

Tree ring dynamics in mountain birch

Licentiate thesis

Faculty of Natural resources and Agricultural Sciences

Jan Hoogesteger

Swedish University of Agricultural Sciences (SLU)
Department of Crop Production Ecology (VPE)
Uppsala 2006

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Report from the Department of Crop Production Ecology (VPE) • No. 5

Swedish University of Agricultural Sciences (SLU)

Uppsala 2006

ISSN 1653-5375

ISBN 91-576-7179-6

Photo on the cover page: A young mountain birch forest in the Abisko Valley

Photo: Jan Hoogesteger

Editor: Birgitta Båth

Abstract

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ISBN 91-576-7179-6

Jan Hoogesteger
SLU, Department of Crop Production Ecology
Box 7043
SE-750 07 UPPSALA
Sweden

Variation in ring width in tree ring series of mountain birch (*Betula pubescens* ssp. *czerepanovii*) was analyzed and related to climate and herbivory. The effects of different defoliation levels were studied from natural outbreaks of the autumnal moth (*Epirrita autumnata*) and from experimental defoliations.

Short-term variation in ring width was mainly positively correlated with the current year July followed by June temperature. A warm May resulted in wider rings, probably due to earlier budburst.

Low defoliation levels ($\leq 12\%$) and 50% experimental defoliation had no effect on ring widths. The remaining foliage in the experiment showed increased photosynthetic capacity related to increased nitrogen content; this is presumably an important factor in maintaining growth performance after defoliation. Even after a defoliation level of 84% only a one-year reduction in stem growth was observed, but a slightly higher defoliation level (93%) resulted in a growth reduction during at least 4 years, which indicates that the defoliation-growth relationship is non-linear.

Tree ring series display long-term dynamics characterized by regular periods of increased growth. These growth increases are preceded by outbreaks of *Epirrita* with complete defoliation and mortality of old stems and branches, and subsequent rejuvenation by means of sprouts at the tree base and new branches in the crown. This results in a long period of better growth of the surviving and new stems.

The period of rapid growth is followed by a growth decline. Competition between stems within trees seems to be an important factor causing this decline, together with other consequences of tree size. It is suggested that an increased stem and branch surface area/leaf area ratio makes old stands susceptible for *Epirrita* outbreaks.

Sammanfattning

Årsringsdynamik hos fjällbjörk i förhållande till klimat och insektsangrepp

Licentiatavhandling, Fakulteten för naturresurser och lantbruksvetenskap, SLU
ISBN 91-576-7179-6

Jan Hoogesteger
SLU, Institutionen för växtproduktionsekologi
Box 7043
750 07 UPPSALA

Fjällbjörken (*Betula pubescens* ssp. *czerepanovii*) är det dominerande trädslaget i stora delar av norra Sverige och dess tillväxt kan variera mycket från år till år. Detta beror dels på variationer i klimatet och dels på populationsstorleken av larver till fjällbjörksmätaren (*Epirrita autumnata*), en blad ätande insekt. Mätarlarver uppträder periodvis i höga antal och kan förstöra stora områden av fjällbjörksskog genom nästan total avlövningsgrad följt av stamdöd. Effekten av varierande avlövningsgrad på årsringsbredden studerades utifrån både experimentell avlövningsgrad och naturlig avlövningsgrad orsakad av mätarangrepp.

Årsringbredden visade sig vara positivt korrelerad med medeltemperaturen i juli och till viss del i juni. Även en högre medeltemperatur under maj kan leda till bredare årsringar, förmodligen på grund av tidigare lövsprickning.

Vid låga, experimentella avlövningsnivåer ($\leq 12\%$ och 50%) påverkades inte årsringsbredden. De kvarvarande löven utmärktes av förhöjt kväveinnehåll och därigenom förhöjd fotosynteskapacitet, vilket antagligen är en viktig faktor för att upprätthålla en hög tillväxtförmåga efter avlövningsgrad. Vid 84% avlövningsgrad påverkades björkens stamtillväxt bara under påföljande året. Däremot orsakade 93% avlövningsgrad minskad stamtillväxt under minst 4 år. Detta visar att förhållandet mellan avlövningsgrad och tillväxt är icke-linjärt.

Årsringserierna illustrerar långtidsdynamiken i tillväxttakt och visar att det regelbundet förekommer perioder av förhöjd tillväxt. Dessa perioder föregås ofta av populationstoppar hos mätarlarver med fullständig avlövningsgrad och många döda stammar och grenar, följt av föryngring genom nya stubbskott. Dessa år med snabb tillväxt följs ofta av en period med starkt minskad tillväxt: Konkurrens mellan stammar inom samma träd och andra storleksrelaterade faktorer bidrar troligen till denna minskade tillväxt. Gamla bestånd av fjällbjörk är ofta mer utsatta för mätarangrepp än yngre bestånd. Som en orsak till den ökade mottagligheten diskuteras en ökad kvot mellan stammyta (eller grenmyta) och bladmyta.

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Appendix

Paper I – III

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Eckstein, D., Hoogesteger, J. & Holmes, R.L. 1991. Insect-related differences in growth of birch and pine at northern treeline in Swedish Lapland. *Holarctic Ecology* 14, 18-23

II. Hoogesteger, J. & Karlsson, P.S. 1992. Effects of defoliation on radial stem growth and photosynthesis in the mountain birch (*Betula pubescens* ssp. *tortuosa*). *Functional Ecology* 6, 317-323

III. Karlsson, P.S., Tenow, O., Bylund, H., Hoogesteger, J. & Weih, M. 2004. Determinants of mountain birch growth in situ: effects of temperature and herbivory. *Ecography* 27, 659-667

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Introduction

Defoliating insects can have a strong impact on tree growth (Kulman 1971, Schowalter *et al.*, 1986). Heavy defoliations cause growth reductions or even mortality. Light defoliations, however, often do not have much impact, or they may even enhance growth (Haukioja & Koricheva, 2000).

The autumnal moth (*Epirrita autumnata*) plays a significant role in the mountain birch forest of north-western Europe. Regular outbreaks of this foliage-eating insect are well documented (Tenow, 1972; Kallio & Lehtonen, 1975; Bylund, 1995). In 1954 and 1955 a severe outbreak of the autumnal moth in the Abisko Valley completely defoliated the birch forest, the recovery of which is described by Tenow & Bylund (2000). During an outbreak in northern Finland in 1964 and 1965 vast areas were defoliated, and many trees died (Kallio & Lehtonen, 1975). Similarly, after defoliation in 1965 (here mainly by larvae of the wintermoth, *Operophtera brumata*) birches died over large areas on the northern side of Lake Torneträsk (Sonesson & Hoogesteger, 1983). Such occurrences are, however, rare, and birches mostly recover well after defoliation. After the severe defoliation of 1955, recovery mainly took the form of basal sprouts (Tenow & Bylund, 2000).

Sprouting is a common mechanism by which deciduous woody plants recover after disturbance (Bellingham & Sparrow, 2000; Del Tredici, 2001; Bond & Midgley, 2001). One of the most common types is by “collar sprouts” (Del Tredici, 2001), where the sprouts emerge at the collar, *i.e.* the transition between the root and shoot systems. This results in polycormic (multi-stemmed) individuals. In tree species with a polycormic growth pattern like the mountain birch, main stems may dominate over smaller ones due to both shading and apical dominance (see Haukioja *et al.*, 1990 and references therein). Dominant stems may thus have a better supply of light, nutrients and water than subordinate stems.

The defoliation events mentioned prove the importance of *Epirrita* for the growth dynamics of mountain birch trees and forests. Environmental conditions and past ecological events such as defoliation are recorded in tree ring series (Fritts, 1976; Fritts & Swetnam, 1989). In the current study we use annual ring widths as an indication of the growth of the stem concerned in mountain birch. In this summary “growth performance” means growth as manifest in the ring width.

There are some earlier studies concerning tree ring series in mountain birch, focusing on the relationship with climate (Treter, 1974, 1984; Kuivinen & Lawson, 1982; Millar 1980). More recently, Karlsson & Weih (2003) studied growth dynamics after defoliation by *Epirrita*, and the study by Tenow *et al.* (2004) revealed differences in growth among stems within trees in relation to past defoliation. These studies show that temperature and defoliation have a strong impact on the growth of the mountain birch, and are a great aid to the interpretation of the dynamics of mountain birch tree ring series.

In order to acquire more insight into long-term growth dynamics, it would be interesting to know if and how former defoliations by *Epirrita*, and possibly the severity of these defoliations, can be determined from mountain birch tree ring series. However, the relationship between defoliation level and growth changes remains unclear, as do the mechanisms in the tree related to these changes. The consequences of polycormicity for the differences in growth performance among stems within trees as affected by climate and defoliation also need to be clarified. Furthermore, for a correct evaluation of the growth dynamics, it is necessary to know the effects of stem age and climate at the study sites on the growth of mountain birch.

In the current study we relate tree ring series to climatic factors and different levels of defoliation. The objectives are:

To quantify the effects of age, temperature and precipitation (**I**, **III**).

To quantify the effects of different defoliation levels; this was studied from artificial defoliations (**II**) and from defoliations in natural outbreaks of the autumnal moth (**III**).

To quantify the changes in photosynthesis and leaf nutrient status after defoliation, as mechanisms behind the effect on growth performance (**II**).

To date historical outbreaks of the autumnal moth, by comparing the tree ring series of mountain birch with the tree ring series of pine (**I**).

To study the variation in growth among stems within polycormic trees, among trees within sites, and among sites (**III**).

Material and methods

Study area and species

The studies were carried out in the Lake Torneträsk area in northern Sweden, which has subalpine forests of mountain birch. The mountain birch *Betula pubescens* ssp. *czerepanovii* (Hämet-Ahti, 1987; formerly called *B. pubescens* ssp. *tortuosa* or *B. tortuosa*), is a small tree, usually 4-6 m high when growing on nutrient-poor heaths. At heath vegetation sites with nutrient-poor, acidic soils the birches are usually polycormic, while monocormic individuals dominate on richer soils (Kallio & Mäkinen, 1978; Verwijst, 1988). In northern Europe mountain birch forest constitutes a broad zone between the coniferous forest and the tundra vegetation. Single Scots pines (*Pinus sylvestris*) can be found in the birch forest of the Abisko Valley. More or less continuous pine forest occurs in the eastern part of the Torneträsk area.

