

# Altitudinal and within-crown distribution of insect grazing on Mountain birch (*Betula pubescens* coll.) in SW Greenland and NW Norway

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The distribution of grazing on birch leaves over different altitudes and levels above the ground was studied on valley slopes at three Greenland localities with different degree of oceanity, and compared with three Norwegian localities previously studied. In the Greenland valleys, grazing was concentrated to the lower half of the slopes and to the near-ground foliage, except at the most continental locality where it extended up into the crowns of the tree-sized birches. In the Norwegian valleys, grazing comprised most of the forest-clad slope and the whole crown of the birch trees. In Norway, the grazing insects were *Epirrita autumnata* and *Operophtera brumata* (Lep., Geometridae), their larvae being in outbreak numbers, in Greenland the larvae had left the foliage and therefore remained unidentified. They were in non-outbreak numbers. The importance of these differences for the results is discussed, as well as the effect of climate on grazing and the effect of grazing on growth of birches.

Key words: Mountain birch, *Salix glauca*, Greenland, Fennoscandia, *Operophtera* spp., *Epirrita autumnata*, grazing, outbreaks, zonation.

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The Mountain birch (*Betula pubescens* Ehrh. coll.) forest region is a northern maritime phenomenon which occurs in Fennoscandia, Iceland, northern Ural and, as a westernmost outpost, in south-western Greenland (Hämet-Ahti 1963; Böcher 1979; Ødum 1979). The insect fauna of circumpolar northern birches, including those of Greenland, has been inventoried and compared by Koponen (1978, 1983). In the Mountain birch forests of Fennoscandia, the geometrids *Epirrita* (*Oporinia*) *autumnata* (Bkh.) and *Operophtera* spp. are the most important leaf-eating insects. Thus, larvae of *O. brumata* and *O. fagata* severely defoliate birch forests along the Norwegian coast, while larvae of *E. autumnata* defoliate Mountain birch forests in a more easterly position in the Fennoscandian mountain chain. The outbreaks of these three species are synchronous and recur at intervals of about 9–10 years (Tenow 1972). The outbreaks of *E. autumnata* and *O. brumata* greatly affect the growth and survival of the Mountain birch (e.g. Nuorteva 1963; Kallio & Lehtonen 1973, Vaarama & Valanne 1973; Sonesson & Hoogesteger 1983). In Greenland, one candidate for a similar importance in the birch forest ecosystem could be the Bruce spanworm, *O. bruceata* (Hulst.), a relative and nearctic vicarian of *O. brumata*, known to graze birch and willow severely in North America and Greenland (Koponen

1978; Sippell et al. 1975). In Greenland, the dominant herbivorous insect group on birch is leaf-chewing lepidopterous larvae which made up 67% of the specimens sampled by Koponen (Koponen 1978). Beside *O. bruceata*, larvae of the two tortricid moths *Acleris caryosphena* (Meyr.) and *Eucosma indecorana* (Zett.) were of importance.

A few previous studies have focused on the altitudinal zonation of insect herbivores in the Mountain birch forest and then exclusively in Fennoscandia, centering on differences between species, foremost *E. autumnata* and *O. brumata* (Tenow 1965, 1972; Hågvar 1972, 1976). Bogacheva (1984) mapped within-crown occurrence of insects on birch in forest tundra.

The Greenland part of the present study was performed in 1984. The aim was to compare the distribution of leaf-eating insects on valley slopes with that in the Fennoscandian mountain chain. Fennoscandian data were gathered during the 1962–68 outbreak of *E. autumnata* and *Operophtera* spp. They were obtained from both the southern and northern parts of the mountain chain (cf. Tenow 1965, 1972). From a climatic-phytogeographic point-of-view (Tuhkanen 1984), SW Greenland is similar only to northern Scandinavia. For a comparison, therefore, only data from the northern part is used here.

## Investigation localities

The vegetation of SW Greenland is zoned across a steep climatic gradient from hyperoceanicity at the sea to continentality at the inland ice-cap. The outer hyperoceanic and oceanic zones lack birch growth in any form. Inland of these oceanic zones, three localities were studied in 1984 (Fig. 1 A, B):

1. Kangerdluarssuk, at Lakseelv, ( $60^{\circ}53'N$ ,  $45^{\circ}50'W$ ), close to Narsaq within the suboceanic northern boreal zone (sensu Tuhkanen 1984) but with a strong oceanic influence. The slopes are covered mainly with scattered, dense *B. pubescens* and *Salix glauca* L. shrubs, mostly less than 1.5 m in height, interspersed with some prostrate *Juniperus communis* L. Some of the birches may

