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Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review

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The reviewed studies indicate that small-scale gap disturbance and gap regeneration can be common in boreal forests that have escaped catastrophic fire disturbance for prolonged time periods. Tree regeneration in gaps is enhanced by fine-scale heterogeneity at the forest floor created by soil disturbance and woody debris, which create favourable microsites for seed germination and seedling establishment. The significance of specific microsites for seedling establishment varies among forest types, being smallest in dry Scots pine -dominated forests with scanty understory vegetation and thin humus layer, and greatest in moist Norway spruce -dominated forests with abundant understory vegetation and thick humus layer. In a gap the survival, growth and recruitment of tree seedlings is determined by gap size and long- term below- and above-ground interferences between tree seedlings, understory vegetation and adjacent large trees. Gap disturbance contributes to the structural, functional and species diversity of the boreal forest both at local and areal levels. At local level gap disturbance increases fine-scale variation in soil properties and microtopography. At areal scale gap disturbance creates horizontally and vertically heterogenous forest structures and contributes to the coexcistence of coniferous and broad-leaved tree species.

1. Introduction

Until the first half of the 20th century most ecologists thought that forest succession was a well-defined process leading to a 'climax' stage, which was the normal condition for forest communities (Cajander 1905, 1926, 1949, Weaver & Clements 1938). Although there were individual researchers who opposed this view (e.g. Sernander 1938, Watt 1947), it was not until the 1970s that the importance of ecological disturbance was generally recognized (e.g. Heinselman 1973, Sprugel 1976, Bormann & Likens 1979). At present it is generally acknowledged that natural disturbance is so common that it usually prevents forests from reaching a stable state (Sprugel 1991). Disturbance in forest ecosystems varies spatially and temporally from large-scale catastrophic disturbances operating at landscape level to small-scale perturbations operating at the scale of individual trees.

The Finnish botanist Pehr Kalm (1770), in his book *Travels in North America*, was probably the first to describe the general occurrence and important ecological role of treefall disturbance in primeval temperate forests. During recent years we have witnessed a flood of results demonstrating the fundamental role of disturbance and environmental heterogeneity in different kinds of forest ecosystems (Pickett & White 1985, Kolasa & Pickett 1991). Especially in tropical and temperate forest ecosystems the importance of gap disturbance on forest dynamics has been intensively studied and widely demonstrated (e.g. Runkle 1985, Hubbell & Foster 1986, Platt & Strong 1989). It has become clear that gap disturbance fundamentally contributes to forest ecosystem characteristics, such as structural heterogeneity and species composition of the tree layer, variation in ground microtopography and understory vegetation, and overall species diversity (e.g. Brokaw 1985, Beatty 1984, Denslow 1985, Barik et al. 1992).

In boreal forests the ecological significance of small-scale gap disturbance has until recently received relatively little attention. This may have been due to the fact that large-scale fire disturbance has been considered to be the most important factor regulating forest regeneration in boreal coniferous forests. (Sirén 1955, Zackrisson 1977, Payette 1992). However, there is increasing evidence on the role of small-scale gap disturbances in the regeneration dynamics of these northern ecosystems (e.g. Steijlen & Zackrisson 1986, Hytteborn et al. 1987, Leemans 1991, Liu & Hytteborn 1991). In particular, in areas that have escaped catastrophic disturbance for long periods, one might expect processes occurring at the spatial scale of one to a few trees to play an important role in forest structure and composition. Effective fire prevention and increasing standing stocks of wood volumes are likely to further increase the importance of small-scale disturbances also in managed forests (Steijlen & Zackrisson 1986).

This review is an attempt to summarize mainly early Finnish results and observations concerning the effect of gaps and ground microtopography on natural regeneration and forest community structure in Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) dominated forests. Because the available information is fragmented there is no possibility to cover all the vegetation zones occurring in Finland (see Ahti et al. 1968). Instead a crude division between northern and southern Finland is made, using the 64th latitude as an approximate line of division. The review is not a comprehensive one, but rather aims at collating the most important results. The emphasis is on the processes as they occur in primeval forests but also some studies dealing with managed forests are included since many of the processes are universal. However, studies dealing with mechanical site preparation are excluded. The phenomenon of gap disturbance is viewed at tree, stand and community type levels.

A large part of the reviewed studies are written in Finnish with only brief summaries in English or in German. Especially in studies published before World War II the method of the researchers was to describe individual examples and to make qualitative statements about studied phenomena. Also, some theses prepared for the M.Sc degree in silviculture are cited when they were thought to contain valuable information. In collecting this information the emphasis has been on documented results and specific observations. When untested hypotheses are cited it is clearly indicated. Although the research methods used in some of the older studies reviewed may not meet present standards, it is believed that these early observations may give new insights and catalyze future research on the dynamics of natural coniferous forests in the boreal zone.

2. Characteristics of gap disturbance in boreal coniferous forests

2.1. The concept and characteristics of gap disturbance

In the following, gap disturbance is viewed as a change in stand structure ('minimal structure' *sensu* Pickett et al. 1989) caused by the death of single trees or small groups of trees. In young forests undergoing self-thinning tree death occurs due to competition (*autogenic disturbance*), whereas in old forests trees usually die because of disturbance agents external to stand level (*allogenic disturbance*). The size of the gap depends on both the size of the tree(s), tree density and, in the case of multiple treefall gap ("compound fall"), on the number of dying trees.

The phenomena of gap dynamics and gap phase regeneration were initially described in temperate deciduous forests (Watt 1947). However, in coniferous boreal forests both the physical and biological conditions differ considerably from those in temperate deciduous forests. It is evident that particularly in boreal coniferous forests the term 'gap' cannot be defined as a 'canopy gap', with the emphasis on the aboveground influences such as the availability of radiation on forest floor. This is because, due the predominant low sun angles and the narrow vertically extended tree crowns, trees cast long shadows and can affect the radiation conditions within gaps from considerable distances outside the gaps. Thus, light levels in small gaps may not differ significantly from those in the surrounding forest (Pukkala et al. 1993). Second, in most forests, but especially in boreal forests the canopy cover is usually far from complete and there is a continuum of openings of different sizes throughout the forest (e.g. Aaltonen 1919). Third, there is ample evidence that, for example, in Scots pine dominated dry heathlands it is not light but belowground interactions that determine seedling growth initially (Aaltonen 1919, Björkman 1945, Björkman & Lundeberg 1971, Kuuluvainen et al. 1993). This points out that gap size may not always be proportional to crown size, but to the size of the root system, the influence zone of which usually far exceeds the crown projected area.

