

# Tree Mortality Agents in Pristine Norway Spruce Forests in Northern Fennoscandia

Antti Länneppää, Tuomas Aakala, Heikki Kauhanen and Timo Kuuluvainen

---

**Länneppää, A., Aakala, T., Kauhanen, H. & Kuuluvainen, T.** 2008. Tree mortality agents in pristine Norway spruce forests in northern Fennoscandia. *Silva Fennica* 42(2): 151–163.

We examined tree mortality agents in pristine old Norway spruce (*Picea abies* (L.) Karst.) forests in northern Finland and northwestern Russia. The data was collected on nine 40 m × 400 m transects. The primary mortality agents of recently dead trees were recorded and their frequencies were calculated. The pattern of tree growth prior to death was studied based on increment core samples and compared with the growth of healthy dominant trees. Of all recently dead trees, 72% could be associated with a primary mortality agent. In both study areas the most common primary mortality agent was a *Coniophora* (Mérat) DC. -genus fungi, which was found on average in 33% of trees sampled. The fungi *Phellinus chrysoloma* (Fr.) Don and *Onnia leporina* (Fr.) H. Jahn as mortality agents were more common in the Finnish area compared to the Russian area. Analysis on the growth patterns indicated weak differences between different pathogens' influence on prior-to-death growth of trees, so that fungi rotting the whole tree decreased tree growth more rapidly than fungi rotting only the heart wood. The results demonstrated that in old Norway spruce forests of northern Fennoscandia the most common primary tree mortality agents were wood rotting fungi, which weaken the mechanical stability of tree stems until they fall due to snow or wind, which should be considered only as secondary mortality agents. It is evident that tree death in pristine forest typically results from a long-lasting process involving both biotic and abiotic factors.

**Keywords** *Coniophora*, mortality agent, northern Fennoscandia, *Picea abies*, pristine forest

**Addresses** *Länneppää, Aakala & Kuuluvainen*: Dept. of Forest Ecology, University of Helsinki, Finland; *Kauhanen*: Kolari Research Unit, Finnish Forest Research Institute, Finland

**E-mail** tuomas.aakala@helsinki.fi

**Received** 6 July 2007 **Revised** 5 December 2007 **Accepted** 3 January 2008

**Available at** <http://www.metla.fi/silvafennica/full/sf42/sf422151.pdf>

---

# 1 Introduction

Forest dynamics are driven by three main processes: regeneration, growth and death of trees. Understanding all these processes is needed for a comprehensive picture of forest dynamics. From these three processes, tree death is probably the most difficult one to predict (Dobbertin and Biging 1998). Many external factors may affect the weakening and eventually the dying of a tree. These factors can be divided into primary mortality agents that are capable of killing healthy trees, and secondary mortality agents that kill only weakened trees. However, this division is often problematic from an ecological point of view, because in many cases both are needed to finally kill a tree. When taking into account all the agents involved in the death of a tree, it is reasoned to say that tree mortality often is a complex chain of cause and effect (Franklin et al. 1987, Manion 1991, Kuuluvainen 1994).

Northern boreal Norway spruce (*Picea abies* L. Karst.) forests are growing in harsh environmental conditions, where the growing season is short, the angle of solar radiation is low and temperatures remain low throughout the year. In these conditions all ecological processes are slow and tree growth is retarded. Particularly in old Norway spruce forests the thick and poorly decomposing moss layer decreases soil temperatures and slows down the nutrient cycle (Sirén 1955). In such stressful environment trees are also constantly susceptible to fungal diseases (Norokorpi 1979).

It has been a common belief that tree mortality and regeneration in old Norway spruce forests naturally occurs through large and forceful disturbances such as high-severity fires (Sirén 1955). However, recent studies demonstrate that wildfires are rare in these forests (Syrjänen et al. 1994, Hyvärinen and Sepponen 1988, Wallenius et al. 2005) and that their dynamics are driven by small-scale mortality of trees (Kuuluvainen 1994). The establishment of seedlings in the northern boreal Norway spruce forests is generally limited by seedbed availability (Hofgaard 1993). Thus, tree mortality plays a major role also in facilitating regeneration by creating suitable seedbeds in the form of nurselogs and

exposed mineral soil. Similarly, tree mortality is important for biodiversity, as it creates the dead wood many organisms depend on (Siitonen 2001). Therefore, understanding both regeneration and dead wood dynamics requires understanding the mortality process.

The purpose of this study was to examine the causes and process of tree mortality in old pristine Norway spruce forests in northern boreal Fennoscandia. We asked the following specific questions: 1) what are the most significant tree mortality agents? and 2) how do different mortality agents affect tree growth prior to death?