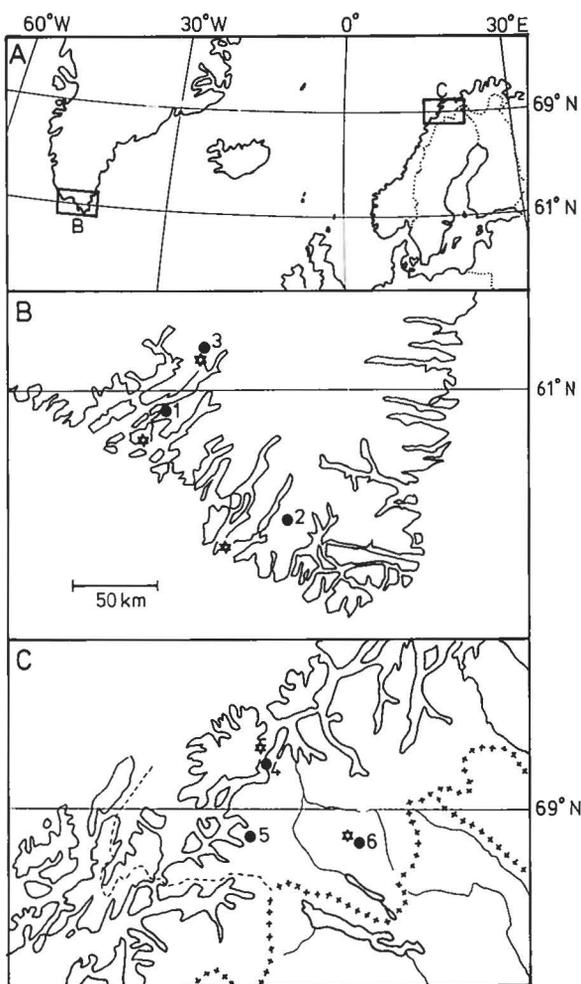


Fig. 1. Maps of investigation localities (●) with nearby weather stations (\*). A: General overview of investigation regions. B: SW Greenland with 1) Kangerdluarssuk (weather station: Qaqortoq/Julianehåb), 2) Qingua-dalen (Nanortalik), 3) Hospital Valley (Narsarsuaq). C: NW Norway with 4) Trollvika (weather station: Gibostad), 5) Engmo, 6) Frihetsli (Dividalen).

be intermediate with *B. glandulosa* Michx. Studies were performed on July 22–24 at two sites on the northern side of the Lakseelv valley, one on a west-facing slope at the fiord head near the GGU (Greenland Geological Survey) camp site where the birch “tree” line is at about 75 m a.s.l., and the other on a southeast-facing slope 1 km up the valley, with the valley floor at 30 m and the “tree” line at about 100 m. The herbivorous insect fauna of Kangerdluarssuk was studied by Koponen during an outbreak of *O. bruceata* on *B. pubescens* and *S. glauca* in 1976 (Koponen 1978).

2. Qingua-dalen, ( $60^{\circ}16'N$ ,  $44^{\circ}30'W$ ), in the same climatic/vegetational zone as Kangerdluarssuk but in a sheltered situation 10 km SE of Tasermiut fiord. Here, stands of polycormic *B. pubescens* trees have a luxuriant growth with heights and stand densities approaching those of Scandinavian birch forests. The tallest trees near the valley bottom are 6–8 m in height and even reach 12 m (Rosenvinge 1898; Oldendow 1935; Kuivinen & Lawson 1982). Between the birch stands are vast areas of dense *S. glauca* thickets. Specimens of *Sorbus groenlandica* (Schneid.) and *J. communis* occur scattered in the birch stands. On July 28 – August 2, insect grazing was studied on the slope of both sides of the valley about 1 km upstream of the valley river outlet into Lake Tasersuaq (23 m). Here the valley bottom is at 25 m a.s.l. and the “forest” line at about 275 m and 180 m on the northwest and the southeast side of the valley, respectively. A detailed description of the lower part of the valley is given by Oldendow (1935).

3. Hospital Valley, ( $61^{\circ}16'N$ ,  $44^{\circ}30'W$ ), within the subcontinental northern boreal zone. The study site is situated 6 km northeast of Narsarsuaq Airport, on a slope exposed to the north. Dense thickets of *B. pubescens* and *S. glauca* extend on the slope with sparse trees, 3–4 m in height in sheltered positions. The valley floor and the “forest” line are situated at app. 40 m and 170 m a.s.l., respectively. The study was performed on July 17–18 and July 20.

Comparisons are made with the spatial distribution of insect grazing at three localities in the county of Troms, NW Norway, at about the same distance from the sea as in Greenland (Fig. 1 A, C) and with about the same length of growing season (120–160 days and about 120 days, respectively, with a mean daily, or monthly, temperature above  $+5^{\circ}C$ , according to Tuhkanen 1984).

