

Artificial Infection and Development of Snow Mold Fungus (*Phacidium infestans*) in Container-grown Norway Spruce Seedlings

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Petäistö, R.-L., Lilja, A. and Hantula, J. 2013. Artificial Infection and Development of Snow Mold Fungus (*Phacidium infestans*) in Container-grown Norway Spruce Seedlings. *Baltic Forestry* 19(1): 31–38.

Abstract

Phacidium infestans causes common snow mold in Scots pine (*Pinus sylvestris* L.), its main host in Finland. Recently, a mycelial web similar to that occurring on pine has been observed on Norway spruce (*Picea abies* L.) seedlings in some forest nurseries of Finland. In this study, we showed that *Ph. infestans* can cause snow mold in container seedlings of Norway spruce exposed to treatments that simulated natural infection by ascospores borne on Scots pine saplings. In the following spring after infection, inoculated seedlings stored in the freezer (-3 °C) were generally more diseased than those stored outdoors during the 2006/2007 winter, suggesting that *Ph. infestans* does not require snow cover to develop on spruce seedlings. Diseased needles were grey-green in early spring. After death, diseased needles soon became yellow-brown or grey-brown and seedlings often died. In contrast to the disease in Scots pine of the same age, infected Norway spruce needles were dropped mainly during the summer of 2007. Although the final examination took place about two years after artificial infection, we did not observe any mature fruiting bodies of *Ph. infestans* on spruce or pine seedlings included in the experiment as a reference.

Key words: *Phacidium*; nursery practice; snow blight; ascospore infection; overwintering; *Picea*

Introduction

The snow mold or snow blight fungus, *Phacidium infestans* P. Karst. (Phacidiaceae, Ascomycota), is a common and serious pathogen of *Pinus* in parts of Eurasia, North America and Japan that experience prolonged snow cover (Petraik 1955, Bazzigher 1978). The fungus also infects *Abies*, *Picea* and *Juniperus* growing close to diseased pines (Björkman 1948, Roll-Hansen 1987, 1989). In Baltic forests, *Ph. infestans* is known to occasionally cause damage during winters with thin and short-term snow cover (Hanso 2000, McLaughlin and Šica 1993).

Snow mold ascospores spread during wet weather with high relative humidity (RH). Dispersal begins in September and continues until the apothecia are covered by snow or the spore production capacity is exhausted (Kurkela 1996). Growth of *Ph. infestans* occurs as low as -5 °C and beyond +25 °C (Björkman 1948, Butin and Söderholm 1984), with the optimum being +15 °C at 98–100 % RH. Thus, conditions at ground level under thick snow cover and during snowmelt enable infections to develop and appear in the spring (Keränen 1920, Vuorinen and Kurkela 1993).

Technology and growing practice in commercial seedling production have changed considerably over the last 20–30 years in Finland (Tervo 1999). Today, over 99% of seedlings are grown in containers, germinated in greenhouses and later transferred outdoors (Lilja et al. 2010). Two thirds (about 100 million) of seedlings produced are Norway spruce (*Picea abies* Karst) (Finnish Statistical Yearbook 2011). Approximately one third of seedlings are stored in freezers at about -3 °C over winter and the rest outdoors under natural or artificial snow cover (Lilja et al. 2010).

Recent years have brought long, warm and humid autumns that encourage infection by pathogens such as *Ph. infestans* (Björkman 1949, Jylhä et al. 2009). In some nurseries, groups of diseased Norway spruce seedlings have been found after snowmelt with symptoms typical of Scots pine seedlings damaged by *Ph. infestans*. In response to this, we sought to determine whether *Ph. infestans* pose a risk to Norway spruce seedlings stored outdoors over winter or in the constant, snow-free environment of a freezer. This study also aimed to describe disease symptoms on Norway spruce seedlings, a new putative host of this pathogen in Finnish nurseries.