## 2 Material and Methods

### 2.1 Study Areas

The research was carried out in two locations in northern Fennoscandia, in northwestern Finland in the Pallas-Yllästunturi National Park, and in northwestern Russia in the Murmansk Oblast. The study area in the Pallas-Yllästunturi National Park was chosen because it harbors some pristine Norway spruce forests. The area belongs to the northern boreal vegetation zone (Ahti et al. 1968). The yearly mean temperature is  $-1^{\circ}\text{C}$ , the effective temperature sum is 650–700 dd. and the annual precipitation is about 550 mm (Vadja and Venäläinen 2003).

The study area in northwestern Russia was chosen with the help of information from Russian colleagues and satellite images. This remote area is located by the Kazkim-river  $68^{\circ}18'N$ ,  $30^{\circ}22'E$ . The area is in the northern boreal vegetation zone, and its climatic key figures are: yearly mean temperature  $-2^{\circ}\text{C}$ , the effective temperature sum 400–430 dd. and the annual precipitation about 600 mm. (Vadja and Venäläinen 2003). The Russian study area is thus influenced by a considerably harsher climate compared to the Finnish study area.

## 2.2 Site Selection and Stand Characteristics

In the study areas, the stands for sampling were searched based on information from maps (Finland) and satellite images (Russia), and the final selection was done by field surveys. The forests that were accepted for sampling fulfilled the following requirements: 1) The dominant tree species was Norway spruce, 2) the forest had a continuum of decayed trees, and old standing trees, indicating long development without major external disturbances, and 3) the forest had no signs of direct anthropogenic influence.

The sampling unit was a transect of 40 m × 400 m. In the selected stands the starting points and directions of the transects were randomized so that the whole transect fitted in the same type of forest. All four Finnish transects were established in 2005, and the five Russian transects in 2006.

In the Pallas-Yllästunturi National Park the sites of sampling are located south of Lake Pyhäjärvi, 67°40'N, 24°22'E. The studied stands are sparse, with mean volume of 99.5 m<sup>3</sup>ha<sup>-1</sup> (range: 88.9–108.2 m<sup>3</sup>ha<sup>-1</sup>; unpublished data). Stands are dominated by Norway spruce (on average, 74% of volume; *Picea abies* L. Karst), and there is an admixture of birches (20%; *Betula pendula* Roth, *Betula pubescens* Ehrh.) and also a small number of pines (7%, *Pinus sylvestris* L.) especially on drier locations. The forest floor is dominated by blueberry (*Vaccinium myrtillus* L.), lingonberry (*Vaccinium vitis-idaea* L.) crowberry (*Empetrum nigrum* L.) marsh ledum (*Ledum palustris* L.) and bog bilberry (*Vaccinium uliginosum* L.).

In the sites in northwestern Russia the mean volume is 65.7 m<sup>3</sup>ha<sup>-1</sup> (range: 54.5–71.5 m<sup>3</sup>ha<sup>-1</sup>). Tree species composition is similar to the Finnish sites, on average 77% of volume is Norway spruce, 19% birch, and 3% pine (unpublished data). However, there is a difference in the composition of the forest floor vegetation, so that marsh ledum and bog bilberry were notably more abundant than on the Finnish sites. Also the raw humus and layer of bryophytes were thicker than in the Finnish sites (pers. obs.).

## 2.3 Identification of Mortality Agents

To study the causes of tree mortality in the transects, we recorded all standing dead and fallen trees over 10 cm DBH (diameter at 1.3m height). These trees were classified into decay classes (Table 2) following a modification of the classification of Imbeau and Desroches (2002). The most important mortality agent, i.e. the primary mortality agent, was determined for each tree (Table 1). If signs of several different primary mortality agents were visible, or the tree had died without external signs, it was considered as having died with no clear cause. In practice, identifying a primary mortality agent was possible only for trees that had died relatively recently. Therefore, the determination of primary mortality agents was limited to standing dead trees in decay classes 4 and 5, and fallen trees in decay classes 9 and 10 (see Table 2).

The identification of biotic mortality agents was mainly done using the presence of polypore fruiting bodies and insect galleries. When fruiting bodies were found the fungi species could easily be determined. If the primary agent was clearly a rotting fungi, but no fruiting bodies were found, the identification was based on decay characteristics. In these cases, the agent was identified only to the genus level. In particular, the typical brown rot of the genus *Coniophora* (Eriksson 1958) was repeatedly found in the recently dead trees.

The observed causes of tree death were summed and the results were converted into proportional values so that the two study areas could be compared. When interpreting the results it should be kept in mind, however, that the identification of the primary mortality agent involved an unavoidable element of uncertainty, because it was done qualitatively based on external indicators.