4. Trollvika ( $69^{\circ}15'N$ ,  $18^{\circ}00'E$ ), 3 km north of Finnsnes Commune and situated within the suboceanic sector of the northern boreal zone (Tuhkanen 1984). The meadow *B. pubescens* forest, mainly of monocormic birches 10–18 m in height and interspersed with *Sorbus aucuparia* L., *Salix* sp. and *J. communis* specimens, extends from sea level up to about 320 m. The study, performed on July 4, 1965, was complemented on June 25, 1966.

5. Engmo (68°43'N, 18°05'E), in the Salangdalen on the east-facing slope of the fjell Trosen is in the suboceanic middle boreal zone (Tuhkanen 1984). The forest is a rich heath *B. pubescens* forest with monocormic trees, 5–15 m in height, extending from the valley floor at about 110 m up to about 420 m a.s.l. At lower levels, small *Pinus sylvestris* L. stands occur. The study was made on June 28–29, 1964 and completed on June 27–28, 1965.

6. Frihetsli (68°46'N, 19°43'E) on the west-facing slope of the fjell Anaskåla in the Dividalen valley. This site is in the middle boreal zone but under a more continental influence than the two previous localities (Tuhkanen 1984). The *B. pubescens* forest extends from the Di-helva river at 200 m a.s.l. up to about 560 m. It is a heath forest of polycormic and monocormic birches, 6–10 m in height, including *P. sylvestris* trees at lower altitudes. The study was performed on July 1 1964.

In Fig. 2, mean monthly temperature curves are given for weather stations which are close to some of the investigation localities (Fig. 1 B, C). The temperature data for Narssarsuaq should be representative of the nearby Hospital Valley, and the oceanic Qaqortoq/Julianehåb is somewhat more extreme than Kangerdluarsuk. The Norwegian Gibostad and Dividalen are good representatives of Trollvika and Frihetsli, respectively. Weather stations that are representative of Qingua-dalen and Engmo are lacking. The exposed oceanic Nanortalik, 40 km WSW of Qingua-dalen, shows the extremes of the outer coast.

## Materials and methods

At each investigation locality, the occurrence of leaf-eating insects was quantified at 2–4 stations at different altitude levels from the valley floor to altitudes near the forest line. At each station 10 birches were sampled, except in Norway in 1964 when only 6 birches were used. In the valley of Qingua-dalen, the sampling plots, laid out parallel with the slope, were 100 × 100 steps in size. The trees to be sampled were identified by using the sides of the plot as a grid for randomly selected coordinates and by taking the tree closest to each of the ten pairs of coordinates, paced out on the plot. All other plots were 50 × 50 m, sometimes modified according to the topography. The sampled trees were selected by "random walk" and pointed out blindly from a distance to prevent a subjective choice. Neither selection is truly random. However, they are erratic in relation to the distribution of larvae and consumption, and should not bias a comparison among sites. At some exceptionally steep plots (Trollvika) and in birch forest outliers (Kangerdluarsuk and Hospital Valley) all accessible and available trees of the plot had to be sampled to get  $n = 10$ . On the Greenland plots, but not on

