

- LONGTON, R. E. & HOLDGATE, M. W. 1967: Temperature relationships of Antarctic vegetation. — Phil. Trans. Royal Soc. London B, 252: 237—250.
- LUNDAGER, A. 1912: Some notes concerning the vegetation of Germania Land: north-east Greenland. — Medd. om Grönl. 43: 349—414.
- LYE, K. A. 1966: A quantitative and qualitative investigation of oceanic bryophyte communities and their relation to the environment. — Nytt Magasin for Botanikk 13: 87—133.
- MIYATA, I. & HOSOKAWA, T. 1961: Seasonal variations of the photosynthetic efficiency and chlorophyll content of epiphytic mosses. — Ecology 42: 766—775.
- PAOLILLO, D. J. Jr. & BAZZAZ, F. A. 1968: Photosynthesis in Sporophytes of *Polytrichum* and *Funaria*. — The Bryologist 71: 335—343.
- PISEK, A. & KEMNITZER, R. 1968: Der Einfluss von Frost auf die Photosynthese der Weisstanne. — Flora B 157: 314—326.
- PODPERA, J. 1954: Conspectus muscorum europaeum. — 297 pp. Praha.
- RASTORFER, J. R. 1970: Effects of light intensity and temperature on photosynthesis and respiration of two Antarctic mosses, *Bryum argenteum* and *Bryum antarcticum*. — The Bryologist 73: 544—556.
- , — 1972: Comparative physiology of four west Antarctic mosses. — Antarctic Res. Ser. 20: 143—161.
- , — & HIGINBOTHAM, N. 1968: Rates of photosynthesis and respiration of the moss *Bryum sandbergii* as influenced by light intensity and temperature. — Amer. J. Bot. 55: 1225—1229.
- ROMOSE, V. 1940: Ökologische Untersuchungen über *Homalothecium sericeum*, seine Wachstumsperioden und seine Stoffproduktion. — Dansk. bot. arkiv 10: 1—134.
- RUDOLPH, E. D. 1965: Antarctic lichens and vascular plants: their significance. — BioScience 15: 285—287.
- SMITH, D. C. 1962: The biology of lichen thalli. — Biol. Rev. 37: 537—570.
- STEELE, W. C. 1954: Bryophytes. — Bot. Rev. 20: 425—450.
- STÄLFELT, M. G. 1937: Der Gasaustausch der Moose. — Planta 27: 30—60.
- , — 1960: Flechten und Moose. — In RUHLAND, W. (ed.): Handbuch der Pflanzenphysiologie V/2: 364—375.
- STÖRMER, P. 1940: Bryophytes from Franz Josef Land and eastern Svalbard. — Norges Svalbard. og Ishavs-Undersökelse 47: 1—16.
- SØRENSEN, T. 1941: Temperature relationships and phenology of the northeast Greenland flowering plants. — Medd. om Grönl. 125: 1—305.
- TALLIS, J. H. 1958: Studies in the biology and ecology of *Rhacomitrium lanuginosum* Brid. I. Distribution and ecology. — J. Ecol. 46: 271—288.
- , — 1959: Studies in the biology and ecology of *Rhacomitrium lanuginosum* Brid. II. Growth, reproduction and physiology. — J. Ecol. 47: 325—350.
- , — 1964: Growth studies on *Rhacomitrium lanuginosum*. — The Bryologist 67: 417—422.
- TAMM, C. O. 1953: Growth, yield and nutrition in carpets of a forest moss (*Hylocomium splendens*). — Meddel. från Statens Skogsforskningsinst. (Stockholm) 43: 1—140.
- , — 1964: Growth of *Hylocomium splendens* in relation to tree canopy. — The Bryologist 67: 423—427.
- TIKHOMIROV, B. A., SHAMURIN, V. F. & SHTEPA, V. S. 1960: Temperatura arktitsheskih rastenii. — Isv. Akad. nauk. SSSR, Ser. Biol. 3: 429—442.
- WARREN WILSON, J. 1960: Observations on net assimilation rates in arctic environments. — Ann. Bot. N.S. 24: 372—381.

Birch forest damage caused by *Oporinia autumnata* (Bkh.) in 1965-66 in Utsjoki, N Finland

PAAVO KALLIO and JUHANI LEHTONEN

Department of Botany, University of Turku, SF-20500 Turku 50, Finland

Received April 4, 1973

Printed December 15, 1973

Abstract

KALLIO, PAAVO & LEHTONEN, JUHANI. (Botany Dept., Univ., 20500 Turku 50, Finland) Birch forest damage caused by *Oporinia autumnata* (Bkh.) in Utsjoki, N Finland.

REP KEVO SUBARCTIC RES STAT 10. 55—69. Illus. 1973. — In 1965—1966 the caterpillars of the geometrid *Oporinia autumnata* defoliated vast areas of birch forests in Finnish Lapland. The damage areas in Utsjoki, the northernmost district of Finland, were studied more thoroughly. About 1350 km² were defoliated and large areas of this will be changed into treeless "tundra". Apparently due to temperature inversion, the valleys of the bigger rivers are totally saved. Owing to a less prominent capacity for adventive shoot formation the monocormic trees are more sensitive to the damage than the polycormic ones. There are also areas of earlier damage, particularly from the years 1955 and 1927. Vast treeless areas in the NW part of the study area were earlier birch forests; the remnants are still to be seen. Effects of the damage on field vegetation and in particular on juniper are discussed.

1. Introduction

Utsjoki, the northernmost administrative district of Finland, about 5000 km² in area and situated S of the latitude of 70°, was in 1965—66 the scene for what is probably one of the most abrupt changes in the landscape and in the balance of the subarctic birch zone ecosystem; in this area, the caterpillars of *Oporinia autumnata* (Bkh.) geometrid (autumnal moth) defoliated an area of ca. 135,000 hectares, and approximately 5000 square kilometers in whole Finnish Lapland (cf. NUORTEVA & JUSSILA 1969). This area will largely be changed into treeless "tundra". The Kevo Subarctic Research Station of the University of Turku (KALLIO 1964), situated in the centre of Utsjoki, undertook to classify and map the damage and to study its biology. The present paper gives

some preliminary data about the main features of the change that is taking place, and its distribution.

Among different attacks of insects in Lapland, the mass occurrences of *Oporinia autumnata* are known best; reports of these cover a period of more than a century. TENOW, in his excellent work (1972), gives a good survey of the history of *Oporinia* damages in Fennoscandia. In fact, the outbreaks have occurred at intervals of ca. ten years on an average. TENOW's work also provides much local data concerning the area investigated in this paper. Other reports about the same area include works by KALLIO (1941), NUORTEVA (1963; 1966; 1971), SILVOLA (1967), NUORTEVA & JUSSILA (1967; 1969), JUSSILA & NUORTEVA (1968), KALLIO et al. (1969), and KALLIO & MÄKINEN (1974).

The investigation area is in the centre of the *Oporinia* problem, because the pure birch zone is widest in the whole Fennoscandia (cf. HÄMET-AHTI 1963; KALLIO et al. 1969), and birch constitutes by far the most important host plant for the autumnal moth. The area is situated north of the continuous pine forest line. Its topography shows typical features of a "peneplane" with the top level of rounded mountains at ca. 300–500 m, the highest tops being 640 m, and the lowest parts (Tenojoki valley in the NE corner) 15 m a.s.l. Most of the land area is covered by birch forests consisting of more or less typical *Betula pubescens* ssp. *tortuosa*. The areas above ca. 300–500 m are beyond the climatic birch line, but some areas below this limit are also treeless. These areas are partly different types of bogs and fens, but the dry ecosystem also includes secondary treeless areas.

The birch forest type varies in different zones and belts. A more maritime and moss-rich forest type is met in the northernmost periphery of the area and continues to Norway, whereas a more continental and lichen-rich, dry forest prevails in the interior (HÄMET-AHTI 1963). Scattered pines occur in many valleys and slopes. Some isolated, small pine forests are also met in the Utsjoki-Kevojoiki valley.

There are two morphologically different types of spp. *tortuosa*: a bush-formed or polymorphic, and a more tree-like or monocormous form (cf. HÄMET-AHTI 1963; KALLIO & MÄKINEN 1974). There are some areas, particularly E and N of Paistunturit, called the Jeskaddam area, where monocormous trees are dominating. Some parts of NE Utsjoki also have plenty of monocormous birches, while polymorphic birches typically prevail in the continental parts, e.g. in the Utsjoki valley and on mountain slopes in the Petsikko area, and N of it.