## 2.4 Growth Pattern Measurements and Analyses

To characterize the influence of different primary mortality agents on tree growth patterns prior to death, a sub-sample of all sampled recently dead trees was selected for coring. Only trees whose mortality could be unambiguously assigned to a specific agent were sampled. Therefore, we

**Table 1.** The causes of tree mortality and the criteria used for their identification.

Mortality agent	Used criteria
No clear cause	The tree has died without any visible cause. No polypores are found, and there are no traces of insects in the phloem
Competition	A standing dead tree in a clearly suppressed position
Wind, uprooted	Tree fallen with a root plate, no signs of rot in the broken roots.
Wind, root breakage	Breakage at, or just below the root collar, no root plate
Wind, break < 1,3 m	The tree has broken below 1.3 meters
Wind, break > 1,3 m	The tree has broken above 1.3 meters
Snow	The snapped crown has been fallen to the direction where branches are in an asymmetric crown
<i>Fomitopsis pinicola</i> (Sw.:Fr) P. Karst.	A fruiting body was found
<i>Phellinus chrysoloma</i> (Fr.) Don	A fruiting body was found
<i>Onnia leporina</i> (Fr.) H. Jahn	A fruiting body was found.
<i>Armillaria</i> spp.	A fruiting body or mycelia was found
<i>Stereum sanguinolentum</i> (Fr.) Alb. & Schw.	A fruiting body was found
<i>Heterobasidion parviporum</i> Niemelä & Korhonen	A fruiting body was found in the roots of a fallen tree
Coniophora sp.	Cubical brown rot was found
Unidentified brown rot	Unidentified brown rot was found
Unidentified white rot	Unidentified white rot was found.
<i>Tetropium</i> sp.	Larvae galleries were found in the phloem
<i>Callidium coriaceum</i> Paykull	Larvae galleries were found in the phloem
<i>Dendroctonus micans</i> Kugel.	Larvae galleries were found in the phloem, which had turned to a hard mixture of wood dust
<i>Ips typographus</i> L.	Larvae galleries were found in the phloem
Other biotic	Another biotic factor was found
Other abiotic	Another abiotic factor was found

**Table 2.** Decay classification and explanation of classes. For both standing and fallen trees Classes 1–3 were reserved for living trees and were not used in this study. Classes 4–8 for standing dead trees, and classes 9–14 for fallen trees. All trees taller than 1.3 m were classified as standing trees.

Class	Explanation
4	Recently dead: small branches with at least some foliage (red/brown) still attached
5	Foliage absent. Small twigs still present, cambium dried or absent
6	Smallest twigs absent, largest branches still present
7	Snapped. Only largest branches possibly present
8	Less than 2m high. Branches gone
9	Similar to standing dead 4
10	Similar to standing dead 5
11	Similar to standing dead 6
12	Only largest branches possibly present, log shape round
13	No branches, loss of log shape
14	Covered with ground vegetation

sampled only fallen trees, where the stem cross-section was visible due to breakage so that the role of rotting fungi could be assessed. Using these selection criteria our sampling was limited to only a few mortality agents, but on the other

hand we minimized problems associated with assigning death of trees to a single agent. To pinpoint the exact year of tree death, a further effort was made to select trees that had apparently died fallen during previous fall or winter,

**Table 3.** The basal area growth series, their abbreviation and the number of trees in the series.

Formed series	Abbreviation	Number of trees
Finnish master	Fm	14
Russian master	Rm	22
Finnish <i>Coniophora</i>	Fc	12
Russian <i>Coniophora</i>	Rc	15
Finnish white rot	Fw	6
Finnish heart rot	Fh	5

by using the presence of remnant green needles as the main criterion. Because a fallen tree can retain its needles for several years after falling (pers. obs.), additional indicators were used. Light colored wood, resin, and small, flexible fibers in the stem breaking point were considered useful determinants. Similar indicators have been used in earlier studies (Eriksson 1958). The sampling of trees for growth patterns was expanded outside the transects so that a sufficient number of trees that fulfilled the criteria could be sampled. Core samples were taken with a standard size increment borer, and as low in the stem as possible. However, due to the large amount of decay in the lower portion of the stem in many cases, samples were often taken at breast height or higher. As the interest was in the growth pattern prior to death, the variation in coring height was not considered a problem. Healthy canopy dominant trees were cored in both study areas to facilitate comparisons of growth patterns.

The collected increment cores were mounted on channeled wood, and sanded so that the tree ring structure was clearly visible. Tree-ring widths were measured with a stereomicroscope, using a Velmex™-measuring bench (accuracy 0.001 mm), and Measure J2X-software. Master series for crossdating were constructed from the measurements obtained from living trees (Fritts 1976). Cores extracted from recently dead trees were crossdated against the master series to assign tree-rings to correct calendar years (Fritts 1976). The crossdating was done visually using a set of index years (i.e. years characterized by exceptionally narrow or wide rings) derived from the master series. Ring-widths of the dead trees were compared to these index years, so that the calendar year of formation of each ring could be established. This facilitated comparisons of growth

patterns of correct years between the sample trees, despite the occurrence of missing rings. The formation of tree rings may stop for decades prior to mortality (Cherubini et al. 2002). These missing rings in the end of the ring series (i.e. prior to death) cannot be detected by crossdating. By using our set of external criteria, we aimed in accurately determining the year of death despite the lack of production of annual rings prior to death. The discrepancy between the externally determined year of death and the calendar year of the formation of the last tree ring (derived from dendrochronology) was then interpreted as zero growth.