Study sites

The larval or adult population densities of the autumnal moth (*Epirrita autumnata* L. Lepidoptera: Geometridae) have been monitored in the Abisko Valley in most years since 1955 (Tenow, 1972; Douwes, 1975; Bylund, 1995; Bylund & Tenow,

(unpubl.). Based on these sources, and average per capita *E. autumnata* leaf consumption (Haukioja & Niemelä, 1974), the proportional foliage loss could be estimated for five autumnal moth population peaks (III):

1955: 100% defoliation (at one of our sites [VN, cf. below] the outbreak began in 1954 already, Tenow *et al.*, 2004), Abisko,

1965: 12%, Abisko

1975, 1987 and 1993: ca. 3%, Abisko

1995: 84-93% in the vicinity of Torneträsk Railway Station (see Karlsson & Weih, 2003).

Table 1. *Origin and characteristics of the mountain birch tree ring width series analyzed. All the sites were located at ca 360-400 m a.s.l. in the Torneträsk area, northern Sweden (from III)*

Series	Abbreviation	No. of stems	No. missing rings (%)	Annual ring series
Abisko 1	ANS 1	16	0.9	1940-2001
Abisko 2	ANS 2	73 ¹	2.3	1920-1988
Vuoleb Njakajaure	VN	116 ¹	1.6	1920-1988
Torneträsk railway stn 1	TRS 1	5	1.5	1990-2001
Torneträsk railway stn 2	TRS 2	5	0	1990-2001

¹Sampled from 15 polycormic tree individuals. For all other series one stem per tree was sampled.

Five series of annual ring widths were analyzed from five sites in the Lake Torneträsk area (referred to below as ANS 1, ANS 2, VN, TRS 1 and TRS 2; Table 1). All the sites were relatively dry, nutrient-poor heath dominated by polycormous trees and with a field layer dominated by *Empetrum hermaphroditum* and *Vaccinium vitis-idaea*. The forests at all the sites were of similar age and structure. Two of these (the TRS-series) were used only to estimate the effect of autumnal moth defoliation during 1995 and have been published previously (Karlsson & Weih, 2003). The ANS 1 series was collected over a relatively flat area ca 200 m south of the Abisko Scientific Research Station in 2001, while the ANS 2 series was collected on a north-facing slope ca 100 m north of the Station in 1988. The habitat conditions at ANS 1 were more similar to those of VN than of ANS 2. Further information on the ANS 2 and VN series can be found in Tenow *et al.* (2004).

In order to date historical outbreaks, samples were taken from three sites: one dry and one wet site about 1 km south of the village of Abisko, and one dry site near the Kamajokka River, 14 km southwest of Abisko (I). The defoliation experiments were situated within two kilometres of the Abisko Scientific Research Station, at an altitude of 400-450 m (II).

Defoliation experiments

Effects of defoliation on radial growth (Experiment 1)

Within a 1-ha area 36 uniform trees 3-5 m high were selected. These trees were randomly assigned to one of seven defoliation treatments (Table 2). The trees were defoliated at the beginning of the growing season, just after the leaves had appeared, *i.e.* the stage at which they are usually defoliated during an *Epirrita* outbreak. All the leaves were removed (by hand) in the 100% treatment. Although the intention was to leave all the buds at the end of the shortshoots intact, a few were inadvertently removed. For the 50% defoliation treatment the leaves of every second shortshoot were removed. In natural outbreaks initial longshoots are eaten long before the leaves are consumed; these initial shoots were therefore removed in all the treatments. To estimate recovery in terms of leaf area, all the leaves on six 100%-defoliated trees were counted at the time of defoliation and in July one and two years afterwards. The mean area per leaf was determined by measuring the area of each leaf on ten shortshoots per tree.

Table 2. *Design of defoliation experiment 1 (From II)*

Treatment	Defoliation (%)			<i>n</i>
	1985	1986	1987	
1	50	0	0	3
2	0	50	0	6
3	100	0	0	6
4	0	100	0	6
5	50	100	0	3
6	0	50	100	6
Control	0	0	0	6

Photosynthesis in defoliated trees (Experiment 2)

In the vicinity of the Abisko Scientific Research Station, young trees ranging in height between 0.3 and 0.5 m were selected. In June 1989, some days after the leaves had appeared, seven saplings were 100% defoliated and seven were 50% defoliated in the way described above, while another seven saplings were left intact to serve as controls.

The photosynthetic rate was measured in the laboratory using an open-flow IRGA (Mark II series 225, ADC Co Ltd, Hoddesdon, UK) system with Osram HQI-TS 400 W daylight lamps. During the first two weeks of August, small branches were cut from the trees and their cut ends immediately immersed in tap water. They were then transported to the laboratory. Before being mounted in the measuring cuvettes the shoots were cut once more under water. The leaf temperatures were kept at 18°C, and the photon flux density was successively increased from 50 to 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in five steps. The photon flux density was measured using a quantum sensor (LI-190B, Li-Cor Inc.). The leaf area was determined on fresh

leaves and the dry weight was determined after drying for 24h at 70°C. Seven to nine replicate measurements were made on each treatment type, i.e. control, 50% defoliated and 100% defoliated.

Diurnal photosynthetic assimilation was estimated using the light-response curves and a diurnal course of photon flux densities occurring in mid-August at this site. Whole-plant carbon incomes were estimated by multiplying the diurnal assimilation with the whole-plant leaf area, assuming that all the leaves were horizontal and not shaded by other foliage. The potential photosynthetic nutrient-use efficiency (PPNUE, Field & Moony, 1986) was estimated as the quotient of the light saturated photosynthetic rate divided by the leaf nitrogen or phosphorus concentration.

For nitrogen and phosphorus analysis, leaves were collected from each tree included in experiment 1 in August 1986, 1988 and 1989. For experiment 2 the leaf material for analysis was collected in June and August 1989. The material was digested in sulphuric acid and analyzed by flow injection (FIA-star, Bifok AB, Höganäs, Sweden).

Ring width analysis

The ring series were obtained from discs taken ca 10 cm above ground (the sites mentioned in **III**) or from discs taken at a height of ca 1 m (**I**). The discs were prepared according to standard dendrochronological techniques (Stokes & Smiley, 1968). The ring series used in the defoliation experiment (**II**) were obtained from microcores (diameter 1.2 mm) taken between 0.5 and 1 m above ground. The cores were sliced using a microtome. The ring widths were measured with a micrometer to 0.01 mm accuracy. The ring series were crossdated visually and checked for missing rings (cf. Table 1 for frequency of inserted missing rings). The ring series of each tree was corrected for age-related trends assuming a linear relationship between age and ring width (**III**) or by applying the ARSTAN computer program (Cook, 1985; **I**).

Ring width versus climate

In order to analyze the relationships between climate and mean ring width for each site (the sites mentioned in **III**) the following procedure was performed: after age correction, the ring series was normalized to obtain annual ring series with averages of zero and standard deviations (SD) of one (Cook & Kariukstis, 1990). From these age-corrected and normalized values an average annual ring series was calculated for each tree. This step was performed for the ANS 2 and VN series where several stems were sampled from each tree (see Table 1). In all the other series only one stem was randomly selected from each tree. A mean ring series for each site was then calculated as the mean of all sampled trees. These mean series were back-transformed into their original scale by first multiplying each value with the SD and then adding the mean of the original ring width of each stem.

The series of mean annual rings were then related to climatic conditions using multiple regressions. The RESPO program (Lough & Holmes, 1994) was used for

this analysis in the birch-pine comparison study (I). Preliminary analysis revealed no significant effect of precipitation, which was therefore excluded from the further analysis (III). Ring widths were related to the monthly means of air temperature from January to July the year a ring was produced and monthly values for May-December the preceding year. The ring width of the previous year was also included in the list of x-variables to be used in the analysis. In addition, date of budburst (Karlsson *et al*, 2003) was evaluated for the ANS 1 and ANS 2 and VN series. The period used in comparing ring widths with temperature varied among series (*cf.* Table 1). When date of budburst was included in the regression models, the analysis was restricted to 1958-2001 since budburst data is available from 1958 only. The statistical analyses (III) were performed using SPSS (version 11.5).

The growth performance of individual stems was related to the June and July temperatures using age-corrected ring widths. These two months were selected since the analysis of mean ring widths indicated that these months were the most important. The effects of these two months were thus calculated for each individual stem using a multiple regression model. The regression slopes and R^2 were further related to stem characteristics (main vs. subordinate stem, diameter and age). The main stem(s) was defined as the thickest stem in each polycormic tree or the stems with a diameter >90% of the thickest stem. According to this definition, most trees had only one main stem, but some had two or three.

Ring width versus herbivory

The effect of the autumnal moth population peaks was estimated by normalizing the birch rings so that the mean ring width for year -7 to -2 (III) or year -5 to -2 (II) relative to a peak density year was 1.0. In the defoliation experiment the ring widths were further corrected for differences between years by dividing the ring width of each tree by the mean ring widths of the control trees for the same year (II).

Ring width versus stem characteristics

The ANS 2 and VN series included samples of several stems from each tree and were thus suitable for comparing the variation in growth performance between sites, among trees within sites and among stems within trees. Thus, variation in mean growth performance (mean ring width from 1958 to 1988) among stems, trees and sites was compared using a nested analysis of variance and variance component analysis where trees were nested within sites and stems within trees (III).

Sprout growth in relation to insect outbreaks

After the 1954-1955 autumnal moth outbreak, some old stems died and a flush of basal sprouts emerged. This was more prominent at the VN site than at ANS (Tenow & Bylund, 2000; Tenow *et al*, 2004). The growth performance of sprouts produced during or just after this outbreak (1954-1957) was compared with the growth performance of sprouts produced before 1950 or after 1960 (III).