Another important difference between temperate and boreal forests is related to the growth habit of trees. Temperate deciduous species generally show considerable flexibility in branching and overall crown shape that allow them rapidly to exploit nearby gaps in the forest canopy. In contrast, coniferous trees with their monopodial growth habit have a much more rigid architecture and show only limited ability for 'light foraging' through flexible modifications in branching (Waller 1986). Accordingly, a crown gap in the boreal coniferous forests is likely to be filled more slowly by neighboring canopy trees when compared to deciduous temperate forests, where two or more gap episodes are usually required for seedlings to grow into the main canopy (Runkle & Yetter 1987). Thus, a gap in a boreal coniferous forest is characterized by lower light levels but possibly longer duration of increased light supply when compared to a similar gap in temperate deciduous forest.

The ecological properties of a gap also depend on the primary disturbance agent. For example, trees killed by fungi and/or insects may remain standing for prolonged periods thus forming 'resource gaps' with little change in the microhabitat availability. Only when a sufficiently large tree falls, may regeneration microsites become available (e.g. Sirén 1955).

2.2. Causes of gap disturbance

In boreal coniferous forests allogenic gap disturbance agents include wind, snow and ice, insects, various pathogens, large animals and fire. Surface fire can obviously create small gaps by killing individual trees or small groups of trees selectively. Catastrophic fire, however, usually operates at a higher spatial level (landscape) of ecosystem hierarchy.

A gap can be created by a single factor, such as wind, but usually it is the final event in a process involving several factors forming a complex network of cause and effect. Obviously, the relative importance of gap disturbance agents change as a function of tree age, geographic and topographic location, tree species, stand structure and time of year. For example, in the moist northern *Hylocomium-Myrtillus* spruce dominated forests fungi and insect are the major agents causing tree death (Sirén 1955, Juutinen 1958, Norokorpi 1979a). However, especially in high elevation wind-exposed sites heavy snow loads frequently break the tops of healthy trees and thereby initially trigger the attack by fungi and insects (Cajander 1917, Heikinheimo 1922). Trees weakened or killed by fungi and insects are eventually felled by even moderate winds and/or snow loads. The importance and occurrence of different disturbance agents also vary according to geographic location and local conditions. For example, according to Heikinheimo (1922) windthrows of living spruce trees in northern Finland are more common in low altitude than in high altitude forests which have to resist heavy snow loads.

Snow damage is frequent in specific regions, such as the high altitude forests in north-eastern Finland, where atmospheric moisture concentrates directly on tree crowns forming heavy ice and snow loads (Cajander 1917, Heikinheimo 1920b). Occasionally, heavy snow loads can cause widespread damage also in low altitude sites and in southern Finland (Suominen 1963). Sometimes large animals, especially moose, can cause uprootings of smaller trees.

In Scots pine dominated forests on dry sites surface fires can be important in creating small gaps by killing individual trees or small groups of trees while leaving the majority of trees largely undamaged. For example the irregular and patchy structure of dry Scots pine forests in northern Finland studied by Aaltonen (1919) can apparently be largely attributed to frequent surface fires. Surface fire may also damage the root systems of Scots pine trees making them more susceptible to windthrow, as suggested by Sarvas (1938).

2.3. Distribution of gap disturbance in space and time

A gap disturbance is usually a relatively discrete event in time that locally changes tree population structure, resources, substrate availability or the physical environment (White & Pickett 1985). The occurrence and characteristics of gap disturbance are obviously related to the successional stage of the forest. Although young forests often have high mortality rates due to self-thinning, the small gaps are usually rapidly occupied. Only in older forests become large enough trees susceptible to disturbance so that sufficiently large gaps for tree regeneration are created. For example, Sirén (1955) found, when studying the primary succession of northern *Hylocomium-Myrtillus* spruce forests, that although dead trees occurred throughout succession the death of large trees started when the trees reached the age of about 300 years. This was also the stage when gap regeneration started (Sirén 1955). However, surface fires and heavy snow loads may create regeneration gaps also in younger forests. Evidently young pine trees with thin bark are more susceptible to death by fire than older trees with thick bark. According to Suominen (1963) pine and spruce forests in the age class 60–100 years are most susceptible to snow damage, while older trees appear to be more resistant in this respect.

Laiho (1987) studied the wind damage caused by the October 1978 storm in western Finland within an area of 9000 ha of managed forest. Although there existed variation in the spatial distribution of disturbance, the windthrows were in general scattered across the forest. Large spruce trees were most susceptible to windthrow, while in Scots pine the diameter of trees was not related to the frequency of windthrow. This can be due to the fact that Scots pine is usually dominant on poor and most wind-exposed sites. However, in general wet sites experienced more damage than drier sites. This can be due to superficial root systems of trees and/or their higher stature in wet sites. In the study area every 56th tree (1.7% of basal area) fell. Most of the trees were uprooted and only 4% of the trees were snapped (Laiho 1987). Similarly, in the virgin spruce forest of Jaurujoki in Lapland 93% of the windthrown trees were uprooted (Kauhanen 1991). Thus, most windthrows caused by large-scale wind storms appear to create an uprooting, which most affects ground microtopography.

Studies dealing with large-scale wind disturbance suggest that the occurrence of gap disturbance due to windthrow peaks at early to late autumn when high wind speeds are most frequent and soils are wet but still unfrozen (Laitakari 1952, Laiho 1987, Kauhanen 1991). There are also latitudinal differences in the timing of the storm damage due to differences in soil freezing from south to north. For example, in southern Finland wind damage still occurs in October and December, while in northern Finland very little damage takes place at this time of the year because the soil is already frozen (Laitakari 1952).

In general, these studies would suggest that gap disturbance regimes vary greatly in space and time, depending on factors like tree species, forest age and structure, soil conditions, water table, topography and geographic location.

3. Effect of gap disturbance and ground microtopography on forest regeneration

3.1. Scots pine dominated forests

Scots pine (*Pinus sylvestris* L.) is distributed throughout Finland. On dry and dryish sites Scots pine naturally forms almost pure stands which commonly have a persistent bank of small seedlings in the understory (Vaartaja 1951, Lähde et al. 1991). In suppressed conditions these seedlings grow extremely slowly, have short needles, and suffer frequently from insect and pathogen damage (Aaltonen 1919). The turnover rate among the understory seedling population is high, but some seedlings may survive up to 60–80 years (Vaartaja 1951).