The success of visual crossdating was controlled using the Cofecha computer program (Holmes 1986). When both methods gave the same result, the crossdating was considered successful. However, in some cases with very narrow growth rings the visual crossdating failed, and Cofecha results alone were used.

For studying tree growth patterns the radial increment measurements obtained from core samples were converted to basal area increment. Basal area increment is considered a better indicator of long-term changes in tree growth than raw ring width measurements, as deviations from constant growth can be detected more easily (Visser 1995). The basal area increments were calculated by considering the stem cross-section as a circle. The basal area growth patterns prior to tree death were grouped according to the primary mortality agent. These grouped series represent the average basal area increment of trees killed by a given mortality agent. The series were formed only for those primary mortality agents for whom a sufficient number of recently dead trees were sampled. In addition, similar series from both areas were formed from basal area increments of the living tree master series. These series represent the growth level and pattern of healthy dominant canopy trees.

Basal area growth trends were analyzed using linear regression of the last 25 years of each of the averaged growth series. This time period was chosen based on visual assessment of the growth patterns, and was similar to time spans used in earlier studies (Cherubini et al. 2002). By comparing the series to each other and to the master series, we examined the differences in tree growth

**Table 4.** The frequencies of identified causes of tree death, percentages are presented in brackets. The recognition percentage is the percent of trees that was not categorized as “no clear cause”.

Abiotic factors	Russia	Finland	Total
No clear cause, or multiple causes	84 (35)	1 (1)	85
Competition	2 (1)	3 (4)	5
Wind, uprooted	22 (9)	2 (3)	24
Wind, root breakage	1 (0)	0 (0)	1
Wind, stem breakage < 1,3 m	1 (0)	0 (0)	1
Wind, stem breakage > 1,3 m	0 (0)	0 (0)	0
Snow	0 (0)	3 (4)	3
Knocked down by other tree	3 (1)	0 (0)	3
Biotic factors			
<i>Fomitopsis pinicola</i>	7 (3)	0 (0)	7
<i>Phellinus chrysoloma</i>	1 (0)	6 (9)	7
<i>Onnia leporina</i>	6 (2)	18 (26)	24
<i>Armillaria</i>	0 (0)	0 (0)	0
<i>Heterobasidium parviporum</i>	1 (0)	0 (0)	1
Other brown rot	0 (0)	1 (1)	1
Other white rot	4 (2)	0 (0)	4
<i>Tetropium</i> sp.	7 (3)	1 (1)	8
<i>Callidium coriaceum</i>	0 (0)	6 (9)	6
<i>Dendroctonus micans</i>	4 (2)	3 (4)	7
<i>Ips typographus</i>	1 (0)	0 (0)	1
<i>Coniophora</i> spp.	80 (33)	23 (34)	103
Heart wood white rot	17 (7)	1 (1)	18
Total trees	241	68	309
Recognition percentage	65%	99%	72%

reduction caused by mortality agents. The differences between the slopes of the linear regression were tested with analysis of variance using SPSS software. The analysis among the growth series of dead trees was done using contrast analysis in SAS software.

## 3 Results

### 3.1 Tree Mortality Agents

The primary mortality agent was studied on 309 dead trees. Of these, 68 were recorded from the four Finnish transects, and 241 from the five Russian transects. The factor that had caused tree death was successfully determined for the majority of dead trees (Table 4). In Russia 65% and in Finland 99% of the dead trees was categorized to a primary cause of death.

Of abiotic causes of mortality, uprootings were

the most common representing 9% of the cases in Finnish sites, and 4% in the Russian sites. The role of other abiotic mortality agents was only minor, with sporadic observations of various types of stem breakages, and deaths due to fallen neighboring trees (Table 4).

The most frequent cause of tree death in both study areas were the fungi in the genus *Coniophora*, causing dark brown cubical heart rot (Eriksson 1958). These fungi were considered the primary cause of death for 34% and 33% of the studied trees in Finland and in Russia, respectively (Table 4). In the Finnish transects, the fungi *Onnia leporina* was the primary mortality agent on 26% of the trees, and *Phellinus chrysoloma* on 9% of the trees. Both of these fungi were practically absent from the Russian transects, but in these stands *Fomitopsis pinicola* was considered as the primary mortality agent for 3% of the cases. Unidentified white rots and brown rots were considered as the primary mortality agent on 1% of the trees in Finnish stands, and unidentified white



**Table 5.** Basal area increment series and their abbreviations, linear regression slope parameters and coefficient of determination of the linear regression models.