Birches are used as firewood only near permanent settlements, but the forests constitute an important pasture land for the ca. 17,000 reindeers in Utsjoki.

The climate in our investigation area is more continental than on the Norwegian coast. A more detailed description of the topography, vegetation, climatology and hydrology is given by KALLIO et al. (1969) and KÄRENlampi (1972).

2. Methods

The investigation of the damaged area was started in 1969, i.e. four years after the outbreak. The ecology of the *Oporinia* caterpillars is, therefore, not included in this work, and the important birch physiology will be included in the programme of the Kevo Research Station later. However, some important entomological work has been carried out by NUORTEVA and JUSSILA (cf. literature cited).

To map the damage, excursions were made in the whole 5000 km² wide area of Utsjoki. Centres of damage are found around the rivers Utsjoki—Kevojoiki, around the river Pulmankijoki in NE Utsjoki, and around the river Kaamasjoki, the last centre being a less coherent area than the first two. As seen in Fig. 1, there are some smaller areas in addition to these, and the mapping also includes Inari, which was, however, studied less thoroughly.

To get a general view of the area, flights at 600 m were used to some extent before planning an excursion to the area. In the excursions, plots of 50 m × 50 m were taken randomly or 100 birches were taken from both sides of the selected route, not further than about 5 m from the route. Degrees of damage of the trees were estimated using the following scale:

- 0 = without any damage (i.e. "untouched")
- 1 = 1–10 % of the tree without leaves
- 2 = 11–80 % of the tree without leaves
- 3 = 81–99 % of the tree without leaves
- 4 = total damage (no leaves)

A damaged birch may recover to some extent afterwards (the recovery in the first two years after the damage has not been studied). Both twigs and parts of the basal stem are able to form adventive shoots, the latter being, however, more important (cf. MIKOLA 1942). Consequently, the number of basal shoots was taken as an indication of the degree of recovery. The following scale was used for this:

- 0 = no shoots
- 1 = 1–5 shoots
- 2 = 6–20 shoots
- 3 = more than 20 shoots

Birch seedlings were also counted in every plot in two random squares, one (i.e., 10 × 10 m) each. Only rarely was there a problem in classifying a "seedling". In most cases, there is a thickening of the stem base without connection to any bigger birch bush, indicating that their age may be many years, but even this type of the seedling is easily drawn up with all the roots.

The number of monocormous birches is indicated as per cent of all birches. Notes were also made of bushes and the field layer in every plot. The number of the investigated plots is 204. The gaps between these plots were filled by visual estimation. The maps (Figs. 3. and 5.) about the intensity of the damage and the recovery of birches in Utsjoki are based on the averages for the degree of damage and recovery for every plot and on visual estimations and observations. The line between a damaged and a healthy birch forest is often very sharp, and mostly there are no difficulties in placing it on the map. In wide areas, and particularly during the first few years of the study, the only map available was the General Economic Map of Finland; in the last two years, however, air photos, given to our disposal by military authorities, were used to complete the General Map. Good topographical maps, scale 1:20,000, were published first in 1972.

Some information is based on discussions with people from different villages, but the notes were, in most cases, checked by excursions. In order to observe changes over a long period, 9 enclosures were constructed in the birch damage areas for the purpose of eliminating reindeer influence (Map 2.). These enclosures, only ca. 400 m², are too small to eliminate all the "border effects". Evidence from Kevonsu Farm shows, however, that a dense birch seedling stand has developed in small fenced areas in a few years, while no birch seedlings are found outside these in the pasture land of reindeer. Vegetation analyses were made in the enclosures after constructing the fences, which took place in 1969–1971.

3. Results

3. 1. The damage areas

Fig. 1 shows the damage areas of the 1965—66 outbreaks in the whole of Inari Lapland, and those in Utsjoki birch forests are given in more detail in Fig. 2. The intensity of the damages in Utsjoki is indicated in Fig. 3. The Kevo and Pulmankijoki areas are typical damage centres, whereas the third main area around the Kaamasjoki draining area shows a less continuous grouping of damages. Typically, river valleys have remained untouched and thus split the defoliate areas as narrow belts from some metres to a few hundred metres in breadth. This is clearly seen in Fig. d, Plate I. The Kevojoki valley, with very little damage near Njaggaljärvet (Fig. 4), Madjohka, and Tsarsjoki, are examples of such quite healthy areas. Similarly, in the Pulmankijoki area, the Pulmankijoki, Aškassjohka, Loktajohka and Morišveijohka valleys form narrow bands of green in the almost totally defoliated

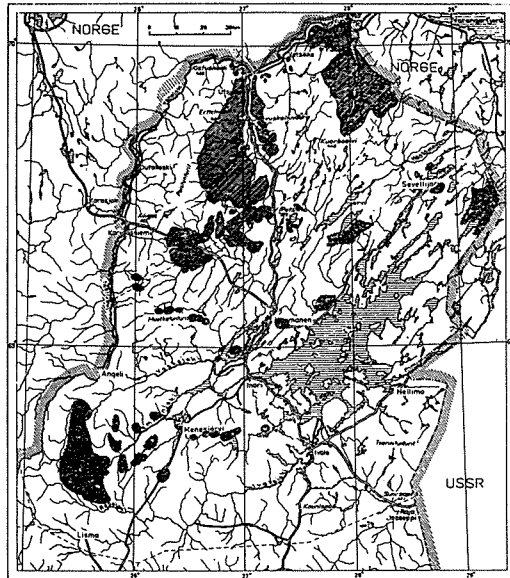


Fig. 1. The most important *Oporinia* damage areas from 1965—1966 in Inari Lapland. The areas in Utsjoki are studied in more detail.

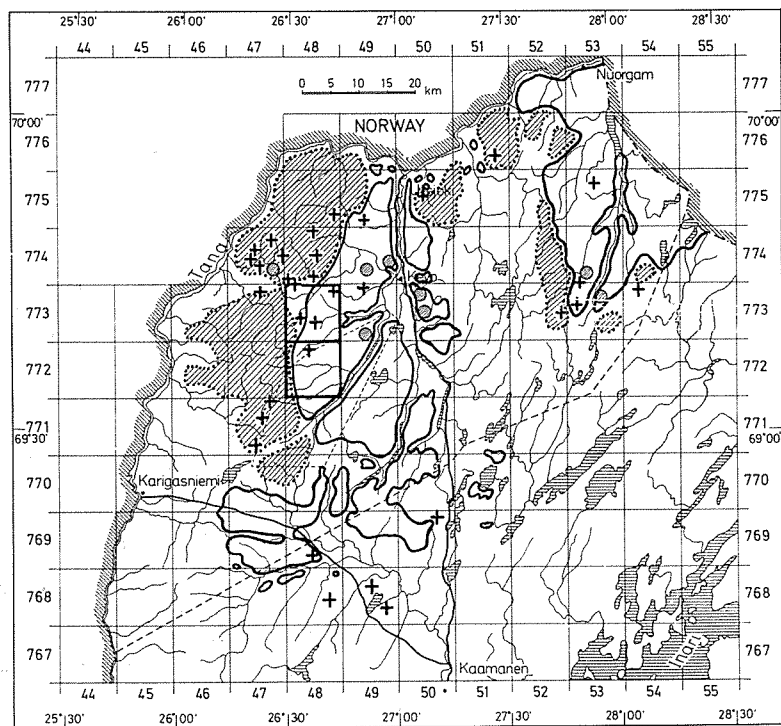


Fig. 2. The *Oporinia* damage areas from 1965—1966 in Utsjoki. The damage areas are drawn by thick continuous lines. Diagonal lines show recent treeless areas, which are partly of secondary origin. Crosses indicate older birch damages. Circles indicate the sites of fences. The two squares indicate the locations of the maps in Fig. 6.