Several studies on dry pine forests have demonstrated that large vigorous trees are surrounded by 'interference zones', where the amount and growth of seedlings is retarded in the trees' vicinity (Aaltonen 1919, 1920, Kalela 1942, Vaartaja 1961, Kuuluvainen & Pukkala 1989, Kuuluvainen et al. 1993). Accordingly, on dry and dryish sites the size and spatial distribution of large trees usually have a strong effect on the understory seedling population. When a sufficiently large gap in the forest is formed the suppressed understory seedlings have immediate access to released resources. However, the acclimation of pine seedlings to changed microclimate and the consequent recovery in growth takes time, being faster on better sites and in small seedlings when compared to dry sites and big seedlings (Vaartaja 1951). For example, Vaartaja (1951) reported that only after 1–4 years after full release may small (5–25 cm) seedlings show increased growth.

3.1.1. Northern Finland

Aaltonen (1919) was probably the first to carefully examine and describe the spatial patterns of Scots pine regeneration in the dry heathlands of northern Finland. The occurrence of different disturbances in these forests is unknown, but in natural condition fires occur frequently and are important for tree regeneration. These forests are generally irregular in pattern and consist of patches of trees of different age. Apparently recurrent surface fires, that kill individual trees or small groups of trees, strongly contribute to the patchy structure of these forests. The patchy structure of the forest, and the underlying fire disturbance history (van Wagner 1978), is also reflected in the size distributions of the trees on the plots studied by Aaltonen (1919).

Aaltonen (1919) studied 32 subjectively selected sample plots totalling 34 ha. The average canopy cover on the studied plots was only 11–24%, reflecting the extremely poor site conditions. The ground vegetation consisted mainly of feather mosses, dwarf shrubs (*Calluna vulgaris, Empetrum nigrum, Vaccinium vitis-idaea, Arctostaphylos uva-ursi*) and lichens (*Cladonia* sp.).

Small seedlings were found mainly in old stands and much less in young and middle-aged stands which Aaltonen considered to be too dense. The abundance of the bank of small seedlings was variable and did not bear any apparent relation to tree density. However, the growth and survival of seedlings was related to the spatial distribution of canopy trees. If the canopy trees were uniformly distributed the seedlings stayed in suppressed condition. Only if the canopy was irregular and formed gaps, the seedlings could grow further depending on gap size and site conditions. Aaltonen concludes that in gaps of 15–20 meters in diameter (0.017–0.031 ha) the seedlings in the middle grew well but the seedlings close to the edges of the gap stayed in suppressed stage (see Fig. 1). In larger gaps a group of seedlings was able to grow and form patches of younger forest among older forest. A recent forest fire diminished the effect of canopy trees and then seedlings were able to grow also under rather dense canopy if the site was not the poorest lichen type. The small-scale fertility gradients in soil were also demonstrated to affect seedling distribution, abundance and growth (Aaltonen 1919).

Aaltonen (1919) lists three microsites where seedlings are most abundantly found in the dry heath forests of Lapland: 1) Along decomposed fallen trunks (often in rows) and beneath fallen crowns, 2) in uprooting sites (pits/mounds) and 3) under old canopy trees growing in rather wide spacing. When an old pine tree falls its heavy trunk and thick, crooked and spreading branches

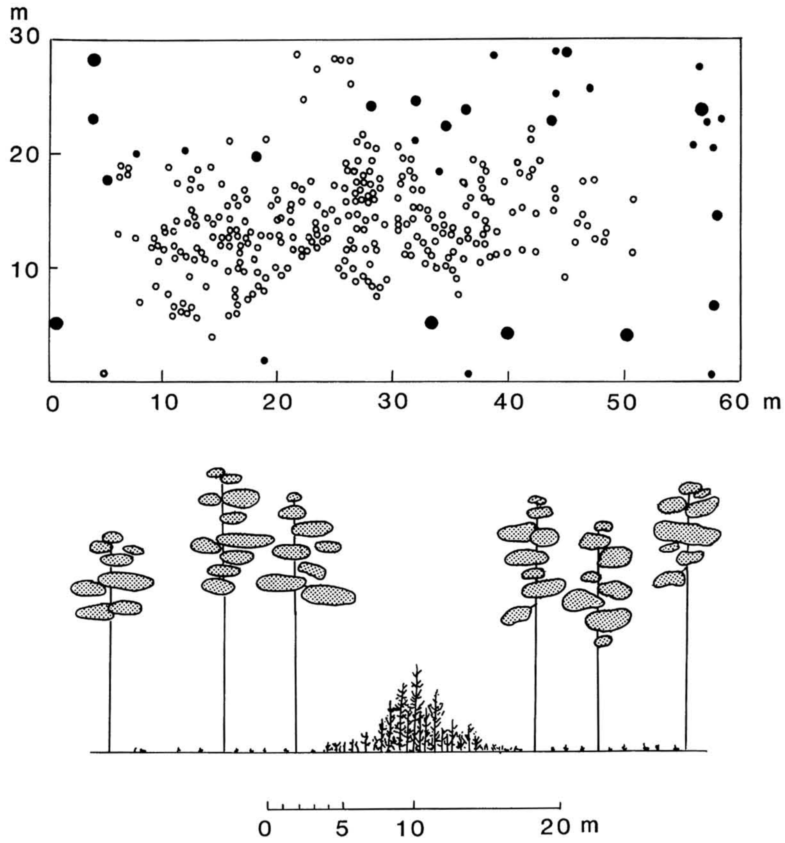

Fig. 1. An example of the spatial and height distribution of pine seedlings in a small gap in dry Scots pine forest in northern Finland. Redrawn from Aaltonen's (1919) figs. 32 and 33.

easily break the scanty ground vegetation and thin humus cover, thus exposing the mineral soil and creating microsites for seed germination. The slowly decomposing branches also give shelter against reindeer and moose browsing (Sarvas 1938) and desiccation caused by excess radiation and wind. Furthermore, the growing conditions are beneficial close to fallen trunks and crowns due to changes in microclimate (increased moisture) and increased nutrient availability from decomposing litter (bark, needles, small branches) at these locations (Fig. 2). This was indicated by the notion that adjacent to fallen trees the plant species like *V. vitis-ideae, V. Myrtillus, Calluna vulgaris* and mosses were more abundant than in the rest of the site (Aaltonen 1919).

Aaltonen (1919) also emphasizes the advantage of uprooting sites for regeneration and mentions that in these sites one can find seedling age classes which cannot be found elsewhere in the forest. However, no distinction was made between pits and mounds as regeneration microsites.