Name	Abbreviation	Slope	r <sup>2</sup>
Finland master	Fm	3.376	0.111
Russia master	Rm	3.047	0.136
Finland heartwood white rot series	Fh	-2.337	0.357
Finland whole wood white rot	Fw	-4.162	0.802
Finland <i>Coniophora</i> -series	Fc	-1.328	0.225
Russia <i>Coniophora</i> -series	Rc	-1.138	0.293

**Table 6.** The results of the contrast analyses. The comparison pairs are: Finland heart wood white rot series (Fh) vs. Finland whole wood white rot series (Fw), Finland heart wood white rot series (Fh) vs. Finland *Coniophora*-series (Fc) and Finland whole wood white rot series (Fw) vs. Finland *Coniophora*-series (Fc).

Compared series	Fh vs. Fw	Fh vs. Fc	Fw vs. Fc
Sum of squares	2165	662	5222
Degrees of freedom	1	1	1
p-value	0.245	0.519	0.072

rots on 9% of the cases in Russia.

*Callidium coriaceum* was the most frequent insect found in the Finnish transects; it was the primary mortality agent on 9% of the cases. Other insects of lesser importance in these sites were *Dendroctonus micans* (4%), and *Tetropium* spp. (1%). In the Russian transects, the insects were less frequent as main causes of mortality, with observations of *Tetropium* spp. (on 3% of the trees), and *D. micans* (2%). Competition was of minor importance as a cause of mortality in both study areas.

### 3.2 The Effect of Mortality Agents on Prior-to-Death Tree Growth

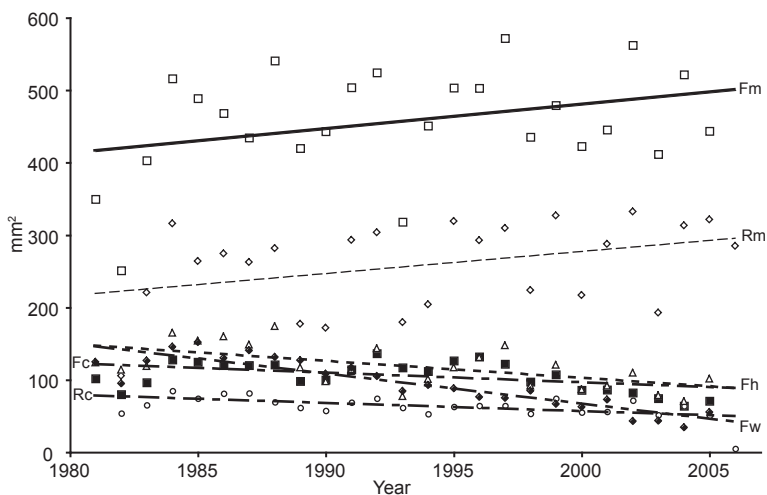
Basal area growth before death was studied and compared by constructing average basal area growth series for trees associated with different primary mortality agents. These mortality agent specific growth series were formed for trees with the *Coniophora* spp. as the primary mortality agent in both study areas, and for trees with heartwood white rot, and whole wood white rot in the Finnish study areas. Sample trees with other mortality agents were too few for proper comparisons of growth series (Table 4). The basal area growth series, formed specifically for each

mortality agent, were then compared against the two master growth series (i.e. those formed from healthy dominant trees), and against one another. The comparison was based on the slopes of fitted regression lines (Fig. 1).

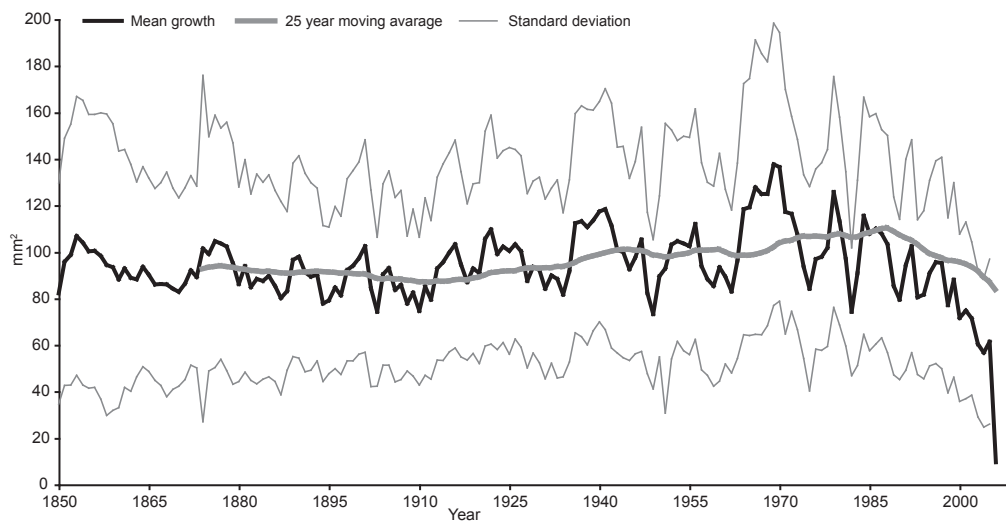
Overall, the slopes of the regression lines of the constructed mortality agent specific series and those of the master series were significantly different in both study areas (ANOVA,  $p < 0.05$ ; Table 5, Fig. 1). Also, when growth series was calculated for all dead trees in Finland and compared with those of the master series, the slopes of the regression lines were found to be significantly different (ANOVA,  $p < 0.05$ ).

