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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-

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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

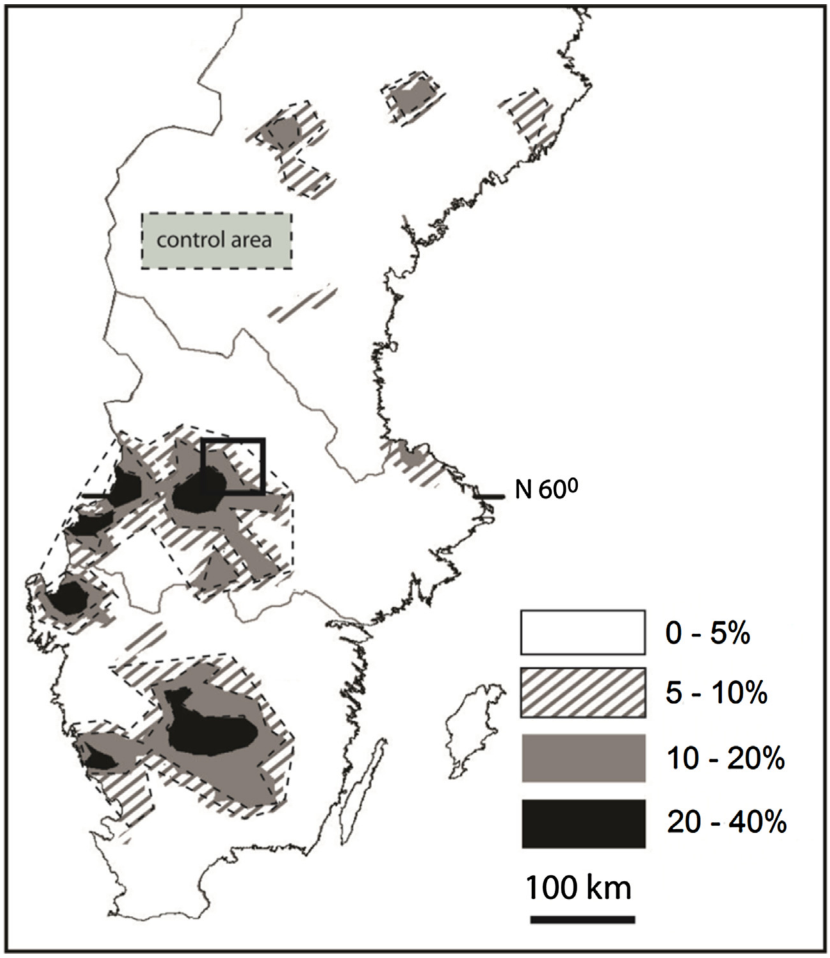

Fig. 1. Distribution of *GA* infection in Swedish pine forests according to the National Forest Inventory (NFI) during 2002–2003 (Wulff et al., 2006) and the region where four studied stands were located (black square). Tree-ring records of Scots pine and Norway spruce trees were extracted from the polygons representing the stands with 5–10% (bars), 10–20% (grey), and 20–40% (black) trees with >25% crown defoliation, respectively. The rectangle marked "control area" indicates the area used to extract the control data.

tree age at year *t*. Third, we calculated annual tree volume using the equation for a solid paraboloid: Volume = (Height * Basal Area)/2. Last, we subtracted total volume at year *t-1* from volume at year *t* to derive chronology of annual volume increment. Such chronologies of volume increment estimated from the ring-width chronologies of the tree base or around the breast height were termed as $EVI_{R\text{-}1st}$ and $EVI_{R\text{-}2nd}$ respectively (Table A3).

2.3. Definition of decline period and assessment of volume loss

We ran piecewise linear regression of the OVI chronologies versus calendar years to date the actual onset of the decline in the volume growth rate. We assumed that volume growth rate increased linearly with time and that the *GA* epidemic caused its temporal decline. We identified the change-point in this relationship as a breakpoint value in piecewise linear model. For each sample tree, the model attempted to split its entire chronology into two segments and to yield two separate, but connected linear functions, one for each segment. These two functions were connected by breakpoint pointing to the onset of the growth decline. The piecewise analyses were performed in Statistica 6.0 (StatSoft, 2007).

To detect the termination of the growth decline, we first performed a regression between OVI and cambial age (years) over the period prior to 2000 (termed as the *pre-infection period*) and used regression parameters to project volume growth over period from 2000 to 2012 (termed as the *post-infection period*), and then the growth decline was defined to terminate at the moment when the annual volume increment regained or exceeded the respective value projected based on the growth trends prior to infection. Subsequently, we considered the *decline period* as time between the actual onset and the termination of the growth decline.

The growth of each tree in the *pre-infection period* occurred at various growth rates. We integrated tree growth performance during that period by either linear or quadratic model selected among a range of linear or non-linear options as the model with the highest R^2.