The groups of seedlings found around stems of old standing canopy trees in the dry heath forests of Lapland are called tarhat ("yards") by local people (Aaltonen 1919). Seedlings were found to be more abundant on the southern side of trunks and they grew as well as seedlings in the openings. Laitakari (1927) and Kalela (1942) give evidence that the occurrence of seedlings adjacent to large trees on poor sites is related to low vigor and damaged root system of large canopy trees.

Aaltonen (1919) concludes that root influences (competition for water and nitrogen) apparently have a dominating effect (compared to light) on the spatial pattern of forest regeneration in these dry heath forests and that the effect of below ground influences increase with decreasing site quality. Consequently, also the dependence of the spatial distribution of regeneration on the

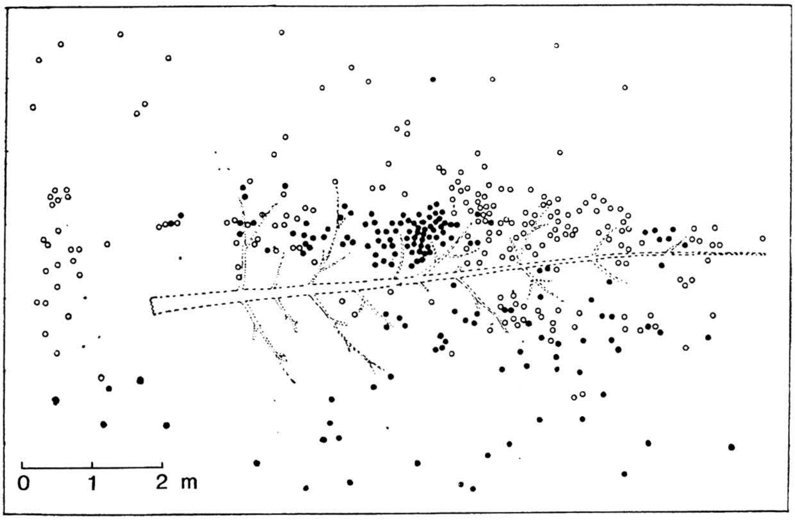

Fig. 2. The distribution of pine seedlings around a fallen crown in a dry Scots pine forest in northern Finland. The height of the seedlings is 10–20 cm. Open circles represent live seedlings, filled circles represent dead seedlings. Redrawn from Aaltonen's (1919) fig. 40.

arrangement of canopy trees tends to increase toward poorer sites.

The study of Sarvas (1950) on the regeneration in selectively cut dry heath forests gives areal-mean information on the potential quantity of regeneration in patchy pine stands. The sample plots of Sarvas (1950) were taken in pure Scots pine dominated stands on dry *Ericaceae-Cladinae* type (13 plots), in pure pine stands on dryish *Empetrum-Myrtillus* type (7 plots) and in mixed pine-spruce stands on *Empetrum-Myrtillus* site (17 plots). The mean canopy coverage percentages from ground area on these types were 9%, 17% and 17%, respectively, i.e. the forests were very sparse. On dry Scots pine dominated sites on average 57000 pine seedlings per hectare were found. The respective seedling number on dryish pine sites was 21700. In mixed pine-spruce stands on dryish site only 1860 seedlings per hectare were found. The decrease in the amount of regeneration with improving site quality and the shift in tree species proportions from almost pure pine stands to mixed pine-spruce stands, was attributed to the increase in the thickness of the humus layer, the mean of which changed from 1.4 cm and 1.5 cm in the dry and dryish pine sites to 3.6 cm in the mixed pine-spruce sites. (Sarvas 1950). These results suggest that the occurrence of regeneration in gaps is strongly affected by site quality, humus thickness and tree species composition. The conditions for regeneration appear to be very beneficial on pine-dominated dry sites, but deteriorate both toward extremely dry lichen sites and toward better mixed-species sites (Aaltonen 1919, Sarvas 1950).

3.1.2. Southern Finland

In southern Finland Scots pine occupies similar sandy upland sites as in the North but the stands are in general denser and more productive.

In the 1930's and 40's three masters theses concentrated on the regeneration of Scots pine in gaps in the middle and southern parts of the country (Braxén & Kärkkäinen 1932, Halinen & Harjama 1937, Honkavaara et al. 1948). Since these studies were based on limited and varying material and used partly inconsistent methods, only some basic observations are mentioned here. Seedling height and abundance was found to be generally highest in the middle or in the northern part of the gap (Halinen & Harjama 1937, Honkavaara et al. 1948). On the northern side of the gap seedlings were even occasionally found under the large canopy trees ("yards", Aaltonen 1919). These patterns were suggested to be due to distribution of light within the gap so that the northern side received more radiation than the southern side.

Braxén & Kärkkäinen (1932) suggested that the increase in density of the surrounding forest depressed seedling growth within the gap. Halinen & Harjama (1937) found that the number of small seedlings (shorter than 25 cm) and thus total seedling number in gaps was much higher in poorer *Vaccinium* and *Vaccinium-Myrtillus* sites when compared to better *Myrtillus* and *Oxalis-Myrtillus* sites. However, the seedlings were of better 'quality' in better sites and the number of taller seedlings (25–200 cm) in gaps was only little affected by site quality, except in the richest *Oxalis-Myrtillus* site where seedling number was very low (Halinen & Harjama 1937).

Some areal-mean estimates of the potential quantity of regeneration in gap-structured old pine stands are given by Sarvas (1944) and Lehto (1956). Sarvas (1944) studied the regeneration of selectively cut stands in southern Finland. On dry *Calluna* sites four plots (0.25 ha each) had the mean of 5700 seedlings per hectare while on the dryish *Vaccinium* type on nine plots had on average 3300 seedlings per hectare. The respective mean stand densities from 'full density' (=1.0) were 0.42 and 0.32. Thus, the seedling number decreased toward better sites, a tendency also detected by Lehto (1956) in southern Finland, and Halinen & Harjama (1937) and Sarvas (1950) in northern Finland.

Sarvas (1944) also found that in selectively cut stands the age-class distribution of the seedlings was related to site quality. On dry *Calluna* type there was much more older seedlings than on dryish *Vaccinium* site, suggesting a slower turnover rate for the dryer *Calluna* type.

