

Age and susceptibility of Fennoscandian mountain birch (*Betula pubescens*) towards insect outbreaks

Babst, F.^{1,2}, Frank, D.C.¹, Parlow, E.² & J. Esper^{1,3}

¹ Swiss Federal Research Institute WSL

² Institute of Meteorology, Climatology and Remote Sensing, University of Basel

³ Institute of Geography, University of Mainz

E-Mail: flurin.babst@wsl.ch

Introduction

Epirrita autumnata is one of the few Lepidoptera species that regularly reaches outbreak levels in northernmost Fennoscandia (e.g. Bylund 1997), where mountain birch (*Betula pubescens*) is the dominant tree species (Tenow et al. 2004). *E. autumnata* has a very high potential population growth rate (6 to 10-fold in one generation, Bylund 1995) and its leaf-eating caterpillars may cause massive defoliation over large areas (Tenow 1972, Karlsson et al. 2004). To reach outbreak level, at least three consecutive years of population growth are needed (Virtanen et al. 1998). High reproduction rates are mainly prevented by cold winter temperatures. The lethal temperature for the eggs is -36.5 to -35.1°C in high winter (December and January) and -29.8 to -28.3°C in late winter (February to April) (Eckstein et al. 1991). These facts make the population dynamics of *E. autumnata* subject to regional climate change, and suggest that the frequency and abundance of outbreak events is likely to be enhanced in a warmer future.

Disturbances caused by *Epirrita* fundamentally affect the forested ecosystems along the Scandes range and may cause tree mortality and trigger rejuvenation if an outbreak occurs in an unfavourable growth season (Kallio & Lehtonen 1975). Severe defoliation (more than 80% loss of foliage) reduces the annual ring width considerably for one or more years (Hoogesteger & Karlsson 1992).

Tenow (1972) and Bylund (1997) discovered that the susceptibility of mountain birch towards defoliation was tree-age dependent during the biggest known event in 1955. Stand age does not directly influence larva mortality but mature trees are generally more attractive for adult insects because they offer more places for oviposition (Ruohomäki et al. 1997). The eggs have a higher survival rate if they are laid into cracks, lichens or on scarred surfaces. Therefore, trees older than 60 years generally suffered from more severe defoliation in 1954/55 than young individuals because the larval density was higher (Tenow 1972, Tenow 2004).

Here, we investigate for the first time the different impact of *Epirrita*-caused defoliation on radial growth in old and young trees along altitudinal transects and for the four most recent outbreak events in the research area. These took place in 1954/55 (Tenow 1972), 1986, 1994 and 2004 (Babst et al. in prep.) and locally were of different intensity and distribution. In Babst et al. (in prep), the ring-width series of both transects was compared to local climate data in order to distinguish between outbreak effects and variability caused by changing growth season temperatures. Our goal in this study is to reinvestigate the connection between tree age and vulnerability towards insect outbreaks in terms of a general validity of the findings from the 1954/55 event. If the stand age structure is found to be a key parameter steering susceptibility, this has implications in forest stability and management with regard to a warming regional climate.

Materials and Methods

Study area

Research was conducted in the area of Lake Torneträsk (68°19'6"N, 19°16'44"E; 341m a.s.l.) and the Abisko National Park in Swedish Lapland. The region of interest is situated on the Eastern

slope of the Scandes. There are two types of pure mountain birch (*Betula pubescens*) forest in the research area. Most slopes are covered by the dense meadow type whereas the lower areas are dominated by the heath type (Vegetationskarta 1981). Apart from small villages along the south side of the main lake, the area of interest is mainly unsettled. **Figure 1** shows a schematic view over the study area. Temperature and precipitation data available back to 1913 from the Abisko Scientific Research Station (ANS), which is located at the southern margin of Lake Torneträsk, characterize the cold and dry climate in this region. Despite the low annual precipitation sum (304 mm) due to the lee setting, water is not a limiting factor to tree growth. The average annual air temperature is -0.55°C and mean summer temperature (JJA) is 9.98°C allowing tree growth up to about 650m a.s.l. Mean JJA temperature is the most important factor steering tree growth. Together with natural growth variability, summer temperature accounts for 80% of the variance in detrended ring-width series (Eckstein et al. 1991, Karlsson et al. 2004). Strong growth-climate relationships allow disturbances to be identified as significant deviations from temperature modelled growth.

