

14 Rates and Processes of Natural Regeneration in Disturbed Habitats

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14.1 Introduction

Surface disturbance from recreational hiking and camping has been reported from a number of ecosystems in various parts of the world, and is also common in the Nordic mountain birch ecosystem. This will be of increasing importance in the future as the use of these birch forests and adjacent alpine-arctic areas for tourism purposes has grown dramatically in recent decades (Bäck et al. 1989; Ilyina and Mieczkowski 1992; Sippola et al. 1995; Gniesser 2000; Godde et al. 2000; Prokosch 2001; Monz 2002; Chaps. 15 and 24). Recovery after surface disturbances in the high altitude and latitude mountain birch systems is normally slow due to the generally low temperatures, short growing seasons, and the often nutrient-poor soil (see below). In dense mountain birch forests also low light intensity may reduce the recovery rate.

Very few controlled field experiments have been carried out on the ecological effect of surface disturbance within the northern mountain birch forest itself. However, it may be postulated that the effects will be of the same order as in similar vegetation types above and north of the present tree line. The Nordic mountain birch forest is also expected to expand in response to climate change to higher elevation and further north, as stressed in several chapters in this volume (see, e.g., Chaps. 1 and 21). This means that the plant field and bottom layers of today's low alpine-arctic ecosystems in the future may be within the subalpine-subarctic mountain birch forests in Fennoscandia.

Ecological impacts of surface disturbance, natural or man-made, are many and include, among others, reductions in the diversity and abundance of plant species (Liddle 1997), growth forms (Bayfield et al. 1981; Forbes 1992b) and soil fauna (Bayfield 1979a; Kevan et al. 1995), changes in vegetation cover, structure and productivity (Cole and Bayfield 1993; Forbes et al. 2001), floristic convergence among sites and colonization by non-native species (Schreiner 1982; Gorchakovskii 1985; Gorchakovskii and Korobeinikova

1997), and increases in soil erosion (Bryan 1977; Liddle 1997; Grieve 2000), soil compaction and concomitant reductions in porosity and infiltration (Monti and Mackintosh 1979; Gellatly et al. 1986a).

Most studies of foot and vehicle traffic have been short term and few controlled experimental studies of recreation impact have, as mentioned, been conducted in the Nordic mountain birch forest and even beyond the northern tree line (Liddle 1997; Yorks et al. 1997). More common have been experiments with camping and associated pedestrian trampling in these and related ecosystems (Bayfield 1979a,b; Cole and Bayfield 1993; Cole 1995a,b; Marion and Cole 1996; Arnesen and Moen 1997), as well as more retrospective descriptions of 'recovery' from sites of long-term impact where levels of use can only be estimated (Hoogesteger 1984; Gellatly et al. 1986a,b; Forbes 1996; Gorchakovskii and Korobeinikova 1997; Wielgolaski 1998).

Findings from around the circumpolar North are seen as generally comparable, in contrast to studies from the southern hemisphere, because of the many floristic and environmental similarities in arctic and subarctic regions (Gnieser 2000) like the Nordic mountain birch forest. However, blanket generalizations on the ostensible 'fragility' of tundra plants have been criticized and dictate that a more local approach be taken (Oksanen and Virtanen 1995). Furthermore, experimental methods have varied widely, making comparisons difficult even among closely situated sites with similar soils and vegetation types (e.g. Emanuelsson 1984; Tolvanen et al. 2001). In response, there has been an effort to institute common sampling protocols (Cole and Bayfield 1993) and this has been adopted in more recent studies in Nordic mountain birch forests (Finland; Tolvanen et al. 2001) and more arctic areas (Gnieser 2000; Monz 2002). Yet, of the few genuine experimental studies conducted in subarctic or arctic ecosystems (Emanuelsson 1984; Gnieser 2000; Monz 2002), monitoring for periods longer than a few years remains uncommon (see, however, Tarnocai and Veldhuis 1998). This chapter will focus on rates and processes of natural regeneration in habitats disturbed by recreation impacts, with special emphasis on the subarctic mountain birch forest and neighbouring zones in Fennoscandia.

Dahl (1975) observed that the erosional features resulting from human trampling were relatively unimportant in Fennoscandia as a whole. Similarly, Emanuelsson (1984) felt that, except in areas in the immediate vicinity of roads, trails and tourist infrastructure, trampling effects on vegetation in the Swedish mountains seemed to be of "limited importance". In fact, damages tend to be concentrated at and above the tree line – where tourist tracks are typically channelled along the most favourable ascension routes from forested areas to higher ground for unobstructed views of the surrounding lowlands. A recent survey in Swedish Lapland has found that over 30% of multi-day hikers reported "significant wear" on the natural surroundings and 50% of all respondents agreed partly or completely that tourists' wear on vegetation in the mountain "is a problem" (cf. Chap. 15). Similar patterns of

impact and erosion are perhaps more noticeable in Finland, which is much less mountainous than either Norway or Sweden and thus contains limited high-elevation terrain. As a result, most of the sizable and accessible mountains in northern Finland ('vaara' in Finnish) are characterized by tourist developments entailing extensive networks of summer hiking and winter skiing and snowmobiling trails (Helle and Särkelä 1993; Ukkola 1995; see also Chap. 15).