Material and methods

Seedling material

Experiments were performed at the Suonenjoki nursery of the Finnish Forest Research Institute. Qualified seed from seed orchards of Norway spruce (SV177 EY/FIN TO3-00-0446 useable for 1080-1280 d.d.) and Scots pine (SV337EY/FIN T03-03-0215) were sown on 25 April 2006 in PL-81F containers (81 seedling cells per tray, in 9 rows, each cell 85 cm³; Lannen, Iso-Vimma, Finland) filled with low-humified *Sphagnum* peat. Seedlings of both conifer species were grown in a greenhouse prior to the experiment and moved outdoors 26 July 2006. Control seedlings remained in an unheated greenhouse to avoid natural infection. We also measured the height of nine spruce in each tray on 14 May and 29 September 2007 to monitor seedling growth during the summer after artificial infections performed the previous autumn (Figure 1).

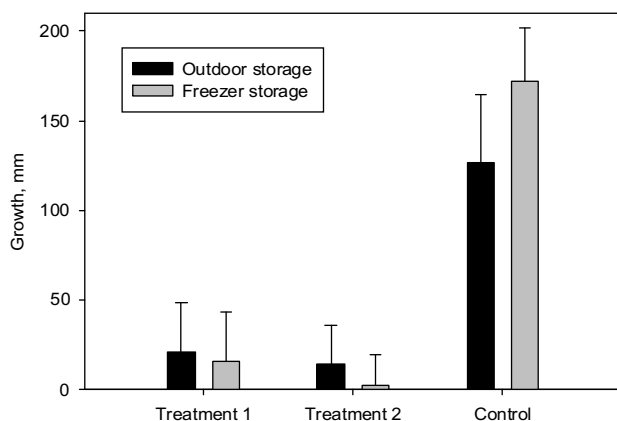


Figure 1. Growth increment of Norway-spruce seedlings during summer 2007 following infection treatment in 2006 and winter storage; measurements from nine seedlings in each of four trays per treatment × storage combination

Artificial infection with *Ph. infestans* ascospores

In 2006, seedlings were exposed to inoculation treatments, one of them simulating infection by ascospores. Branches with diseased needles providing the inoculum were collected from Scots pine saplings in a nearby forest that were naturally infected by *Ph. infestans* a year earlier. Treatments were: 1) artificial ascospore infection by placing Norway spruce seedlings under the 2–3 layers of diseased Scots pine branches on an iron mesh covering the containers about 1.2 m above soil level on August 16; 2) inoculation 1 + inoculation with diseased needles at the time of transfer to winter storage (about 2 dl of pine needles bearing ascocarps were scattered over each seedling tray on October 20); 3) control seedlings were sheltered from infection in an

unheated greenhouse about 50 m from a pine forest edge. One tray with 81 seedlings was a replicate and each treatment was replicated eight times for Norway spruce and treatment 1 and 2 twice for Scots pine. At the time of inoculation, needle ascocarps were closed but had begun to open on 22 August and about 20% were open a month later.

Winter storage treatments

Norway spruce trays (81 seedlings/tray) representing each inoculation treatment with four replicates (12 trays together) and treatment 1 and 2 with one tray of Scots pine, each representing one inoculation treatment were stored over winter outdoors and in a freezer. Outdoor trays were randomly placed in three rows spaced 50–70 cm apart and embedded in a peat layer to protect seedling roots against frost damage. In the freezer, each tray was packed into a separate cardboard box and randomly placed on shelves. A temperature/RH sensor (Hobo, MicroDAQ.com Ltd., PO Box 439, Contoocook, NH 03229, USA) was placed between seedlings in one tray in the freezer and in one tray outdoors. The freezer maintained a constant temperature of about -3 °C (Figure 2 a). The RH sensor in the cardboard box reported 100% in the first two days but subsequently malfunctioned. RH was most probably 100% during the entire winter as cardboard boxes were closed all the time and the temperature remained constant. Outdoor temperature, RH (average daily means) and snow depth (measured on weekdays) during winter storage are shown in Fig. 2 b, c. The RH sensor typically showed about 100% RH.

Seedling condition after winter and second growing season

Thawing of freezer-stored seedlings took place in April, with material increasing in temperature from -3 to +4 °C. During the last week of thawing (27 April – 2 May), seedlings were placed outdoors in a shaded location with ventilation holes of the boxes open. On 4 May, inoculated seedlings were removed from the boxes and evaluated, and likewise control seedlings on 8–9 May. Trays were moved to the nursery field adjacent to the seedlings that had spent the winter outdoors. Seedlings stored outdoors over winter were evaluated after snow had melted at the beginning of April 2007.