Lehto (1956) looked at the amount of regeneration in approximately 100 year old managed Scots pine forests of varying density. He measured 39 plots (0.25 ha each) on the *Calluna* site and 37 plots on *Vaccinium* site type. The numbers of pine seedlings were comparable to the those found by Sarvas (1944), but there was a high variation from one stand to another; in general the amount of regeneration decreased as a function of tree density. Lehto (1956) emphasized the beneficial influence of small disturbances of the ground layer on Scots pine regeneration. Thus, both ground disturbance and the occurrence of gaps contribute to regeneration in Scots pine dominated forests in southern Finland.

3.2. Norway spruce dominated forests

3.2.1. Northern Finland

The spruce dominated forests of northern Finland occur predominantly on moist watershed areas (Heikinheimo 1920a). These peculiar forests are growing on strongly podsolized glacial tills and are characterized by poorly decomposed humus layer reaching the thickness of about 8–9 cm at stand age 200–300 years (Sirén 1955). Stands are generally uneven-aged and sparse and old trees carry significant amounts of epiphytic lichens (Heikinheimo 1920a, Havas & Kubin 1983). The ground and bottom layer vegetation comprise a considerable portion of the biomass and primary production of the ecosystem (Havas & Kubin 1983). The fire rotation of these moist forests is exceptionally long in Finnish conditions; for example, in the Kivalo area only four fires could be recoqnized during the past 1700 years (Hyvärinen & Sepponen 1988).

Heikinheimo (1922) examined the regeneration of northern spruce forest on 38 sample plots located predominantly in primeval forests. Both vegetative and sexual reproduction occurred in most plots. Seedlings formed by layering, i.e. from branches forming adventitious roots and detached from stems, accounted from 0–50% of the total seedling number, the average proportion being 13%. Seedlings of vegetative origin were most abundant on sites with thick moss cover and their proportion diminished with decreasing tree number and moss thickness. Seedlings of sexual origin were distributed in different microhabitats in the following proportions: on decomposed stumps and downed logs 15.5%, under fallen crown 4.8%, adjacent to stones 1.7%, in uprooted spots 2.8%, under standing trees 12.0% and in 'open' ground 63.2%. The seedlings growing on stumps, logs and in uprooted spots were most vigorous, while seedlings growing in the 'open' among ground vegetation were least vigorous. In general, the most vigorous seedlings were found where the moss and humus layer had been disturbed. The forests had typically

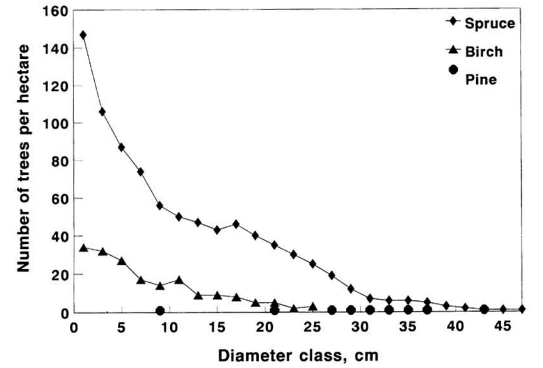

Fig. 3. Stem diameter distribution of spruce, birch and pine in primeval spruce dominated forests in northern Finland according to Heikinheimo (1922).

an all-size structure suggesting a continuous recruitment of new individuals (Fig. 3). (Heikinheimo 1922).

Sirén (1955) used stand chronosequences to study the successional dynamics of virgin spruce forests growing on humid *Hylocomium-Myrtillus* sites in northern Finland. Two major pathways of spruce regeneration were noted: 1) large-scale regeneration after catastrophic fire disturbance (primary succession) and 2) small-scale regeneration in old and declining stands (start of secondary succession). According to Sirén (1955:34) (large-scale) wind-, insect- and pathogen damage are rare "but on a smaller scale they are present in connection with the natural regeneration of almost all old spruce stands" (Sirén's 1955 figs. 32, 33). The death of large trees started when the trees had reached the age of about 300 years during the 'post-climax' stage (Table 1). Insect and fungi are the major agents of tree death (see also Juutinen 1958, Norokorpi 1979a); however, especially on high elevation wind-exposed sites heavy snow loads frequently break the tree tops thus facilitating the attack by insects and fungi (Cajander 1917, Heikinheimo 1922). Whatever the primary cause, tree death is eventually followed by treefall; "Mass death results usually in a stock of dead standing trees which soon fall, giving a forest picture highly reminiscent of the tangled thicket following storm damage" (Sirén 1955:34).

Sirén (1955) found practically no seedlings in the understory of undisturbed old spruce stands on the *Hylocomium-Myrtillus* site and regeneration was almost completely restricted to specific microsites created by small-scale disturbances. He states: "Young growth makes its appearance almost exclusively in uprooted spots, in the neighborhood of stumps and on sufficiently decomposed fallen logs; in exceptional cases only does the ground community afford an adequate germination substratum for tree seeds" (Sirén 1955:33 and figs. 34, 35). In this respect it was noted that especially in old open-canopied stands the proportion of dwarf shrub roots in the humus was remarkably high (Sirén 1955:159). According to Havas & Kubin (1983) in old spruce stands of this type about 70% of total root mass is attributable to ground-layer vegetation. The average number of spruce seedlings per hectare in old primary spruce stands detected by Sirén (1955:108) was 178 in the 240–300 years age class and 530 in the 300–330 years age class.

The occurrence of logs laying on the forest floor also reflects the frequency of treefall disturbance and the availability of regeneration microsites in the forest. Sirén (1955, table 22) found that birch logs were most abundant (about 880 logs/ha) at stand age of about 100 years and declined thereafter during the primary succession of the northern *Hylocomium-myrtillus* forests. The number of fallen spruce logs peaks in the end of the primary succession at stand age of 300–330 years (about 750 logs/ha), and in the beginning of the secondary succession. Correspondingly,

Table 1. Average number of dead standing spruce trees per hectare in 'medium dense' forests as a function of mean stand age during primary succession in the northern *Hylocomium-Myrtillus* type; according to Sirén (1955, Table 20).