Defoliation history

To detect former outbreaks of *Epirrita*, tree ring series of mountain birch were compared with tree ring series of pine (**I**). Since *Epirrita* does not feed on pine, the normalized pine ring series was subtracted from that of birch in order to eliminate variance due to climate (Nash *et al*, 1975). The residual series should enhance the effect of the outbreaks. The success of this approach depends on how similarly both species respond to climatic variables. The pines were sampled at various localities along Lake Torneträsk (for more information about the pine series see Bartholin & Karlén, 1983).

Results

Variation in mean ring width and sprout growth

The mean ring width varied between 0.32 and 0.64 mm (**III**). A decline in ring width with increasing stem age was found at all heath forest sites. Trees at VN showed the largest decline ($-8.6 \mu\text{m yr}^{-1}$), while the smallest decline was found at ANS 1 ($-1.9 \mu\text{m yr}^{-1}$). On average 12-22% of the inter-annual variation in ring width could be attributed to age.

Significant variation of mean ring width among individual trees was found: 19% of the variation in stem mean ring width was due to variation among trees. However, the variation among stems within trees was considerably larger (81%), while <1% was due to differences between the two sites (VN and ANS2). The variation among stems could partly be related to differences among main and subordinate stems; main stems grew faster and were more responsive to climate than subordinate stems.

During the first years after emergence, the radial growth of sprouts was considerably faster than in mature stems (Fig. 1). Furthermore, sprout growth was affected by the conditions during which the sprouts emerged (were “born”, Fig. 1). At VN sprouts emerging between 1954 and 1957 had wider rings than sprouts born before or after the outbreak in the mid-1950s (Fig. 1). At ANS 2 the pattern was different; here sprouts born in or after 1960 displayed slower growth than sprouts emerging earlier.

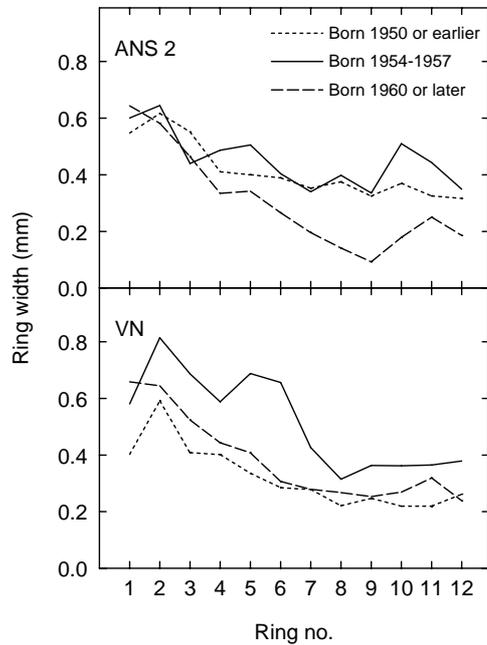


Fig. 1. Ring widths of basal sprouts produced (born) during the 1954-1957 autumnal moth outbreak as compared to sprouts born before and after the outbreak. Each line is based on between 23 and 41 sprouts, except that only eight sprouts emerged at ANS after 1959. (From III).

Effects of climate on ring width

The main climate factors influencing stem radial growth were (in order of importance) the July, June and May temperatures for all ring series (III) (Fig. 2). The mean May temperature could be replaced by the Julian day of budburst, with similar regression results; in fact R^2 increased for all series when the May temperature was replaced by the date of budburst. For all series, the ring width was correlated to that of the previous year, although the relative importance (partial R^2) varied between 0.03 and 0.19.

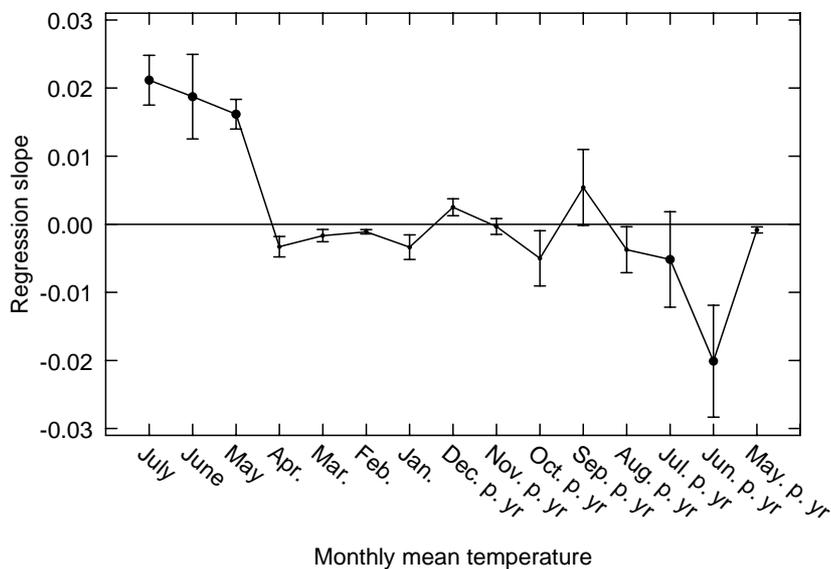


Fig. 2. The effect of temperature on mountain birch ring widths. Each ring series (ANS 1, ANS 2 and VN) was analyzed separately, relating ring width to monthly mean temperature for each month from July the year a ring was formed, back to May the year before and to ring width previous years. The mean effect (regression slope) for the three series is shown (vertical bars indicate ± 1 SD). Filled circles indicate that two thirds or more of the regression coefficients for that month were significant. (From III).

Recorded effects of defoliation

Foliage regrowth

In the defoliation experiment (II), 100%-defoliated trees produced new leaves in mid-July, about one month after defoliation. New leaves emerged from the shortshoots and were fewer in number compared with the primary foliage. Although most of the new leaves were larger than the primary foliage, the variation in size was great. These new leaves were also considerably lighter in weight per unit leaf area, 55 vs. 80 g m⁻². Shortshoots from which the bud had accidentally been removed died without producing new leaves. The whole tree leaf area was back to pre-treatment levels two years after defoliation. Trees defoliated by 50% did not produce any new leaves in the year of defoliation. The remaining buds stayed alive. None of the defoliated trees produced new longshoots in the year they were defoliated. The remaining foliage on 50%-defoliated trees did not grow between June and August. The weight/area ratio of leaves from these trees two months after defoliation was similar to that of leaves from the control trees.

Ring width

In the defoliation experiment, the rings in 50%-defoliated trees did not show any significant decrease in width compared with the control trees (II). The two more severe defoliation treatments resulted in large reductions in ring widths: the relative ring widths of trees subjected to defoliation treatments of 100% and 50+100% (50% and 100% defoliation treatments during two subsequent years) were only 15-25 % of the control widths. Many of the trees did not show any growth on one side of the stem in the year of defoliation and/or the following year. No differences in responses were found between the 100% and the 50+100% treatments. In trees defoliated 100% or more, the rings were still less than their normal width 2-3 years later.

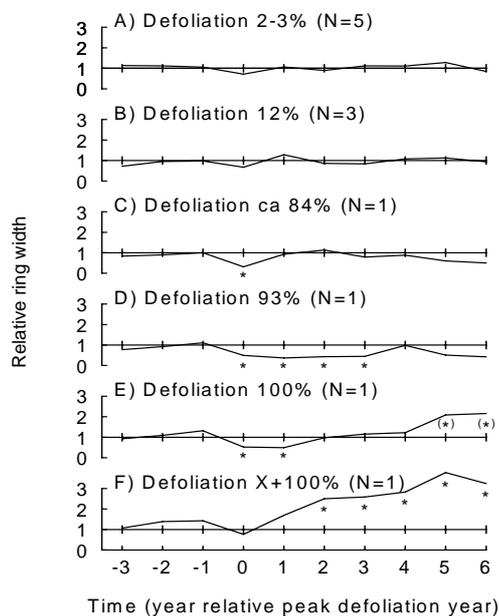


Fig. 3. Relative ring widths of mountain birch trees during population peaks of the autumnal moth. The ring widths were normalized to have a mean of 1.0 when not defoliated by *Epirrita* (cf. Material and methods). The defoliation level “X+100%” indicates substantial defoliation in two consecutive years (VN 1954 and 1955) but the defoliation level in the first year is unknown. N indicates the number of sites and events used for each curve. The mean for each site and event is based on 5 to 116 stems (cf. Table 1). Asterisks indicate rings significantly different from 1.0 ($p \leq 0.05$, asterisks within brackets $p = 0.07-0.08$). Defoliation events and series used for the different panels: A) ANS 1, ANS 2 and VN in 1975 and ANS 2 in 1987 and 1993; B) ANS 1, ANS 2 and VN in 1965; C) and D) the TRS 2 and 1 respectively in 1995; E) ANS 2 in 1955 and F) VN in 1955. (From III).

In natural *Epirrita* outbreaks, low defoliation levels (3-12% defoliation, Fig. 3) did not result in any significant reduction in ring width (III). The 84% defoliation caused a reduced ring width for one season only. When the defoliation level was

slightly higher (ca 93%), the ring widths were reduced during four years. The pattern changed after more severe defoliation: at ANS (100% defoliation in 1955) the ring widths were reduced by ca 50% during two years, and followed by a tendency towards increased ring widths ($p=0.07-0.08$ for years 5 and 6). At VN (strong defoliation in 1954 and 100% defoliation in 1955) the positive effect of defoliation dominated over the negative effects. A weak reduction (-24%) occurred in the year of defoliation, thereafter (years 2-6) the rings were 2-3 times wider than the pre-outbreak rings and were still almost 80% wider than expected even ten years after the outbreak.