To compare the volume loss at the same temporal scale (13 years, 2000–2012), we aggregated the volume loss over the whole *post-infection period* for each sample tree. The estimate of cumulative volume increment over the *post-infection period* was referred to as the *projected volume increment*, PVI (Table A3). The same procedures were used to obtain the projected volume increment of $EVI_{R\text{-}1st}$ and $EVI_{R\text{-}2nd}$ ($PVI_{R\text{-}1st}$ vs. $PVI_{R\text{-}2nd}$) over the *post-infection period* (Table A3). The tree-specific volume loss was derived by integrating the difference between observed and projected volume increments over the *post-infection period*. More specifically, we used the following equations to calculate volume loss based on stem analyses (VL_{PVI}) and its percentage form (VL_{PVI} %) (Table A3):

$$VL_{PVI} = \sum_{i=2000}^{2012} (PVI_i - OVI_i) \tag{1}$$

$$VL_{PVI}\% = VL_{PVI} / \sum_{i=2012}^{2012} PVI_i \quad (2)$$

where OVI_i and PVI_i represented observed and projected volume increments, respectively in year *i*. By averaging volume losses on the four sample trees within the same CT class, we derived mean volume loss (MVL) per tree for each CT class. To assess the using of regular ring-width chronologies in estimating volume growth dynamics, we used the same algorithm to calculate volume losses from ring-width data obtained at the two lowest cross-section ($VL_{PVI\text{-}1st}$ and $VL_{PVI\text{-}2nd}$) (Table A3). To evaluate the quality of these estimates, we checked the linear relationships between volume losses that were estimated from stem analysis (x) and volume increment reconstructions using ring-width data (y), assuming that perfect prediction would correspond to y (*i*) = x (*i*), where *i* is a tree within a particular CT class.

To evaluate the effect of *GA* infection on tree height growth, which was not considered in estimating volume losses from regular ring-width chronologies, we calculated average annual height increment between the uppermost cross-section used for the stem analysis and the tree height at the time of sampling. The respective time period included the *GA* outbreak and was therefore viewed as characteristic of post-outbreak height growth. For each sampled tree, we divided the difference between total tree height and the uppermost cross-section height by the number of rings on that cross-section (which varied between 4 and 14 years). We then compared that estimate with the average annual height increment over the tree life span prior to moment the tree reached the height of the uppermost cross-section.

2.4. Analysis of tree-ring data from NFI and estimate of volume loss over slightly affected pine forests

We used NFI tree ring records to compare BAI response of infected Scots pine and Norway spruce forests at the national scale. NFI contains information on tree cores sampled between 2006 and 2010 on temporary plots systematically distributed over Sweden. We selected tree-ring records using the *GA* outbreak map, based on interpolation of data from 4865 forest observation plots from the 2002–2003 NFI and National Forest Damage Inventory (Wulff et al., 2006). We delineated areas with affected pine forests (>65% of the stand area, Fig. 1) and retrieved all NFI tree-ring records available in these areas. NFI database yielded 223 pine and 733 spruce chronologies (Table A4). As a control dataset we used 155 pine and 20 spruce chronologies from a region where trees were either seemingly uninfected or only slightly defoliated, located in the vicinity of the affected areas (Fig. 1). We note that NFI uses CT < 25% as the limit for slightly defoliated trees.

We limited the analyzed period by the year 2006 in all the chronologies to address the differences in the timing of the tree core sampling (varying between 2006 and 2010). To calculate BAI we selected only trees with ages equal to or above 20 years for pine and 10 years for spruce, taking into account fewer chronologies of spruce in the dataset. The ring-width chronologies were transferred into BAI series using the R package *dplR* (Bunn, 2008). We performed a linear regression between years (as predictor) and BAI series (as dependent variable) prior to year 2000, then used this regression to project BAI over 2000–2006, assuming no disturbance (outbreaks) occurred. We calculated the *relative growth* ($RELA_{BAI}$) as a percentage of observed BAI in the projected BAI accumulated over 2000–2006, using tree-level data:

$$RELA_{BAI} = \left(\sum_{i=2000}^{2006} OBS_i^{BAI} / \sum_{i=2000}^{2006} PRO_i^{BAI} \right) \cdot 100\% \quad (3)$$

where OBS_i^{BAI} and PRO_i^{BAI} were the observed and projected BAI in a year *i*, respectively.

The use of projected values helped us avoid direct comparisons between infested and control stands/trees, which could be influenced by a variety of tree/stand specific factors (e.g. local soil conditions and local density), interacting with outbreak-induced growth signal. To check for the sensitivity of the results to the quality of growth trend approximation by empirically derived functions we ran the analyses three times: for the complete dataset, and for two subset of samples representing trees with values of R^2 above 0.5 and 0.7, respectively.