The condition of each Norway spruce seedling was evaluated individually. Each seedling shoot was divided into approximately equal quarters: 1 = top quarter, 2 = second quarter, 3 = third quarter and 4 = lowermost quarter. The condition of each quarter was then classified: 1 = healthy; 2 = ≤10% diseased needles; 3 = <50% diseased needles; 4 = >50% diseased

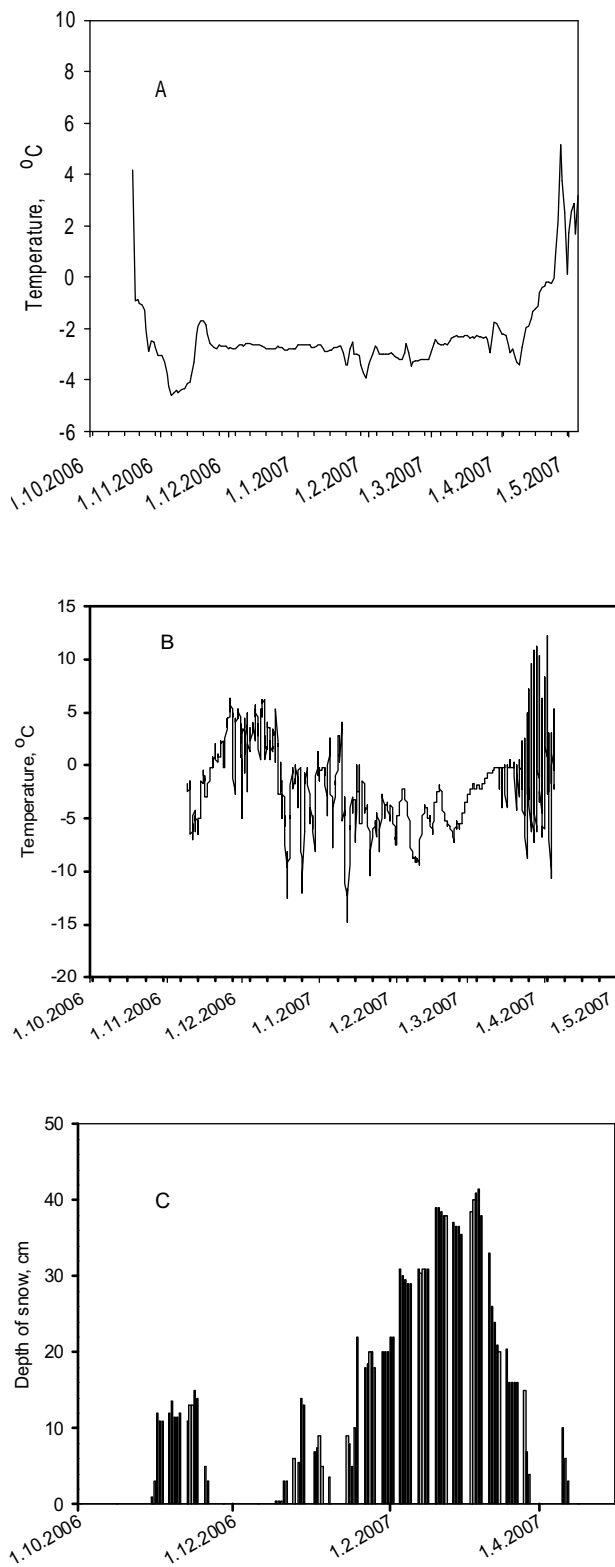


Figure 2. Freezer (A) and outdoor (B) daily mean temperature in seedling canopy (left) and snow depth (C) during winter 2006/2007

needles; 5 = dead. Scots pine seedlings were observed more generally, i.e., evaluating each tray rather than individually. Spruce and pine needle samples were collected from each tray for fungal isolations. Twelve needles from four seedlings per inoculation/storage treatment were rinsed in 70% alcohol for 6 seconds and three times with sterile water. Needle fragments of 2–3 mm were cut from each surface-sterilized needle and placed on PDA-media (Potato dextrose agar, 39 g/l, Difco, MI, USA) in Petri dishes and incubated at 10–15 °C in the dark.