Nutrient status and photosynthesis

The more severely the defoliation to which the trees were subjected was in the defoliation experiment, the higher the leaf nitrogen concentration was in mid-August of the same year (**II**; Fig. 4). The nitrogen concentration of trees defoliated 50% was ca 15% higher than that of the control trees, while the nitrogen concentration of the regrowth foliage after 100% and 50+100% defoliation was ca 1.5 times higher than the concentration in the leaves of the controls. One year after defoliation the leaf nitrogen concentrations of the 50% and the 100%-defoliated trees were similar to that of the control trees. In the trees exposed to 50+100% defoliation, the leaf nitrogen concentration had decreased to 50% of the control trees. Two years after defoliation, the leaf nitrogen concentrations were normal again. The leaf phosphorus concentrations showed a similar pattern, but with smaller differences between treatments.

The photosynthetic rate (per unit leaf area) of the remaining foliage on the 50%-defoliated trees exceeded that of the control trees at photon flux densities above $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 5). At maximum photon flux density ($800 \mu\text{mol m}^{-2} \text{s}^{-1}$) the difference was 35% and significant. The area-based photosynthetic rate of the regrowth foliage on 100%-defoliated trees was intermediate and was no different from that of either the control or 50%-defoliated trees. When expressed on a weight basis, clear differences in photosynthetic maximum rates were found between treatments, the rate of leaves from the 100% defoliation treatment being almost 85% higher than that of the control leaves.

Photosynthetic rate was correlated with leaf nitrogen concentration. The differences in leaf nitrogen concentration were proportional to the differences in photosynthetic rate, resulting in similar photosynthetic production per unit leaf nitrogen or phosphorus in all treatments.

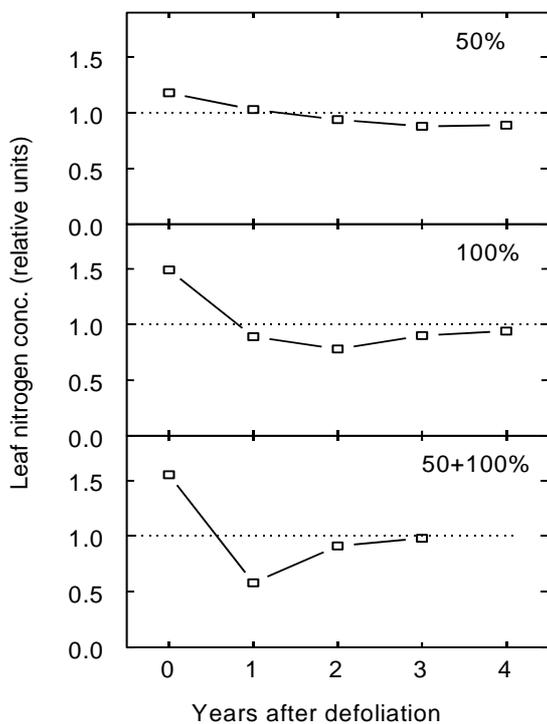


Fig. 4. Time course of leaf nitrogen concentration after different degrees of defoliation in relation to those of controls (control=1.0). The 50+100% defoliation treatments consist of 50%+100% defoliation in two subsequent years. (From II).

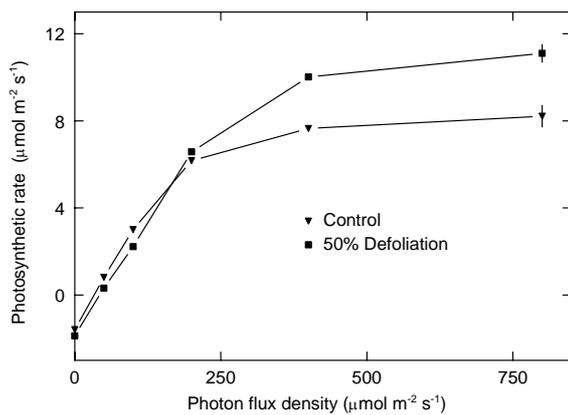


Fig. 5. Response of photosynthetic rate to photon flux density in 50%-defoliated trees and control trees. Trees defoliated 100% showed an intermediate response. Vertical bars indicate standard error. (From II).

Tree ring series and defoliation history

The climatic response in the tree rings of pine has many similarities with that of mountain birch: in both species the summer temperature is the most important factor affecting ring width, while precipitation is of minor importance (I). The pine chronology was subtracted from that of the birch, and the residual chronology shows the growth of birch in relation to that of pine (I, Fig. 6). Comparison with *Epirrita* outbreaks, documented since 1880 for different parts of the Fennoscandian mountain area (Tenow, 1972; Fig. 6), reveals that six out of ten outbreaks are clearly evident (nos. 1, 2, 4, 7, 8, and 10 in Fig. 6). Three others coincide with intervals where the residual curve runs above the zero line (nos. 3, 6, and 9 in Fig. 6).

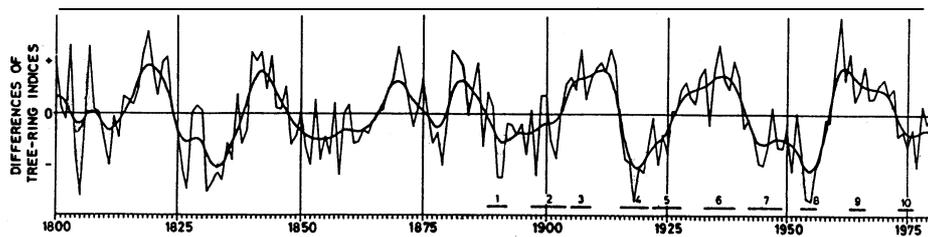


Fig. 6. Birch-minus-pine chronology, annual differences and low-pass filtered data. The bars along the time axis indicate documented outbreaks of the autumnal moth. (From I).

Discussion

Effects of defoliation

Foliage and photosynthesis

It seems to be a general behaviour in plants that after disturbance such as defoliation or pruning, after some time the original relationship between aboveground and underground mass (shoot/root ratio) is restored (Brouwer, 1962; Poorter & Nagel, 2000). Mountain birch defoliated by more than 50% displayed foliage regrowth in the year of defoliation (II; Karlsson & Weih, 2003), thus apparently seeking to restore the shoot/root ratio. Trees defoliated by 50% did not produce any new leaves in the year of defoliation.

In the remaining foliage of 50%-defoliated trees the photosynthetic rate increased; it was also higher in the regrowth foliage of 100%-defoliated trees than in the control trees. The photosynthetic rate was correlated with leaf nitrogen content, and the increased nitrogen content in defoliated trees was probably a consequence of the decreased leaf area. The photosynthetic production per unit leaf nitrogen was similar in all treatments, so the increased photosynthetic capacity of the defoliated trees must have been a response to the increased leaf nitrogen content. This partial compensation for the lost foliage, in the form of an increased photosynthetic capacity, probably occurs only during the year of defoliation, since

the leaf nitrogen concentration decreases to normal or below-normal values in subsequent years. The photosynthetic capacity would be expected to show a similar pattern (Karlsson & Nordell, 1988; Karlsson, 1991).

I have no data on possible nitrogen content changes in branches, bark or sapwood after defoliation, and nor could I find any information about this in the literature. Woody tissue maintenance respiration is closely related to nitrogen content (Ryan *et al*, 1995; Maier *et al*, 1998; Ceschia *et al*, 2002). Hence, any nitrogen increase in these tissues, too, as a consequence of decreased leaf area would increase the branch and stem respiration.

Radial stem growth

Low defoliation levels did not result in any significant reduction in ring width (3-12% defoliation, Fig. 3). Even no growth reduction was found after 50% experimental defoliation. Similar observations have been made for poplars (Bassman *et al*, 1982; Gao *et al*, 1985) and oaks (Hilton *et al*, 1987; see also Mattson & Addy, 1975).

In the remaining foliage of the 50%-defoliated trees, the photosynthetic rate increased by 35% (II). Similar responses to defoliation were found by Heichel & Turner (1983) in red maple and red oak. However, increased photosynthesis cannot fully explain why the 50%-defoliated trees in our experiment showed nearly normal diameter growth. Under normal light conditions, the whole-tree daily CO₂ assimilation in mid-August was estimated to be 67% of that of the control trees. These trees must have had other sources of carbon to be used in wood formation. Some of this carbon may have been obtained at the expense of root and longshoot growth: the defoliated trees did not produce any longshoots, whereas the control trees did. Carbon may also have been obtained through the mobilization of stored carbohydrates (*cf.*, *e.g.*, Kozlovski & Winget, 1964; Willard & McKell, 1978) or by diverting reserves destined for other plant parts. In grasses and other plants, root growth is known to decrease after defoliation (Crawly, 1983; Poorter & Nagel, 2000).

At defoliation levels above 80% in natural outbreaks a significant reduction was observed in radial stem growth. After ca 84% defoliation a reduction was observed in one year only (TRS 2), while it was reduced ca 50% for four years after 93% defoliation (TRS 1). The 100% and 50+100% artificial defoliations in the experiment (II) yielded responses similar to those of the 93% natural defoliation at TRS 1.

One striking feature in the responses to defoliation is the difference between TRS 1 and TRS 2. This is larger than might be expected from the percentage of defoliation alone (93% and 84%). Why did the 93%-defoliated trees show a reduction for so many years, while the 84%-defoliated trees did only in the defoliation year? At the more severely defoliated site, from the third year after defoliation onward, also the leaf area is significantly lower than at the other site and in the control trees (Fig. 1 in Karlsson & Weih, 2003). A notable feature of

this figure is the very constant level of lowered leaf area. The ring width pattern of TRS 1 in fact looks like that of VN after the defoliation in 1944 (Fig. 4 in Tenow *et al.*, 2004). This, together with the leaf area pattern mentioned, suggests that a structural change has taken place in the trees of TRS 1, resulting in a new shoot/root balance. The striving towards a constant shoot/root ratio in plants does, if applied to trees, obviously also have consequences for the stem. The amount of foliage is proportional to the amount of conductive tissue in the stem (Shinozaki *et al.*, 1964a, 1964b; Waring *et al.*, 1982; Waring & Schlesinger, 1985). Because every living cell needs maintenance, it is logical to assume that, if the amount of leaf area in a defoliated tree is not restored within a certain time, the excess sapwood will be abandoned and transformed into heartwood. Perhaps this is what happened in the trees of TRS 1. This may also explain the increase in ring width in the fourth year after defoliation (1999, see Fig. 7 in Karlsson & Weih, 2003): nitrogen and other mineral nutrients are recycled from senescing sapwood (Meerts, 2002), so the ring width increase might be an indication of this. Another possible but related way of achieving structural change is by forming false heartwood, a well-known phenomenon in arboriculture (Shigo & Hillis, 1973) that can be induced by injury or dying branches. Also this leads to a thinner sapwood layer. Heartwood in birch is colourless, but false heartwood may be coloured differently from heartwood (Shigo, 1984). Indeed, mountain birch stems that have experienced heavy defoliation often have a dark centre which may be sharply bordered by the ring formed in the year of defoliation (J.H., unpubl.)