To estimate country-wide loss of pine volume increment and its economic equivalent we used data from the Swedish NFI and current timber prices. Our estimation was based exclusively on the dominant type of affected forest areas, so-called "slightly affected pine forests". This group accounted for 87% (or $4.23{*}10^5$ ha) of all *GA* affected forests and was defined by NFI as stands with more than 10% of the trees exhibiting CT of 25–60% (Wulff et al., 2006). Trees with CT below 20%, analyzed in this study, provided volume data to assess country-wide effect of *GA* outbreak. To simplify calculation, we assumed that all "slightly affected forests" had exactly 10% of affected trees and their volume dynamics could be represented by trees in the least infected class (trees with CT below 20%) of trees sampled for stem analyses. All assumptions reflected a conservative approach in estimation of volume losses. We considered 800 stems ha^{-1} as the average stand density in Swedish pine production forests (Gong, 1998). Finally, we used the 2008 average selling price of pine sawlogs that were delivered at the forest roadside in middle Sweden (500 SEK or 55 Euros per m^3, Classon and Gjerdrum, 2013) to estimate the corresponding economic loss by multiplying the total volume loss by this price.

3. Results

3.1. Growth decline period in Scots pine

For Scots pine trees in CT class I, volume growth rate either declined for three or seven years following the outbreak (Trees 281 and LK7) or did not exhibit any breakpoint behavior (Trees 614 and 796); rather, growth of the latter continuously increased towards the end of our observation period (Fig. 2, Table A5). For pine trees in CT class II, there was an average decline period of nine years (range: 5–13 years) and, by the year 2012, two chronologies had regained annual volume increments that were equal to or higher than values that projected based on growth trends prior to the infection (Fig. 2, Table A5). For pine trees in CT class III, the growth decline lasted from ten to eleven years (Fig. 2, Table A5). In none of four trees annual volume increment reached the projected levels by 2012 (Fig. 2, Table A5).

3.2. Dynamics of Scots pine volume increment as revealed by stem analysis

We computed cumulative volume loss under a 13-year timespan (2000–2012) for each tree (Table A6). In CT class I, some trees exhibited only marginal volume losses (0.1% and 1.6%, respectively, in Trees 281 and 796), whereas others (614 and LK7) had volume losses ranging from 10 to 30%. In CT class II, volume loss varied from 12% (Tree 618) to almost 80% (Tree 293). In CT class III, volume losses exceeded 50% for all sample trees, reaching 75% in Tree 280. During the period 2000–2012, mean volume losses were 10 ± 12%, 44 ± 32% and 62 ± 10% for CT class I, II and III, respectively. In terms of absolute values, these percentages corresponded respectively to 10 ± 10 dm^3 $tree^{-1}$ for CT class I, 60 ± 47 dm^3 $tree^{-1}$ for CT class II, and 59 ± 24 dm^3 $tree^{-1}$ for CT class III.