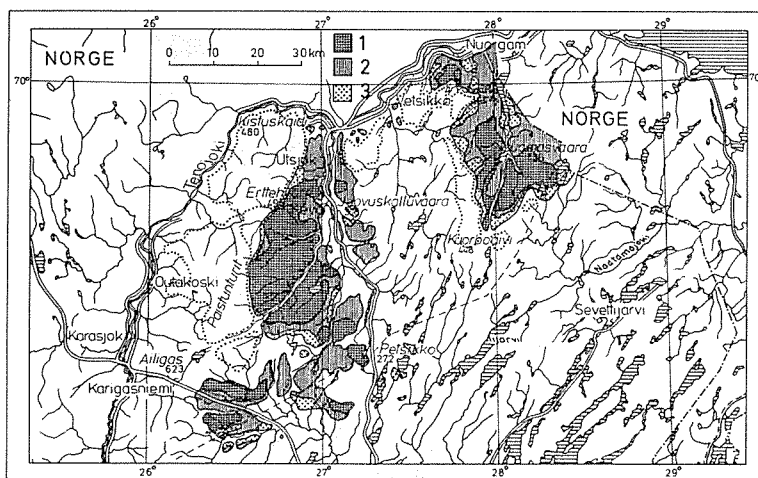


Fig. 3. The degrees of damage in Utsjoki after the *Oporinia* damage in 1965—1966. The different approximate degrees of damage are indicated by following symbols: 1. degree of damage 4.00—3.51, 2. degree of damage 3.50—2.51, 3. degree of damage 2.50—1.51 (see the scale in chapter 2.).

birch areas. The wide area of Lake Vetsijärvi district, with many bogs and rather low forest land, is all undamaged. The unmarked areas between the marked ones on the map do not mean that they are completely undamaged; in the Petsikko area, for instance, there are many isolated trees with more or less damage near the main road. Similar scattered examples are also found N of the western Utsjoki damage area, and W of the Pulmankijoki area.

There are many examples of the effect of local topography on the damage. In the northernmost part of the skaidi between the rivers Pulmankijoki and Morišveijohka, in an area which is 100 per cent defoliated, there is a small pond which is almost dry in summer and is surrounded by gently rising slopes. This pond has a narrow belt of untouched birches around it. Quite healthy or only slightly defoliated birches, mostly bushformed, are also found in continuous damage areas on tops of isolated mountains reaching near the climatic birch limit (ca. 300—350 m). Typical examples of this occur E of Kenespahta (E of the river Utsjoki) and near the border of Inari, W and E of the highway to Utsjoki. Similarly, some fells (height 300—350 m) W of the Kevo Subarctic Research Station have a green top of small birch bushes or rich shoots after the damage, while all the slopes are totally covered by dead birches. In the Utsjoki valley, the lower damage limit joins the upper pine limit.

The birch forests of the Tenojoki valley and the mountains in the Finnish side are mostly well preserved, with only some local damage

areas on high slopes E of Outakoski. In the northernmost corner of Finland (Nuorgam), the Pulmankijoki damage centre reaches to the banks of the river Teno, and at Harrematšohkka close to the Teno, the damage is 100 % and recovery ca 5 %.

As seen in Fig. 2, the almost continuous Kevo damage area is separated from the Teno birch forest area by an almost treeless heath area, which is partly climatically determined and partly of secondary origin. The Pulmankijoki damage centre continues east to the Norwegian side, where there are also vast areas

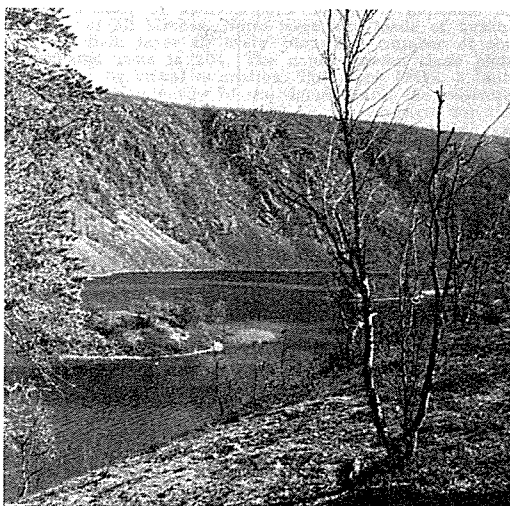


Fig. 4. In some places the damage has also taken place in bottom of the Kevojoki valley. The shore of Lake Njaggajärvi. 31. 7. 1971. P. Kallio.

of damage. The damage in some areas in NE Inari is almost total; the widest of these is the area around Lake Äälisjävi, Lake Nanabeljävi, and Vätsäri mountains, where the varying topography does not give any local differences in the intensity of damage: the damage is in many places total also on lake shores and on small islands (Fig. 1; cf. also Fig. e in Plate I).

As regards the degree of damage, the two main centres are rather similar. Around a central area with the highest degree of damage, there are transitional zones with gradually diminishing intensities of damage; often, however, the distinctions are sharp. Owing to the scale of the map, Fig. 3, it is often impossible to make the transitional zones discernible.

About half of the damaged area shown in the map, Fig. 3., has a damage index of 3.51—4.00; ie. more than 90 % of the green has been destroyed. The most typical areas of total damage are in the western part of the Kevo Nature Park, where the average of many areas sampled for this study is 100 % (no leaves). This is particularly the case in areas of monocormous birches (cf. Plate I, Fig. a). A high degree of damage is also seen in some central parts of the Pulmankijoki area and also in Utsjoki Ailigas (cf. Fig. 7), while the damage has not been so severe in areas E of the Utsjoki valley, (e.g. Kenespahta, cf. Fig. 8).

Two areas in the Kevo damage centre were investigated in more detail, and the mapping was carried out in scale 1:20,000 (pages

3914 07 and 3913 09 in Fig. 6). These areas are typical of the region; the narrow valleys of small brooks are almost untouched, and there are occasional transitional areas. The same maps also have areas of earlier damage and tops reaching over the climatic birch limit.

3.2. The recovery of birches

The recovery of birches, i.e. shoot formation, is shown in the map, Fig. 5. There are no continuous areas of high recovery. High damage values and low recovery values often coincide (cf. Figs. 7, and a, b, in Plate I), and areas with high recovery values are often seen as transitional zones around low recovery centres. The Kevo Nature Park area has the lowest recovery, and even the polycormic trees show low recovery values (Fig. 9).

At Kenespahta, in an area where the number of totally defoliated trees is more than 95 % of all, the recovery is also very high; 80—100 % of trees show at least some recovery. There are rather few monocormic trees scattered among the polycormic ones. When monocormic trees are taken separately, their recovery is under 10 % (16 of 165 trees show at least a single shoot). W of the Kevo Station near the valley of Tsarsjoki (NE from the point 322), all the totally defoliated monocormic trees (100 counted) had not a single basal shoot while the per cent value is 52 in the polycormic birches. Although the differences are not always as clear as in these examples, some differences are normally seen.