False heartwood is known to contain protective substances in many tree species, in hardwoods mostly phenolic compounds (Shigo, 1984). Phenolic compounds in the leaves of mountain birch are known to enhance the resistance to *Epirrita* (Ruohomäki *et al.*, 1996; Ossipov *et al.*, 2001). A possible allocation of these substances in the wood of mountain birch could have implications for their production in other parts of the tree and maybe decrease their production in the leaves, and thus reduce the resistance to *Epirrita*.

The new leaf area will be smaller, but the new sapwood cross section area/leaf area ratio will, once the balance has been restored, be the same as before. However, the stem and branch surface area/leaf area ratio will be bigger. Since most of the sapwood maintenance respiration is concentrated near the surface, especially in branches (see section on growth increase), the new respiration costs per leaf area will be much bigger than before. Moreover, less sapwood means less storage space for reserves. These may be the reasons for growth at a constant lower level. If the stem growth reduction were due to the depletion of carbohydrates alone, the ring width would be expected to return to pre-outbreak levels much sooner. The strong growth increase at VN after the defoliation in 1955 resulted in a larger leaf and sapwood area and thus better proportions and a better energy balance, which probably enabled the trees to maintain growth at a higher level for at least ten years (Fig. 3F). This did not, however, happen until after the dieback of one or some old stems.

Stem mortality

In view of the above-mentioned properties, it is not surprising that the trees at VN experienced higher stem mortality than those at ANS 2 after defoliation in 1955. Interesting in this context is the fact that several trees which had experienced heavy defoliation and stem mortality in northern Finland in 1965-1966 and were analyzed by Millar (1980) showed a similar growth reduction for about ten years before the outbreak. This indicates that they had already experienced defoliation in the 1950s as well (Fig. 3 in Millar, 1980). Similar abrupt growth reductions in other trees have been reported elsewhere, and could partly be related to disturbances such as intense pathogen attacks or severe drought (Pedersen, 1998; Villalba & Veblen, 1998).

The decrease in sapwood layer inevitably affects the growth rate. Relative growth rate in its classical sense, i.e. growth in relation to living biomass (Poorter, 1989), is difficult to apply to big trees. Sapwood cross sectional area can be used as a function of leaf area (see above), or living biomass. Thus the relative growth rate can be expressed as the ring cross section area in relation to the sapwood cross section area. This relationship has been used as a measure of the production efficiency of the tree crown (e.g. Waring *et al.*, 1980, 1981; Kaufmann, 1996). After the decrease in width of the sapwood layer, the relative growth rate may be about the same as before, but the absolute growth rate will be much smaller. In a tree ring series (which is an expression of the yearly absolute growth) this is visible only as narrow year rings or 'low growth rate'.

Several studies have analyzed growth rate and/or growth pattern before tree mortality (e.g. Pedersen, 1998; Wyckoff & Clark, 2002; Bigler & Bugmann, 2003, 2004). Long periods of low, stationary growth do not necessarily imply an increased mortality probability (Bigler & Bugmann, 2003). Abrupt growth reductions are, however, often soon followed by tree mortality, though lowered growth rates can sometimes persist for many decades (Kaufmann, 1996; Bigler & Bugmann, 2003). It is very likely that mountain birches that have experienced sapwood reduction will experience stem mortality after the next *Epirrita* outbreak. Presumably, the trees at TRS 1 were severely defoliated again in the recent outbreak of 2003-2004 and are now experiencing crown dieback and stem mortality.

Strongly weakened trees after defoliation are often attacked by wood-boring insects such as *Hylecoetus dermestoides* (Palm, 1959). This insect attacks weakened stems and feeding larvae destroy the phloem tissue, which finally kills the stems.

There may be several reasons why 100% and even 50+100% defoliation in the experiment (II) did not result in any stem mortality. Artificial defoliation differs in several aspects from natural defoliation by *Epirrita*, for instance in the time span within which the defoliation is completed. Real insect feeding may have a bigger impact on, for example, water loss (Hammond & Pedigo, 1981; Haukioja *et al.*, 1990). The buds on the shortshoots, on which refoilation occurs, were also left

almost intact in the experiment, whereas in a severe *Epirrita* attack a large proportion of these buds is also eaten once most of the leaves have been consumed (Haukioja *et al.*, 1990). Another reason may be tree size or age. The trees in the experiment were much younger than those that experienced mortality in the natural defoliation. Dormant buds are important for recovery in subsequent years (Lehtilä *et al.*, 1994; Borg, 2005), but older trees are less able to produce new shoots from dormant buds (Thomas, 2000). Furthermore, the growth rate is mostly higher in younger trees. A higher growth rate may promote tree resistance or recovery from defoliation by rapid regrowth (Chen *et al.*, 2001).

One potential cause may be the weather before the outbreak. A correlation has been shown between severe outbreaks and cool preceding summers (Niemelä, 1980). Defoliation in combination with cool summers before or during outbreaks has been suggested as a mortality risk (Sandberg, 1963; Kallio & Lehtonen, 1975).

Sprout growth

The defoliation during the outbreak in the 1950s was more severe at VN than at ANS. As a result, many stems died at the VN site and foliage recovery was achieved mainly through the production of basal sprouts (new stems) in the polycormic trees, while at ANS 2 sprouting was less important (Tenow & Bylund, 2000; Tenow *et al.*, 2004). This difference in the formation of new sprouts is probably related to the differences in the growth performance of sprouts seen at the two different sites. Thus, at VN sprouts emerging between 1954 and 1957 had a relatively high radial growth; this was probably achieved by a release of the suppression of new sprouts by older stems and/or by a better nutrient supply from a root system that was oversized following the dieback of old stems. In contrast, more old stems survived the insect outbreak at ANS 2 and the growth of sprouts emerging during or just after the defoliation was similar to those emerging before the insect outbreak. At ANS 2 the sprouts produced in or after 1960 showed slower growth than the sprouts emerging earlier. This response pattern is similar to that of older stems, where the growth promotion of surviving stems was larger at VN than at ANS 2.

Effects of temperature

The high significance of the June and July temperatures confirms previous investigations of the climatic effects on birch seedling growth (Weih & Karlsson, 1997; Weih, 2000a) and ring widths (Kuivinen & Lawson, 1982). Furthermore, it is consistent with the observation that mountain birch wood formation in the Abisko area occurs mainly during July (Gellineck, 1997). The significant effect of the May temperature on growth is its effect on the date of budburst (Karlsson *et al.*, 2003) and thus how early in the season the foliage starts assimilating CO₂. June and July temperatures can affect growth through the effects on photosynthetic rates (Sveinbjörnsson, 1983), soil decomposition and nutrient release (van Cleve *et al.*, 1981; Hobbie, 1996), birch nutrient uptake from soil (Karlsson & Nordell, 1996; Weih & Karlsson, 2001a) and also affect directly on growth processes. The temperature during August and September did not affect the current year growth performance, and neither could any effect of these two months on growth

performance be detected in the following year (Fig. 2). However, an effect of growth performance in the previous year (previous ring width) was found in all the series analyzed. Similarly, mountain birch seedling growth has been found to be affected by the growth conditions in the previous year (Weih, 2000a) and the ring widths of birches in southern Greenland correlated to the ring widths of the previous year (Kuivinen & Lawson, 1982).

In arctic environments, Chapin (1983) concluded that the length of the growing season is more important than the summer temperatures. In contrast, we found a larger effect of early summer temperature (June and July) than of length of the growing season for the subarctic mountain birch growth. Also Weih (2000b) arrived at the conclusion that the environmental conditions during the growing season are more important than duration of the growth period for growth rate and survival of mountain birch seedlings. Nevertheless, my results showed that also the length of the growing season was significant for mountain birch growth. Budburst is related to May temperature (Karlsson *et al.*, 2003), and can be regarded as the main determinant of the length of the period with green leaves for the mountain birch at Abisko, since date of leaf fall is less variable than date of budburst and also shows a less clear relation to climate (Karlsson unpubl.).

The general importance of the summer temperature in the subarctic is evident from the similarity in the climate response function of two such different tree species as birch and pine (I). This similarity enables the construction of a birch-minus-pine chronology (see section “Historical perspective”).

Long-term dynamics

Growth increase

After the natural 100% defoliation at ANS 2 in 1955 some stems died. In the surviving stems, the ring widths were initially reduced, but then followed a long period of increased radial growth (Fig. 3E). At VN the defoliation was more severe (in 1954 and 1955), and even more stems died (cf. Tenow & Bylund, 2000; Tenow *et al.*, 2004); the surviving stems showed only a weak reduction in the year of defoliation; thereafter the rings were 2-3 times wider than the pre-outbreak rings. The higher stem mortality is, the more the growth performance of the surviving stems apparently benefits from the outbreak, despite severe defoliation. This is probably achieved by the same mechanisms as those discussed earlier for sprouts: release of suppression by older stems, and/or a better nutrient supply from a root system that was oversized following the dieback of old stems.

Another potential explanation for the increased ring widths is a fertilization effect through nutrients released from dead larvae and pupae (Wickman, 1980; cf. Tenow, 1972). However, it was concluded from studies on nitrogen mineralization from gypsy moth frass in oak forests that nitrogen may be unavailable to plants for a long time (Lovett & Ruesink, 1995; Christenson *et al.*, 2002). It is thus possible that the same applies in birch forests defoliated by *Epirrita*. Further, there was no fertilization effect after the also rather severe defoliations at the TRS sites (see Fig.