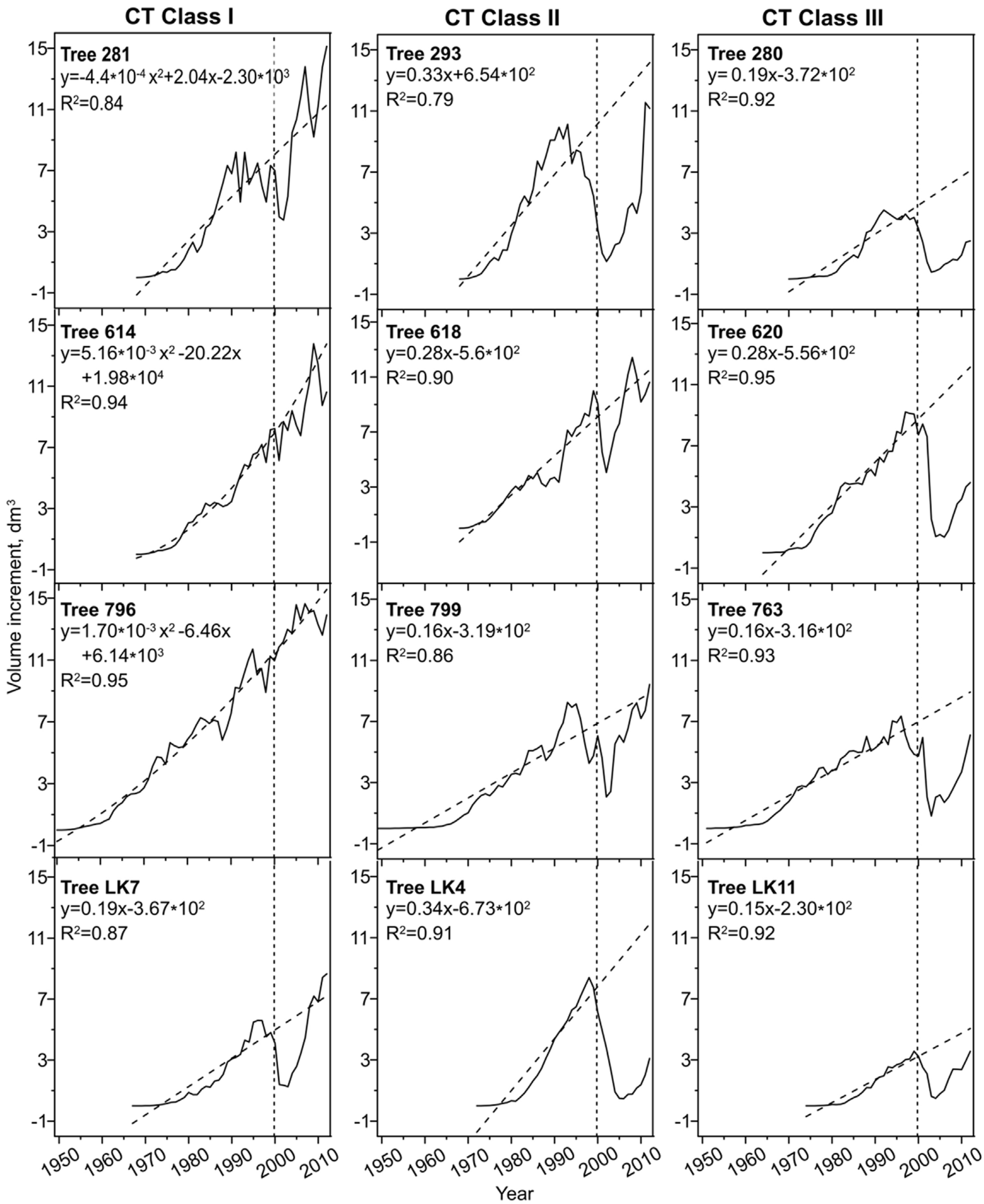

Fig. 2. Reconstruction of volume dynamics through the stem analysis. Observed volume increment (OVI, solid line) and the regression line fitted for the pre-infection period (broken line). Regression line over the post-infection period (2000–2012) represents projected volume increments (PVI) based on projecting the pre-infection linear growth trend into the post-infection period (under the assumption of no infection). Regression models and model R^2 are shown for each tree. The vertical dashed line marks year 2000. Tree ID shown in the upper left corner of each panel.

3.3. Effects of GA outbreak on stem growth of Scots pine and Norway spruce at country scale

Analysis of NFI data revealed that in the forests affected by *GA* outbreak the relative BAI was 78.7% for Scots pine and 97.1% for Norway spruce over 2000–2006. In forests considered not infected by *GA*, the relative growth in BAI was 88.7% for pine and 98.0% for spruce. With analyses done on the subsets of data with better growth approximation by an empirical function (R^2 in regression between time and BAI above 0.5 and 0.7), the relative growth ($RELA_{BAI}$) was 78.5% and 77.6% for pine, and 96.8% and 96.7% for spruce. Variability in regression skill had therefore little influence on the growth estimates.

The total volume loss over slightly infected pine forests (CT < 20%) was estimated to be on average $0.8\,m^3\,ha^{-1}$ or $3.38^*10^5\,m^3$ over the whole Sweden following the *GA* outbreak. The associated corresponding economic loss reached 16.9 million SEK or 18.6 million Euros.

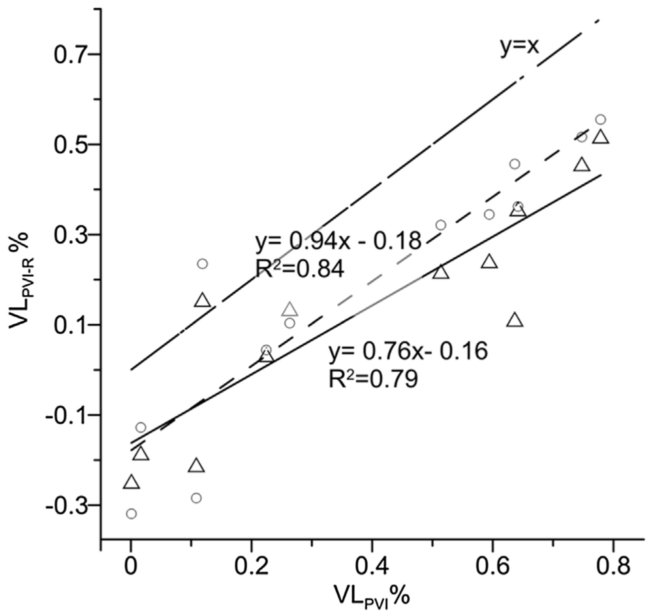

Fig. 3. Relationships between volume losses estimated from stem analyses (VL_{PVI}) and reconstructions based on ring-width data from a regular ring-width chronology (VL_{PVI-R}). Regressions that were obtained on the base cross-section ($VL_{PVI-1st}$) and the second lowest cross-section ($VL_{PVI-2nd}$) are shown as solid lines (triangles) and broken lines (circles), respectively. The dashed line represents the regression model, which assumes a perfect correspondence between results that were obtained through analyses of volume and ring-width chronologies ($VL_{PVI-R} = VL_{PVI}$).