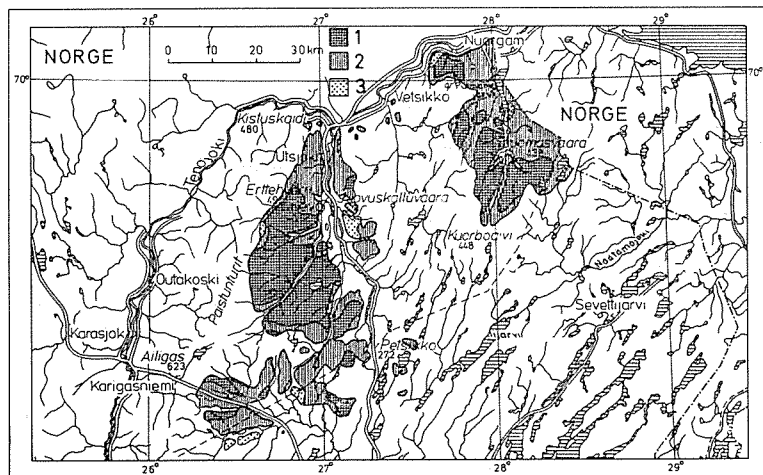
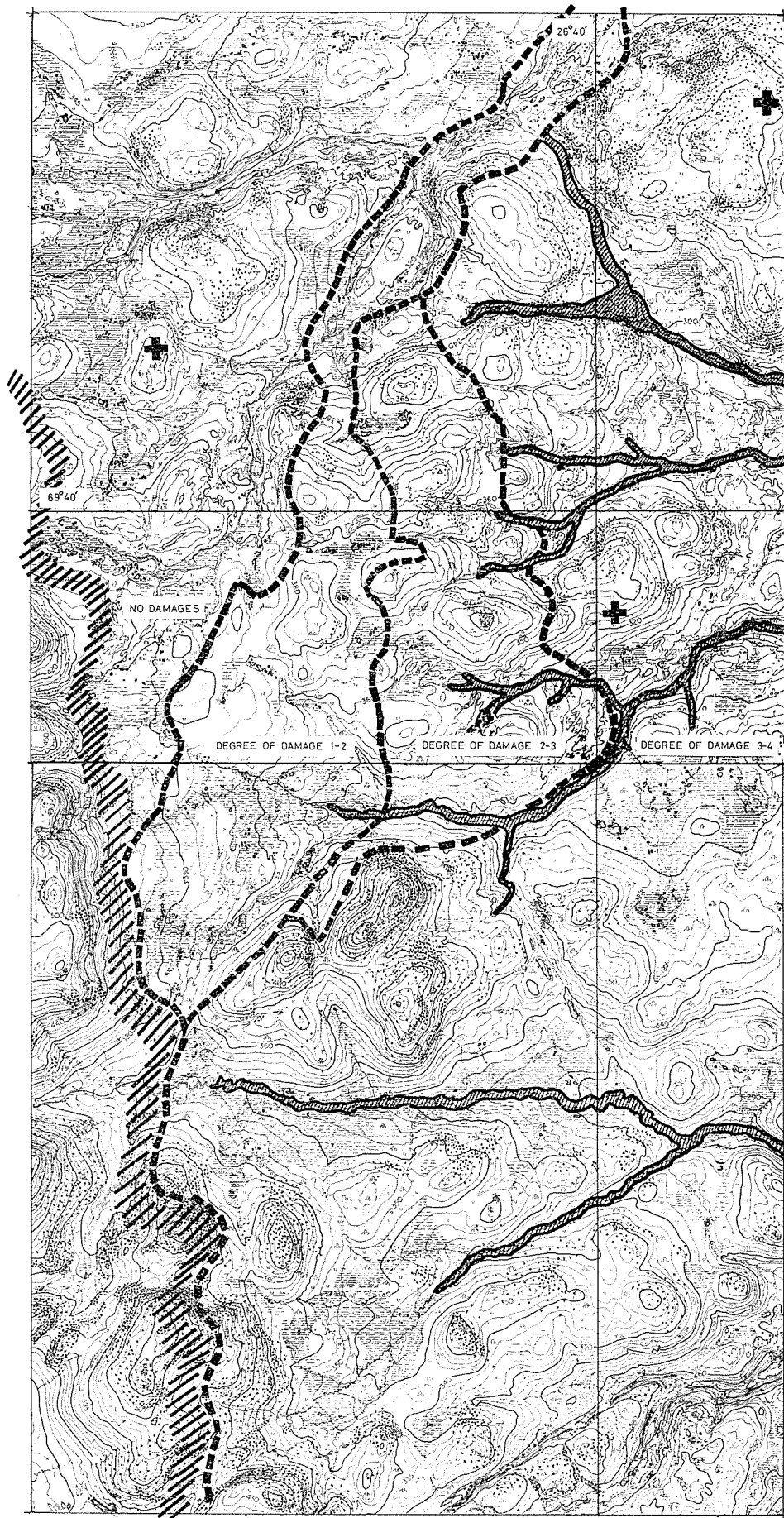


Fig. 5. Recovery of birches after the *Oporinia* damage in 1965—1966. The approximate degrees of recovery are indicated by following symbols: 1. degree of recovery 0.00—0.50, 2. degree of recovery 0.51—1.50, 3. degree of recovery 1.51—2.50 (see the scale in chapter 2.).



In our linear survey estimations, altogether 14,800 birches were studied in 148 sites: 3044 monocormic and 11,756 polycormic trees. Of all the trees, 51,2 % were totally defoliated (damage class 4).

Table 1. Damage and recovery of monocormic and polycormic birches.

	Number of totally de- foliated trees (class 4), %	Mean degree of damage	Number of trees with no recovery (class 0), %	Mean degree of recovery
Monocormic birches	77.1	3.5	88.6	0.13
Polycormic birches	44.5	3.2	50.1	0.83

Mean degrees of damage and recovery are based on estimated values for all the studied monocormic and polycormic trees.

It is naturally clear that the damage per cent is higher in monocormous than in polycormous trees, but the higher recovery per cent is more dependent on different responses of the two birch forms to the damage. A difference in the succering capacity is apparently involved. This has been discussed in KALLIO & MÄKINEN 1974.

3. 3. Reafforestation by seedlings

Numbers of seedlings vary according to the vegetation and soil. Continuous thick layers of mosses and lichens as well as dense dwarf shrub vegetation (*Vaccinium myrtillus*) lower the number of seedlings to the minimum of almost 0 per are. On the other hand, higher values are found in places where the vegetation is broken by bare soil, e.g. on reindeer paths, in camp fire places (where fire has burnt the peat and the vegetation), on slopes with moving soil or in sandy areas where the wind erosion has blotted some spots, and on river banks. For instance, 110 seedling per are were found near Kaldaudšjävri, and almost as many at a brook band on the slope of Ailigas.

Fig. 6. *Oporinia* damage areas from 1965—1966 in the western part of the Kevu Nature Park and N of this (cf. Fig. 2). The river valleys are almost untouched (narrow shaded areas limited by continuous lines). The boundary between undamaged valleys and totally destroyed slopes is mostly very sharp. Some transitional areas are also seen. The climatic treeless area in the west (Paistunturit-area) is limited by diagonal lines. The maps used have been reduced from the topographical map No. 3913 09 and 3914 07. Reproduced with the permission of the Cartographical Department of the National Survey Board.

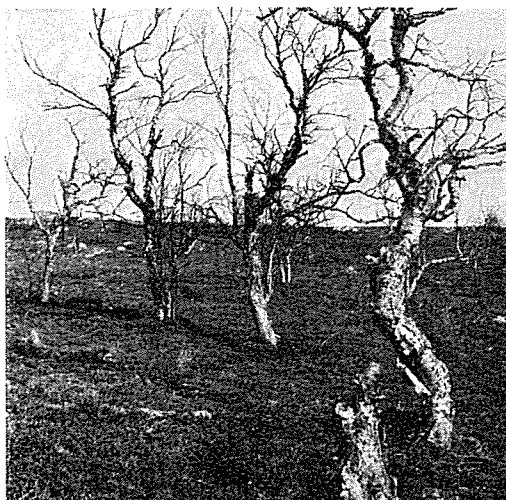


Fig. 7. Totally damaged birches at the W-slope of Utsjoki-Ailigas near the birch forest limit. The degree of recovery is 0. 30. 7. 1971. P. Kallio.

Normally, however, the number of seedlings in the investigated plots was between 0 and 5, the average being 2. The seedlings are often badly damaged, partly eaten by voles and reindeer, and the base of the young stem is often swollen. Fig. 11 shows typical seedlings, age 5—6 years. As the number of seeds in the centres of the damage areas is small at present and is dependent on long distance dispersal

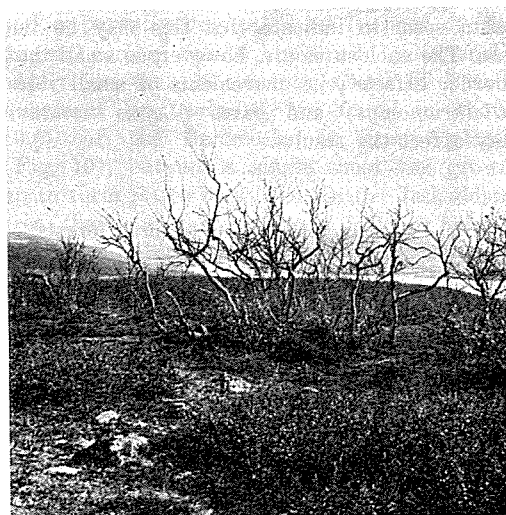


Fig. 8. *Oporinia* damage from the NW slope of Utsjoki-Ailigas. The polycormic birches have been totally defoliated and the stems are dead, but the basal shoot formation is vigorous. 30. 7. 1971. P. Kallio.

