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SUSCEPTIBILITY OF *Picea abies* AND *Pinus sylvestris* SEEDLINGS OF VARIOUS ORIGINS TO *Heterobasidion annosum* AND *H. parviporum*

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Five-year-old Norway spruce and four-year-old Scots pine seedlings of various origin were inoculated with Heterobasidion annosum *s.s. and* H. parviporum *to estimate whether the susceptibility of seedlings to* Heterobasidion *was affected by origin of seeds. In total, 520 spruce and 538 pine seedlings from different seed sources and provenance regions of Latvia were tested. Four months after inoculation the fungal growth was measured. The results highlight differences between development of* H. annosum *and* H. parviporum *in spruce and pine seedlings. We did not find any seed source that was more resistant than others.*

Key words: *pine, spruce, Heterobasidion root rot, resistance test.*

INTRODUCTION

Norway spruce (*Picea abies* (L.) H. Karst) forests of Latvia are divided into three geographically distinct provenance regions and Scots pine (*Pinus sylvestris* L.) forests into two (Fig. 1). The provenances differ from each other in productivity and quality, such as in stem straightness and branch thickness (Baumanis u.c., 2001). In establishing new plantations local seedlings are recommended, because they may be better adapted to site conditions and more resistant to pathogens (Gonthier and Thor, 2013). It is known that environmental factors can influence tree susceptibility to fungal pathogens (Lindberg and Johansson, 1992; Santini *et al.,* 1997; Karlsson *et al.,* 2008)).

Root and butt rot caused by several species of *Heterobasidion* is one of the most destructive diseases of conifers in the northern temperate regions (Gonthier and Thor, 2013). In Latvia, a sample of 25 000 stumps of Norway spruce was investigated (Arhipova *et al.,* 2011); 21.8% of them contained butt rot. *Heterobasidion parviporum* Niemelä & Korhonen was the most common decay-causing fungus. Another *Heterobasidion* species, *H. annosum* (Fr.) Bref. *sensu stricto*, is common in Scots pine stands of Latvia but occurs also on spruce (McLaughlin and Šica, 1993; Zaļuma *et al.,* 2015).

Adaptation of *H. parviporum* for growth in spruce is well documented (Swedjemark *et al*., 2007) and it has been shown that fungal growth in sapwood varies significantly between spruce clones (Swedjemark *et al.,* 1997; Swedjemark and Stenlid, 1997) and families (Swedjemark and Karlsson, 2004; Skrøppa *et al.,* 2015). In many artificial inoculation experiments, the growth rate of many isolates of *Heterobasidion* in *P. abies* and *P. sylvestris* seedlings has been investigated in relation to the virulence of the pathogen (Swedjemark *et al.,* 1999). In order to test a wide collection of seedlings and origins we used only one isolate of

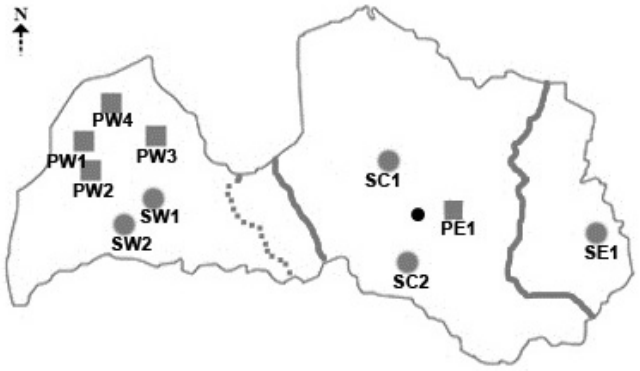

Fig. 1. Seed sources and provenance regions for *Pinus sylvestris* and *Picea abies* in Latvia. Dashed line separates provenance regions of *P. sylvestris* and solid line separates provenance regions of *P. abies*. Grey square — seed source of *P. sylvestris*, grey circle — seed source of *P. abies,* black circle — Forest Research station in Jaunkalsnava.