A second inventory of spruce seedlings was completed at the end of the 2007 growing season; 12 months after seedlings were inoculated. Since only a few needles remained at this time, seedlings were scored as either alive or dead. In addition, needle samples of both tree species were taken from shoots and the soil surface (i.e., fallen) to check for the presence of fruiting bodies. The last samples to check for the presence of fruiting bodies on both conifer species were collected in September 2008, ca. 24 months after inoculations.

DNA analysis and identification

Partial sequence of the 18S rDNA gene as well as culture morphology of two isolates from Norway spruce seedlings reminiscent of *Ph. infestans* were obtained and compared with those of three confirmed Norwegian isolates from *Pinus* (originally isolated by Prof. F. Roll-Hansen and Dr. H. Roll-Hansen, provided by Prof. H. Solheim). DNA was isolated as described in Vainio et al. (1998) and part of the 18S rDNA gene was amplified using primers NS1 (White et al. 1990) and FR700 (complementary to primer FF700: Vainio and Hantula (2000)) and sequenced with primers NS1 and FR1100 (complementary to primer FF1100: Vainio and Hantula (2000)). Sequence data were deposited with GenBank.

Data analysis

Univariate ANOVA and Tukey HSD was conducted using SPSS 16.0. The dependent variable was the arcsin-transformed proportion of diseased Norway spruce seedlings (i.e., the proportion of seedlings exhibiting disease classes 3–5), and the factors (independent variables) were inoculation and storage. Statistical analyses of storage and inoculation treatments were conducted separately for each seedling quarter. Tray was used as the experimental unit.

Results

Symptoms and isolates

In 2007, typical symptoms for *Ph. infestans* infection were seen on seedlings of both tree species exposed to ascospores the previous year. In early spring,

it was possible to see mycelial web on seedlings (Figure 3). Mycelia later disappeared but needles of infected seedlings remained grey-green or later grey-brown with small dark patches or uniformly yellow-brown with fewer patches (Figures 3, 4). Most inoculated Scots pine seedlings were totally brown after winter, only the tray with inoculation treatment 1 and stored outdoors had more greenish seedlings. In contrast to Scots pine the infected spruce needles were typically largely shed already in June 2007, while brown needles stayed attached on pine.



Figure 3. Abundant surface hyphae on diseased Norway spruce shoots in spring 2007 after freezer storage



Figure 4. A diseased Norway spruce seedling in outdoor winter storage in early spring 2007

Isolations from artificially infected needles yielded similar culture morphology to that exhibited by control isolates of *Ph. infestans* from diseased needles of Scots pine from Finland and Norway. Isolates from all inoculated trays, but one stored outdoors, exhibited the same culture morphology consistent with *Ph. infestans*. The partial 18S rDNA sequences ob-

tained from Norway spruce (an isolate from our experiment, and from a Finnish forest nursery) and those from pine (three Norwegian isolates of *Ph. infestans*) were 100% identical. GenBank accession numbers of isolates are GQ266406-GQ266410. The pathogen could not be isolated from control seedlings, although some had brown needles.

Occurrence and distribution of symptoms in the shoot of Norway spruce

According to the 2007 spring inventory, Norway spruce seedlings that received either of the inoculation treatments 1 and 2 had fewer healthy needles than the control seedlings in all four shoot quarters ($p < 0.057$ and $p < 0.001$; $p < 0.002$ and $p < 0.001$; $p < 0.001$ and $p < 0.001$; $p < 0.001$ and 0.001 Tukey HSD), Figures 5 and 6. Inoculation 2, in which needles with apothecia were also scattered over the seedlings prior to winter storage, resulted in a greater incidence of disease than inoculation 1 ($p < 0.001$) in all shoot quarters (Figures 5 and 6). The means of arcsin transformed proportion of disease in inoculation treatments 1, 2 and 3 were in quarter 1: 0.172; 0.490; 0.010, in quarter 2: 0.362; 0.772; 0.007, in quarter 3: 0.552; 1.085; 0.012, in quarter 4: 0.771; 1.368; 0.055.