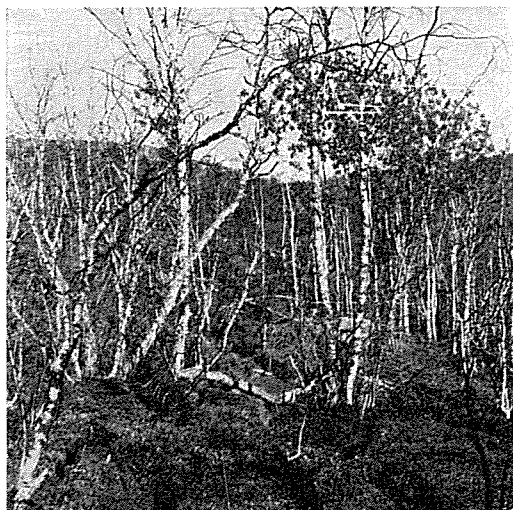


Fig. 9. Damaged *Betula tortuosa* forest at the NW slope of the Kevojoki valley near Lakes Njaggaljärvet. No basal shoots. 31. 7. 1971. P. Kallio.

only, it is probable that some of the seedlings are, in fact, of pre-damage origin. However, the number of seedlings does not seem to be higher at the margins of the damaged areas, where distances to healthy forests are shorter. A possible explanation is that reindeer grazing may to some extent impede reafforestation by seedlings. The enclosures seen in map, Fig. 2, will provide information about this factor. The first, quite preliminary observations in Kenespahta seem to indicate that this may be the case. The enclosures are, however, so small that "border effects", i.e. movements of small voles (*Clethrionomys*) and hares (*Lepus timidus*) may affect the results.

3. 4 Previous destructions of birch forests

Previous damages by *Oporinia* in Utsjoki have been described by KALLIOLA (1941) in the Karigasnjarga-Ailigas area and north of that. The damage occurred in 1927, and clear signs of the lowering of the birch forest limit were seen in 1950, when Nuorteva visited the area. According to his measurements in 1962, the dead birch forest belt on the slopes of Ailigas was 0.6–1 km wide and comprised an area of 15.5 km² (NUORTEVA 1963). Nuorteva also supposed that forests in the Paistunturit area N of Ailigas had disappeared,

possibly "as a result of the damage done by *O. autumnata* during the years 1927". However, no direct evidence of this was found.

The senior author made, in 1954, an excursion in the area between Madjokskaidi and Kuivi and observed many largely decayed birch stems still standing in the area E of Paistunturit; this area at present has very few birches. It seems that some stems (possibly the thickest ones?) may stay nearly 30 years after the damage. TENOW's study (1972, Fig. 21, p. 60) shows that dead stems of 20 years are totally branchless. There may be local differences in this respect, however (cf. NUORTEVA 1963). Accordingly, the forest killed in the big damage in 1955, e.g. around the Kaamanen—Karigasniemi road near Kaamas-



Fig. 10. A shoot grown in a fairly decayed birch trunk, apparently dating the *Oporinia* damage in 1927 or before that. The basal globe is an isolated part of the trunk. — Drawn by Marketta Lehtikainen.



Fig. 11. Typical seedlings from the Jeskaddam area. The seedlings have been broken several times by voles and reindeer. — Marketta Lehtikoinen.

mukka and Aksujävri and particularly in the Rastigaissa area W of the river Geidnojhka, was still standing in 1971—72.

We have made observations of earlier birch damage in places shown in Fig. 2. Wide areas of such ancient birch forests are to be found in the Jeskaddam area, (cf. Plate I, fig. f) E and N of Paistunturit. This is very typically represented in the Skierrevadda mountains: in an area of many square kilometres, there is not a single birch tree to be seen. Wide areas are covered with dwarf birch (*Betula nana*), and typical oligotrophic dwarf shrub heaths with *Empetrum hermaphroditum*, *Phyllodoce*, *Loiseleuria*, *Juncus trifidus* and lichens, particularly *Cladonias* and *Cetrarias*. Remnants of ancient birches, long bits of bark, indicate that quite thick birches have grown in the area. Small hummocks are also found, usually covered by crustaceous lichens and *Vaccinium vitis-idaea*, *Empetrum hermaphroditum*, and other typical representatives of dry heath vegetation. These hummocks contain clear remnants of *Betula*.

The number of such hummocks may be as high as 300 per ha, i.e. 30,000 per square kilometre, and apparently only a (small?) part of the original birches can be identified. Quite small, mostly less than 10 cm long shoots of *Betula pubescens* ssp. *tortuosa*, are found in about 10 % of the hummocks in many places (Fig. 10), but not a single shoot has grown up to form a tree or a bush. In the Jeskaddam area, there are, however, some isolated birches and birch groups.

All these trees are monocormous (eg. Tuolba Njaugoaiivi, Holgadanoaiivi, the bog area W of Koddigvarri, W of the point 322, Linkki-varri, Skierrevadda, Nuvvusaittivarri, Kirje-ädna, Nuvvušvaara, Rušogalggi, Pirkkoaiivi, Paddaskaidi and Ertteharri).

Large areas of Jeskaddam belong to the climatical birch zone, which is also seen in that there are isolated birches on some mountain tops. The question arises why the birches have not recovered in this area and why it has not been reafforested later by seedlings.



Fig. 12. A typical "table"-juniper from the area between Koddigvaara and Kamaoalvi. — Marketta Lehtikainen.

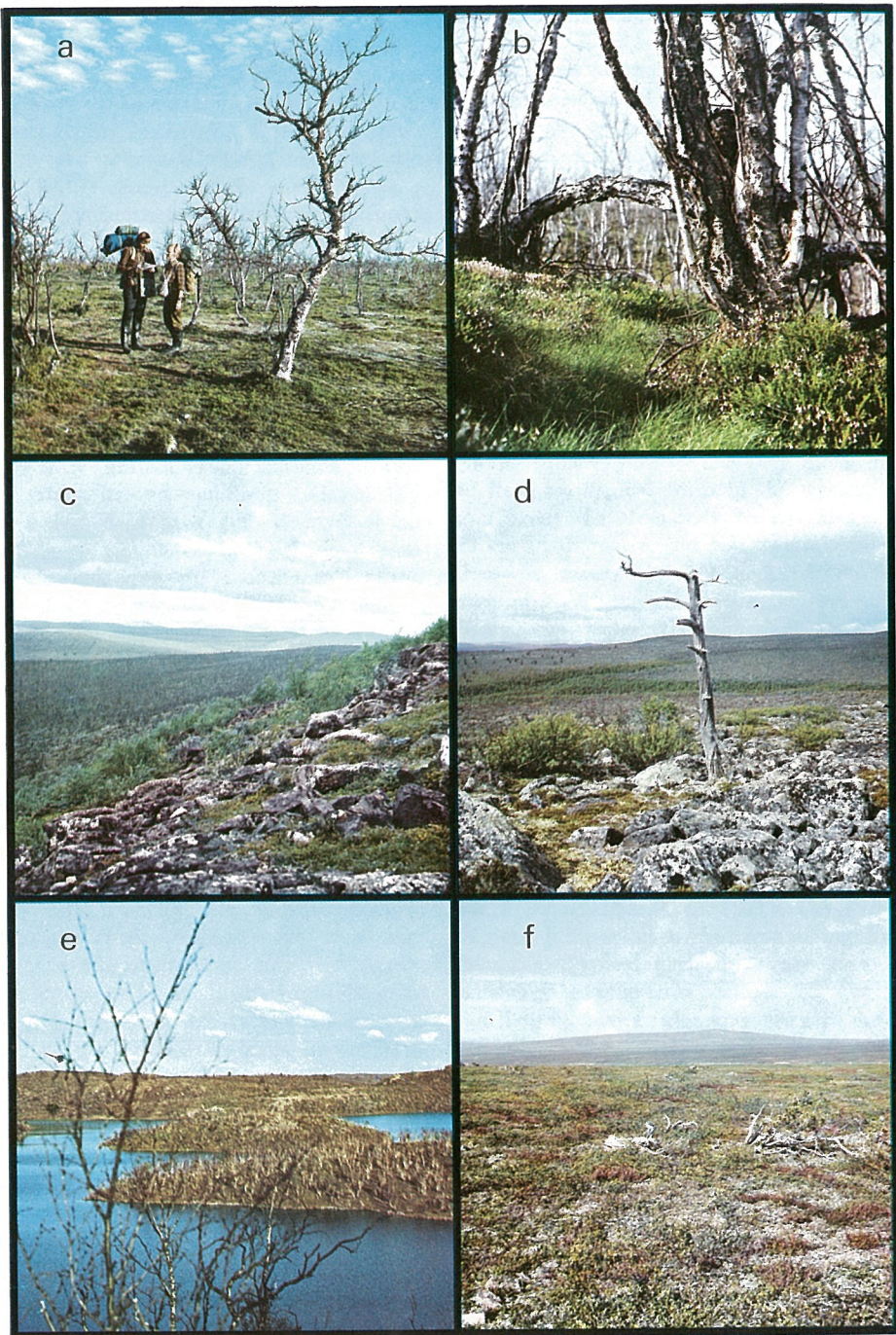
In addition to the damages from 1955 and 1927, there are signs of older damages. Old people in Talvadas village and other villages in the Teno valley tell about big birch damages that occurred in the first decade of this century. This means that the damage period 1905—1909, known from Sweden and Norway (cf. TENOW 1972: map 13 VI, p. 30), also reached as far as Utsjoki. However, there has been an earlier "tundra" area in this region, known e.g. in the map of KIHLMAN (1884). It seems that the area discussed forms a very labile ecosystem, and that recent development has not favoured birch forests.