Table 1

CHARACTERISTICS OF *Pinus sylvestris* AND *Picea abies* SEEDLINGS USED IN THE STUDY

Tree species	Provenance region	Seed source (coordinates)	Number of seedlings	Code	
				Provenance region	Seed source
*P. sylvestris**	Eastern	Sāvienas seed orchard (N 56.4093, E 26.0465)	84	PE	PE1
*P. sylvestris**	Western	Zlēkas seed orchard (N 56.4910, E 24.5547)	84	PW	PW1
*P. sylvestris**		Dravas seed orchard (N 57.0357, E 21.5641)	89		PW2
P. sylvestris		Andumi seed orchard (N 57.9195; E 22.4292)	176		PW3
P. sylvestris		Ezernieki seed orchard (N 57.2058, E 21.5658)	105		PW4
*P. abies**	Eastern	Ludza forest district, Ludza forestry (N 56.30, E 27.45)	107	SE	SE1
*P. abies**	Western	Remte seed orchard (N 56.4477, E 22.4745)	99	SW	SW1
*P. abies**		Saldus forest district, Sesile forestry (N 56.36, E 21.35).	106		SW2
*P. abies**	Central	Cēsis forest district, Zaube forestry (N 57.02, E 25.45)	108	SC	SC1
*P. abies**		Jēkabpils forest district, Brieži forestry (N 56.23, E 25.47)	100		SC2

* Seedlings used also in earlier experiment (Zaļuma *et al.,* 2015)

H. annosum and *H. parviporum* in inoculation experiments. The aim of this study was to compare the development of *H. annosum* s.s. and *H. parviporum* in spruce and pine seedlings, and to determine whether the susceptibility of seedlings to *Heterobasidion* is affected by origin of seedlings.

MATERIALS AND METHODS

Plant material. In the experiment, 520 five-year-old spruce seedlings from five seed sources and 538 four-year-old pine seedlings from five seed sources were used (Table 1, Fig 1). All seedlings were cultivated in the experimental forest nursery of the Forest Research Station in Jaunkalsnava ($56^{o}68'$N, $25^{o}96'$E) (Fig. 1) under field conditions (Zaļuma *et al.,* 2015).

Fungal isolates. The isolates were selected on the basis of strong disease symptoms that these fungal genotypes caused in the forest from which they were isolated. Heterokaryotic pure culture of *H. parviporum* (strain S37) was isolated in central Latvia from living *P. abies* with a long decay column extending up to 9.8 m (Arhipova *et al*., 2011). Heterokaryotic culture of *H. annosum* s.s. (VStr2821aP) represented a genotype that had infected seven *P. sylvestris* trees within a 9-m radius in eastern Latvia (K. Pāruma, unpublished data). The pure cultures were identified by pairing with homokaryotic tester isolates (Korhonen, 1978).

Inoculation of seedlings. Inoculum (pieces of spruce sapwood) was prepared using a procedure of Swedjemark and Stenlid (1995); the only difference was the size of the inoculum: length 0.8 cm and diameter 0.3–0.4 cm. For inoculation, the lower part of the seedling stem was surface disinfected with 70% ethanol. A circular wound (diameter 0.4 cm, depth 0.5 cm) was made 1–2 cm above the soil surface using a disinfected drill positioned at an angle 45 degrees to the surface. A wood block colonised by *Heterobasidion* was inserted into the wound, which was then covered and sealed with gardening wax. Controls were treated similarly, using sterile wood blocks (Zaļuma *et al.,* 2015). A total of 213 pine seedlings and 201 spruce seedlings were inoculated with *H. annosum*; 216 pine seedlings and 199 spruce seedlings were inoculated with *H. parviporum.* As controls we used 109 pine and 120 spruce seedlings. Plants were grown under normal field conditions and regularly watered (1–2 times per week) until harvested. The experiment was started in 13 September, 2011. Mean air temperature was 13.6 ^{o}C in September, 8.7 ^{o}C in October, 5.1 ^{o}C in November, 2.6 ^{o}C in December and 1.2 ^{o}C in the beginning of January, according to data from LLC "Latvijas, Vides, ģeoloģijas un meteoroloģijas centrs" (Latvian Environment, Geology and Meteorology Centre).