The effect of storage on proportion of disease was significant in quarters 1–3 ($p < 0.01$). Proportion of disease was greater in the freezer in quarters 1–3 compared to those stored outdoors (Figures 5 and 6). In the lowest shoot quarter, the effect of storage on the proportion of disease was not significant ($p < 0.23$). Overall, snow mold seemed to be worse in seedlings stored in the freezer (mean of 45.8% diseased) than outdoors (mean of 32.3% diseased).

In spring 2007, we found seedlings in all disease classes although only two of 1944 seedlings were dead (class 5). In the top and second quarter, the effects of storage, inoculation treatment and also their interaction on the diseased (condition classes 3–5) proportion were all statistically significant ($p < 0.01$). In inoculation 2, the proportion of the condition class 4 was greater in freezer-stored seedlings than in those stored outdoors in the uppermost two quarters (Figures 5 and 6). In quarter 3, effects of inoculation and storage were both significant ($p < 0.01$ and $p < 0.025$) but the effect of their interaction was not ($p < 0.107$). In the lowermost quarter (4), the effect of inoculation and the interaction of storage and inoculation were significant ($p < 0.01$ and $p < 0.027$), but the effect of storage was not.

In autumn 2007, seedlings were classified to two classes: alive and dead, because most of the infected needles had been shed during the summer. From the inoculated seedlings, whose bottom quarter had been classified into condition class 4 during the spring evaluation, (see Figures 5 and 6) about 60% were dead

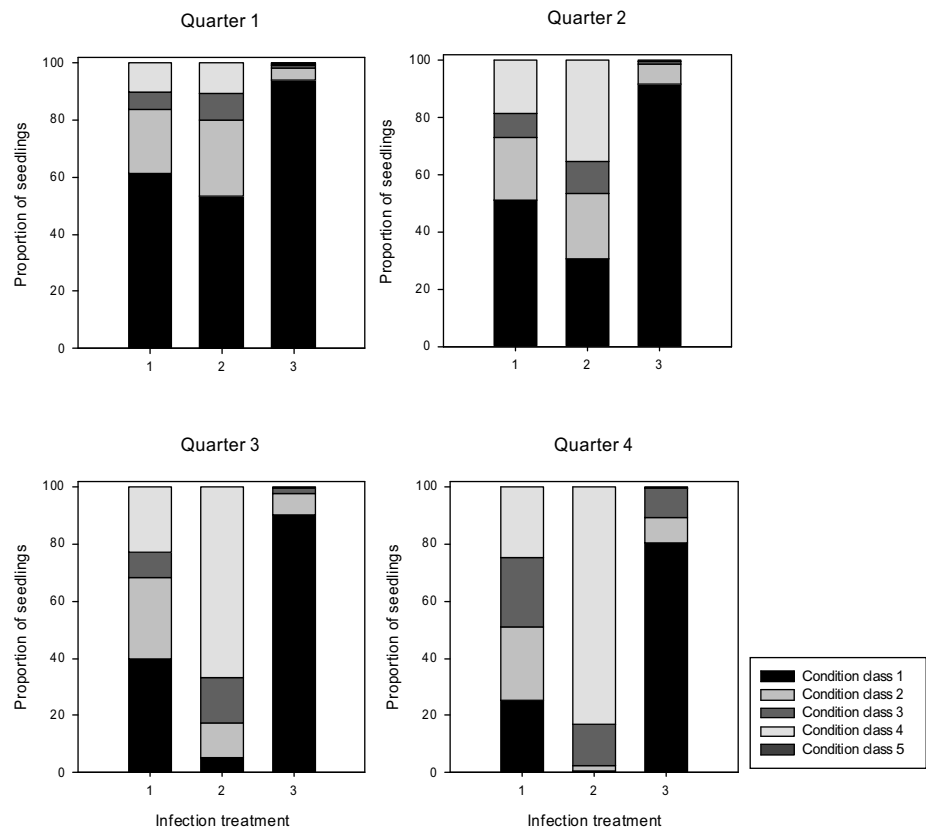


Figure 5. Health conditions of seedling quarters (quarter 1 is the top part and quarter 4 the lowest part) following infection treatment and outdoor winter storage, spring 2007. Proportion of seedlings, condition class 1=black (healthy), class 2=light grey, class 3=dark grey, class 4=lightest grey, class 5=darkest grey (dead)