	Age group, years					
DBH class, cm	80–104	125–137	145–150	180–195	240–270	300–330
height<1.3 m	48	13	23	8	8	14
1–5	11	166	137	56	20	21
5–10	3	51	13	10	12	9
10–15	2	1	4	13	5	15
15–20	–	3	2	8	5	14
20–25	–	2	–	1	5	13
25–30	–	–	–	–	4	17
>30	–	–	–	–	10	15

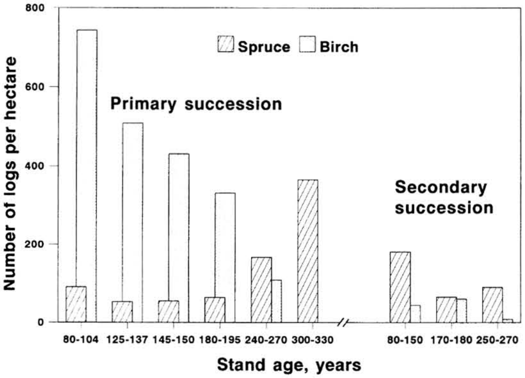

Fig. 4. Number of spruce and birch stems of decay classes 2 ("wood soft — disintegrated"[1]) and 3 ("wood semi-decomposed and sunk into ground"[1]) laying on forest floor during the primary and secondary succession in the northern *Hylocomium-Myrtillus* forest. Logs in these decay classes presumably provide favourable microsites for tree regeneration. Redrawn from Sirén's (1955) table 22. [1]From Sirén's (1955) table 21.

in a similar spruce forest Kubin (1981) found 700 downed logs per hectare; the number of logs on the forest floor was twice the number of large (dbh>20 cm) standing trees. However, not all downed logs provide suitable regeneration habitats, but only those in suitable stage of decay (Fig. 4).

According to Sirén (1955) the regeneration of old spruce stands on *Hylocomium-Myrtillus* site may be delayed if regeneration microsites are not formed because trees killed by pathogens and/or insects remain standing for prolonged periods. However, on the general importance of small-scale regeneration he states: "The regeneration of these forests is scanty and accidental, but given enough time it results in a more or less unevenaged seedling stand which just covers the site" (Sirén 1955:34). Kubin (1981) sudied an old forest of the same type and concluded that in the studied forest the irregular forest structure is largely due to small-scale gap disturbance and gap regeneration. These observations suggests that these old spruce forests are generally self-replacing (see also Heikinheimo 1922), although the seedling densities naturally could not meet the management standards required for clear cut regeneration (Sirén 1955:159).

3.2.2. Southern Finland

In southern Finland Norway spruce naturally dominates fertile and medium fertile sites. In contrast to the moist 'raw humus' forest of the north, these spruce forests are denser, have thinner humus layer, and except for mosses the understory vegetation is usually rather scarce. Early seedling establishment succeeds also when disturbances are absent; however, the disturbance of vegetation and soil greatly enhances regeneration in this case too (Yli-Vakkuri 1961). Old spruce stands in middle and southern Finland frequently have small suppressed seedlings in the understory (Pöntynen 1929, Lähde et al. 1991). Mikola (1966) has shown, using data from the four first national forest inventories, the great importance of spruce undergrowth for spruce forest regeneration especially in southern Finland.

Kalela (1934) examined the effect of gap size on the average height growth of understory spruce seedlings after release, i.e. gap creation ; altogether 52 small sample plots were studied. Kalela concluded that if the gap was smaller than 0.01 ha no growth improvement could be seen. In gaps of 0.01–0.02 ha the seedlings showed slow recovery. Only in gaps of 0.04–0.05 ha most of the seedlings were able to grow vigorously. Seedling height at the time of gap disturbance also had a strong effect on height growth, so that the taller the seedling at release the faster was their height growth after release (Fig. 5).

Kalela's (1934) results suggests that a gap created by the disturbance of a group of trees is required to facilitate the growth of understory seedlings into the main spruce canopy. However, the poor ability of adjacent mature spruce trees to fill the gap may allow even slowly growing seedlings to ultimately reach the dominant canopy even in a rather small gap. The gap regeneration process may also be a gradual one in which a single treefall first facilitates seedling establishment and the subsequent enlargement of the gap finally lets the seedlings grow and fill the gap. According to Jonsson (1990), in northern Sweden about half of the gaps were formed by the fall of two or more trees.

Kalela (1934) also found that the height of seedlings increased from the edges of the gap outward but the tallest seedlings were generally found

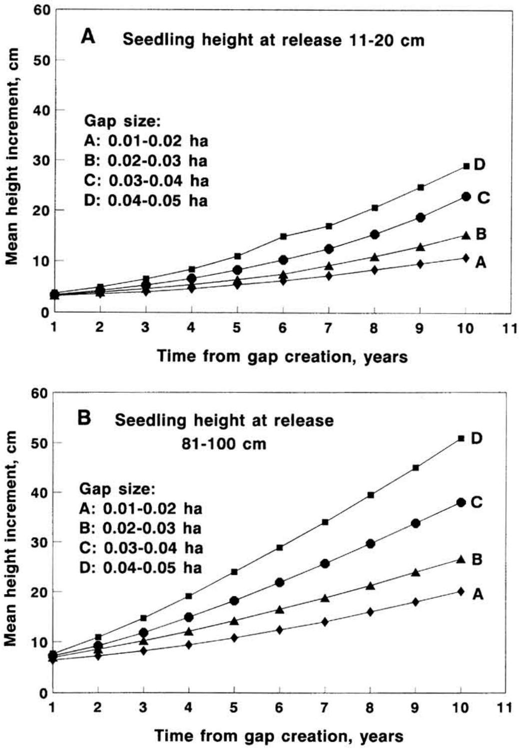

Fig. 5. The effect of gap size and height of understory spruce seedlings at the time of gap disturbance on the subsequent mean annual height increment: (a) 'small' seedlings (height at the time of gap disturbance 11–20 cm) and (b) 'large' seedlings (height at the time of gap disturbance 81–100 cm). Redrawn from Kalela's (1934) table 8.

in the northern part of the gaps, i.e. the height distribution of seedlings was not symmetrical within the gap. This agrees with the observations made in Scots pine forests by Halinen & Harjama (1937) and Honkavaara et al. (1948).

Myllymäki & Virkkunen (1950) examined the effect of fallen logs, stumps, and uprooted spots on the occurrence of spruce seedlings on *Vaccinium* and *Myrtillus* sites and in spruce swamps in middle Finland. They placed rectangular plots around fallen logs and circular plots around stumps and uprooted spots. A similar reference plot was subjectively placed nearby at each site. Altogether 80 plots of 1.7–6.0 m^2 in size were examined. In *Vaccinium* and *Myrtillus* sites all the three mircosite classes contained more and better growing seedlings when compared to the reference plots. The more decomposed the wood material, the more seedlings were found.