Sampling. In 12 January 2012, plants were removed from pots, and their length and diameter at root collar were measured. The spread of fungus above and below the point of inoculation was also measured. Plants were cut at root collar level, branches were removed, and the stem surface was flamed to sterilise. An approximately 15–20-cm long piece from stem base was cut into 0.2–1.1-cm thick discs with disinfected secateurs. The discs were surface sterilised by quick flaming and placed on moist sterile filter paper in Petri dishes. After seven days incubation at room temperature, the discs were examined under stereo microscope for conidiophores of *Heterobasidion*. Re-isolation of inoculated isolate was attempted from 10 pine and 10 spruce plants; half of them had been inoculated with *H. annosum* and the other half with *H. parviporum* (Zaļuma *et al.,* 2015). Obtained isolates were paired with the original strain on malt agar medium to test for somatic compatibility (Stenlid, 1985).

At the time of sampling, *Heterobasidion* had already spread outside of the sampled region (upwards or downwards or both) in stems of 123 spruce seedlings. These seedlings were excluded from calculations concerning differences in spread of mycelium in different directions. Mean growth upwards, downwards and total longitudinal growth in both

tree species and in each seed source was calculated. Total longitudinal growth of *Heterobasidion* was calculated also for spruce and pine in each provenance region.

Statistical analysis. Kruskal-Wallis chi-squared and Mann–Witney U, Tukey HSD tests were used to test for differences in growth of *Heterobasidion*. Graphical and mathematical processing and statistical analysis were carried out using Microsoft Excel 2010 and R version 3.1.2 (Anonymous, 2014).

RESULTS

Mean height of pine seedlings was 70.4 cm ± 0.54 cm (n = 538) and root collar diameter was 1.34 cm ± 0.01 cm (n = 538). Mean height of spruce seedlings was 70.7 cm ± 0.58 cm (n = 520) and root collar diameter was 1.38 cm ± 0.01 cm (n = 520). The differences between spruce and pine in diameter and height were not significant ($p > 0.05$).

Die-back of the inoculated and control seedlings was not observed during the incubation period. All re-isolations of the fungus from inoculated seedlings were vegetatively compatible with the inoculated strain, indicating that the re-isolated strain was identical with the inoculated one.

Both *Heterobasidion* species spread significantly faster in spruce than in pine (Table 2). In spruce, *H. parviporum* was slightly but not significantly faster than *H. annosum,* and both *Heterobasidion* species spread significantly faster upward from the inoculation point (Table 3). In pine, *H. annosum* spread significantly faster than *H. parviporum*, and the spreading of both species was slightly but not significantly faster downward.

Growth of *Heterobasidion* in seedlings from different seed sources. Pine. In pine seedlings, growth of *H. annosum* was significantly faster in seedlings from the western seed source PW3 compared to eastern PE1, but between other seed sources of pine we did not detect significant differences. Also, the growth of *H. parviporum* was fairly similar in all pine seed sources (Fig. 2).

Spruce. In spruce seedlings, growth of *H. annosum* was a little faster in western seed sources SW1 and SW2 compared to central and eastern ones SC1, SC2 and SE1, but the differences were not significant. *H. parviporum* spread significantly faster in SW2 seedlings compared to SC, and in SE1 seedlings compared to SC1, SC2, and SW1. Differences between seedlings from other sources were not significant (Fig. 2).

Table 2

MEAN LONGITUDINAL GROWTH OF *Heterobasidion annosum* AND *H. parviporum* IN SEEDLINGS OF *Pinus sylvestris* AND *Picea abies*

Species	Growth of *Heterobasidion* ± SE, cm*	
	P. sylvestris	*P. abies*
H. annosum	1.78 ± 0.07 a	7.73 ± 0.25 c
H. parviporum	1.24 ± 0.06 b	8.03 ± 0.24 c

*For each variable, means with different letter subscripts, whether in rows or column, are significantly different ($p < 0.05$). SE, standard error.

Table 3.