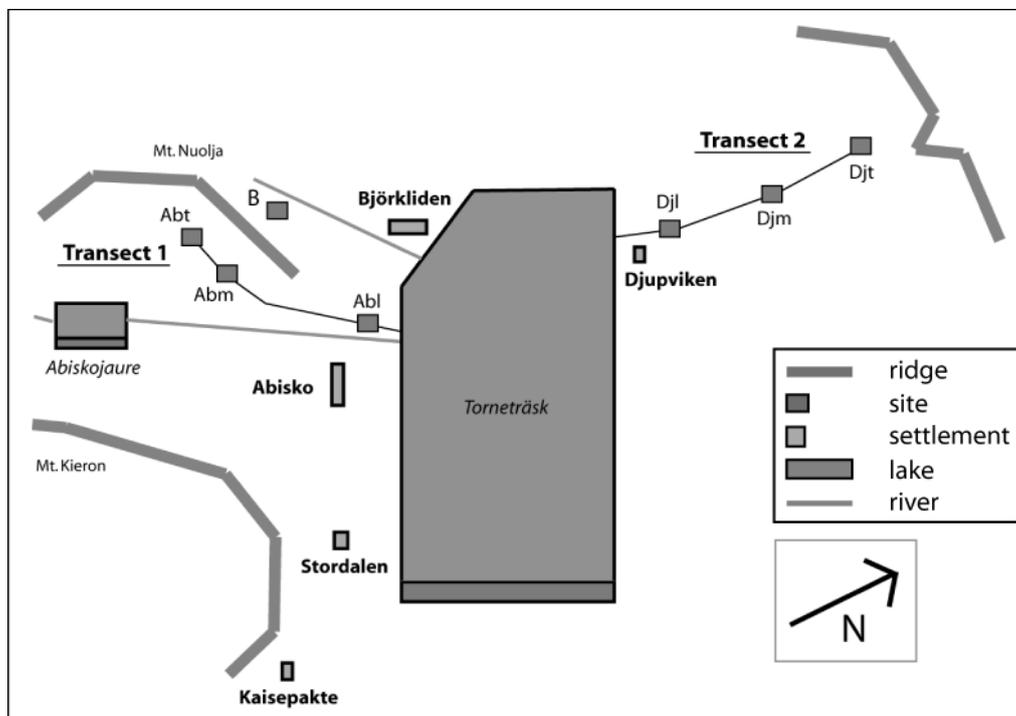


Figure 1: Schematic view over the research area. Transect 1 (Abisko) is located south of Lake Torneträsk, Transect 2 (Djupviken) covers the slope above its north-west end.

Sites and chronologies

Samples were taken along two transects with three sites at different elevations each (see **Figure 1**). This sampling strategy accounts for a potential impact of elevation on the susceptibility of young and old trees towards insect outbreaks. Transect 1 (Abisko) with the sites Abl (low), Abm (middle) and Abt (top) was set up south of Lake Torneträsk on the east-facing slope of Mt. Nuolja. Transect 2 (Djupviken, sites Djl, Djm and Djt) is located at the south-facing slope above the north-western end of the main lake. At each site, increment cores from 18-20 trees (four radii per tree) were taken and later measured, crossdated, and detrended in order to produce reliable site chronologies. For this purpose, the programs COFECHA (Holmes 1983) and ARSTAN (Cook & Holmes 1986) were used and 50-years smoothing splines (Cook & Peters 1981) applied in order to remove low-frequency trends and preserve short-term variation. Additionally, variance was

adjusted (Cook & Peters 1997) to avoid biases due to replication and cross-correlation changes during the calculation of arithmetic means (Frank et al. 2007). **Table 1** provides some basic information on series length, mean inter-series correlation (R-bar), expressed population signal (Wigley et al. 1984) and the number of radii from main and side stems (in case of polycormic individuals) included in each site chronology.