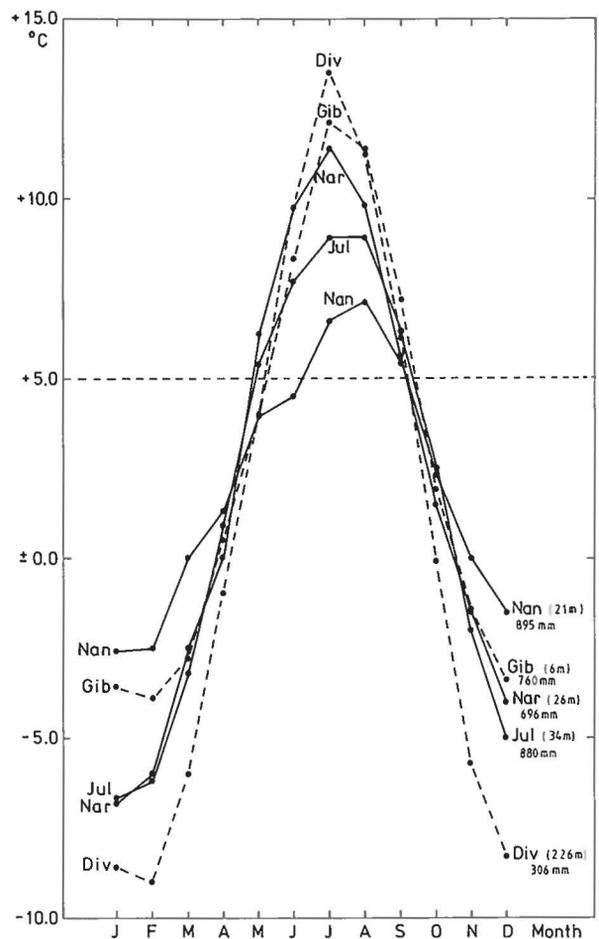


Fig. 2. Mean monthly temperature curves for typical Greenlandic and Norwegian weather stations, according to Sestland (1970). Lufttemperaturen i Norge 1861–1955. I. Middeldverdi, Oslo 1957, and Nedbøren i Norge 1895–1943. I. Middeldverdi og maksima, Oslo 1949. SW Greenland: Jul = Qaqortoq/Julianehåb. Nan = Nanortalik. Nar = Narssarsuaq. NW Norway: Gib = Gibostad, Div = Dividalen. Figures within parenthesis after name = altitude above sea level; figures below name = average annual precipitation. Horizontal, dashed line at +5°C marks lower temperature limit for the growing season, according to Tuhkanen (1984). Position of weather stations, see Fig. 1.

the Norwegian ones, 10 *S. glauca* bushes were selected for sampling, viz., the one closest to each of the selected birches.

Generally, birches of the NW Norway localities were taller than those of the Greenland localities and while the polycormic Greenland birches formed thickets with much of the leaves near the ground, the mainly monocormic NW Norwegian birches carried their foliage well lifted up from the ground. On the Norwegian plots, one twig (on average with 50–70 leaf-carrying shoots) per tree was taken from the lower half of the crown at 2–3 m above the ground, by climbing the tree with a ladder. On the Greenland plots, with their low birches and

willows, one twig per tree or bush was taken from the middle part of the crown, reached by hand 1.5–2.0 m above the ground. In addition, at the Qingua-dalen sites, each selected birch and willow was also sampled for one twig within 0.5 m from the ground.

Each sampling unit was kept apart, either treated on the spot (Greenland) or put into a transparent plastic bag and transported to a separate handling place. The investigation in Norway was made during the on-going 1964–66 outbreak and the number of shoots and larvae of different species was counted per twig and the counts transformed to the number of larvae per 100 shoots. In addition, the representativeness of the estimates for different altitudinal zones of a site was checked from merely visual evaluation of the damage inflicted to the foliage at return visits later in the summer. In Greenland, the spring and summer of 1984 were extremely early and warm, and all leaf-eating larvae had already terminated their feeding and had left the foliage prior to the investigation. Thus, no counting of larvae was possible. As a substitute, the leaves of 100 shoots per twig were examined for gnawing marks and the number of grazed shoots per 100 shoots was recorded. Neither was it possible to identify the insect species causing the damage.

The altitude above sea level of the valley floor, forest line and sampling plots was determined from current topographical maps (Greenland 1:250 000 and 1:100 000; Norway 1:50 000) and with a pocket altimeter (Lambrecht Höhenmesser 1304).

Data were not transformed for normality. The ( $2 \times$  s.e.) bars of average values in Figs. 3–5 below therefore more likely correspond to a confidence interval of 80–90% than to one of 95% (cf. Axelsson et al. 1975). Data were tested for significant differences with appropriate non-parametric statistical methods (Zar 1984). The following are used: K-W test = Kruskal-Wallis test, W test = Wilcoxon paired-sample test, and M-W test = Mann-Whitney test.

## Results

### Greenland

At the main investigation locality, Qingua-dalen, insect grazing on tree-sized birches (Fig. 3 A) was concentrated to the lower part of the slope ( $p < 0.01$ , K-W test) and to low levels above the ground ( $p < 0.01$ , W test), on both sides of the valley. The highest frequency of gnawed shoots, 34%, was on the northwest side of the valley (southeast-facing slope) closest to the valley floor. Near the “forest” line, 250 m a.s.l. on the northwest side and 175 m on the southeast side, the frequency of gnawed shoots was less than 10%. Similarly, in the upper part of the crowns, at 1.5–2 m above the ground, the grazing frequency was less than 10% and this was the case at all investigated altitudes. This difference in grazing as a function of altitude reappeared in *S. glauca* (Fig. 3 B, northwest side:  $p < 0.01$ , K-W test), as well as