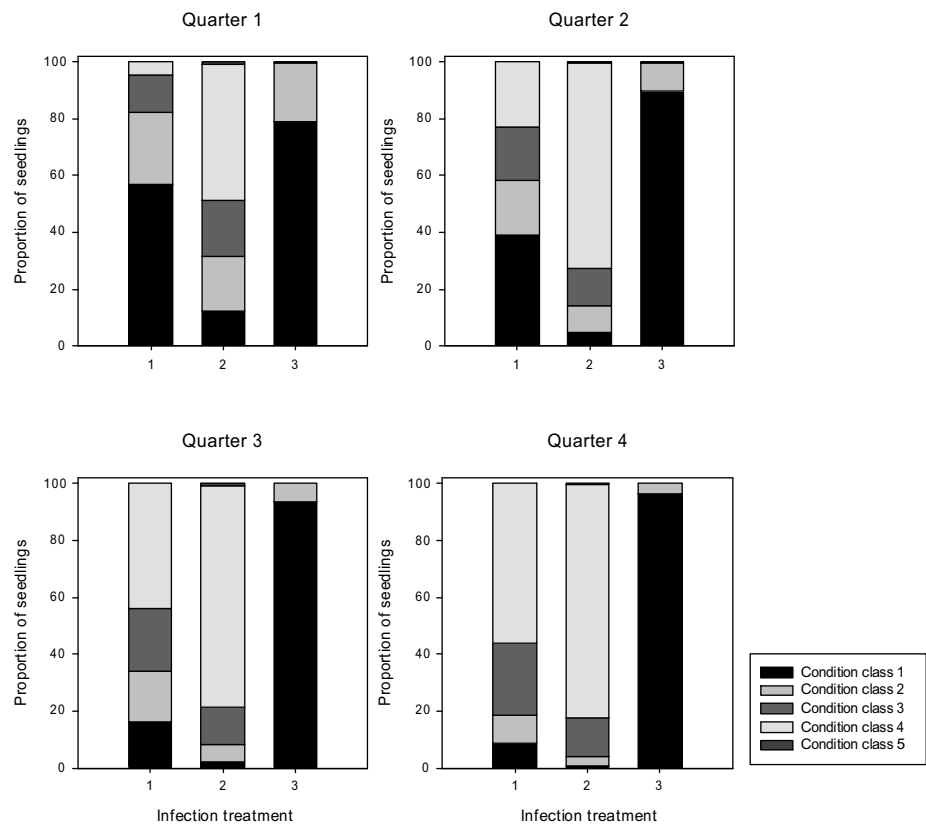


Figure 6. Health conditions of seedling quarters (quarter 1 is the top part and quarter 4 the lowest part) following infection treatment and freezer winter storage, spring 2007

by the autumn except in seedlings in treatment 2 stored outdoors the percent was 20 (Figure 7). Although some artificially infected seedlings remained alive in autumn 2007, their growth during the summer 2007 was minimal (Figure 1). We did not find any *Ph. infestans* fruiting bodies in the needles of spruce or pine seedlings, collected in autumn 2007 and 2008. However, it was possible to see black small spots on needles (Figures 3 and 4).

In Norway spruce seedlings of this study, diseased needles were typically grey-green and thin mycelial hyphae were visible on the surface in early spring. After death and drying, needles soon became yellow or grey-brown and many seedlings died. According to our observations, in contrast to diseased Scots pine of the same age, diseased needles of Norway spruce seedlings were mostly dropped early in the first summer following infection. However, ascocarps could not