Table 1: Inventory of the curves included in the chronologies of the individual sites. Length of the chronologies with a replication >5 trees and EPS > 0.85. Additionally, the R-bar is displayed.

Site	Length of Chronology	R-bar	EPS	Number of trees	Number of radii (main-stem)	Number of radii (side-stem)
Abl	1915-2007	0.67	0.93	13	46	13
Abm	1900-2007	0.53	0.91	12	30	18
Abt	1971-2007	0.71	0.97	17	66	21
Djl	1939-2007	0.71	0.94	11	26	3
Djm	1877-2007	0.59	0.92	15	35	1
Djt	1950-2007	0.49	0.92	22	40	4

Analysis of age and vulnerability

Potential differences in the reduction of radial growth in old and young birch individuals due to an *Epirrita autumnata* population peak were investigated. As proposed by Tenow (1972) and Bylund (1997), a threshold age of 60 years at the time of the outbreak was considered, allowing young and old trees at all sites (except Abt) to be separately analysed. **Table 2** provides information about the number of young and old individuals at each site. Since the number of trees in each age class was not sufficient at all plots, the chronologies of equal elevations were combined to ensure a suitable replication. Additionally, possible bias induced by differing site properties is reduced.

Table 2: Number of young and old birch trees (threshold age 60 years in 2004) at the individual sites at both transects. The total number of the combined sites and the average age in 2004 are displayed.

Site	No. trees > 60 years	No. trees < 60 years
Abl	9	4
Abm	11	1
Abt	0	18
Djl	6	6
Djm	8	9
Djt	8	16
Total low	15 (av. age 89)	10 (av. age 45)
Total mid	19 (av. age 140)	10 (av. age 38)
Total top	8 (av. age 130)	34 (av. age 29)

A superposed epoch analysis was carried out which covered the four most recent outbreaks in 1954 (Tenow 1972, Bylund 1997), 1986, 1994 and 2004 (Babst et al. in prep.). The correct dating of the outbreaks was ensured by calculating residuals from instrumental temperature data and from non-host species (not shown here). This way, the possibility of reduced growth due to unfavourable conditions was excluded. Three years preceding and following each outbreak were included in order to visualize the differences in reduction of the tree-ring indices between young and old trees during an outbreak. This analysis also enabled the inter-comparison of the four events in terms of intensities and recovery periods.

Results

The reduction in radial growth due to insect outbreaks was compared for old and young birch individuals. Despite the present noise in the data, a distinct defoliation signal was clearly visible in all outbreak years. Generally, the impact of the disturbance appeared to be dependant on age, as well as elevation.