3.4. Comparison of two volume assessment metrics

We compared the accumulated volume losses on pine trees that had been obtained through stem analysis (OVI) and tree-ring chronologies that had been developed at two heights (EVI_{R-1st} and EVI_{R-2nd}) (Table A6). In general, estimated volume increment (EVI_{R-1st} and EVI_{R-2nd}) chronologies tended to underestimate volume losses by about 25–30% as compared to OVI chronologies (Fig. 3, Table A6). Underestimation was consistent across all CT classes (Fig. 3). *GA* outbreak reduced the height growth of surviving trees. The averaged reduction was 68.1% for trees in the lowest CT class (<20%), 85.2% in intermediate CT class (20–80%) and 64.4% for the most severely affected trees (CT > 80%).

4. Discussion

4.1. Growth decline and recovery in Scots pine

We analyzed growth dynamics of Scots pine trees that survived *GA* infection, i.e. individuals that typically were not considered when estimating pathogen-induced damage. By extending analyses of post-infection effects on pine over 13 years (2000–2012) and analyzing the outbreak effects on pine at the country scale, we demonstrated considerable and largely overlooked effects of infection on the growth of surviving trees. In severely damaged Scots pine trees, the *GA* outbreak negatively affected the annual volume increment over a period of or exceeding a decade (with CT exceeding 80%). In general, higher CT was associated with a longer period of growth decline. A number of studies involving a range of pathogens or pests have indicated that growth recovery depends upon defoliation intensity. For example, in a previous 5-year-long study of *GA* infection, the growth rate of pine trees with medium CT (40–79%) regained pre-outbreak levels within five years, while the growth of trees with severe CT (>79%) had not even started to recover (Sikström et al., 2011). Scots pine trees that had sustained complete defoliation by pine sawfly (*Diprion pini* L.) in two consecutive years of attack showed a seven- to eight-year decline in diameter growth (Långström et al., 2001). Similarly, trees with crowns that had been severely damaged by European pine sawfly (*Neodiprion sertifer* Geoffroy) exhibited an average nine-year period of growth decline (Austarå et al., 1987). These studies and our own results indicate the importance of having an observation period exceeding one decade to adequately assess the growth response of trees to pathogen infections.

4.2. Crown conditions and volume dynamics following Gremmeniella outbreak in Scots pine

CT condition was a good indicator of volume loss, as volume loss generally increased with an increasing degree of crown transparency. In our study, pine trees with slightly (CT < 20%) to severe (CT > 80%) crown damage showed volume losses of less than 10% up to 63% over 2000–2012. A study in a Swedish Scots pine forest reported a volume loss of 42–73% for trees with CT exceeding 60% after the 2000 outbreak (Sikström et al., 2011), similar to results that had been obtained in a Finnish study (Riihinen and Uotila, 1992). Another Swedish study linked defoliation levels ranging from 30% to 70% to losses in mean diameter increment ranging from 10% to 50%, respectively (Bernhold, 2008).

4.3. Effects of the GA outbreak on stem growth of pine and spruce

GA outbreak caused considerable decline in stem growth of surviving pine trees while it had little impact on spruce. Analysis of the NFI dataset revealed an average BAI reduction of 21% on pine trees over the 7-year period (2000–2006). We speculate that the actual growth loss might be even larger, as this assessment has been obtained on increment core data, which underestimate the actual growth loss (see section Value of regular tree-ring data in assessing volume losses). A 10% growth reduction observed in non-infected forests may be attributed to (a) an impact of minor infection in the forests considered "healthy" in the inventory, or (b) factors not related to *GA*, e.g. to climatic conditions during the start of the 21st century, or both. We argue that the impact of minor infections was a more likely reason for that reduction, considering the lack of regional growth declines in spruce. Indeed, spruce trees in both the infected and control forests did not exhibit obvious growth reductions, which would be indicative of *GA* infection in the early 2000s, with an average difference in the observed vs. projected BAI of c. 2%. Our results indicate that spruce was more tolerant to *GA* infection than pine, confirming the pattern reported earlier (Barklund and Rowe, 1981; Barklund and Unestam, 1988). The pathogen has been mostly observed on spruces growing in the understory of pine-dominated stands, affecting mainly the leading shoots (Barklund and Rowe, 1981). We conclude that mixing of pine and spruce at the stand level may help mitigate effects of future *GA* outbreaks. Since spruce displayed lower growth reduction than pine, including both tree species could reduce overall production losses following GA outbreaks. We did not study secondary damaging agents in this study, although we acknowledge their potential importance. For example, the pine shoot beetle, *Tomicus piniperda*, as a secondary damaging agent colonizing *GA* affected trees, may further contribute to the growth decline (Bernhold, 2008; Sikström et al., 2011).