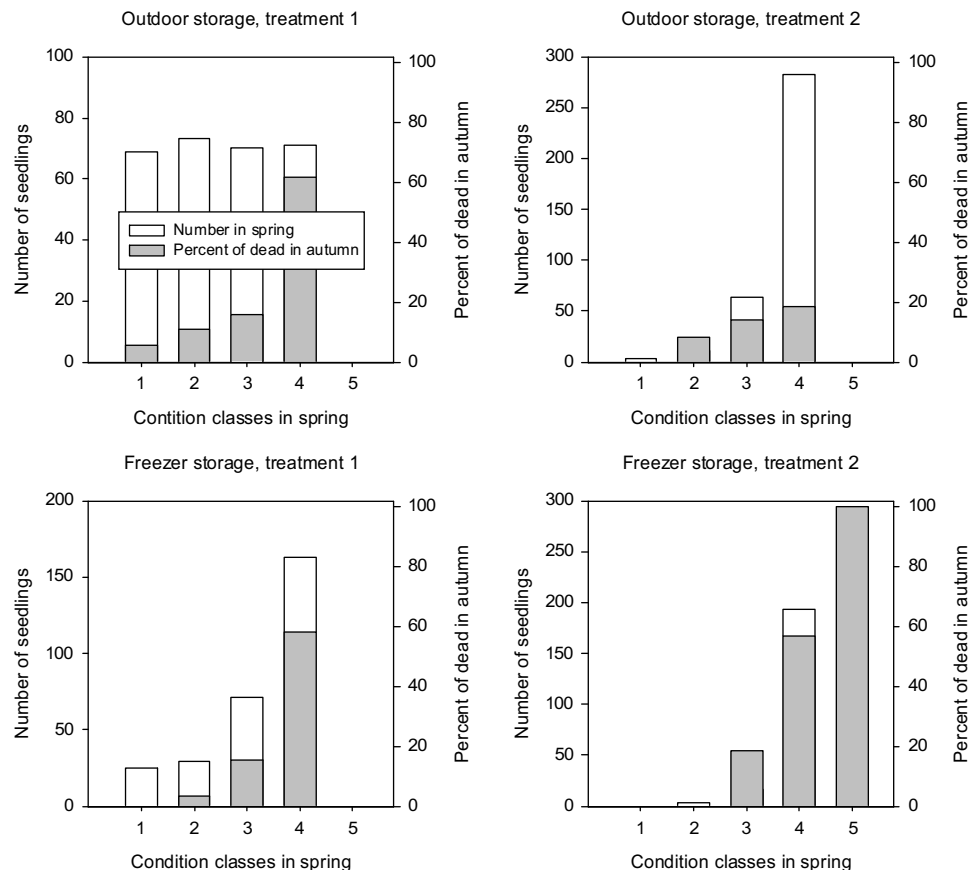


Figure 7. Health conditions of lowermost quarter of shoots in spring 2007 and in the following autumn (seedlings (percent) in each condition class that died during summer); storage × treatment combinations

Discussion

This study showed that *Ph. infestans* can infect and cause disease on containerized Norway spruce seedlings via ascospores borne on Scots pine saplings. Our results confirm the threat this pathogen poses to nursery production and underlines its importance to the commercial production of Norway spruce seedlings in Finnish nurseries. Earlier studies have mainly focused on *Ph. infestans* in Scots pine and have shown how, in the nursery, it can pose a threat to species of *Pinus* and *Abies* (Roll-Hansen 1975, Kurkela 1995, 1996, Burdon et al. 1992, Nef et al. 1999, Hansson 2006).

be found the following autumn on Norway spruce seedlings or their fallen needles or on brown needles of Scots pine. In accordance with this, Jamalainen (1961) found that *Ph. infestans* does not typically produce apothecia on 1- to 2-yr-old Scots pine seedlings. Additional studies with older seedlings of Norway spruce and Scots pine are necessary to determine the dependence of ascocarp formation on the age of needles and/or seedlings, since the life cycle of the pathogen is commonly 1 year (Björkman 1994, Roll-Hansen 1989). Snow mold can infect several conifers but ascospores have only been found on *Pinus*, *Abies* and *Juniperus* (Roll-Hansen 1987, 1989, Nef et al. 1999). In Finnish forests, ascocarps of *Ph. infestans* develop on

Scots pine saplings and trees during the summer, depending on weather and microclimate conditions. High mean temperatures in June–August must be followed by a humid autumn to support ascocarp production and maturation (Kurkela 1995, 1996). Mature ascospores are released from September until snow cover or apothecia are emptied (Kurkela 1995, 1996).