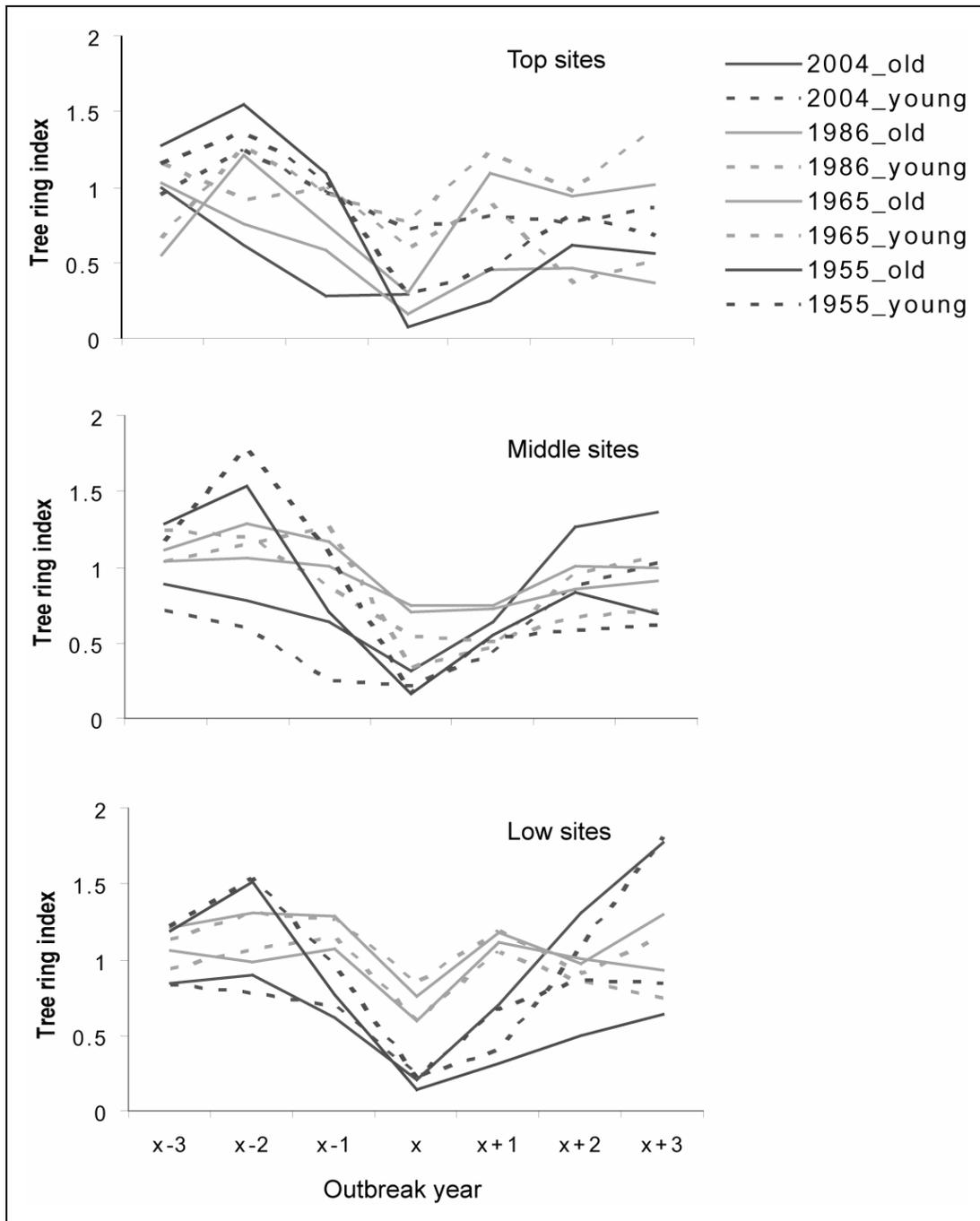


Figure 2: Superposed epoch analysis of the four most recent *Epirrita autumnata* outbreaks (1954/55, 1965, 1986, 2004). Tree-ring indices of three years preceding and following an outbreak event are displayed. Young trees are marked with dotted lines, old trees with continuous lines.

At the low-elevation sites, the difference in the intensities of the *Epirrita* population peaks is clearly visible (**Figure 2**). The absolute radial growth during the 1954/55 and the 2004 event were lower than the in 1965 and 1986. In terms of the age classes, no clear difference in the susceptibility was

found in the outbreak years themselves. The recovery period after the 1954/55 event, however, appears to have been significantly longer for old individuals whose growth remained low in three consecutive years. On contrary, young birches approached purely climate determined growth already one year after the outbreak. After the large 2004 event, young trees appeared to have taken one year longer to recover than old individuals. The difference between the age classes, however, was less pronounced than after the mid-century outbreak.