The mortality agent specific growth series from the study area in Finland were compared using ANOVA contrast analyses (Table 6). The slopes of the *Coniophora* series, and heart wood rot series did not differ significantly ( $p = 0.529$ ). Neither did the heartwood white rot series and the whole wood white rot series ( $p = 0.245$ ). The clearest difference was found between the *Coniophora* series and that of the whole wood white rot, which was statistically weakly significant ( $p = 0.072$ ).

The *Coniophora* series from the study areas in Finland and in Russia did not differ significantly from each other (ANOVA). The similarity of these two series was evident (Fig. 1 and Table 5).



**Fig. 1.** Basal area increment, and the fitted regression lines of the last 25 years growth of live trees, and dead trees grouped according to primary mortality agent. The abbreviations are: Fm Finnish master series, Rm Russian master series, Fh Finnish heart rot series, Rc Russian *Coniophora*-series, Fw Finnish whole wood white rot series and Fc Finnish *Coniophora*-series.



**Fig. 2.** The average growth of all dead trees, the 25 year moving average, and standard deviation.





**Fig. 3.** Dark brown cubical rot, associated with *Coniophora* spp.  
Photo: Antti Lännpää.

## 4 Discussion

### 4.1 Tree Mortality Agents

The most common recorded primary cause of tree death in both study areas were fungi that caused dark brown cubical heart rot (Fig. 3). Based on the descriptions of rot of different fungi in studies from northern boreal forests (Eriksson 1958, Juutinen 1958), we interpreted that the fungi causing this type of rot were from the genus *Coniophora*. This interpretation was supported

by the high occurrence of these fungi in earlier studies from the same region (Norokorpi 1979), and further by expert opinions in the field (Håkan Berglund, University of Helsinki, pers. comm.; Reijo Penttilä, Finnish Environment Institute, pers. comm.). According to Eriksson and Strid (1969), and Norokorpi (1979), the *Coniophora* species that could appear in our study sites were *C. arida* (Fr.) P. Karst., *C. olivacea* (Fr.) P. Karst., and *C. puteana* (Schumach.) P. Karst. We considered these species as one group due to their convergent behavior, and difficulty of species-



**Fig. 4.** Interaction of fungi and wind was the main cause of tree death in both study areas. A thin shell of fresh wood surrounds a rotten core. Wind usually breaks the tree before it is killed by the rotting fungi. Photo: Tuomas Aakala.

level identification.

*Coniophora* spp. cause heartwood rot, which weakens the mechanical stability of trees. A tree is not directly killed by the fungi, but the structural weakening of the stem predisposes it to wind-induced stem breakage, and wind is often the final agent killing the tree (Fig. 4). In our study sites the relationship between the largely decayed

trunk and stem breakage was clearly visible, and the decay appeared to be responsible for the mechanical failure of the stem (cf. Worrall et al. 2005). Similar to the findings of Eriksson (1958) these trees showed stem breakages with decayed centres surrounded by a layer of fresh wood, indicating that the trees must have been alive when felled by wind. In these cases, the fungi were



considered as the primary mortality agent. In a recent study in northern boreal Norway spruce forest in Sweden, Edman et al. (2007) found that *P. chrysoloma* was the most common mortality agent. Although the species was different, the mechanism was the same as in our study: the fungi predisposed trees to wind-induced mortality. This species-difference could be caused by the high spatial variability in the occurrence of different polypore species in this forest type, as demonstrated by Norokorpi (1979).

Although the proportional occurrence of *Coniophora* spp. as a tree mortality agent was similar in the two study areas, there were also some differences related to other mortality agents. The first one was the more frequent appearance of *Phellinus chrysoloma* and *Onnia leporina*, which were relatively common in the Finnish study area, but practically absent from the Russian study area. The differences could be due to the natural distribution of these species, or related to the species microclimatic requirements that commonly affect the distribution of fungi (Boddy 2000, 2001). On the other hand, the fungi were classified as primary mortality agents based on the presence of fruiting bodies. Thus, differences in the occurrence of the fruiting bodies could have been a reason as well. For example, the results of Gustafsson et al. (2002) showed that the occurrence of fruiting bodies on Norway spruce reflect only approximately 1/3 of the total fungi populations living in trees. In general, insects as primary mortality agents were rare; the larger numbers of *Callidium coriaceum* in the Finnish sites could be explained by the fact that the species prefers trees that are over 25 cm in diameter (Heliövaara et al. 2004), which were more common in the Finnish sites.