One problem is connected with the variation and adaptation of birches, particularly the problem of monocormic versus polycormic forms. It is of particular importance that the monocormic birch is prevalent in the Jeskaddam; the solitary forest remnants and isolated trees in the area, as well as the decaying stems, represent monocormic forms, and almost the whole margin of the area is bordered by monocormic birches or forests where monocormic trees dominate. Also the widening of the tundra after the 1965—66 damage is most pronounced in the areas of monocormic trees.

There are very few seedlings in the Jeskaddam area. In the periphery, where their number is higher (e.g. in the westernmost enclosure), almost every seedling has been damaged (many times?) by reindeer and/or small voles (Fig. 11). As the number of reindeers has continuously increased in Utsjoki, the grazing pressure is obviously an important factor prohibiting the reafforestation of the damaged birch forests in the Jeskaddam area.

Plate I

- a. Total damage, recovery excluded, in W part of the Kevo Nature Park. 31.7. 1971 P. Kallio.
- b. Rich grass and herb vegetation (*Linnaea* in bloom) under birches after the *Oporinia* damage. Upper slope of the Kevojoki valley, near lakes Njaggäljärvet. 31.7. 1971 P. Kallio.
- c. West slope of Jesnalvaara. Only a few birches are green in the front; the rest of the landscape totally destroyed birch forests. 29.7. 1971 P. Kallio.
- d. Paaalvaara seen from south. The river valleys (Kitisjoki) are green, but all mountain slopes are covered by totally dead birch forests (at the left some isolated pines). 27.7. 1971 P. Kallio.
- e. The total damage of birch forests around lake Nanabeljärvi in Nö-Inari, seen from the north. 25.7. 1972 Juhani Lehtonen.
- f. Earlier birch forest area with 300 remnants of birches per hectare. West border of the Kevo Nature Park, view to the north. Even junipers are mostly dead. 1.8. 1971 P. Kallio.





3.5. Chances in vegetation

The changes in the vegetation after the birch damage are dramatic in the birch forests of *Myrtillus-Hylocomium* type and other mesic or hydric types, while only slight changes are seen in forests dominated by lichens and *Empetrum*. Same features are seen in these changes in the whole of Fennoscandia: the biomass of *Deschampsia flexuosa*, *Festuca ovina*, and some herbs increases. This has been mentioned e.g. by HOLMGREN (1905), KALLIO (1941), SANDBERG (1958; 1963), HÄMETÄHTI (1963), NUORTEVA (1963), TENOW (1972), KÄRENLAMPİ & KAUMANEN (1972) and KALLIO & MÄKINEN (1974). No detailed analyses are given in this paper, but the changes are drastic, particularly in forests in more humid localities, e.g. in Lake Pulmankijärvi area, especially around Tsuomasvaara, which deviates from its surroundings edaphically as being a less acid area (cf. KALLIO et al. 1969). Many places have been changed into *Deschampsia* meadows on the slopes of the Kevojoki valley as well as on the lower slopes of the fells around the river Tsarsjoki and in Kenesvaara. In 1972, these meadows were still different from untouched areas; during the first 4—5 years especially *Trientalis europaea*, *Linnaea borealis*, *Solidago virgaurea*, and in some places, *Chamaenerion angustifolium* bloom more than on average (cf. Fig. b in Plate I). In some places, e.g. around Lake Äälisjävri damage area in Inari, the leaves of *V. myrtillus* were red in early summer 1972, while this colour change was almost missing in undamaged areas. *Empetrum* was also damaged in some places, but this was partly due to the outbreak of small voles in 1969—70.

Oporinia caterpillars are rather selective in their food plants. When the birch leaves have been totally used, caterpillars often move to *Betula nana*. In some large areas, *B. nana* stands are defoliated completely and killed. Such areas are found particularly between the lower course of the river Kevojoki, and Paistunturit mountains. These stands are regularly situated near ssp. *tortuosa* damage. In an open boggy area in the upper course of the river Niljok, there was a small but totally defoliated area of *B. nana* stand which was far from ssp. *tortuosa*. Willows have been only occasionally damaged. *Salix borealis* is often the only

green tree in totally defoliated birch forests, and *S. glauca* has never been damaged. *Sorbus aucuparia* does not seem to be a host plant for *Oporinia* either. It was seen abundantly in bloom in a totally damaged birch forest on the upper slope of the Kevojoki valley, though it has been mentioned as a host plant for *Oporinia* by SEPPÄNEN (1954), for instance. *Vaccinium myrtillus* and *V. uliginosum* are damaged in many places, e.g. in Kaktasavari and Stuuravdši. It seems that dwarf shrubs have mostly recovered after damage. *Populus tremula* has never been damaged by *Oporinia*. It seems to take advantage of the *Betula* damage; for instance, young adventitious shoots had grown rapidly near the Fiello waterfalls after the damage of birches.

Juniperus communis is a common plant in *Oporinia* damage areas. The thick-stemmed and "table-formed" juniper has, in Utsjoki, developed its most typical form in the western mountain area; the stem may be as thick as 25—29 cm in diameter, but the whole plant is less than one metre high. (Fig. 12). The form is determined by the macroclimatic desiccation effect of the winter; the only parts that stay are the ones protected by snow against desiccation. Good examples of the effect of winter were seen e.g. in 1969, when the snow cover was thin.

Although the most typical table junipers are met particularly in the Jeskaddam area, N and E of Paistunturit, some areas in the SW corner of Utsjoki and e.g. Stuuravdši area also have similar junipers. The junipers are old; the oldest ones are more than 1000 years (cf. KALLIO & al. 1971). Large numbers of dead junipers occur in areas of big *Oporinia* damages. Typical such areas are seen e.g. in Aittivarri at the NW border of Jeskaddam.

All these juniper damages seem to date from 1927 (or older) *Oporinia* outbreaks. One possible factor in the destruction of junipers is the change that took place in the local climate after the birch damage. In the Nuvvusvaara—Kirjeädna area, almost all the dead junipers — more than 200 of them have been counted — are not as upright as they were originally; the wind effect has increased, and the wind has pressed the junipers so that the ancient "tables" are badly slanting. The upper part has died first. It is also possible that snow relations changed after the birch damage so that the snow was blown to the valleys. Damage of roots,

and the consequent desiccation effect, may also have played some role. Some quite continuous, dense juniper stands in the *Oporinia* damage area have been preserved under favourable conditions, the damage being mainly confined to stands of isolated table junipers. Apparently in the dense stands in the valleys, the wind effect is not so strong as in the damage areas described, and the birch shelter has not the same ecological significance.

3.6. Changes in fauna

Birch damage also had an effect on the fauna. SILVOLA (1967) showed that the bird population in the defoliated birch forests decreased almost to 50 % in 1966, while the population density increased in the closely situated undamaged birch forests. The population of small rodents in the subarctic *Betula pubescens* ssp. *tortuosa* forest near the Kevo Research Station showed following relative biomass values in 1970, which was the year of great rodent populations (private communication by K. NYGRÉN):

	D	C
<i>Clethrionomys rufocanus</i>	5617	5957
<i>Clethrionomys rutilus</i>	987	843
<i>Microtus oeconomus</i>	4041	33

The numbers indicate biomasses in grams per similar areas; abbreviations: D = damaged area, C = control area. It is seen that there are no significant differences in the *Clethrionomys* species in the compared areas, but the third species, *Microtus oeconomus*, has in the *Oporinia*-damaged area a population density more than hundred times as high as in the control area. Differences are also seen in the invertebrates; the question is discussed by NUORTEVA (1966).