At mid-elevation, again the 1954/55 and the 2004 population peaks led to the strongest growth reduction. Young and old birches were equally affected and showed similar recovery patterns. For the moderate 1965 and 1986 outbreaks, there is a clear difference in the reaction of the two age classes. In 1986, young trees reduced growth more strongly than old trees which produced nearly average ring-width. The ring-width reduction in the young individuals was as strong as during the two severe events. The growth pattern of the 1965 defoliation was similar to 1986, though less pronounced.

The tree-line sites showed a clear age-dependence of the *Epirrita*-caused damage. During all four most recent insect outbreaks, old trees reduced growth much more strongly than young individuals who, apart from the 1954/55 event, grew almost averagely. Despite the different general intensities of the events, which became evident at the low- and mid-elevation sites, the old tree-line birches were equally affected during all four outbreaks. Growth remained low for several years after the 1954/55 and the 2004 events. Furthermore, it became evident, that – for some unknown reason – the trees older than 60 years already suffered reduced productivity prior to the 2004 incident. None of them survived the heavy defoliation which matches the observations during field work.

Discussion

Dendrochronological analysis proved an ideal tool to assess the degree of growth reduction in old and young birch trees due to insect outbreaks. Earlier investigations (e.g. Tenow 1972, Bylund 1997) suggested that old individuals generally suffer heavier defoliation since they offer more suitable places for oviposition and therefore are more attractive for female *Epirrita autumnata*. Our results confirm these findings only partly. While they assess the different intensities of the outbreak events correctly (Karlsson et al. 2004, Eckstein et al. 1991), they indicate that, apart from age, defoliation intensity strongly depends on elevation. At the lowest sites, young and old trees are equally defoliated during moderate and severe events. The top sites on the other hand, show distinctly heavier damage to older individuals. These findings indicate that the vulnerability of old birches increases towards the treeline where growth conditions are already harsh due to climatic circumstances. This is confirmed by the longer recovery phases and by the fact that none of the elder individuals survived the 2004 outbreak at the top site, whereas all of them recovered at middle and low elevation. The low growth of old trees prior to 2004 suggests that – for some unknown reason – trees have been weakened in advance which is likely to have promoted mortality in the outbreak year itself. Analysis of defoliation intensity (Babst et. al. in review) indicated that the top sites were equally or less disturbed than the lower parts of both transects.

When analysing these results, it is important to consider the differing replication and average age at both transects. The Abm site has only one young tree for the most recent outbreak in 2004, whereas the Abt site contains no old trees at all. This puts more weight onto the age classes of the Djupviken transect. Although the site properties at equal elevations do not differ considerably, the varying age distribution could slightly alter the tree-ring indices. For the 2004 event, the average age of the "old tree" category differed by 51 years between the low and the mid sites. However, no substantial difference in susceptibility towards insect-related defoliation is to be expected due to this age differences (Tenow 1972). Additionally, other disturbing influences like reindeer grazing (Stark et. al. 2007) may not be excluded. However, the consistent patterns found in this study, suggest that these biases are rather small. Furthermore, the considerable noise in the data which is likely to be caused by local differences in the *Epirrita* population density within the transects, did not prevent a conclusive interpretation of the results.

Another forest Lepidoptera species that reaches outbreak population levels is the larch budmoth (LBM, *Zeiraphera diniana*). Esper et al. (2007) developed a 1200-year reconstruction of LBM outbreaks in the Swiss Alps. Similar to *Epirrita autumnata* (Ruohomäki et al. 2000), Esper et al. (2007) discovered a cyclicity in LBM population peaks every 9 years until 1981. The absence of mass outbreaks since the 1980s to the present is explained by the exceptional warming trend (Büntgen et al. 2005) disturbing the moths population cycle. In the case of *Epirrita autumnata*, a regional warming is likely to have the opposite effect. *E. autumnata*'s abundance is limited by egg-killing winter temperatures (Hoogesteger & Karlsson 1992) which suggests that outbreaks are likely to become more frequent and expand into hitherto unaffected areas (Klemola et al. 2006, Tenow & Nilssen 1990). Such differing impacts of regional climate warming on related species complicate the prediction of the ecological consequences of a changing climate in Europe.

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