



Resilience of *Phialocephala fortinii* s.l. – *Acephala applanata* communities – Effects of disturbance and strain introduction



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ABSTRACT

Members of the *Phialocephala fortinii* s.l. – *Acephala applanata* species complex (PAC) are ubiquitous endophytes forming complex communities in roots of conifers and ericaceous shrubs across the Northern hemisphere. Two kinds of disturbances (clear-cutting and drought) and their effects on the resident PAC community, as well as on the introduction of alien strain 7_45_5, were investigated using mesocosms with natural Norway spruce (*Picea abies*) regeneration, both under controlled climate chamber conditions and natural conditions in the forest.

This is the first record of successful strain introduction into a well-established forest ecosystem. Introduction was more successful when planting inoculated living spruce saplings, compared to inoculation using autoclaved colonized roots. 7_45_5 was less assertive in the forest, where *Phialocephala subalpina* clearly dominated. Clear-cutting favored *A. applanata* and simultaneously reduced the overall frequency of PAC. Drought only had a significant influence on 7_45_5, which was more abundant in dry than moist, non-clear-cut plots. To conclude, disturbances and arrival of foreign strains can alter resident PAC communities significantly.

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1. Introduction

Ecological disturbances are events that influence competition, as well as substrate and resource availability within ecosystems (White and Jentsch, 2001). In forest ecosystems, especially in the boreal regions of North America, the effect of clear-cut logging and wildfire disturbance has been widely studied (Jones et al., 2010; Barker et al., 2013). Since the colonization of roots by mycorrhiza evidently improves establishment and growth of forest tree species, the effects of disturbance on the root systems are crucial for forest management practices, along with climate change (Talbot, 2017). Tree roots are also colonized by a large variety of endophytic fungi and bacteria with various effects on their hosts ranging from beneficial to harmful (Sieber and Grünig, 2006; Tellenbach et al., 2011; Mayerhofer et al., 2012; Gaiero et al., 2013). A large group of root colonizing endophytes of coniferous trees in boreal forests belong to a helotialean ascomycete species complex of dark

septate endophytes (DSE) (Stoyke and Currah, 1991) called *Phialocephala fortinii* s.l. – *Acephala applanata* (PAC) (Sieber and Grünig, 2006), consisting of at least 21 morphologically indistinguishable cryptic species (CSP) (Grünig et al., 2003, 2007; Grünig and Sieber, 2005) of which eight have been formally described (Grünig and Sieber, 2005; Grünig et al., 2006). Recently, the genome of *Phialocephala subalpina* (CSP6) has been sequenced (Schlegel et al., 2016). Factors shaping the community structure of PAC species are still unknown, yet, local PAC communities are highly diverse (Queloz et al., 2005, 2008; Grünig et al., 2006; Queloz, 2010; Stroheker et al., 2016). The influence of ecological factors on PAC community assembly seems to be low (Queloz et al., 2008). The mode of dispersal of PAC remains unknown and no sexual states have been found even though mating type loci and evidence for reproduction exist (Grünig et al., 2004, 2006). Asexual spores are rarely formed, are not known to be airborne and have never been found to germinate (Grünig et al., 2004). Long distance transfer may occur through relocation and planting of colonized seedlings from either nurseries or other forest sites (Brenn et al., 2008; Stenström et al., 2014).

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When talking about fungal invasions, establishment of pathogenic fungi in a new environment is most commonly considered (Desprez-Loustau et al., 2007). Unintentional introduction of fungi through propagative plant material within areas with comparable climates is a well-recognized dispersal means (Palm and Rossmann, 2003). Prominent examples being *Hymenoscyphus fraxineus*, the cause of European ash dieback, *Cryphonectria parasitica* causing chestnut blight or *Ophiostoma novo-ulmi* responsible for Dutch elm disease (Anagnostakis, 1987; Gross et al., 2013). Within their native range, these pathogens unusually show low virulence on their hosts (Zhao et al., 2012), though, once introduced into a new environment, they can be highly virulent due to lack of co-evolution of pathogen and host (Queloz et al., 2011; Gross et al., 2013; Landolt et al., 2016).

A considerable number of non-pathogenic fungi are also assumed to have been transported from their native geographical location to other foreign habitats. These translocations, however, are often difficult to assess due to a lack of local reference data (Desprez-Loustau et al., 2007). In addition, little attention has been paid to fungal transplantations within their native range. Even less attention is being paid to the dispersal of fungal endophytes.

Another means of introduction, although much slower, is spreading via root contact between infected stumps and healthy Norway spruce tree individuals as reported for the root-and-butt-rot-causing fungus *Heterobasidion annosum* s.l. (Hodges, 1969; Stenlid, 1987; Garbelotto and Gonthier, 2013), or the root-rot-causing *Armillaria* species (Morrison and Mallett, 1996).