MEAN GROWTH OF *Heterobasidion annosum* AND *H. parviporum* IN SEEDLINGS OF *Pinus sylvestris* AND *Picea abies* UPWARD AND DOWNWARD FROM INOCULATION POINT

	Growth in *P. sylvestris* ± SE, cm*		Growth in *P. abies* ± SE, cm*	
	Upward	Downward	Upward	Downward
H. annosum	0.87 ± 0.04 a	0.92 ± 0.04 a	3.57 ± 0.18 b	2.76 ± 0.23 d
H. parviporum	0.62± 0.04 a	0.63± 0.04 ab	3.62 ± 0.11 c	3.09± 0.11 e

*For each variable, means with different letter subscripts, whether in rows or column, are significantly different ($p < 0.05$). SE, standard error.

Growth of *Heterobasidion* in seedlings from different provenance regions. Pine. There were no significant differences in the growth of *Heterobasidion* species in pine seedlings from different provenance regions. *H. annosum* grew slightly faster in western PW seedlings in comparison to eastern PE seedlings, and *H. parviporum* grew faster in PE compared to PW seedlings ($p = 0.079$) (Table 4).

Spruce. *H. annosum* spread significantly faster in SW seedlings compared to SC seedlings, while there was no significant difference between SW and SE seedlings ($p = 0.065$) and between SC and SE seedlings. Growth of *H. parviporum* was significantly faster in SE seedlings than in SC

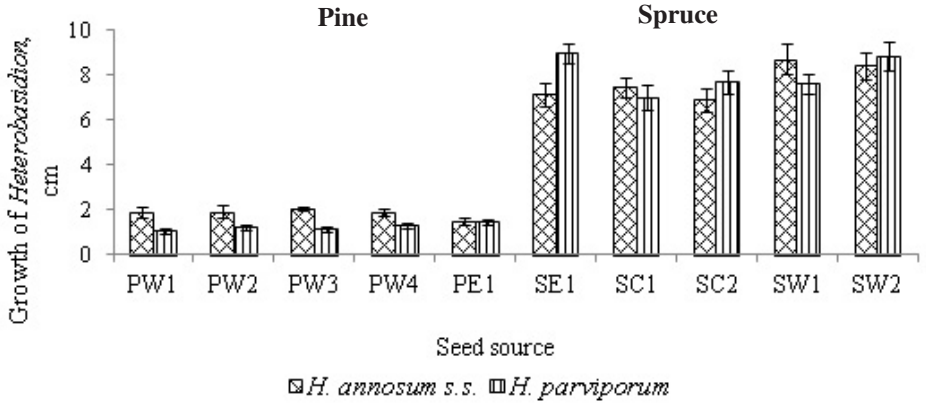

Fig. 2. Mean longitudinal growth of *Heterobasidion annosum* and *H. parviporum* (in 122 days) in different seed sources of *Pinus sylvestris* and *Picea abies*, standard error included.

Table 4.

MEAN LONGITUDINAL GROWTH OF *Heterobasidion annosum* AND *H. parviporum* IN SEEDLINGS OF *Pinus sylvestris* AND *Picea abies* FROM DIFFERENT PROVENANCE REGIONS

Seed source	*H. annosum*	*H. parviporum*
	Growth of *Heterobasidion* ± SE, cm*	Growth of *Heterobasidion* ± SE, cm*
PW	1.84 ± 0.07 a	1.20 ± 0.06 b
PE	1.52 ± 0.15 b	1.47 ± 0.05 b
SW	8.57 ± 0.45 ce	8.25 ± 0.40 cde
SC	7.18 ± 0.33 d	7.34 ± 0.38 d
SE	7.15 ± 0.54 cd	9.00 ± 0.45 e

*For each variable, means with different letter subscripts, whether in rows or column, are significantly different ($p < 0.05$). SE, standard error.

seedlings and slightly faster than in SW seedlings ($p = 0.082$) (Table 4).

DISCUSSION

In the present work seedlings were inoculated by *Heterobasidion* through stem wounds, but in nature *Heterobasidion* invades conifer stands by basidiospores through newly cut stumps or fresh wounds on roots. Stem wounds are colonised only occasionally (Redfern and Stenlid, 1998). However, stem wound infection may be more significant in unmanaged forests, where fresh stumps are rare or absent (Garbelotto and Gonthier, 2013).