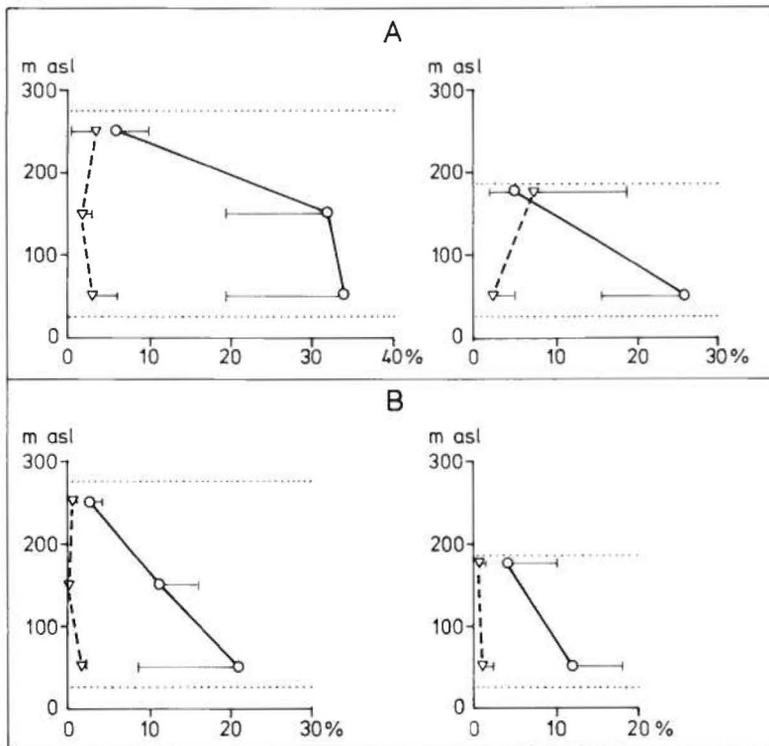


Fig. 3. Percentage of grazed shoots at 0.5 m (circles) and 1.5–2.0 m (triangles) above the ground at different altitudes above sea level (a.s.l.) in Qingua-dalen. A: *Betula pubescens* on NW side (left diagram) and SE side (right) of valley. B: *Salix glauca* on NW side (left) and SE side (right) of valley. Altitudes of valley floor and upper limit of *B. pubescens* stands are indicated by dotted lines. Horizontal bars =  $2 \times$  s.e.

the difference in grazing as a function of height above the ground (northwest side:  $p < 0.005$ , southeast side:  $p < 0.05$ , W tests), in spite of the willow shrubs being only about half the height of the birches.

At the two subsidiary localities, with either a lack of tree-sized birches (Kangerdluarssuk), or a clumped occurrence of birch trees (Hospital Valley, upper slope), no separation was made between "low" (below 0.5 m above the ground) and "high" insect grazing (at 1.5–2 m above the ground).

At Kangerdluarssuk, the height of the birches (*Betula* spp.) was low, 0.2–0.8 m near the head of the fiord and 0.2–1.5 m about 1 km up the valley, the birches attaining the higher values in sheltered positions near rocks and stones. Consequently, the grazing occurred mainly within 0.5 m above the ground.

The grazing frequency on birch (Fig. 4 A) was highest at the outer study profile and at the lowest altitude (25%), although the difference between altitudes within the profile was not significant. Grazing was lower on *S. glauca* than on *Betula* (inner profile:  $p < 0.05$ , outer profile:  $p < 0.001$ , M-W tests), i.e. less than 5% (Fig. 4 A).

In Hospital Valley, which is the only investigated inland locality, the grazing frequency at 2 m above the ground on the 3–4 m high *B. pubescens* trees (Fig. 4 B) was highest in the lower half of the slope, ( $p < 0.001$ , K-W test), apparently with a maximum 50 m above the valley floor, however not significantly different from the grazing intensity at the lowest situated station. Insect grazing was generally lower on *B. glandulosa* and *S. glauca* shrubs (0.5–2 m in height), than on *B. pubescens* ( $p < 0.01$ , M-W tests) although data are lacking for the lowermost station (Fig. 4 B).

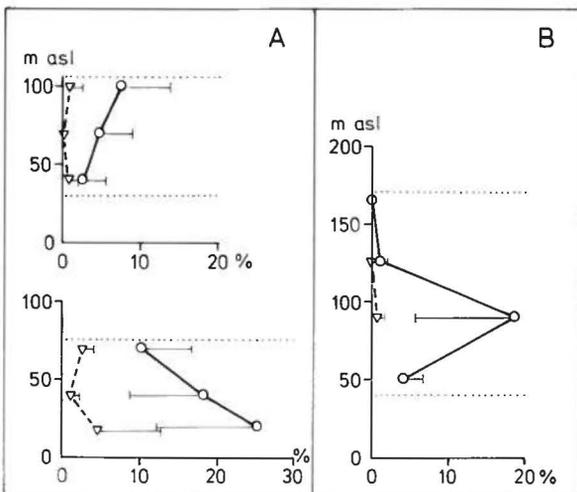


Fig. 4. Percentage of grazed shoots of *Betula pubescens* (circles) and *Salix glauca* (triangles) at different altitudes above sea level (a.s.l.). A: Kangerdluarssuk, inner part (upper diagram) and outer part (lower) of the Lakseelv valley. B: Hospital Valley. Altitudes of valley floor and upper limit of *B. pubescens* stands are indicated by dotted lines. Horizontal bars =  $2 \times$  s.e.