3), and neither at VN after defoliation in the 1940s (Fig. 4 in Tenow *et al.* 2004). Hence release of suppression by the main stem(s) is a more plausible explanation.

There is, however, one interesting feature that may further speak in favour of a fertilization effect: increased ring widths (years 5 and 6) after the defoliation in 1955 were also observed in main stems of ANS trees that did not experience stem mortality (J.H., unpubl.). Released competition from neighbouring trees is one explanation. However, foliage recovery occurred in these trees mainly in the crowns of the main stems, whereas in VN recovery occurred mainly in the secondary stems and new sprouts (Tenow & Bylund, 2000; Tenow *et al.*, 2004). At ANS about one-fifth of the branches had died (Tenow *et al.*, 2004). Recovery in the crown takes place from shortshoots and dormant buds (Lehtilä *et al.*, 1994; Haukioja, 2003; Borg, 2005). Heavy herbivory may rejuvenate the canopies of trees and is comparable to artificial pruning to maintain the viability of old trees (Haukioja & Koricheva, 2000). Rejuvenation involves the ample production of longshoots from pruned stems and large branches. This damage-induced reiteration (Halle *et al.*, 1978) is familiar in many tree species. In this way the birches get rid of old branches, and also of their respiration. Reiteration is also a way by which old trees may try to slow down the aging process (Ishii & Ford, 2001; Thomas, 2000). Stem and branch respiration plays a major role in the carbon balance of trees (Ryan, 1990; Damesin *et al.*, 2002). Until now, woody tissue respiration has been difficult to assess due to the interaction between CO₂ efflux from woody tissues and transport of respiratory CO₂ in the transpiration stream, and may be an important source of error in respiration calculations (McGuire & Teskey, 2004; Bowman *et al.*, 2005). Moreover, recent studies show that maintenance respiration is higher in inner bark than in sapwood, and higher in outer than in inner sapwood (Pruyn *et al.*, 2002; Bosc *et al.*, 2003 and references therein), and also that branches and stems in the crown have a much higher respiration rate on a volume mass base than the stem at breast height (Ceschia *et al.*, 2002; Damesin, 2003). This suggests that the role of branch respiration in a tree's carbon balance may be more significant than has previously been recognized. It follows from this that replacement of old branches by young branches at the branch base or directly at the stem greatly benefits the tree. The increase in stem ring width in the 5th and 6th year after defoliation in trees that only experienced branch mortality may therefore be a result of the growth enhancement caused by rejuvenation in the crown. Because of the strong positive correlation of birch growth with warm summers (see earlier), the above-average mean summer temperatures in 1960 and 1961 undoubtedly contributed to the great growth increase during these years.

Growth decline

According to Berger *et al.* (2004), the main cause of age-related growth decline in a forest at the start of the process is competition among neighbouring trees. Their study concerned monocormic tree species, but also in polycormic mountain birch this competition may be important, since 19% of the variation in stem mean ring width was due to variation among trees (III). The mountain birch is known to show large variation among individual trees (Karlsson & Nordell, 1988; Suomela

et al., 1995; Weih & Karlsson, 2001b); hence the genetic variation among trees also contributes to this variation. Anyhow, the variation among stems within trees was considerably larger (81%), so competition among stems within trees is more important for growth performance than competition among trees.

The variation among stems could partly be related to differences among main and subordinate stems: main stems grew faster and were more responsive to climate than subordinate stems. This is in accordance with the general situation in forests, where dominant trees contain more climatic information than suppressed trees (Fritts, 1976). Obviously, the suppression of subordinate stems by main stems is an important factor in the competition.

The growth increase in the mountain birch stems in the 1960s is followed by a growth decline (Fig. 6). In the *Epirrita* population peak in 1975, defoliation was only 3% and did not affect birch growth, but it coincides with a downward trend in growth. Obviously, *Epirrita* is not the only cause of the growth decline. More likely, this downward trend in growth is caused by keener competition among trees and among stems within trees, as discussed above, together with other consequences of the increase in tree size (Weiner & Thomas, 2001), like increase of respiration-to-photosynthesis ratios (see earlier), hydraulic limitations and architectural complexity (Ryan & Yoder, 1997; Rust & Roloff, 2002; Mencuccini *et al.*, 2005).

Historical perspective

In the birch-minus-pine chronology (Fig. 6) growth dynamics are emphasized, because the subtraction from the pine curve has largely removed the effect of climate. The more or less regular waves in this figure express the variation in birch growth performance of the sampled forest site. Clearly visible is the growth decrease that coincides with the documented *Epirrita* outbreak in the 1950s, and its close similarity with the pattern in Fig. 3E (defoliation 100%, ANS 2, 1955). Obviously, mortality in the outbreak period and the subsequent increase in growth in the surviving stems after the outbreak is the start of a new wave. The documented outbreak of 1944-45 is also visible in this figure, but not followed by a strong upward growth trend, indicating that mortality was absent or negligible.

Though *Epirrita* populations regularly peak with an interval of about ten years, outbreak levels usually occur in older stands, and can leave adjoining stands with only young birches unaffected (Bylund, 1997; Ruohomäki *et al.*, 1997). This means that the wave pattern is strongly site-specific. The reason why old birch forests are more susceptible than young ones is not yet clear. Bylund (1997) suggests as a possible reason the higher structural complexity and presence of more lichens in older trees, and the preference of the moth females to deposit their eggs on a rough surface. Another possible reason could be the bigger size of old trees. This means that there is simply more space for the moths to rest, copulate and deposit their eggs. Not only is there a bigger absolute difference in size (shoots and branches/m², Tenow & Bylund, 2000), but also – and this may be more important – a much bigger stem and branch surface area in relation to leaf area (Whittaker & Woodwell, 1967). Because females are poor fliers and do not

disperse far from their sites (Tammaru *et al.*, 1995), only few subsequent years with circumstances favourable for *Epirrita* would create an outbreak-critical difference in larvae numbers between old and young forests.

Concerning the impact of historical outbreaks, no explicit conclusions can be drawn from this figure about degrees of defoliation. First, there may be spatial differences, because this curve is the mean of surviving stems from a relatively large area bordering both the VN and ANS sites. Second, when defoliation is below 100%, there is always some variation in degree of defoliation between the trees (personal observation), so a calculated degree of defoliation for a certain area represents always a mean value. This implies that in evaluating the growth response, the relation between the degree of defoliation and the growth response is assumed to be linear. This is not the case (see discussion on effects of defoliation), and there may be large variation in growth response among trees with apparently the same degree of defoliation (**II**). Moreover, there is the threshold of the sapwood area (see earlier). Furthermore, there are dramatic differences in response, whether or not mortality occurs.

Some general conclusions can be drawn from the figure. There were in the 100-year period from 1880 to 1980 three periods with increased growth. The outbreaks inducing this increased growth are probably nos. 1 and/or 2, 4 and 8 (Fig. 6). Further, it is evident that periods with increased growth occurred with a certain regularity. The intervals between these periods are longer than the *Epirrita* outbreak cycles, because outbreaks occur in old forests (see earlier). However, they are shorter than the lifetime of a single (main) stem, which is often more than 100 years (Sonesson & Hoogesteger, 1983).

References

- Bartholin, T. & Karlen, W. 1983. Dendrokronologi i Lappland. *Dendrokronologiska Sällskapet, Meddelanden* 5, 3-16. In Swedish.
- Bassman, J., Myers, W., Dickman, D. & Wilson, L. 1982. Effects of simulated insect damage on early growth of nursery-grown hybrid poplars in northern Wisconsin. *Canadian Journal of Forest Research* 12, 1-9.
- Bellingham, P.J. & Sparrow, A.D. 2000. Resprouting as a life history strategy in woody plants communities. *Oikos* 89, 409-416.
- Berger, U., Hildebrandt, H. & Grimm, V. 2004. Age-related decline in forest production: effects of growth limitation, neighbourhood competition and self-thinning. *Journal of Ecology* 92, 846-853.
- Bigler, C. & Bugmann, H. 2003. Growth-dependent tree mortality models based on tree rings. *Canadian Journal of Forest Research* 33, 210-221.
- Bigler, C. & Bugmann, H. 2004. Predicting the time of tree death using dendrochronological data. *Ecological Applications* 14, 902-914.
- Bond, W.J. & Midgley, J.J. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution*. 16, 45-51.
- Borg, C. 2005. Structural Growth in Mountain Birch, *Betula pubescens* ssp. *czerepanovii*. *Ph.D. thesis, Uppsala University*.
- Bosc, A., De Grandcourt, A. & Loustau, D. 2003. Variability of stem and branch maintenance respiration in a *Pinus pinaster* tree. *Tree Physiology* 23, 227-236.

