stands (Slodičák and Novák, 2007). Half of the locations were in the thicket stage (10–24 years old), and half were in the small pole stage (26–41 years old). Half were at low altitude (about 300 m), and half were at high altitude (about 500 m) (Table 1). Half of the locations had a "moderate" habitat, and half had an "extreme" habitat. The moderate habitats had a flat terrain and nutrient-rich loamy soils that were normally developed mesotrophic to eutrophic cambisols; these soils had good water-holding capacity and were permeable and deep. The extreme habitats were exposed and stony cambisols with slopes > 30°.

Two sites were established at each location and were separated by about 30 m. At each site, a group of about 50 spruces taller than 1.3 m were de-branched and assigned a serial number (shorter spruces were excluded). The first tree selected was in the centre of the area, and other trees were selected on a curve spiralling from the centre. These were the trees that were evaluated as described in the following sections.

2.2. Evaluation of crown symptoms

Dieback, which was indicated by an absence of leaves at the terminal and adjacent whorls of branches, was evaluated as follows: 0 – loss of leaves is not apparent; 1 – loss at the terminal; 2 – loss at the terminal and on the first whorl; 3 – loss at the terminal and on the first and second whorls; and 4 – loss at the terminal and on the first to third and potentially other whorls. If leaves were missing only on the youngest shoots of some of the whorls beyond the terminal, a value of 1 was recorded. If the tree was dry, other tree parameters were not evaluated (Appendix A).

Discoloration of foliage was evaluated based on the dominant leaf colour of the entire crown: 1 – healthy green; 2 – light green to slightly yellow; 3 – yellow; and 4 – rusty (usually with active bark beetle