## Norway

In Norway, the insects still occurred on foliage when the field work was performed. Two of the localities were studied in two years. For the first year, counts of the most important grazers, *O. brumata* and *E. autumnata*, are reported separately, for the second year they are pooled.

At Trollvika, which is the most seaward investigation site, grazing obviously was high over most of the slope, as judged from the larval counts (Fig. 5 A). In 1965, the birch forest was brown-eaten from sea level up to about 100 m a.s.l. In 1966 the larval population was still high up to the forest line, but declining compared to the preceding year (Fig. 5 A).

At Engmo, grazing in 1964 (Fig. 5 B) was high at both the upper and the middle altitudes of the slope and significantly lower near the valley floor ( $p < 0.05$ , K-W test). The forest became brown-eaten only in a middle, horizontal zone. This damage pattern was recorded at a

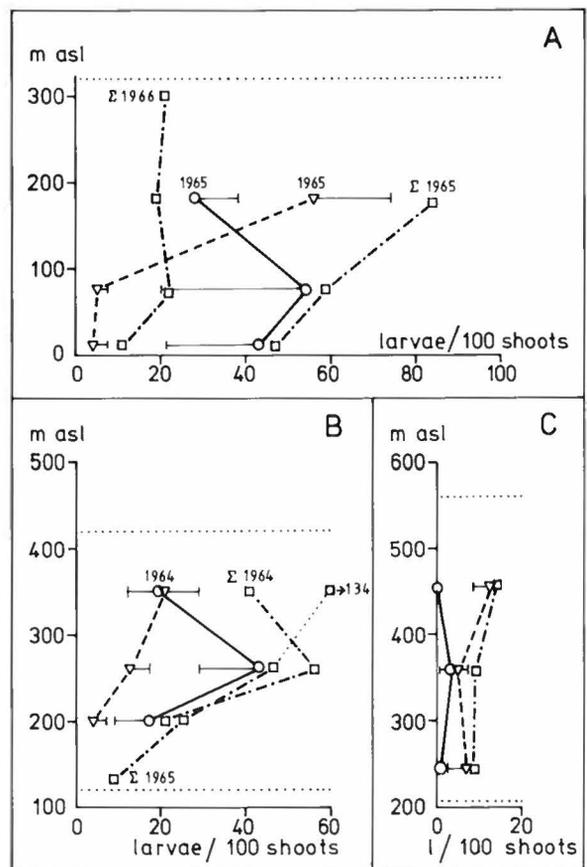


Fig. 5. Abundance of larvae of *Operophtera brumata* (circles) and *Epirrita autumnata* (triangles), separately, and summed up (squares) on *Betula pubescens* at different altitudes above sea level (a.s.l.). A: Trollvika 1965, with addition data from 1966. B: Engmo 1964, with addition data from 1965. C: Frihetsli 1964. Altitudes of valley floor and upper limit of *B. pubescens* forests are indicated by dotted lines. Horizontal bars =  $2 \times$  s.e.

visit later in the season when grazing had ceased, on August 10 1964. The outbreak culminated in 1965 with very large numbers of larvae at the highest station (Fig. 5 B). On a return visit on August 12 1965, it was observed that the brown-eaten zone this summer had shifted up-slope, now extending vertically from about 325 m a s.l. to near the forest line.

In contrast to the situation at the two former localities, the population at Frihetsli had not reached outbreak numbers in 1964 (Fig. 5 C). There were no obvious differences in total larval numbers along the slope. A return visit in 1982 revealed the occurrence of many dead birch trees in the upper half of the slope, killed by an outbreak, probably in the middle of the 1960's. The birch forest became severely defoliated in the upper part of the slopes on the eastern side of the river also in the 1940's and on the western side in 1955 (Tenow 1972).

At Trollvika, *E. autumnata* larvae dominated in number in the upper half of the slope ( $p < 0.01$ , W test) in 1965 and *O. brumata* in the lower half ( $p < 0.01$ ) (Fig. 5 A).