The pathogen is generally believed to cause damage only under deep and long-lasting snow cover during the winter and spring snow melt (Björkman 1948, Roll-Hansen 1975). In Baltic countries, the pathogen can survive winters with thin and short-term snow cover only in the poor forest types and nursery damage has occurred only after snow-rich winters (Hanso 2000). Our results show that snow cover is not required as the disease also developed during freezer storage, although we stress that the temperature and humidity experienced during thawing in cardboard boxes is suitable for disease development.

Although not a prerequisite for infection, conditions under snow cover are important for the disease in nature. In Scots pine, the amount of infection is inversely related to the rate of snow melt, as the melting period provides optimal conditions for the hyphal growth and disease development (Mattsson-Mårn and Netzell 1941). In our study, it seemed that freezer storage provided slightly better conditions for disease development than those experienced outdoors, as infection clearly caused more damage on freezer seedlings on the upper parts of the shoot than on the upper parts of seedlings stored outdoors. This could be due to more constant conditions in the freezer in relation to the intermittent snow cover and winds during the winter of 2006–2007. It should also be noted that storage in the freezer lasted approximately 1 month longer than outdoors, because seedlings were evaluated at the beginning of April, immediately after snow melt whereas seedlings in the freezer were thawed more slowly, according to standard practice, and their condition was evaluated at the beginning of May.

Infection with *Ph. infestans* caused clear symptoms on all shoot quarters of spruce seedlings. Winter storage outdoors or in the freezer did not differ with respect to symptom frequency in the lowest part of the shoot, where RH is likely to be more uniform than in the upper parts. We noted that more seriously diseased seedlings weakened during the summer and by autumn had lost their vigor or died.

Nursery managers seeking to reduce the use of fungicides should increase ventilation, reduce the frequency of irrigation in chronic sites of high infection, and destroy diseased pine seedlings whenever they occur nearby.

Acknowledgements

Ms Marja-Leena Jalkanen, Ms. Marja-Leena Santanen and Ms. Hanna Ruhanen are thanked for their skillful assistance. Juha Lappi provided helpful comments on data analysis. Thanks also to Prof. Halvor Solheim for the Norwegian Phacidium isolates collected by Dr. Helga and Prof. Finn Roll-Hansen. The English revision by Dr. Michael Hardman is gratefully acknowledged.

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Received 11 July 2012

Accepted 07 June 2013

ИСКУССТВЕННЫЕ ИНФЕКЦИИ И РАЗВИТИЕ ГРИБА (*PHACIDIUM INFESTANS*) В СЕЯНЦАХ ЕЛИ ОБЫКНОВЕННОЙ, ВЫРАЩЕННОЙ В КОНТЕЙНЕРАХ

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Резюме

Гриб *Phacidium infestans* является причиной возникновения снежного шютте – болезни, которая в Финляндии поражает, как правило, хвою сосны обыкновенной (*Pinus sylvestris* L.). В последнее время в некоторых лесных питомниках Финляндии на сеянцах ели обыкновенной (*Picea abies* L.) наблюдался паутинистый мицелий, схожий с тем, который появляется на сосне. В нашем исследовании мы показываем, что гриб *Ph. infestans* может вызвать снежное шютте у выращенных в контейнерах сеянцев ели обыкновенной, подверженных обработке, имитирующей естественное заражение посредством аскоспор саженцев сосны обыкновенной. Следующей весной после заражения инфицированные сеянцы, хранившиеся в морозильной камере (-3 °C), были наиболее подвержены большому заражению, по сравнению с сеянцами, хранившимися зимой 2006-2007 гг. на открытом воздухе. Это дает основание полагать, что для развития гриба *Ph. infestans* на сеянцах ели не требуется снежного покрова. Ранней весной зараженная хвоя приобрела серо-зеленый цвет. После засыхания зараженная хвоя приобрела желто-коричневую или серо-коричневую окраску, многие больные сеянцы погибли. В отличие от заражения сосны обыкновенной того же возраста, большая часть хвои зараженных сеянцев ели обыкновенной опала летом 2007 года. Несмотря на то, что заключительный осмотр состоялся спустя два года после искусственного заражения, мы не наблюдали зрелых плодовых тел гриба *Ph. infestans* на сеянцах ели или сосны, включенных в исследование для сравнения.

Ключевые слова: *Phacidium*; работа в питомниках; снежное шютте; заражение аскоспорами; перезимовка; *Picea*