4.4. Hidden growth losses due to the GA outbreak

Our study demonstrated that apart from losses associated with heavily declined trees, there were considerable growth losses due to a decade-long growth recovery of less affected pine trees. Stem analyses showed an average growth loss of 7.5%, or 9.74 dm^3 $tree^{-1}$, for healthy-looking pine trees (CT < 20%) over 2000–2012. Similarly, calculations based on the NFI dataset revealed an average of c. 10% reduction in BAI of pine trees, observed in the forests considered unaffected by *GA*, i.e. forests with at least 95% of the canopy trees exhibiting defoliation below 25%. The consistency of obtained results argues for the inclusion of slightly infected or seemingly healthy pine forests in assessments of overall stand-level damage assessment. Indeed, estimated volume loss of $3.38*10^5$ m^3 (0.8 m^3 ha^{-1}) was "hidden" in slightly infected forests, and the associated economic loss (169 million SEK or 18.6 million Euros) would increase the initial economic losses (one billion SEK or 110 million Euros, Wulff et al., 2006) by 17%.

4.5. Value of regular tree-ring data in assessing volume losses

Reconstruction of the *GA* impact on volume increment of Scots pine using regular ring-width chronologies at two stem heights resulted in persistent underestimation of volume losses by 25–30%, questioning the value of this non-destructive approach for growth decline analyses. Assumption of the constant height growth, which we used to assess decline estimation on radial growth data obtained at a single height, was likely responsible for the underestimation of the *GA* outbreak impact. Indeed, height growth was reduced by at least 65% following the *GA* outbreak. However, the reductions in height growth does not appear to immediately follow the dynamics of crown conditions. For example, the trees belonging to the intermediate CT class (20–80%) showed the most dramatic decline in height growth, 85.2%. Earlier studies have reported a positive correlation between height loss of Scots pine and the severity of pathogen (*GA*) or pest (*Bupalus piniaria* L., a pine looper moth) infection (Kurkela, 1984; Bernhold, 2008). Height growth reduction in our study (64.4–85.2%) was generally higher than in pine trees that had experienced 60–100% defoliation due to pine looper attack (40–70%, Cedervind, 2003). The reduction in height growth indicated high sensitivity of tree height growth to environmental stresses.

We conclude that year 2000 outbreak of *G. abietina* in Sweden led to a decade-long decline in growth of surviving Scots pines, considerably affecting pine trees which are commonly classified as "slightly affected", while leaving little impact on spruce stands. Using regular ring-width chronologies as the predictor of stem growth in damage assessment likely underestimates the pathogen impact, which calls for development of more precise methods for assessment of forest productivity declines.

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Appendix A.

Table A1
Properties of the studied stands.

Stand	Coordinates	Elevation, m a.s.l.	Year planted	Site index	Area, ha	Species composition	Species density, stems ha^{-1}	Species mean basal area, m^2 ha^{-1}	Mean DBH, cm	Mean height, m
Ljungkullen (LK)	60°10′N, 14°28′E	400	1969	T24	34.20	Scots pine	–	–	–	10.50
Bekens (BK)	60°19′N, 14°13′E	400	1963	T24	10.10	Scots pine	1233	27.51	19.73	12.00
Säfsbacken (SB)	60°09′N, 14°26′E	300	1946	T22	20.10	Scots pine	640	18.40	21.75	16.90
						Norway spruce	160	4.60	22.66	16.90
Västansjö (VT)	60°09′N, 14°24′E	300	1959	T22	6.50	Scots pine	875	21.60	20.26	13.70
						Norway spruce	97	2.40	20.97	13.70

Note: Data obtained from the Stora Enso Skog AB inventory carried out in September 2001; dash indicates missing data.

Table A2
Characteristics of trees sampled for stem analyses in Bergslagen area. Crown transparency (CT) classes are <20% (I), 20–80% (II), and >80% (III).

Stand	LK			BK			SB			VT		
Tree ID	LK7	LK4	LK11	281	293	280	796	799	763	614	618	620
CT	I	II	III	I	II	III	I	II	III	I	II	III
Age	46	41	39	45	45	43	62	61	61	44	45	44
Height, m	11.20	10.30	9.30	14.70	12.50	11.50	19.20	15.00	15.20	16.30	15.60	14.20

Table A3
List of variables used in the analyses.