- Bowman, W.P., Barbour, M.M., Turnbull, M.H., Tissue, D.T., Whitehead, D. & Griffin, K.L. 2005. Sap flow rates and sapwood density are critical factors in within- and between-tree variation in CO₂ efflux from stems of mature *Dacrydium cupressinum* trees. *New Phytologist* 167, 815-828.
- Brouwer, R. 1962. Distribution of dry matter in the plant. *Netherlands Journal of Agricultural Science* 10, 361-376.
- Bylund, H. 1995. Long-term interactions between the autumnal moth and mountain birch: the role of resources, competitors, natural enemies, and weather. *Doctoral thesis, Swedish Univ. of Agricultural Sciences, Uppsala*.
- Bylund, H. 1997. Stand age structure influence in a low population peak of *Epirrita autumnata* in a mountain birch forest. *Ecography* 20, 319-126.
- Ceschia, E., Damesin, C., Lebaube, S., Pontailler, J-Y. & Dufrene, E. 2002. Spatial and seasonal variations in stem respiration of beech trees (*Fagus sylvatica*). *Ann.For.Sci.* 59, 801-812.
- Chapin, F.S. III 1983. Direct and indirect effects of temperature on arctic plants. *Polar Biology* 2, 47-52.
- Chen, C., Kolb, T.E. & Clancy, K.M. 2001. Mechanisms of Douglas-fir resistance to western spruce budworm defoliation: bud burst phenology, photosynthetic compensation and growth rate. *Tree Physiology* 21, 1159-1169.
- Christenson, L.M., Lovett, G.M., Mitchell, M.J. & Groffman, P.M. 2002. The fate of nitrogen in gypsy moth frass deposited to an oak forest floor. *Oecologia* 131, 444-452.
- Cook, E.R. 1985. *A time-series analysis approach to tree-ring standardization*. Ph.D.Diss. Univ. of Arizona, Tucson.
- Cook, E.R. & Kairiukstis, L.A. 1990. *Methods of Dendrochronology*. Kluwer Academic Publishers, Dordrecht. 394pp.
- Crawley, M.J. 1983. Herbivory. *The Dynamics of Animal-Plant Interactions*. Blackwell Scientific Publications, Oxford.
- Damesin, C. 2003. Respiration and photosynthesis characteristics of current-year stems of *Fagus sylvatica*: from the seasonal pattern to an annual balance. *New Phytologist* 158, 465-475.
- Damesin, C., Ceschia, E., Le Goff, N., Ottorini, J-M. & Dufrene, E. 2002. Stem and branch respiration of beech: from tree measurements to estimations at the stand level. *New Phytologist* 153, 159-172.
- Del Tredici, P. 2001. Sprouting in temperate trees: a morphological and ecological review. *Botanical Review* 67, 121-140.
- Douwes, P. 1975. Ljusfällfångst av Fjärilar i Abisko. *Entomologen* 4, 2. In Swedish.
- Field, C. & Moony, H.A. 1986. The photosynthesis-nitrogen relationships in wild plants. In: *On the economy of plant form and function*. (Ed. T.J. Givnich). Cambridge University Press, Cambridge, pp. 25-55.
- Fritts, H.C. 1976. *Tree rings and climate*. – Academic Press, London, New York, San Francisco. 567 pp.
- Fritts, H.C. & Swetnam, T.W. 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. *Advances in Ecological Research* 19, 111-189.
- Gao, R.T., Qin, X.X., Li, J.Z., Hao, W.Q. & Wang, X.Z. 1985. A preliminary study on the relationship between artificial defoliation of poplar trees and their growth. *Scientia Silvae Sinicae* 21, 199-205.
- Gellineck, H. 1997. Untersuchungen zur Holzbildungsdynamik von Birke und Kiefer an der Nördlichen Waldgrenze mit Hilfe der "Pinning"-Methode. *Diplom-Arbeit, Univ. Hamburg*.
- Halle, F., Oldeman, R.A.A. & Tomlinson, P.B. 1978. *Tropical trees and forests. An architectural analysis*. Springer, Berlin Heidelberg NewYork. 441 pp.
- Hämet-Ahti, L. 1987. Mountain birch and mountain birch woodland in NW Europe. *Phytocoenologia* 15, 449-453.
- Hammond, R.B. & Pedigo, L.P. 1981. Effects of artificial and insect defoliation on water loss from excised soybean leaves. *Journal of the Kansas Entomological Society* 54(2), 331-336.

- Haukioja, E. 2003. Putting the insect into the birch-insect interaction. *Oecologia* 136, 161-168.
- Haukioja, E. & Niemelä, P. 1974. Growth and energy requirements of the larvae of *Dineura viridorsata* (Retz.)(Hym., Tenthredinidae) and *Oporinia autumnata* (Bkh.)(Lep., Geometridae) feeding on birch. *Annales Zoologici Fennici* 11, 207-211.
- Haukioja, E. & Koricheva, J. 2000. Tolerance to herbivory in woody vs. herbaceous plants. *Evolutionary Ecology* 14, 551-562.
- Haukioja, E., Ruohomäki, K., Senn, J., Suomela, J. & Walls, M. 1990. Consequences of herbivory in the mountain birch (*Betula pubescens* ssp. *tortuosa*): importance of the functional organization of the tree. *Oecologia* 82, 238-247.
- Heichel, G.H. & Turner, N.C. 1983. CO₂ assimilation of primary and regrowth foliage of red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.): response to defoliation. *Oecologia* 57, 14-19.
- Hilton, G.M., Packham, J.R. & Willis, A.J. 1987. Effects of experimental defoliation on a population of pedunculate oak (*Quercus robur* L.). *New Phytologist* 107, 603-612.
- Hobbie, S.E. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs* 66, 503-522.
- Ishii, H. & Ford, E.D. 2001. The role of epicormic branching in maintaining foliage in old Pseudotsuga menziesii (Douglas-fir) trees. *Canadian Journal of Botany* 79, 251-264.
- Kallio, P. & Lehtonen, J. 1975. On the ecocatastrophe of birch forests caused by *Oporinia autumnata* (Bkh.) and the problem of reforestation. In: *Fennoscandian tundra ecosystems. Part 2: Animal and system analysis*. (Ed. F.E. Wielgolaski) Springer, pp. 174-180.
- Kallio, P. & Mäkinen, Y. 1978. Vascular flora of Inari Lapland. 4. Betulaceae. *Report from the Kevo Subarctic Research Station* 14, 38-63.
- Karlsson, P.S. 1991. Intraspecific variation in photosynthetic light response and photosynthetic nitrogen utilization in the mountain birch, *Betula pubescens* ssp. *tortuosa*. *Oikos* 60, 49-54.
- Karlsson, P.S. & Nordell, K.O. 1988. Intraspecific variation in nitrogen status and photosynthetic capacity within mountain birch populations. *Holarctic Ecology* 11, 293-297.
- Karlsson, P.S. & Nordell, K.O. 1996. Effects of soil temperature on the nitrogen economy and growth of mountain birch seedlings near its presumed low temperature distribution limit. *Ecoscience* 3, 183-189.
- Karlsson, P.S. & Weih, M. 2003. Patterns of recovery after insect herbivory in the mountain birch. *Functional Ecology* 17, 841-850.
- Karlsson, P.S., Bylund, H., Heino, S. & M. Tjus. 2003. Climatic response of budburst in the mountain birch at two areas in northern Fennoscandia and possible responses to global change. *Ecography* 26, 617-625.
- Kaufmann, M.R. 1996. To live fast or not: growth, vigor and longevity of old-growth ponderosa pine and lodgepole pine trees. *Tree Physiology* 16, 139-144.
- Kozlowsky, T.T. & Winget, C.H. 1964. The role of reserves in leaves, branches, stems and roots on shoot growth of red pine. *American Journal of Botany* 51, 522-529.
- Kuivinen, K.L. & Lawson, M.P. 1982. Dendroclimatic analyses of birch in south Greenland. *Arctic and Alpine Research* 14, 243-250.
- Kulman, J.H. 1971. Effects of insect defoliation on growth and mortality of trees. *Annual Review of Entomology* 16, 289-324.
- Lehtilä, K., Tuomi, J. & Sulkioja, M. 1994. Bud demography of the mountain birch *Betula pubescens* ssp. *tortuosa* near tree line. *Ecology* 75(4), 945-955.
- Lovett, G.M. & Ruesink, A.E. 1995. Carbon and nitrogen mineralization from decomposing gypsy moth frass. *Oecologia* 104, 133-138.
- Lough, J.M. & Holmes, R.L. 1994. RESPO. In: *Dendrochronology program library – Users manual*. (Ed. R.L. Holmes). Laboratory of Tree Ring Research, Tucson, Arizona, USA. pp. 41-42.
- Mattson, W.J. & Addy, N.D. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190, 515-522.

- Maier, C.A., Zarnoch, S.J. & Dougherty, P.M. 1998. Effects of temperature and tissue nitrogen on dormant season stem and branch maintenance respiration in a young loblolly pine (*Pinus taeda*) plantation. *Tree Physiology* 18, 11-20.
- McGuire, M.A. & Teskey, R.O. 2004. Estimating stem respiration in trees by a mass balance approach that accounts for internal and external fluxes of CO₂. *Tree Physiology* 24, 571-578.
- Meerts, P. 2002. Mineral nutrient concentrations in sapwood and heartwood: a literature review. *Annals of Forest Science* 59, 713-722.
- Mencuccini, M., Martinez-Vilalta, J., Vanderklein, D., Hamid, H.A., Korakaki, E., Lee, S. & Michiels, B. 2005. Size-mediated ageing reduces vigour in trees. *Ecology Letters* 8(11), 1183-1190.
- Millar, A. 1980. Annual rings of birch (*Betula pubescens* ssp. *tortuosa* (Ledeb)(Nyman)), climate and defoliation: an exploratory study. *Merlewood Research and Development Paper, Number 77*. ISSN 0308-3675.
- Nash, T.H., Fritts, H.C. & Stokes, M.A. 1975. A technique for examining nonclimatic variation in widths of tree rings with special reference to air pollution. *Tree-Ring Bulletin* 35, 15-24.
- Niemelä, P., 1980. Dependence of *Oporinia autumnata* (Lep., Geometridae) outbreaks on summer temperature. *Reports from the Kevo Subarctic Research Station* 16, 27-30.
- Ossipov, V., Haukioja, E., Ossipova, S., Hanhimäki, S. & Pihlaja, K. 2001. Phenolic and phenolic-related factors as determinants of suitability of mountain birch leaves to an herbivorous insect. *Biochemical Systematics and Ecology* 29, 223-240.
- Palm, T. 1959. Följdverkningar av fjällbjörkmätarens härjning i Abiskodalen 1954-56. En koleopterologisk undersökning somrarna 1958 och 1959. *Entomologisk Tidskrift* 34, 120-136.
- Pedersen, B.S. 1998. The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. *Ecology* 79, 79-93.
- Poorter, H. 1989. Plant growth analysis: towards a synthesis of the classical and the functional approach. *Physiologia Plantarum* 75, 237-244.
- Poorter, H. & Nagel, O. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO₂, nutrients and water: a quantitative review. *Australian Journal of Plant Physiology* 27, 595-607.
- Pruyn, M.L., Gartner, B.L. & Harmon, M.E. 2002. Within-stem variation of respiration in *Pseudotsuga menziesii* (Douglas-fir) trees. *New Phytologist* 154, 359-372.
- Ruohomäki, K., Chapin, F.S., Haukioja, E., Neuvonen, S. & Suomela, J. 1996. Delayed inducible resistance in mountain birch in response to fertilization and shade. *Ecology* 77, 2302-2311.
- Ruohomäki, K., Virtanen, T., Kaitaniemi, P. & Tammaru, T. 1997. Old mountain birches at high altitudes are prone to outbreaks of *Epirrita autumnata* (Lepidoptera: Geometridae). *Environmental Entomology* 26, 1096-1104.
- Rust, S. & Roloff, A. 2002. Reduced photosynthesis in old oak (*Quercus robur*): the impact of crown and hydraulic architecture. *Tree Physiology* 22, 597-601.
- Ryan, M.G. 1990. Growth and maintenance respiration in stems of *Pinus contorta* and *Picea engelmannii*. *Canadian Journal of Forest Research* 20, 48-57.
- Ryan, M.G. & Yoder, B.J. 1997. Hydraulic limits to tree height and tree growth. *Bioscience* 47, 235-242.
- Ryan, M.G., Gower, S.T., Hubbard, R.M., Waring, R.H., Gholz, H.L., Cropper, W.P. & Running, S.W. 1995. Woody tissue maintenance respiration of four conifers in contrasting climates. *Oecologia* 101, 133-140.
- Sandberg, G. 1963. Växtvärlden i Abisko nationalpark. In: *Natur i Lapland*. (Ed. K. Curry-Lindahl). Bokförlaget Svensk Natur, pp. 885-908.
- Schowalter, T.D., Hargrove, W.W. & Crossley, D.A. 1986. Herbivory in forested ecosystems. *Annual Review of Entomology* 31, 177-196.
- Shinozaki, K., Yoda, K., Hozumi, K. & Kira, T. 1964a. A quantitative analysis of plant form – the pipe model theory. I. Basic analyses. *Japanese Journal of Ecology* 14, 97-105.