The proportion of all inventoried trees that were assigned with a primary cause of mortality was clearly higher in Finland (99%) compared to Russia (65%). Although we do not know the exact reason, there are at least two possible factors that may have contributed to this. First, because of the harsher climate in the Russian study area, the trees are under constant climatic stress, and possibly more susceptible to death due to harmful agents compared to the more southern Finnish sites. Second, the fruiting bodies of *O. leporina* and *P. chrysoloma* were common in Finland,

but absent from Russia. The absence of fruiting bodies does not necessarily mean that these fungi could not have caused tree mortality, but rather that such cases would have been classified as no clear cause.

#### 4.2 Mortality Agents Affecting Prior-to-Death Tree Growth

The average prior to death growth trends (as described by the slopes of the regression lines) of trees, and the mortality agent specific ones differed from those of the healthy dominant trees (i.e. the master growth series, Table 5). The slopes of the regression lines were negative, i.e. descending for all the dead tree series, and positive for the live tree series. While this clearly indicated that, on average, trees were weakened prior to death, generalizations are difficult to make. This is because at individual tree level there were both ascending and descending growth trends for growth prior to death (not shown). It appears that the pathogens do not explain the inter-tree variation of the growth pattern very well and the presented trends only describe averages of several trees.

Overall, the differences in growth trends between the dead tree series, grouped according to primary mortality agent, were not significant (ANOVA). The only difference that was weakly significant was that between the *Coniophora* and the whole wood white rot series (ANOVA contrast analysis,  $p = 0.072$ ). On the other hand, the *Coniophora* series did not differ from the heart wood white rot series ( $p = 0.519$ ). This difference may be explained by the different ways the fungi affect a tree. Heartwood is physiologically dead material, which does not contain nutrient or fluid streams (Fritts 1976). Thus, the decay of heartwood does not affect the growth of trees. In comparison, a fungus rotting the whole stem (such as the fungi in the white rot series) does affect the tree's transport system, which can be seen as a reduction in growth (Agrios 2005). Our observations during fieldwork suggest that the heartwood rotten trees tend to fall before they die, because of the mechanical weakness of the trunk, whereas the whole tree rotten trees mostly die standing.

In addition to the observed differences in growth trends, there was a marked difference in the level of growth between the live and dead trees already at the beginning of the 25 year period that was used in the growth trend analysis (Fig. 1). This suggests that either the trees eventually killed by the fungi were already weakened prior to colonization by the fungi, or the fungi influenced tree growth for a period longer than 25 years. The mean growth level of all dead trees (Fig. 2) had remained at a relatively stable level for the period from 1850 to 1980 (beginning of the decline), which would support the first suggested explanation. Norway spruce is capable for decades of low growth (Cherubini et al. 2002), but low level of growth is also a sign of scarce resources, making the tree less capable of defending itself against harmful agents.

A proper comparison between the two study areas could only be done for trees with the *Coniophora* fungi as the primary mortality agent. The comparison showed that, despite the climatic differences between the regions, these fungi decreased tree growth the same way prior to tree death in both study areas. This can be deduced from the fact that as the slopes of the growth trend lines were almost identical (Fig. 1 and Table 5).

Assessing the timing of tree death is not a trivial task, because of the lack of commonly defined criteria. A tree can keep its needles green for numerous years with the old transporting cells, even if no new ones are formed (Cherubini et al. 2002). For example, Cherubini et al. (2002) found that ring formation can stop 1–31 years prior to death. On the other hand, it is likely that even a fallen tree can grow new rings, if there are intact transport cells left. Thus the definition of a specific year of death is in many cases difficult.

This study focused on the last 25 years of a trees life. Because missing rings are interpreted as years where trees did not grow, they affect the slopes of the growth trends. Since the measurements were done using increment cores, it is possible that some of the missing rings were partial rings. Partial rings are, on the other hand, often narrow (pers. obs.), so the error in the basal area increment calculations, due to interpreting them as missing (i.e. zero growth) is likely to be relatively small.

## 5 Conclusions

In this study we examined the agents and process of tree mortality in old pristine Norway spruce forests in northern boreal Fennoscandia. The most common primary cause of death in the study areas was the heart wood rotting fungi of the *Coniophora* genus. The rot of species of this genus was frequent in recently dead Norway spruce trees. The rot weakens the mechanical stability of tree stems until they fall due to snow or wind, which can be considered only as secondary mortality agents. There were weak indications that growth prior to death was different between trees with heart wood rotting fungi and trees with whole wood rotting fungi. Whole tree rotting fungi decreased tree growth more rapidly than heart wood rotting fungi. In general, the results demonstrated that tree death in pristine Norway spruce forests in northern Fennoscandia results from a long-lasting process involving both biotic and abiotic factors.

## Acknowledgements

This research has been funded by the European Union program: Interreg IIIA Nord (project no. KA 0173). We thank all the fieldwork participants: Jari Hietanen, Matvey Yuntunen, Vladislava Sokolova, Tuomo Wallenius, and all others who shared their knowledge during this study. Bengt-Gunnar Jonsson and John Innes gave valuable comments on an earlier version of the manuscript.