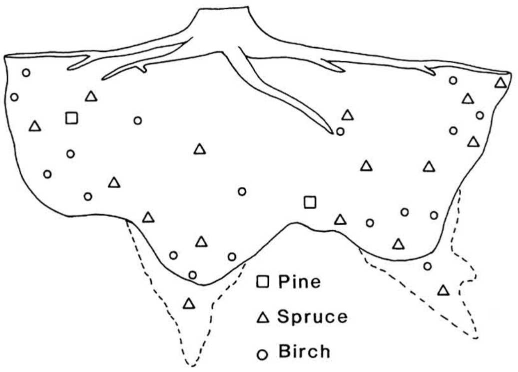

Fig. 6. Distribution of established tree seedlings in an uprooting spot in southern Finland. Redrawn from Purhonen (1947).

Litja (1951) got similar results concerning decomposed stumps and found that stone surroundings had generally less seedlings compared to stumps. This could indicate that the microtopography alone cannot account for these results and that the ecological characteristics of decomposing wood, such as increased nutrient and water availability, are important for seedlings. Myllymäki & Virkkunen (1950) also found that with respect to uprooted spots, spruce swamp was an exception in that the pits contained very few seedlings. This was apparently because the standing water during spring and autumn periods prevented seedling establishment.

In southern Finland Purhonen (1947) examined the effect of windthrow on spruce, pine and birch seedling establishment in spruce dominated forests on 42 uprooted spots in *Myrtillys* and *Vaccinium* site types. The estimated age of the gaps ranged from one to over ten years. Only 40% of the windthrow gaps examined had seedlings outside the uprooted spot while 83% had seedlings in the uprooted spot. Uprootings younger than two years had significantly less seedlings than older uprooted spots. Seedlings were generally most abundant along the fringe of the pit opposite to the mound, while very few seedlings were found close to the mound wall (Fig. 6). Some small seedlings were found on mounds of young windthrows, but they were absent on older mounds. This was suggested to be due to the excess drying of pits in the summer (Purhonen 1947).

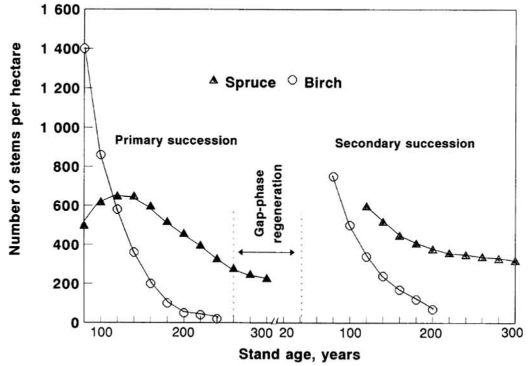

Fig. 7. The development of average stem numbers of spruce and birch in the dominant tree class in primary succession through gap phase (Sirén's 'interregnum phase') to secondary succession in the northern *Hylocomium-Myrtillus* forests according to Sirén's 1955 table 8. Stem numbers for spruce in the primary succession are derived from stands of 'medium dense' spruce storey.

4. Effect of gap disturbance on tree species coexistence

In mainly monodominant Scots pine and Norway spruce forests a gap is apparently eventually occupied with the same tree species as the gap creator(s) (Aaltonen 1919, Sirén 1955). However, especially on richer sites this often seems to be preceded by a gap-scale successional sequence, in which the gap is initially colonized by deciduous species, such as birch, aspen or rowan, which only later give way to the dominant coniferous species. Sirén (1955) gives evidence that in the northern spruce dominated forests on the *Hylocomium-Myrtillus* site type, the gap creation phase, which initiates the secondary succession, is related to a considerable increase in the abundance of deciduous tree species in the forest (Fig. 7). In southern and eastern Finland Purhonen (1947) found that in mixed spruce-pine forests, 20–80% of seedlings growing in uprooted spots were birch. These results suggest that gap disturbance facilitates the recruitment and existence of early successional deciduous species in conifer-dominated forests.

Kubin (1981) studied an old primeval *Hylocomium-Myrtillus* spruce forest (age 200–250 years) in northern Finland and found it to be surprisingly diverse in terms of tree species composition. Six tree species were found, of which spruce and birch dominated the upper layer together with some aspen, rowan and villow. Rowan was by far the most numerous species in the understory, followed by spruce and birch seedlings (Table 2). Considering the great number of logs found on the forest floor (about 700/ha), it was suggested that the small-scale structural heterogeneity and coexistence of several tree species in the forest was largely a consequence of small-scale gap disturbance and gap regeneration. The dependence of Scots pine regeneration on the occurrence of fire was, however, also emphasized. (Kubin 1981).

These observations generally suggest that gap disturbances facilitates the local recruitment of early successional species and therefore contributes to the maintenance of tree species mixtures in conifer dominated forests (Grubb's (1977) 'regeneration niche' hypothesis). The presence of broad-leaved species may also be important for the regeneration of conifers. For example, the height of understory spruce seedlings has been found to correlate positively with the amount of birch in the upper layer (Norokorpi 1979b) and Heikinheimo (1922) found that spruce seedlings grown under birches were most vigorous.

5. Discussion

Appreciation of spatial and temporal scales of disturbances is essential in examining the regeneration dynamics of boreal forests. It has traditionally been considered that the regeneration of

Table 2. The number of trees per hectare of different species in two height classes in an old *Hylocomium-Myrtillus* forest. Numbers estimated from Kubin's (1981) Figs. 1 and 2.

Height:	< 1.3 m	> 1.3 m
Picea abies	615	1140
Betula pubescens	760	1010
Pinus sylvestris	60	410
Sorbus aucuparia	2660	70
Populus tremula	300	70
Salix caprea	50	35

boreal coniferous forest is regulated by large-scale fire disturbance, that initiate a directional succession leading to a relatively stable (climax) community (Cajander 1905, Zackrisson 1977, Payette 1992). Although large-scale fire disturbances have evidently dominated most of the primeval boreal forests, the susceptibility of different forest types and areas to fire vary, and small-scale disturbance dynamics may be common in places and times when catastrophic fire disturbance is infrequent. (Aaltonen 1919, Sernander 1938, Sirén 1955, Hytteborn et al. 1987, Steijlen & Zackrisson 1986).

