ORIGINAL ARTICLE

Outbreaks of *Gremmeniella abietina* cause considerable decline in stem growth of surviving Scots pine trees

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ABSTRACT

In the early 2000s, an extensive epidemic of the fungus *Gremmeniella abietina* (Lagerb.) Morelet occurred in Sweden and caused severe damages to coniferous species. This study aimed to evaluate the impacts of this outbreak on the stem growth of the surviving Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L.) trees, using the country-wide data on pine and spruce from the Swedish National Forest Inventory and data from stem analyses of pine growth in four infected plots ($n_{trees} = 12$) in the Bergslagen area of middle Sweden. Analyses of volume dynamics in the four stands indicated a decade-long negative effect of pathogen infections on volume growth of pine trees. Over 2000–2012, the difference between projected (assuming no infection) and observed volume growth was 10–62%, depending on infection-related crown transparency (varying between less than 20% to above 80%). Height growth of pine in affected stands was reduced by 64–85%, although the reduction did not correlate with levels of crown transparency. The average reduction in basal area increment (BAI) in affected areas country-wide, accumulated over 2000–2006, was ~21% for pine and ~4% for spruce. The use of regular ring-width chronologies, as compared to volume increment chronologies, resulted in underestimation of volume losses by 25–30%.

1. Introduction

Infection of coniferous forests by the ascomycete fungus *Gremmeniella abietina* (Lagerberg) Morelet has been reported in Europe since the early 20th century (Nevalainen, 2002; Sikström et al., 2005), where it is referred to as Brunchorstia disease (Scleroderris canker in North America; Skilling et al., 1979). In northern Europe, two biotypes of *G. abietina* (hence forward *GA*), the small tree type (STT) and the large tree type (LTT), are diagnosed. STT typically infects only seedlings and saplings (Kaitera et al., 2000), causing necroses on the stems and branches covered by the snow (Bernhold, 2008), while LTT attacks trees of all sizes (Kaitera et al., 2000), causing necroses mainly at the base of the buds and in the cortex of the

new shoots. These necroses usually lead to the dieback of buds and the discoloration of needles which subsequently dropped off as a result of the infection (Skilling et al., 1979). Dead shoots are usually concentrated in lower branches, even if the symptoms can appear through the entire crown (Nuorteva et al., 1998; Kaitera et al., 2000).

In Scandinavian forests, pines (*Pinus sylvestris* L. and introduced *P. contorta* Douglas ex Loudon) and Norway spruce (*Picea abies* L.) are among the primary hosts of *GA* (Barklund and Unestam, 1988; Witzell and Karlman, 2000). Scots pine is considered more sensitive than Norway spruce to this pathogen (Barklund and Rowe, 1981; Barklund and Unestam, 1988; Anglberger and Halmschlager, 2003).

In Sweden, several extensive *GA* outbreaks have been documented since the late 1950s (Hellgren and Barklund, 1992; Wulff et al., 2006). In 2000–2003, an epidemic of *GA* was sweeping through Swedish pine forests, with the infestation taking place extensively in the year 2000, and the symptoms became evident in the summer of 2001 (Sikström et al., 2011). This epidemic was recorded as the most severe outbreak so far in Sweden (Bernhold et al., 2011). The Swedish National Forest Inventory (NFI) esti-

mated that almost 6% of pine forests (484,000 ha) were infected during 2001–2003 (Wulff et al., 2006), which resulted in sanitary felling or clearcuts of more than 50,000 ha of Scots pine stands since 2001 (Wulff et al., 2006; Bernhold et al., 2011). In addition, studies have documented high mortality levels (454 trees ha^{-1}) during the first five years following the outbreaks (Sikström et al., 2011), the attack of the secondary damaging agents (e.g. *Tomicus* spp.) being a contributing factor. However, little is known about the long-term growth decline in trees that have survived that outbreak (later referred to as 2000 outbreak). Such a decline is yet another factor that can negatively affect forest productivity. A large proportion of stands that were affected during the 2000–2003 outbreak were young (30–50-year-old) and productive (Sikström et al., 2011), suggesting that growth declines could be considerable. Indeed, during five years following the outbreak, the reduction in volume increment of infected Scots pine was once estimated as 42–73% (Sikström et al., 2011).

Crown transparency (CT), also referred to as defoliation (Sikström et al., 2011), reflects tree growth rates and has been widely used to provide regional assessments of tree growth and vitality following environmentally stressful periods (Drobyshev et al., 2007). In Scots pines, CT has been related to the severity of the *GA* outbreak (Dobbertin and Brang, 2001; Sikström et al., 2005; Sikström et al., 2011). Pines with a CT of 40–59% had stem growth reduced by about 50%, while trees with a CT of 60–79% showed growth reductions up to 70% (Sikström et al., 2011), suggesting that field assessments of CT may be indicative of volume losses following pathogen infections. Infection intensity for spruce forests is generally considered lower than for pine, *GA* targeting mainly the leading shoots of trees growing in the understory of pine-dominated stands (Barklund and Rowe, 1981).