4. Discussion

The periodicity of the *Oporinia* outbreaks has been known for a long time. The interval of these outbreaks in Fennoscandia is about 9–10 years (HOLMGREN 1912; EIDMANN 1957). TENOW (1972) has given a survey of the history of the occurrences. In this century, 4 bigger damages of birch forests have taken place in Utsjoki: in 1965, 1955, 1927, and probably in the first decade of the century.

The synchronous rhythm of the *Oporinia* caterpillar occurrences and the abundance peaks of some of its parasites of the family *Ichneumonidae* point to one of the regulation mechanisms in the ecology of *Oporinia*. This has been studied extensively by Nuorteva and Jussila (NUORTEVA 1966; 1971; NUORTEVA & JUSSILA 1967; 1969; JUSSILA & NUORTEVA 1968). The problem of oscillations in the population densities is characteristic in the Subarcticum. A very well known phenomenon is the oscillation of lemmings and other small voles and their predators. Variations in the primary production level may also have an effect (cf. TAST & KALELA, 1971).

The topography of the calamity may give some hints for detecting the regulative ecological factors. The best preserved areas in Utsjoki are river valleys. TENOW (1972) has pointed to the ecological factor of cold winter conditions for the eggs of *Oporinia*. In deep valleys the winter temperature is assumed to exceed the limit of tolerance (ca. -33° ... -37°) of the eggs (cf. MACPHEE 1967; TENOW 1972). There has been a temporary meteorological observation point in the yard of Tsieskula Farm in the bottom of the Utsjoki valley, at the height of ca. 85 m, and another one at the top of Tsieskulvaara ridge at the height of ca. 250 m, about 3 km from the former. Typical birch bush and polycormic tree vegetation damaged in 1966 by *Oporinia* is seen around the upper

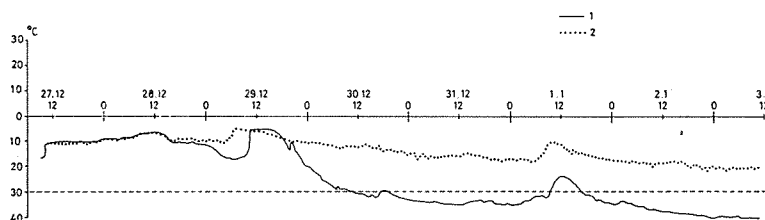


Fig. 13. Curves showing temperatures during 27.12.1965–3.1.1966 in the River Utsjoki valley (1.) and on the top of Kotkapahta ridge, 180 m higher, in the vicinity of the former place (2.). Very strong thermal inversion between these two places can be seen.

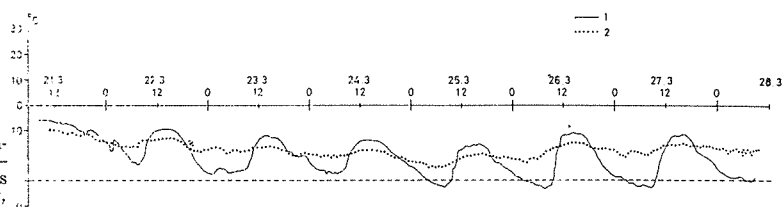


Fig. 14. Curves showing temperatures during 21. 3. 1966—23. 3. 1966 in the same places as in Fig. 13. (1: valley, 2: ridge).

observation point, whereas no damage is found in the Utsjoki valley.

There are very typical temperature inversions in the areas around Kevo, particularly on clear winter nights, and these observation points were used to study this phenomenon. A comparison of the measurements made at these two observation points is very illustrative: in January 1966, there were 10 days in the valley with temperatures below -30°C and 3 below -35°C , and the absolute minimum in the valley was -43°C . At the same time the temperature at Tsieskulvaara ridge was only three times below -30°C , the lowest value being -33°C . The temperatures in January 1965 had been very similar: in the valley, 5 days below -30°C , 3 days below -35°C , the lowest point being -36.8°C ; at the ridge the absolute minimum was -21.6°C .

When all the records of temperature below -30°C are combined in the two winters preceding the top of *Oporinia* damage the result is as follows:

	Valley	Ridge
Winter 1964—65	12	0
Winter 1965—66	52	5

Very likely the temperature minima differences clear up the contrast between valley and mountain when the *Oporinia* damages are compared.

In some valleys the snow cover may be thick enough to protect *Oporinia* eggs. According to the information obtained from Mr. KARI KYRÖ, the forest ranger of the Kevo Nature Park, it is possible that the birches near Njaggäljärvet (cf. Fig. 4), at the bottom of the Kevo-joki valley have totally or at least partly been covered by snow.

The winters preceding the *Oporinia* outbreaks have been colder than the average (e.g. the mean temperatures of February and March in 1966 in Kevo were -23.7°C and -16.7°C , while the mean values for the same months

during the years 1962—1969 were -15.7°C and -11.4°C , respectively). This may have an effect on the contrast between the damages in valleys and on mountains. This contrast is less pronounced in more oceanic areas, e.g. in the lower course of the river Teno as well as in the easternmost part of Inari — in the Äälsjävri area.

Summer temperatures may also be of importance to *Oporinia* damages, and particularly to the recovery. The outbreak of new leaves after the defoliation, and the basal shoot formation in the following years, depend on the energy restored in the roots and stems. The amount of this energy is largely dependent on the environmental conditions controlling the net photosynthesis of the birch. The thermal sum of the year provides a good estimate of this.

The lowest values for the thermal sum, or *dd* (degree days summed for days over $+5^{\circ}$), have been measured in the Finnish Lapland during the last ten years of this century, as shown by the estimated thermal sums in Sodankylä and Inari (from MIKOLA 1971):

	Sodankylä	Inari
1911—20	781	690
1921—30	808	703
1931—40	861	768
1941—50	818	729
1951—60	809	716
1961—70	772	664

In Kevo, the meteorological station was founded only 1962, and the average thermal sum for 1962—1970 is 577, while the two damage summers 1965 and 1966 have given the values of 444 and 589, respectively (KÄREN-LAMPI 1972).

The largest known birch catastrophe in Finnish Lapland in the 1960s hence took place in a period when the average summer temperature was lowest. An explanation for this must be sought from energy balance in birch. The same environmental factor, however, may also affect

the balance at the consumer-predator level; the number of *Ichneumonidae* had decreased apparently because of low temperature (NUORTEVA & JUSSILA 1969).

The distribution of *Oporinia* and *B. ssp. tortuosa* damage areas overlap to a great extent — i.e. the areas of *B. ssp. pubescens* and *B. pendula* are less affected. The ecology, taxonomy and evolution of *B. ssp. tortuosa* has been investigated in Fennoscandia for a long time. One of the most important results is the discovery of the essential role of the hybrid origin between *B. pubescens* and *B. nana*, and the introgression of the *nana* genes to *pubescens* (SULKINOJA, unpubl.; KALLIO & MÄKINEN 1974). Ecologically the most important characteristic that has been more or less transferred to *ssp. tortuosa* is the succering capacity typical to the *Nanae* section, even though it also occurs in the *Albae* section (VAARAMA & VALANNE 1970). In the University Botanical Garden in Ruissalo, Turku, *ssp. tortuosa* seedlings form basal shoots under conditions in which *ssp. pubescens* does not. The capacity to form basal shoots is a feature which is seen in the main morphology of *ssp. tortuosa* in Utsjoki. It is known that the big birch "bush" is a clone which is potentially immortal. The roots only seldom form adventive buds, but the clone can take the advantage of also this form of "dispersal" (cf. KALLIO & MÄKINEN 1974). However, "dispersal" begins more frequently from the adventitious buds of twigs and stems, which are covered by litter and ground vegetation (cf. MIKOLA 1942; KALLIO & MÄKINEN 1974). The normal way for enlargement of a bush is that the shoots isolate and form root systems of their own around the basal enlargement (cf. CAJANDER 1917; MIKOLA 1942). Fig. 10 shows an example of this.

As the introgression is still going on, and the evolution of *B. ssp. tortuosa* is in a very active phase, there is much variation in Lappish birches as regards their ability for clone formation. Because the ability for regeneration is very important in different birch damages, *Oporinia* has become an effective selective factor in the evolution of birches. The monocormic trees show a lower recovery percentage, but on the other hand, they mainly occur in valleys and in the maritime zone of their distributional area. The worst calamities before the one in the 1960s in Utsjoki have occurred in the

Jeskaddam area, where the monocormic trees have dominated and the temperature inversion apparently is not important.