5.1. Gap disturbance, ground microtopography and forest regeneration

Gap disturbance has both short-term and long-term effects on forest regeneration. When a tree falls favourable regeneration microsites are instantly formed due to changes in soil microtopography (pits and mounds) and fall of dead woody material. The change in canopy structure and the local increase in space and resource availability within a gap determine the long-term survival, growth and recruitment of seedlings. Especially the spatial and temporal co-occurrence of 'safe sites' for tree seeds and increased resource levels due to canopy disturbance, contribute to gap-phase regeneration. However, the relative importance of different factors in the regeneration process and the causal mechanisms involved may vary from one forest type and geographic location to another and depending on ecological conditions and disturbance type.

The reviewed studies give some examples of the effect of gap disturbance and ground microtopography on forest regeneration in Finland. In forests where abundant understory vegetation strongly restricts seedling establishment, regeneration microsites created by treefalls are crucial for the whole regeneration process. An example of this forest type is provided by the northern moist *Hylocomium-Myrtillus* spruce forests which have relatively long fire rotation (Hyvärinen & Sepponen 1988), abundant understory vegetation and a thick layer of poorly decomposed humus which practically prevents the establishment of tree seedlings. Regeneration is almost completely restricted to specific microsites produced by treefalls, such as pits and mounds and decomposed trunks (Sirén 1955). In these conditions it is not primarily a gap in the tree layer (which is usually rather sparse) but rather a gap in the ground and bottom layer vegetation that ultimately facilitates regeneration. An event like windthrow obviously produces both, while a standing dead tree may not allow regeneration.

In forests where early seedling establishment commonly takes place under the forest, regeneration occurs mainly through the release of seedlings established under the forest before conopy disturbance. In this case the long-term consequences of gap disturbance on seedling growth and recruitment are apparently more important for forest regeneration than the creation of specific microsites. The detailed study of Aaltonen (1919) on the Scots pine dominated dry heath forests provide an example. These forests have relatively short (surface) fire rotations, scanty understory vegetation and thin humus layer, conditions which contribute to abundant seedling establishment in the understory. In these forests initial seedling establishment is not restricted to specific microsites and there is a persistent seedling bank, especially under older and more open forests; however, also in this case specific microsites enhance regeneration and affect the spatial distribution of seedlings. Most importantly, only in gaps can the seedlings grow into the main canopy (Aaltonen 1919).

Studies conducted in a patchy Scots pine forests in eastern Finland suggests that large trees, understory vegetation, and humus layer develop to form a closely associated complex, in which the effect of large trees is dominating (Kuuluvainen & Pukkala 1989, Kuuluvainen et al. 1993). Thus, the long-term spatial influences of trees in a gap-structured forest apparently largely regulate seedling recruitment from the persistent understory seedling bank (see also Aaltonen 1919, Kalela 1942). These long-term tree influences include both aboveground processes (interception of light and water, litter fall) and belowgroud processes (root uptake of water and nutrients, root turnover, rhizosphere effects). The interactions involved are apparently complex, since large trees affect seedlings both directly through resource competition and indirectly via their effect on understory vegetation and humus properties. In addition, the small-scale spatial variation of mineral soil properties (possibly enhanced by uprootings over long time periods) can also have an effect, further increasing the number of spatial interactions involved (Järvinen et al. 1993, Kuuluvainen et al. 1993).

5.2. Gap disturbance and ecological diversity

Gap disturbance affects the structural, functional and species diversity of the boreal forest at both local and areal scales. At the local scale the change in forest microclimate and the fall of large amounts of woody debris creates fine-scale spatial variation in carbon and nitrogen cycles, which increases the diversity of microhabitats available for plants (Aaltonen 1919, Hertz 1932, Beatty 1984, Pastor & Mladenoff 1992). In addition, decaying wood of different species is important for many insect and fungi species. When a gap is formed in a windthrow, also soil microtopography is modified and new soil microsites are formed due to uprooting (pits and mounds) (Sirén 1955, Troedson & Lyford 1973, Putz et al. 1983, Jonsson & Esseen 1990, Peterson et al. 1990). In fact, the mixing of soil by tree uprootings is a unique disturbance phenomenon in boreal forests, because is reverses the podzolisation process. Treefalls may thus be a significant factor in creating and maintaining small-scale variation in soil properties and microtopography (Troedsson & Lyford 1973, Schaetzl et al. 1989). This above- and belowground heterogeneity have in turn apparent links to the overall community structure of the forest (Jonsson 1990, Jonsson & Esseen 1990). However, the ecological significance of long-lasting soil variation created by uprootings is largely unknown, due to lack of studies and because of the unknown historical windthrow regimes in Finnish boreal forests.

At areal level the disturbance type and regime of a forested area and the consequent regeneration dynamics determine the landscape pattern of forest structure and species composition. The effects of small-scale gap disturbance on forest structure are perhaps most obvious. Small-scale disturbances enhance structural and spatial heterogeneity, i.e. patchy distribution of trees of different age and size, unevenaged stand stuctures and multilayered foliage canopies. Gap disturbance also contributes to the existence of mixed-species forests by facilitating the spotty recruitment of deciduous early successional tree species in conifer dominated forests (Purhonen 1947, Sirén 1955). At particular spatial and temporal scales forests characterized by gap dynamics may have relatively constant tree species composition maintained by repeated small-scale disturbances (Kubin 1981, Steijlen & Zackrisson 1986). This in turn have apparent contribution to both functional and overall species diversity of the forest. Many insects and fungi are known to host on specific tree species and are thus dependent on their continuous presence in the forest (Renvall 1991, Seppänen 1970). Also, even individual trees of different species are known to alter their environments, e.g. by modifying nutrient cycling regimes, thus increasing environmental variability and patchiness.

Although we know next to nothing about the historical gap disturbance regimes in Finnish boreal forests at various scales, it seems relevant to assume that in regions where gap dynamics have been common, the patch mosaic structure has been altered by forest management. This is because forest management tends to homogenize stand structures and tree age distributions while gap disturbance acts to create structurally heterogenous forests. This difference can be important since many boreal organisms may have adapted to forest structures and landscape mosaics created by small-scale gap disturbance (Syrjänen et al. 1994). Accordingly, it has been suggested that the area needed for the natural treefall pattern could be used as a criterion when deciding the size of nature reserves (Jonsson 1990). However, it is also possible that the boreal forests are inherently characterized by non-equilibrium disturbance regimes, in which case the definition of 'natural' disturbance regimes becomes more difficult (Sprugel 1991).

At present our understanding of the ecological significance of small-scale gap disturbances in boreal forests is limited. It seems evident, however, that gap disturbance has an important role in the natural regeneration dynamics as well as in the maintenance of ecological diversity of boreal coniferous forests.

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