Variable, acronym	Variable, full name	Data source
OVI	Observed Volume Increment	Stem analysis
EVI_R	Estimated Volume Increment	Reconstructed ring-width data from cross-sections at two stem heights (at the ground level or at the second lowest level)
$EVI_{R\text{-}1st}$	EVI_R reconstructed from BAI of the basal cross-section	Ring-width data extracted from the basal cross-section
$EVI_{R\text{-}2nd}$	EVI_R reconstructed from BAI of the second lowest cross-section (i.e., the cross-section just above the basal one along the stem)	Ring-width data extracted from the second lowest cross-section
PVI	Projected OVI series during year 2000–2012	Regression models on OVI series before year 2000
$PVI_{R\text{-}1st}$ & $PVI_{R\text{-}2nd}$	Projected $EVI_{R\text{-}1st}$ and $EVI_{R\text{-}2nd}$ series during year 2000–2012	Regression models on EVI_{1st} or EVI_{2nd} series before year 2000

Table A3 (*Continued*)

Variable, acronym	Variable, full name	Data source
VL_{PVI}	Volume loss estimated from stem analysis data	$VL_{PVI} = \sum_{i=2012}^{2012}(PVI_i\text{-}OVI_i)$, PVI_i/OVI_i represented the projected/observed volume increment in year *i*.
$VL_{PVI\text{-}1st}$ & $VL_{PVI\text{-}2nd}$	Volume loss estimated from ring-width data extracted from the first (basal) or second (1.3–2.3 m above ground level) cross-sections	$VL_{PVI\text{-}1st} = \sum_{i=2012}^{2012}(PVI_{R\text{-}1st\text{-}i}\text{-}EVI_{R\text{-}1st\text{-}i})$, $PVI_{R\text{-}1st\text{-}i}$ represented the projected $EVI_{R\text{-}1st}$ in year *i*. The same algorithm for $VL_{PVI\text{-}2nd.}$

CT, crown transparency; GA, Gremmeniella abietina; OVI, observed volume increment; EVIR, estimated volume increment; EVIR-1st & EVIR-2nd, EVIR reconstructed from basal area increment of the basal or the second lowest cross-sections; PVI, projected volume increment; PVIR-1st & PVIR-2nd, projected EVIR-1st & EVIR-2nd series during year 2000–2012; VLPVI, volume loss estimated from stem analysis data; VLPVI-1st & VLPVI-2nd, volume loss estimated from ring-width data extracted from the first or second cross-sections.

Table A4
Numbers of the chronologies extracted from the Swedish National Forest Inventory (NFI), representing infected and control forests. *Percentage of defoliated trees* represents proportion of sampled trees with crown defoliation exceeding 25%. *Respective map shading* refers to Fig. 1 in the main text.

Type of areas	Percentage of defoliated trees and respective map shading	Pine	Spruce
Infected	0.05–0.1 (bars)	168	414
	0.1–0.2 (grey)	45	254
	0.2–0.4 (black)	10	65
	Total	223	733
Control		155	20

Table A5
Observed volume increment (OVI) during post-infection period (2000–2012). Boldface type indicates years with OVI below the breakpoint value, i.e. a change point in time-growth relationship induced by the *GA* outbreak.

CT class	Tree ID	Breakpointvalue	OVI (dm^3) values during 2000–2012												
			2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
I (<20%)	281	5.21	6.99	**3.97**	**3.76**	**5.31**	9.49	10.34	11.86	13.8	10.93	9.2	11.19	13.78	15.13
	614	4.83	8.22	6.14	8.69	8.11	9.4	8.44	7.77	9.77	11.23	13.78	12.46	11.55	11.17
	796	6.25	10.96	11.83	12.18	12.98	12.74	14.57	13.57	14.64	14.08	14.19	13.3	12.62	13.91
	LK7	2.58	4.11	**1.4**	**1.35**	**1.26**	**2.14**	**2.59**	**3.46**	**4.48**	6.52	7.2	6.82	8.42	8.66
II (60–70%)	293	4.61	**3.21**	**1.69**	**1.15**	**1.58**	**2.24**	**2.36**	**3.04**	**4.62**	**4.96**	**4.3**	**5.67**	**7.13**	**8.69**
	618	4.93	9.07	5.56	**4.06**	**5.52**	**6.96**	**7.62**	**9.46**	11.2	12.42	11.04	9.19	9.75	10.62
	799	3.35	6.06	4.61	**2.06**	**2.42**	**5.53**	**6.09**	**5.64**	**6.53**	**7.78**	**8.22**	**7.2**	**7.72**	9.42
	LK4	2.65	6.12	4.96	3.79	**2.4**	**0.91**	**0.49**	**0.47**	**0.75**	**0.76**	**1.16**	**1.38**	**2.03**	**3.1**
III (>80%)	280	1.78	3.3	2.42	**1.13**	**0.45**	**0.53**	**0.67**	**0.95**	**1.09**	**1.29**	**1.24**	**1.57**	**2.41**	**2.49**
	620	3.59	7.72	8.42	7.6	**2.2**	**1.06**	**1.19**	**1.02**	**1.48**	**2.38**	**3.21**	**3.51**	**4.31**	**4.59**
	763	2.91	4.74	5.95	**2.06**	**0.82**	**2.04**	**2.19**	**1.7**	**2.05**	**2.59**	**3.16**	**3.7**	**4.86**	**6.11**
	LK11	1.47	3.24	2.52	2.1	**0.62**	**0.49**	**0.79**	**1.02**	**1.76**	**2.4**	**2.39**	**2.37**	**2.95**	**3.56**