## References

- Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* 5: 169–211
- Agrios, G.N. 2005. *Plant pathology*. Academic Press New York. 922 p.
- Boddy, L. 2000. Interspecific combative interactions between wood-decaying basidiomycetes. *FEMS Microbiology Ecology* 31(2): 185–194.

- 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. *Ecological Bulletins* 49: 43–56.
- Cherubini, P., Fontana, G., Rigling, D., Dobbertin, M., Brang, P. & Innes, J.L. 2002. Tree-life history prior to death: two fungal root pathogens affect tree-ring growth differently. *Journal of Ecology* 90(5): 839–850.
- Dobbertin, M. & Biging, G. 1998. Using non-parametric classifier CART to model forest tree mortality. *Forest Science* 44(4): 507–516.
- Eriksson, J. 1958. Studies in the heterobasidiomycetes and homobasidiomycetes – aphylophorales of Muddus national park in North Sweden. *Sybolae Botanicae Upsalienses* 16(1): 1–172.
- & Strid, Å. 1969. Studies in the aphylophorales (basidiomycetes) of Northern Finland. *Turun yliopiston julkaisu, sarja IIA* 40: 112–158.
- Franklin, J.F., Shugart, H.H. & Harmon, M.E. 1987. Tree death as an ecological process. *Bio Science* 37(8): 550–556.
- Fritts, H. 1976. *Tree rings and climate*. Academic Press, London. 567 p.
- Gustafsson, M., Holmer, J. & Stenlid, J. 2002. Occurrence of fungal species on coarse logs of *Picea abies* in Sweden. In: Gustafsson, M.: *Distribution and dispersal of wood-decaying fungi occurring on spruce logs*. Dissertation. Swedish University of Agricultural Sciences, Uppsala, Sweden. p. 4.1–4.10.
- Heliövaara, K., Mannerkoski, I. & Siitonen, J. 2004. Suomen sarvijäärät. Longhorn beetles of Finland (Coleoptera, Cerambycidae). Tremex Press, Helsinki. 374 p. [In Finnish with English summary].
- Hofgaard, A. 1993. 50 years of change in a Swedish boreal old-growth *Picea abies* forest. *Journal of Vegetation Science* 4(6): 773–782.
- Holmes, R.L. 1986. Quality control of crossdating and measuring: a user's manual for the program COFECHA. In: Holmes, R.L., Adams, K. & Fritts, H.C. (eds.). *Tree-ring chronologies of western North America: California, eastern Oregon, and northern Great Basin*. University of Arizona Press, Tucson, Arizona, USA. p. 41–49.
- Hyvärinen, V. & Sepponen, P. 1988. Tree species history and local forest fires in the Kivalo area of Northern Finland. *Folia Forestalia* 720. 26 p.
- Imbeau, L. & Desrochers, A. 2002. Foraging ecology and use of drumming trees by three-toed woodpeckers. *The Journal of Wildlife Management* 66(1): 222–231.
- Jonsson, B.G. 2000a. Availability of coarse woody debris in a boreal old-growth *Picea abies* forest. *Journal of Vegetation Science* 11: 51–56.
- Kuuluvainen, T. 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. *Annales Zoologici Fennici* 31: 35–51.
- Manion, P.D. 1991. *Tree disease concepts*. Englewood Cliffs, N.J.: Prentice Hall.
- Norokorpi, Y. 1979. Old Norway spruce stands, amount of decay and decay-causing microbes in northern Finland. *Communicationes Instituti Forestalis Fenniae* 97(6). 77 p.
- Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins* 49: 11–41.
- Sirén, G. 1955. The development of spruce forest on raw humus sites in Northern Finland and its ecology. *Acta Forestalia Fennica* 62. 408 p.
- Söderström, L. 1988. Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in northern Sweden. *Nordic Journal of Botany* 8: 89–97.
- Syrjänen, K., Kalliola, R., Puolasmaa, A. & Mattson, J. 1994. Landscape structure and forest dynamics in subcontinental Russian European taiga. *Annales Zoologici Fennici* 31: 19–34.
- Vadja, A. & Venäläinen, A. 2003. Small-scale spatial variation of climate in Finnish Lapland. *Finnish Meteorological Institute Reports* 2003(1). 34 p.
- Visser, H. 1995. Note on the relation between ring widths and basal area increments. *Forest Science* 41: 297–304.
- Wallenius, T., Pitkänen, A., Kuuluvainen, T., Pennanen, J. & Karttunen, H. 2005. Fire history and forest age distribution of an unmanaged *Picea abies* dominated landscape. *Canadian Journal of Forest Research* 35(7): 1540–1552.
- Worrall, J.J., Lee, T.D. & Harrington, T.C. 2005. Forest dynamics and agents that initiate and expand canopy gaps in *Picea-Abies* forests of Crawford Notch, New Hampshire, USA. *Journal of Ecology* 93: 178–190.

*Total of 28 references*