The same trend was seen in 1964 at Engmo (Fig. 5 B), where *E. autumnata* larvae increased significantly in number up-slope ( $p < 0.01$ , K-W test), however, without being more abundant than *O. brumata* at the uppermost station. The abundance of *O. brumata* larvae was higher at the intermediate station than at the lower station ( $p < 0.05$ , K-W test), and the larvae were more abundant than the larvae of *E. autumnata* ( $p < 0.05$ , W test).

Also at Frihetsli, in 1964, the abundance of *E. autumnata* increased with altitude, however, without the increase being significant (Fig. 5 C). Like at Engmo, the occurrence of *O. brumata* larvae peaked at the intermediate altitude station ( $p < 0.05$ , K-W test).

## Discussion

In both regions insect outbreaks have been documented on Mountain birch (Tenow 1972; Koponen 1978). In addition, in 1987 and 1988, after the performance of the present study, outbreaks of *O. bruceata* occurred in SW Greenland, e.g. at Kangerdluarssuk (P. Bjerger pers. comm.; H. Bohse pers. comm. and larval sample).

The results of present investigations are in accordance with previous studies of altitudinal distributions of different insect grazers in Fennoscandia, where outbreaks of *E. autumnata* mainly occur in the upper parts of the forest-clad valley slopes of the Fennoscandian mountain chain, while outbreaks of *O. brumata* centre in the middle or the lower parts, at least during the initial phase of an outbreak (Tenow 1965, 1972; Hågvar 1972).

The altitudinal distribution of outbreak species may change considerably from the initial and the peak years

to the last year of an outbreak, when the original distribution becomes distorted by the effects of virus disease and parasitism on the larval populations, and starvation of the larvae (Tenow 1972). Thus, when comparing the altitudinal zonation of leaf-eating insects, the different conditions prevailing during the study, i.e. an outbreak situation with identified insect species in northern Norway and a near endemic population situation with unidentified species in Greenland, call for caution when interpreting data. However, in Greenland and during the first year of study at the Norwegian localities, the populations were either in the initial or peak phase of a culmination with healthy individuals still essentially unaffected by density dependent factors. A comparison is therefore considered justified. The fact that the two regions were studied during separate time periods and where grazing was evaluated from the percentage grazed shoots and the abundance of larvae, respectively, is assumed not to interfere with large basic similarities or differences.

Furthermore, by comparing SW Greenland localities (Lat. 61°N) with localities in similar climatic-phytogeographical subzones in northern Norway (Lat. 69°N) instead of sites on the same latitude in southern Norway (cf. Fig. 1 A), some effects on distribution of very different vegetational and faunal composition should be reduced.

In Greenland, grazing was mainly at low altitudes of the slopes, either near the sea level as at the two suboceanic localities Kangerdluarssuk and Qingua-dalen, or with a maximum some fifty meters above the valley floor, as in Hospital Valley, the inland-most, subcontinental locality. In contrast, in all Norwegian profiles the grazing was frequent at most altitudes, mainly by *E. autumnata* at the upper levels of the slope and by *O. brumata* at the lower levels.

This difference may simply be due to the absence in SW Greenland of an adapted occupant of the upper parts of the birch zone, like *E. autumnata* (cf. Downes 1988). However, there is one potential leaf-chewing insect, the tortricid *A. caryosphena*, which Koponen found up to the limit of birch, both at Kangerdluarssuk and Narssarssuaq. This species also occurred in Hospital Valley and the inner part of the Lakseelv valley at Kangerdluarssuk (Koponen 1978).

On the other hand, if grazing by *E. autumnata* in Fennoscandia is disregarded, there are large similarities in the grazing patterns of the two regions. This applies at least in the first year of an *O. brumata* outbreak. Thus, grazing by *O. brumata* was mainly at a low altitude on the slope profiles, in the same way as found for the total grazing at the Greenland localities, either close to sea level at Trollvika, the coastal, suboceanic locality, or with a maximum some hundred meters above the valley floor at Engmo and the more continental Frihetsli farthest from the coast.

It is unknown which species caused the grazing observed in Greenland. Outbreak numbers of *O. bruceata*

occurred at Kangerdluarssuk in 1976 (Koponen 1978) and 1987–88 (H. Bohse pers. comm.). On the same occasion *O. bruceata* also occurred at Narsaq and Narsarsuaq but in fewer numbers (Koponen 1978; H. Bohse pers. comm.). Thus, it is reasonable to assume that *O. bruceata* was an important component in the leaf-eating guild in 1984, at least at the suboceanic localities.