It is possible that there have been several damages during the history of the subarctic birch forests, but the latest damage in 1965–66 was one of the most severe; it destroyed areas which have, in all probability, been continuously covered by birch for hundreds of years. A new factor has become increasingly important during the last few decades: the number of reindeer, which has never been so high as it is now. Clear signs of overgrazing are seen in the area (KÄRENlampi & PULLIÄNEN, in preparation). The grazing pressure is too high for the reafforestation of birch forests after so severe a damage as has happened. An additional factor is still to be considered: the very high peak in the population density of lemmings and other small voles in 1969–70. As a result of the joint effect of all these factors, a large area of damaged birch forests will not recover. Treeless tundra has already widened approximately 500–600 square kilometres in Utsjoki, and a little smaller area will be changed into forests with a density of less than half of that earlier.

The whole study of *Oporinia* damages in the subarctic birch forests contains the following sub-studies, which have already been partly included in the research programmes in the Finnish research of the Subarcticum:

1. Mapping and observing the damage of birch forests in detail in relation to topography and local climate and following the development of damages from the beginning, on the basis of knowledge from earlier damages (This time it was not possible to start the investigation at Kevo in the years of the damage).

2. It is most important to know in detail the variations of birches and their evolution in order to understand the significance of *Oporinia* as an agent of selective pressure. The problem of monocormic and polycormic forms in particular has not been cleared satisfactorily. A study of this has started recently at Kevo in the frames of the birch research programme. This programme includes a birch culture garden in Utsjoki, where the monocormic and polycormic trees will be compared.

3. A very detailed observation of *Oporinia* damages (the next one!) to find out their

effects on the physiology of birches, and a simulation of the *Oporinias* by birch defoliation to clear up what is the cause for different effects and degrees of birch damage.

4. Investigation of the effect of rodents and reindeer on the reafforestation of the birch forests. The effect of reindeer can be investigated using the 9 enclosures that have been constructed in the birch areas of Utsjoki and by comparing areas of different grazing pressure.

5. A study of the field layers starting after the defoliation in areas which recover and areas that are changed to treeless tundra. The effect of defoliation on the soil, microclimate and fauna, both vertebrata and invertebrata, must be studied in detail.

Because birch is an important fodder for reindeer and the problem of pasture land has a very close contact with all these changes taking place in the ecosystem, this birch catastrophe has a great effect on the economy of this part of the Subarctic where the Lappish people are one part of the subarctic ecosystem. Therefore this study is also important from the point of view of the Finnish IBP of Tundra Biome.

Acknowledgement. This work was financially supported by SITRA (the Fund established in Connection with the 50:th Anniversary of the Republic of Finland).

References

- CAJANDER, A. K. 1917: Metsänhoidon perusteet II. — 652 pp. Porvoo.
- EIDMANN, H. H. 1957: Om fjällbjörkmätaren (*Oporinia autumnata* Bkh.) och dess bekämpande. — Ent. Tidskr. 78: 222—224.
- HOLMGREN, A. 1905: En insektshärjning och dess inflytande på vegetationen. — Skogsv. Fören. Tidskr. 3: 385—389.
- , — 1912: Studier öfver nordligaste Skandinavien björkskogar. — 156 pp. P. A. Norstedt & Söner, Stockholm.
- HÄMET-AHTI, L. 1963: Zonation of the mountain birch forests in northernmost Fennoscandia. — Ann. bot. Soc. 'Vanamo' 34 (4): 1—127.
- JUSSILA, R. & NUORTEVA, P. 1968: The ichneumonid fauna in relation to an outbreak of *Oporinia autumnata* (Bkh.) (Lep. Geometridae) on subarctic birches. — Ann. zool. fenn. 5: 273—275.
- JUUTINEN, P. 1954: Tunturimittari pahanteossa Lapin koivikoissa. — Metsälehti 32—33: 5.
- KALLIO, P. 1964: The Kevö Subarctic Research Station of the University of Turku. — Rep. Kevö Subarctic Res. Stat. 1: 9—40.
- , —, LAINE, U. & MÄKINEN, Y. 1969: Vascular flora of Inari Lapland 1. Introduction and Lyco-podiaceae—Polypodiaceae. — Rep. Kevö Subarctic Res. Stat. 5: 1—108.
- , — & MÄKINEN, Y. 1974: Vascular flora of Inari Lapland 3. Salicaceae and Betulaceae. — Rep. Kevö Subarctic Res. Stat. 11: 00—00.
- KALLIOLA, R. 1941: Tunturimittari (*Oporinia autumnata*), subalpiinisten koivikoiden tuholainen. — Luonnon Ystävä 2: 53—60.
- KIHLMAN, A. O. 1884: Anteckningar om floran i Inari Lappmark. — Medd. Soc. F. Fl. fenn. 11: 45—135.
- KÄRENLAMP, L. 1972: Comparisons between the microclimates of the Kevö ecosystem study sites and the Kevö Meteorological Station. — Rep. Kevö Subarctic Res. Stat. 9: 50—65.
- KÄRENLAMP, L. & KAUKHANEN, H. 1972: A direct gradient analysis of the vegetation of the surroundings of the Kevö Subarctic Station. — Rep. Kevö Subarctic Res. Stat. 9: 82—98.
- MACPHEE, A. W. 1967: The winter moth *Operophtera brumata* (Lepidoptera, Geometridae), a new pest attacking apple orchards in Nova Scotia, and its control measures. — Canad. Ent. 99: 829—834.
- MIKOLA, P. 1942: Koivun vesomisesta ja sen metsänhoidollisesta merkityksestä Referat: Über die Ausschlagbildung bei der Birke und ihre forstliche Bedeutung. — Acta Forest. Fennica 50: 1—102.
- , — 1971: Reflection of climate fluctuation in the forestry practices of Northern Finland. — Rep. Kevö Subarctic Res. Stat. 8: 116—121.
- NUORTEVA, P. 1963: The influence of *Oporinia autumnata* (Bkh.) (Lep. Geometridae) on the timber-line in subarctic conditions. — Ann. ent. fenn. 29: 270—277.
- , — 1966: Leaf development and leaf pathogens on subarctic birches after a calamity of *Oporinia autumnata* (Bkh.) (Lep. Geometridae). — Ann. zool. fenn. 3: 270—286.
- , — 1971: Decline of the parasite population of the geometrid moth *Oporinia autumnata* (Bkh.) during the second postcalamity year. — Ann. ent. fenn. 37: 96.
- , — & JUSSILA, R. 1967: Seasonal and zonal distribution of Ichneumonidae (Hym.) on a subarctic fell during a calamity of the geometrid moth *Oporinia autumnata* (Bkh.) on birches. — Ann. ent. fenn. 33: 155—163.
- , — & JUSSILA, R. 1969: Incidence of ichneumonids on a subarctic fell after a calamity of the geometrid moth *Oporinia autumnata* (Bkh.) on birches. — Ann. ent. fenn. 35: 153—160.
- SANDBERG, G. 1958: Fjällens vegetationsregioner, vegetationsserier och viktigaste växtekologiska faktorer. In Skuncke, F: Renbeten och deras gradering. Medd. 4, Lappväsensbet, Renforskningen, Uppsala: 36—60.
- , — 1963: Växtvärlden i Abisko nationalpark. In Natur i Lappland ed. by K. Curry-Lindahl. — Almqvist & Wiksell, Uppsala: 885—909.
- SEPPÄNEN, E. J. 1954: Suomen suurperhostoukkien ravintokasvit. — 416 pp. Anim. fenn. 8.
- SILVOLA, T. 1967: Tunturimittarin joukkoesiintymisen vaikutuksesta linnustoon Utsjoella 1964—1966. — Orn. Fennica 44: 65—67.
- TAST, J. & KALELA, O. 1971: Comparisons between rodent cycles and plant production in Finnish Lapland. — Ann. Acad. Sci. fenn. A IV, 186: 1—14.
- TENOW, O. 1972: The outbreaks of *Oporinia autumnata* Bkh. and *Operophtera* spp. (Lep. Geometridae) in the Scandinavian mountain chain and northern Finland 1862—1968. — Zool. Bidr. Uppsala, Suppl. 2, 1972: 1—107.
- VAARAMA, A. & VALANNE, T. 1970: Induced mutations and polyploidy in birch *Betula* spp. Final Report Part V (Project No. ES-FS-47, Grant No. FG-FI-133. Turku: Dept. Bot. Univ. Turku), 7C. On the biology and origin of *Betula tortuosa* Ledeb: 63—97. Mimeogr.