Although high mortality has been observed in many experiments with *Heterobasidion* (Swedjemark and Stenlid, 1995; Swedjemark *et al.* 1999; Werner and Łakomy, 2002), we did not observe any seedling die-back or external symptoms like wilting and needle discolorations in our experiment. Relatively low mortality of seedlings may be explained with low virulence of the pathogen (Kuhlman, 1970; Worrall *et al.,* 1983; Łakomy *et al.,* 2011) or short incubation period (Worrall *et al.,* 1983; Swedjemark *et al*., 2001). The mortality rate increases with length of incubation period. For example, the mortality rate of four-year-old clones of *P. abies* inoculated with *H. parviporum* and incubated at 18 °C was 0.5% after 34 days, and 20% after 83 days (Swedjemark *et al*., 2001). In our experiment the incubation period (122 days) was longer; but average air temperature was lower; so we do not consider that the incubation period was insufficient to cause seedling mortality. Kuhlman (1970) showed that *Heterobasidion* with low virulence is often replaced by *Trichoderma* (in that experiment inoculation holes were made in the root collar). In our research we did not observe the replacement of *Heterobasidion* by *Trichoderma.* Also, an important factor in susceptibility to *Heterobasidion* is vitality of seedlings (Swedjemark and Stenlid, 1997). In their earlier inoculation experiment, where the seedlings of spruce had undeveloped root systems, the mortality caused by *Heterobasidion* was high (Swedjemark and Stenlid 1995).

The growth of both *Heterobasidion* species in spruce seedlings was significantly faster than in pine seedlings, and in spruce seedlings the fungus spread more rapidly upwards. In pine seedlings the situation was rather the opposite. This is mainly in agreement with observations made in other studies (Stenlid and Swedjemark, 1988; Lindberg, 1992; Swedjemark and Stenlid, 1995; Swedjemark *et al.,* 1999). In mature spruce *Heterobasidion* often spreads high up in the stem, up to 12 m (Stenlid and Wästerlund, 1986), but in pine the growth of *Heterobasidion* is usually restricted to the stem base (Korhonen and Stenlid, 1998). Results of our research show that *Heterobasidion* infection in inoculated seedlings spreads in a comparable way, although seedlings do not contain heartwood.

Our results confirm that *H. annosum* is better adapted to *P. sylvestris,* and *H. parviporum* to *P. abies* (partly presented also in Zaļuma *et al*., 2015), as observed previously in inoculation experiments (Stenlid and Swedjemark, 1988; Lindberg, 1992). Similar observations have been made in field conditions. For example, the spread of *H. parviporum* in stems of 60-year-old *P. abies* in Lithuania was more extensive than spread of *H. annosum*: 4.59 ± 1.59 m and 3.27 ±1.01 m, respectively (Vasiliauskas and Stenlid, 1998).

We did not find any seed source that was distinctly more resistant than others. Growth of *Heterobasidion* was about similar in seedlings from the same provenance region, but slight differences occurred between different provenance regions (Table 4). Our results showed that spruce seedlings originating from western and eastern Latvia, and cultivated outside their own provenance region in Jaunkalsnava, central Latvia, were characterized by a higher growth rate of *H. parviporum,* suggesting lower resistance and possibly indicating lower adaption to environmental conditions. This difference may be mainly due to local climatic conditions, as all the seedlings were cultivated in forest nursery. Resistance against pathogens and pathogen growth rate in wood may change in different environments (Lindberg and Johansson, 1992; Santini *et al.,* 1997).

Our research highlights differences between development of *Heterobasidion annosum* and *H. parviporum* in spruce and pine seedlings and show that these differences correspond to the behaviour of these fungi also in mature trees. There is some evidence that differences in susceptibility against *Heterobasidion* might be found between different origins of seeds. This should be considered when regenerating stands on soils that are infected with *Heterobasidion* as well as in planting of new stands on former agriculture land.

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DAŽĀDAS IZCELSMES *Pinus sylvestris* UN *Picea abies* STĀDU UZŅĒMĪBA PRET *Heterobasidion annosum* UN *H. parviporum*

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