The objective of this study was to evaluate the effects of *GA* infection on the stem growth of surviving Scots pine and Norway spruce, using a combination of a detailed study of growth response to infection in four stands and analysis of country-wide NFI data. By using dendrochronological methods we specifically focused on the effects at above-annual scales, which, as we hypothesized, might contribute to underestimation of the overall *GA* impact on forest productivity. At the country scale, we evaluated dynamics of the basal area increment (BAI) over seven years following the outbreak in pine and spruce. To provide a detailed picture of the *GA* effects along the gradient of *GA* infection we compared the decadal dynamics of volume growth following the year 2000 *GA* outbreak at the stand level. We put forward the following questions: (1) what was the growth decline and recovery pattern on the volume growth of the infected pines?, (2) were the volume losses positively correlated with the crown transparency?, (3) did spruce suffer less growth declines in response to *GA* infection, as compared to pine?, and (4) did using regular ring-width chronologies in estimating volume loss provide an unbiased estimate of volume growth dynamics? The rationale for the last question was based on the fact that a large body of annual growth data available from NFI is represented by regular tree-ring width chronologies developed from increment cores, whose conversion to volume estimates involves assumptions about tree allometry parameterized on healthy (not infected) trees.

2. Materials and methods

2.1. Field sampling and sample preparation

We selected four pine-dominated (proportion of pine tree in the total number of trees in the stand above 80%) stands located between 60°09′ and 60°19′N in Bergslagen area, a region affected by the outbreak in 2000 (Fig. 1, Table A1). The selected stands were 40–60 years old and showed a large variability in crown conditions, suggesting large variability in growth responses to the *GA* outbreak.

We visually recorded the CT of all pine trees with binoculars during 2000 (stands LK and BK) and 2001 (stands SB and VT). The degree of CT was assessed as a percentage of the fully developed tree crown, following national inventory protocol (Wulff et al., 2006). Trees were grouped into three CT classes: healthy trees (trees with symptoms of scleroderris canker observed at the less than 20% of the whole tree crown, class I); moderately affected trees (trees with 20–80% of the whole crown with symptoms of scleroderris canker, class II); and heavily affected trees (trees with symptoms of scleroderris canker exceeding 80% of the whole crown, class III). In 2012, within each stand, we randomly selected one tree from each CT class for stem analysis. This resulted in a total of 12 trees (3 CT classes, 4 sites) (Table A2). The low number of analyzed trees at this stage was due to the fact that the sampled stands were private commercial forests. The height of each sampled tree was measured after the felling. When extracting the cross-sections on each tree, the first section was always taken at the base (ground level) and positions of the remaining sections were determined by dividing the height of the tree by ten, resulting in sampling of 11 cross-sections per tree. In the laboratory, all cross-sections and tree-ring cores were polished to obtain fine surfaces with clearly visible ring boundaries.

2.2. Data treatment and calculation of volume increment

Cross-sections were scanned with 1200 dpi resolution and converted into image files for measurements to the nearest 0.001 mm using WinDendro ver. 2005a (Regent Instruments, 2005) and CooRecorder 7.3 (Larsson, 2003). To verify cross-dating and measurement accuracy, we used COFECHA (Holmes, 1983) and CDendro 7.3 (Larsson, 2003) software. On each cross-section, growth was measured along three radii. A first radius was randomly selected and the two remaining radii positioned at a 120° angle to the first. We used WinStem ver. 2005a (Regent Instruments, 2005) to conduct stem analyses and to obtain annual volume increment chronologies for each sampled tree. We later referred to these chronologies as *observed volume increment* (OVI) chronologies, since they represented empirically observed dynamics of volume increment over time (Table A3). While performing stem analyses, we applied linear interpolation to reconstruct tree height dynamics over time (Newton, 2004). We did not use the predictive functions of stem volume already available for Scots pine over the Nordic region (e.g. in Brandel, 1990) as these functions were designed to obtain a single estimate of tree total volume but not the annual dynamics of volume increment. In addition, these functions assumed healthy trees, which was not the case in this study.

Besides reconstructing volume dynamics from cross-sections, we were also interested in developing volume estimates from regular tree cores, a much more abundant, yet less precise source of data on growth dynamics. In this study, we used chronologies obtained from cross-sections at the ground level and at the breast height. These two cross-sections were chosen because in forestry practice, tree cores are typically extracted from either the tree base or the breast height. To develop volume estimates, we followed an earlier proposed four-step approach converting ring chronology from tree core into volume increment series for calculating growth declines (LeBlanc, 1996). First, we computed BAI using the R package *dplR* (Bunn, 2008). Second, we estimated tree height for each year of a tree's lifespan. Assuming linear height increment with time, following LeBlanc's (1996) observation in 50-year-old plantations of Scot pine, we calculated the annual height increment (HI) as HI = (Total height − H$_{cs}$)/Age$_{cs}$, where Age$_{cs}$ was the tree age at a particular cross-section, and H$_{cs}$ was the height of that cross-section, which was set to 0 m for ground level cross-sections or to the actual height of the second lowest cross-sections (within 1.3 and 2.3 m). Tree height in year t was obtained as H$_t$ = H$_{cs}$ + HI * Age$_t$, where Age$_t$ was