- Shinozaki, K., Yoda, K., Hozumi, K. & Kira, T. 1964b. A quantitative analysis of plant form – the pipe model theory. II. Further evidence of the theory and its application in forest ecology. *Japanese Journal of Ecology* 14, 133-139.
- Shigo, A.L. 1984. Compartmentalization: A conceptual framework for understanding how trees grow and defend themselves. *Annual Review of Phytopathology* 22, 189-214.
- Shigo, A.L. & Hillis, W.E. 1973. Heartwood, discolored wood, and microorganisms in living trees. *Annual Review of Phytopathology* 11, 197-222.
- Sonesson, M. & Hoogesteger, J. 1983. Recent tree line dynamics (*Betula pubescens* Ehrh. ssp. *tortuosa* (Ledeb.) Nyman) in northern Sweden. *Nordicana* 47, 47-54.
- Stokes, M.A. & Smiley, T.L. 1968. *An introduction to tree-ring dating*. The University of Chicago Press, Chicago and London. 73p.
- Suomela, J., Ossipov, V. & Haukioja, E. 1995. Variation among and within mountain birch trees in foliage phenols, carbohydrates, and amino acids, and in growth of *Epirrita autumnata* larvae. *Journal of Chemical Ecology* 21, 1421-1446.
- Sveinbjörnsson, B. 1983. Bioclimate and its effect on the carbon dioxide flux of mountain birch (*Betula pubescens* Ehrh.) at its altitudinal tree-line in the Torneträsk area, northern Sweden. *Nordicana* 47, 111-122.
- Tammaru, T., Kaitaniemi, P. & Ruohomäki, K. 1995. Oviposition behaviour of *Epirrita autumnata* (Lepidoptera, Geometridae) in relation to its population dynamics. *Oikos* 74, 296-304.
- Tenow, O. 1972. The outbreaks of *Oporinia autumnata* Bkh. and *Operophtera* spp. (Lep., Geometridae) in the Scandinavian mountain chain and northern Finland 1862-1968. *Zoologiska Bidrag från Uppsala (Suppl. 2)*, 1-107.
- Tenow, O. & Bylund, H. 2000. Recovery of a *Betula pubescens* forest in northern Sweden after severe defoliation by *Epirrita autumnata*. *Journal of Vegetation Science* 11, 855-862.
- Tenow, O., Bylund, H., Karlsson, P.S. & Hoogesteger, J. 2004. Rejuvenation of a mountain birch forest by an *Epirrita autumnata* (Lepidoptera: Geometridae) outbreak. *Acta Oecologica* 25, 43-52.
- Thomas, P.A. 2000. A Tree's Old Age - tree growth and aging - Brief Article. *Natural History*, May 2000.
- Treter, U. 1974. Ökologische Standortsdifferenzierungen auf der Basis von Jahrringanalysen im Baumgrenzbereich Zentralnorwegens. In: *Tagungsbericht und wissenschaftliche Abhandlungen. Deutscher Geographentag Kassel 1973*, 492-507. F. Steiner Verlag, Wiesbaden.
- Treter, U. 1984. *Die Baumgrenzen Skandinaviens*. F. Steiner Verlag, Wiesbaden.
- Van Cleve, K., Barney, R. & Schlenker, R. 1981. Evidence of temperature control of production and nutrient cycling in two interior Alaska black spruce ecosystems. *Canadian Journal of Forest Research* 11, 258-273.
- Verwijst, T. 1988. Environmental correlates of multiple-stem formation in *Betula pubescens* ssp. *tortuosa*. *Vegetatio* 76, 29-36.
- Villalba, R. & Veblen, T.T. 1998. Influences of large-scale climatic variability on episodic tree mortality in northern Patagonia. *Ecology* 79, 2624-2640.
- Waring, R.H., Thies, W.G. & Muscato, D. 1980. Stem growth per unit of leaf area: A measure of tree vigour. *Forest Science* 26, 112-117.
- Waring, R.H., Newman, K. & Bell, J. 1981. Efficiency of Tree Crowns and Stemwood Production at Different Canopy Leaf Densities. *Forestry* 54, 129-137.
- Waring, R.H., Schroeder, P.E. & Oren, R. 1982. Application of the pipe model theory to predict canopy leaf area. *Canadian Journal of Forest Research* 12, 556-560.
- Waring, R.H. & Schlesinger, W.H. 1985. *Forest ecosystems: concepts and management*. Academic Press, Orlando, Florida, USA.
- Weih, M. 2000a. Delayed growth response of mountain birch seedlings to a decrease in fertilization and temperature. *Functional Ecology* 14, 566-572.
- Weih, M. 2000b. Growth of Mountain Birch Seedlings in Early-Successional Patches: A Year-Round Perspective. *Plant Biology* 2, 428-436.

- Weih, M. & Karlsson, P.S. 1997. Growth and nitrogen utilization in seedlings of mountain birch (*Betula pubescens* ssp. *tortuosa*) as related to plant nitrogen status and temperature: a two-year study. *Ecoscience* 4, 365-373.
- Weih, M. & Karlsson, P.S. 2001a. Growth response of mountain birch to air and soil temperature: is increasing leaf-nitrogen content an acclimation to lower air temperature? *New Phytologist* 150, 147-155.
- Weih, M. & Karlsson, P.S. 2001b. Variation in growth patterns among provenances, ecotypes and individuals of mountain birch. In: *Nordic mountain birch ecosystems. Man and the Biosphere Ser. Vol. 27.* (Ed. F.E. Wielgolaski). MAB/UNESCO, The Parthenon Publ. Group, New York, London, pp. 145-156.
- Weiner, J. & Thomas, S.C. 2001. The nature of tree growth and the 'age-related decline in forest productivity'. *Oikos* 94, 374-376.
- Wickman, B.E. 1980. Increased growth of white fir after a Douglas-fir tussock moth outbreak. *Journal of Forestry* 78, 31-33.
- Whittaker, R.H. & Woodwell, G.M., 1967. Surface area relations of woody plants and forest communities. *American Journal of Botany*.54(8), 931-939.
- Willard, E.E. & McKell, C.M. 1978. Sprouting and carbohydrate reserves of two wildland shrubs following partial defoliation. *Journal of Range Management* 31, 141-145.
- Wyckoff, P.H. & Clark, J.S. 2002. The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. *Journal of Ecology* 90, 604-615.

Acknowledgements

First I thank my former supervisor Emeritus Professor Mats Sonesson, who until and even after his retirement supported me in many ways. Without him this work would not have been started. He also gave valuable comments on an earlier version of the thesis. I am also indebted to my former co-supervisor Emeritus Professor Eddy van der Maarel for his support. I am grateful to Emeritus Professors Yrjö Vasari, Marjatta Raudaskoski and Henrik Wallgren and to Dr. Pekka Saranpää for providing workroom and laboratory facilities at the University of Helsinki after my move to Finland.

After a long break I got an opportunity to continue work on my thesis, and for this I am especially grateful to my present supervisor Associate Professor Martin Weih and co-supervisor Professor Theo Verwijst. Without their guidance, advice and support this work would not have been accomplished.

I thank the staff of the Abisko Scientific Research Station for their friendliness and readiness to help, Emeritus Professor Dieter Eckstein and the late Dr. Richard Holmes for their co-authorship and valuable advice, Dr. Thomas Bartholin for introducing me to dendrochronology, Dr. Lutz Eckstein for help with the fieldwork, Emeritus Professor Olle Tenow, Professor Staffan Karlsson and Dr. Helena Bylund for their friendship, valuable discussions and support. Helena even employed her knowledge of Finnish to get my daughter to sleep.

My warmest thanks go to my wife Marketta and our children AnnaKatja, Tom and Paulina. Marketta helped with the fieldwork, read all versions of the thesis, and

with her biological knowledge gave valuable comments. Their endless support and company over the years have been vital to the success of this work.