The newly hatched larvae of *O. brumata* and *O. bruceata* enter and attack opening buds of their hosts (Briggs 1975; Brown 1962) and an early bud burst is considered decisive for the success of *O. brumata* on fruit-trees (Holliday 1977). Bioclimate, and hence the phenology of bud burst and leafing-out, changes systematically up-slope along valley sides. Commonly, on an inland valley slope, the middle zone ("the thermal belt", cf. Geiger 1961) has the warmest climate and, consequently, the earliest flushing of leaves. In the Fennoscandian mountain chain, *O. brumata* outbreaks tend to start within these belts of early leafing (Tenow 1972). A dependence of *O. bruceata* on a similar phenological relationship may partly explain similarities in the form of grazing profiles in SW Greenland and the abundance profiles of *O. brumata* in northern Norway.

Differences in life conditions are perhaps better illustrated by the different distributions above-ground of grazing. At the two suboceanic Greenland localities, grazing on both willow and birch was almost entirely confined to foliage near the ground. At Kangerdluarssuk, this restriction may primarily have been imposed by the mostly low growth of birch and willow. However, it is interesting to note that during the outbreak at Kangerdluarssuk in 1976, with complete defoliation of the low birch shrubbery, the tallest *B. pubescens* formations were in good condition and carried very few herbivores (Koponen 1978). This does not exclude the possibility that starving larvae may sometimes climb trees and to some degree extend grazing upwards. Similarly, in Qingua-dalen, grazing near the ground prevailed in spite of the fact that tree-high birches and tall willow stands dominated along much of the slope profiles. Thus, obviously some factor(s) other than foliage height restricted the vertical extent of grazing. In northern Norway no such restriction was observed; trees were defoliated from the base to the very top of the crowns.

Larvae of *O. bruceata* are more mobile and more easily dislodged from the foliage than those of *O. brumata* (Eidt & Embree 1968). Where both species occur in the same region, as in parts of North America, it has been observed that in forests infested with *O. bruceata*, understory plants are often most heavily defoliated while the wind-exposed portions of the tallest trees may be untouched. On the other hand, in forests infested by *O. brumata*, the understory vegetation is relatively untouched, even when the overstory is completely defoliated (Eidt & Embree 1968). Thus, the different vertical extent of grazing in Greenland may have arisen from influences of the different insect species composition, in

the same way as discussed for differences in the altitudinal extent of total grazing (see above).

However, a direct effect of a more severe and special climate in Greenland can not be ruled out as a contributing cause. The concentration of larvae of *A. caryosphena* on near-ground foliage, especially on leaves close to stones, was ascribed by Koponen (1978) to the warm microclimate in this habitat as contrasted with the conditions at some distance from the ground. The severity of climate is further illustrated by its effect on birch growth. From Fig. 2 it is seen that Narsarsuaq, the most continental of the topical Greenland weather stations, has a summer temperature, a length of growing season and an annual precipitation which is rather similar to that of the most seaward of the two Norwegian weather stations, Gibostad. In spite of this similarity, Narsarsuaq and the nearby Hospital Valley have only smaller, scattered stands of birch trees at a lower altitude, while Trollvika, close to Gibostad, has a luxuriant, continuous meadow birch forest up to more than 300 m a.s.l. Qaqortoq/Julianehåb and Nanortalik lack birch growth due to their exposed oceanic positions (Böcher 1979).

In SW Greenland, hence, birch forests are near their limit of maintenance productivity (Elkington & Jones 1974), the depression of growth to shrubbery or its complete exclusion in coastal areas being caused by too low summer temperatures, too many days with strong winds, and by fog coming in frequently from a sea cooled by drifting ice even in summer (Böcher 1979). In winter, occasional very strong and often long-lasting, warm and dry foehns, blowing from the inland icecap, may desiccate buds and twigs of trees (cf. Ødum 1979).

Reasonably, these special climatic features will affect the insect fauna of birch and willow as well. Thus, candidate factors, acting on one or several life stages irrespective of species, and causing a peculiar, »crouching« form of grazing at the suboceanic localities in Greenland, are windy weather and a chilled air which warms up and keeps warm only in sheltered positions near the ground (cf. Hansen 1973). This assumption is supported by the finding at Hospital Valley, farthest from the sea, that grazing extended up into the crowns in the same way as at the Norwegian localities.

In conclusion, grazing in SW Greenland seems to be mainly in the lower half of the valley slopes, while in Fennoscandia it extends over most of the birch-clad slope. Furthermore, in climatically exposed sites, grazing is concentrated to near-ground foliage, while in Fennoscandia it extends over most of the birch crowns. Only at protected inland localities does it have a similar vertical extent in Greenland.

Hypothetically, then, growth of tree-sized birches in SW Greenland should be significantly affected by outbreaks of leaf-eating insects only at lower altitudes on the slopes at inland sites, while the Mountain birch forest in Fennoscandia is affected over most of its altitudinal and horizontal extent.

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