For PAC, the successful introduction of other non-resident strains into a well-established ecosystem by means of root contact has never been tested. The resident PAC community in roots of living trees is well-established and has shown stability over several years in natural forest ecosystems (Queloz et al., 2005). Thus, artificially introduced PAC strains would probably be unable to integrate themselves into a stable resident PAC community. Nonetheless, disturbances could be potential driving forces creating niches for the establishment of new thalli (White and Jentsch, 2001). Host defoliation resulted, for example, in increased *P. fortinii* colonization of host roots (Saravesi et al., 2013). The dieback of roots due to tree harvesting is thus expected to create new niches for any introduced PAC species. In this context, we would like to test the following two hypotheses: (1) a foreign (alien) PAC strain will be unable to integrate itself into a well-established, resident PAC community; (2) disturbance through tree harvesting and drought will facilitate establishment of an introduced PAC strain. The hypotheses were tested in mesocosms via introduction of an alien PAC strain to natural Norway spruce (*Picea abies*) regeneration under two different disturbance regimes: clear-cutting and drought.

2. Material and methods

2.1. Study sites and experimental setup

The experiment was set-up as a split-plot design with “forest” and “climate chamber” as the two whole-plot factors as follows. Two study sites were established in two geographically separate Norway spruce forest stands (50–80 years of age) with dense natural regeneration (2–10 years of age, 5–30 cm in height) near

Eintürnen, Germany (study site 1: 47° 51' N, 9° 52' E; histic gley soil with intermediate field capacity (LGRB, 2017); study site 2: 47° 5' N, 9° 51' E, para-brown earth with intermediate field capacity (LGRB, 2017); linear distance between sites: 0.5 km). Four subsites (2 × 2 m) were established at each study site, each comprising three study plots (55 × 36 cm) (Fig. S1). For each subsite, two study plots (containing spruce regeneration) were excavated using a spade (topsoil; uppermost 12 cm), placed into plastic boxes (55 × 36 × 12 cm) with holes in the bottom for water drainage and transferred to a climate chamber to be studied under dry and moist conditions, while the third study plot was left in the forest to serve as a control under natural conditions for 1.5 yr. The assignment of the study plots to the different treatments was random. Roots of the resident Norway spruce trees were sampled at the intersections of a 9 × 9 cm grid, which resulted in a total of 24 sampling points in each study plot (Fig. S2). Each study plot was then further divided in three, and two thirds were inoculated with non-resident (alien) PAC strain 7_45_5 (see below) using two different types of inocula (T1 and T2), whereas the last third was left untouched and served as control (T3). One inoculum consisted of sterilized, dead Norway-spruce-root segments colonized by 7_45_5 (T1) and the other one of Norway-spruce saplings with roots colonized by 7_45_5 (T2). Each inoculum was applied to one third of the plot (Table 1). The initial PAC community was assessed prior to all inoculations and plot alterations.

Natural regeneration present within study plots of subsites two and four were clear-cut, with the exception of the newly-planted, inoculated Norway spruce trees (Fig. S1).

Four different climate chamber programs representing the four seasons were defined (Table S1). To account for possible spatial heterogeneity within the climate chamber, two separate complete blocks were set up, all comprising clear-cut and non-clear-cut, as well as moist and dry study plots with random assignment of the plots to the blocks. Moist plots were watered with an average of 30 L/m² per month, whereas dry plots were given half the amount. All study plots in the climate chamber were watered twice a week.

2.2. Preparation of inocula

All inoculations were performed with *Phialocephala fortinii* s.s. (CSP7, strain 7_45_5, Böldmeren, Switzerland), since presence of *P. fortinii* s.s. at the study sites was rare (as shown by a preliminary study) and strain 7_45_5 was not present at the study site prior to experimentation and clearly distinct from other possible *P. fortinii* s.s. strains by its microsatellite profile (Queloz et al., 2010).

Liquid cultures of *P. fortinii* s.s. strain 7_45_5 for treatments 1 and 2 were produced according to Tellenbach et al. (2011): Colonized agar plugs with a diameter of 4 mm were cut out of the margin of a growing colony on Terramycin[®] malt agar (TMA: 15 g/l BECOAGAR[™] (Type 2521), W. Behrens GmbH & Co. KG, Hamburg, Germany; 20 g/l malt, Alpha malt, Klipfel, Rheinfelden, Switzerland; 50 mg/l oxytetracycline, Pfizer Ltd., India). Three agar plugs (4 mm in diameter) were placed into each Erlenmeyer flask containing 50 ml of 2% malt broth. The Erlenmeyer flasks were incubated at 20 °C on a rotary shaker at 90 rpm for 22 d.

Table 1
The three different types of inoculum for each study plot.

Type 1 inoculation	T1	Sterilized Norway spruce root segments colonized by strain 7_45_5 were buried at eight sampling points in each study plot
Type 2 inoculation	T2	A Norway spruce sapling with roots colonized by strain 7_45_5 was planted at each of the eight sampling points
Type 3 inoculation	T3	Left untouched (no inoculum) as the control

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