Table A6
Volume change estimates from $EVI_{R\text{-}1st,}$ $EVI_{R\text{-}2nd}$ and OVI chronologies during the 2000–2012 period. A negative value indicates a volume increment below the expected one.

Tree ID	Chronology type	Actual cumulative volume, dm^3 $tree^{-1}$	Expected cumulative volume, dm^3 $tree^{-1}$	Total volume Change, dm^3 $tree^{-1}$	Total Volume Change, %
Crown transparency class I, <20%					
281	$EVI_{R\text{-}1st}$	190.52	152.81	−37.71	−24.68
	$EVI_{R\text{-}2nd}$	144.95	109.91	−35.04	31.88
	OVI	125.75	125.86	0.11	0.10
614	$EVI_{R\text{-}1st}$	195.34	161.46	−33.87	−20.98
	$EVI_{R\text{-}2nd}$	129.87	101.13	−28.74	−28.42
	OVI	124.38	139.52	15.14	10.85
796	$EVI_{R\text{-}1st}$	219.64	185.55	−34.09	−18.37
	$EVI_{R\text{-}2nd}$	187.96	166.70	−21.26	−12.75
	OVI	171.57	174.43	2.86	1.64
LK7	$EVI_{R\text{-}1st}$	96.32	111.48	15.16	13.60
	$EVI_{R\text{-}2nd}$	66.98	74.72	7.75	10.37
	OVI	58.41	79.28	20.87	26.32
Crown transparency class II, 60–70%					
293	$EVI_{R\text{-}1st}$	97.13	109.50	12.37	11.30
	$EVI_{R\text{-}2nd}$	62.33	114.69	52.30	45.62
	OVI	57.54	158.19	100.65	63.63
618	$EVI_{R\text{-}1st}$	222.29	263.45	41.17	15.63

Table A6 (*Continued*)

Tree ID	Chronology type	Actual cumulative volume, dm^3 tree^{-1}	Expected cumulative volume, dm^3 tree^{-1}	Total volume Change, dm^3 tree^{-1}	Total Volume Change, %
	$EVI_{R\text{-}2nd}$	133.12	174.09	40.96	23.53
	OVI	112.47	127.59	15.12	11.85
799	$EVI_{R\text{-}1st}$	120.64	124.92	4.28	3.42
	$EVI_{R\text{-}2nd}$	92.27	96.54	4.27	4.43
	OVI	79.28	102.21	22.93	22.43
LK4	$EVI_{R\text{-}1st}$	62.64	130.16	67.52	51.87
	$EVI_{R\text{-}2nd}$	52.84	118.82	65.98	55.53
	OVI	28.32	128.06	99.74	77.89
Crown transparency class III, >80%					
280	$EVI_{R\text{-}1st}$	31.25	57.59	26.34	45.74
	$EVI_{R\text{-}2nd}$	24.51	50.67	26.16	51.64
	OVI	19.54	77.42	57.88	74.76
620	$EVI_{R\text{-}1st}$	66.59	103.60	37.01	35.73
	$EVI_{R\text{-}2nd}$	58.66	91.96	33.30	36.21
	OVI	48.69	135.88	87.19	64.17
763	$EVI_{R\text{-}1st}$	70.39	92.91	22.52	24.24
	$EVI_{R\text{-}2nd}$	57.93	88.37	30.44	34.44
	OVI	41.97	103.39	61.42	59.41
LK11	$EVI_{R\text{-}1st}$	45.75	58.56	12.81	21.87
	$EVI_{R\text{-}2nd}$	29.88	44.01	14.14	32.11
	OVI	26.21	53.90	27.69	51.37

Note: $EVI_{R\text{-}1st}$ is the volume increment estimated from ring-width data from the first cross-section (the ground level); $EVI_{R\text{-}2nd}$ is the volume increment estimated from ring-width data from the second lowest cross-section (1.3–2.3 m above ground level); OVI is the observed volume increment derived from stem analyses.

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