14.2 Processes of Regeneration

Disturbance in the Nordic mountain birch forest close to the tree line is important because it produces patches of partially or totally denuded ground that permit propagule establishment but may also open affected areas to erosion (Forbes et al. 2001). In a review of some 400 literature sources from different biomes around the world, Yorks et al. (1997) reported that the greatest general population- and community-level losses in vegetation tend to take place after the first few passes by people or vehicles. This is consistent with research by Cole and Bayfield (1993) who, after repeated experiments in temperate and alpine ecosystems, found no clear evidence to suggest any difference between the effects of trampling all at once and spreading the trampling out over a few months.

Similarly, Tolvanen et al. (2001) report that the negative impact of hiking on subarctic vegetation in both the Nordic mountain birch forest understorey and in nearby dwarf shrub heath is logarithmic: a reduction in species cover and density occurs quickly and at relatively low trampling intensities, after which the measurable level of change is considerably reduced. A visible trail is formed even after 10–25 passes, and a threshold level of a significant cover reduction seems to occur between 75 and 200 passes (Tolvanen et al. 2001). One hundred and fifty passes on flat terrain causes the same relative decrease in vegetation cover as 25 passes on steep slopes, i.e. the impact of trampling is six times greater on the slopes than on flat terrain (Törn et al., unpubl.). It should be noted that, in practice, the numbers of hikers on nature trails in summer are considerably greater than in the experiments, where the maximum number of passes has been 500 (Tolvanen et al. 2001) or 900 (Törn et al., unpubl.). To be realistic, we have to talk about hundreds or thousands of users during a single summer period.

Forest mosses (e.g. *Pleurozium schreberi*, *Hylocomium splendens*) seem to react more slowly than the other plant life-forms to damage from hiking in summer, although skiing has a negative influence on such mesic vegetation (see Chap. 15), but both their decrease and recovery follow the other functional types. Among mosses, *Dicranum* and *Polytrichum* species are most resistant to trampling. The timing of experimental hiking does not seem to

influence the vegetation cover, which decreased similarly independent of whether the hiking treatment was carried out in June, July or August (Törn et al., unpubl.). In an earlier study in northern Sweden, trampling in late summer was found to be more deleterious than early season trampling in meadow vegetation, whereas timing had no influence on the resistance of heath vegetation (Emanuelsson 1984). In the dwarf-shrub-dominated heaths, the seasonal intra-plant translocation of nutrients is apparently not as clear as in the forb-dominated meadows, as dwarf shrubs store a greater amount of their assimilates in their aboveground organs.

In addition to environmental factors, such as low air and soil temperatures, short growing season and often low availability of nutrients near the tree line and above (e.g. Bliss 1962; Billings 1987), regeneration after trampling is constrained by plant characteristics, such as slow growth rates and limited dispersion capabilities through sexual reproduction. Yet, in some cases, disturbance may actually increase plant productivity of graminoids, if not shrubs as well, at least in experimental studies carried out in tundra areas (Chapin and Shaver 1981; Forbes 1992a, 1998), but probably also in similar vegetation types in the Nordic mountain birch forests. Studies have found enhanced productivity to be associated with various substrate changes, such as increases in soil bulk density and decomposition (Gersper and Challinor 1975), radiation absorption and soil temperature (Chapin and Shaver 1981), fluxes of CO₂ to the atmosphere (Zimov et al. 1999), and increase in nutrient availability (Challinor and Gersper 1975; Herbein and Neal 1990).

Plants tolerate disturbances depending on the combined resistance and resilience of each species and the rate of regeneration after disturbance of tundra and Nordic mountain birch understorey plants (Cole 1995a,b; Tolvanen et al. 2001). Many graminoids and deciduous dwarf shrubs have high rates of photosynthesis and growth, and large belowground organs for carbon/nutrient storage (Chapin 1980; Bryant et al. 1983; Karlsson 1985). Such plants normally regenerate well after disturbance and are more competitive than less resilient species, such as cushion plants and evergreen dwarf shrubs (e.g. Chapin 1980).

Recent studies of regeneration by seed in subarctic Fennoscandia provide information relevant to the disturbance and vegetation types discussed here. Welling and Laine (2002) found densities of both seeds and seedlings to be higher in meadow than in heath vegetation at Kilpisjärvi, Finland. In Iceland regeneration of the mountain birch forest by seed is common after soil degradation by sheep grazing (Aradóttir and Arnalds 2001; Magnússon and Magnússon 2001). This was the case in all phases of the 'regeneration pathway' from seed production to standing vegetation. Although seed production, and therefore seed banks, in such habitats can be large, seedling recruitment tends to be negligible in relatively undisturbed vegetation (Molau and Larsson 2000). Rather, studies from different regions and vegetation types across the Arctic indicate that seedling density is generally highest on disturbed ground

and is also typical for the Nordic mountain birch forest (see Chaps. 4 and 17; cf. Kinnaird 1974; Aradóttir and Arnalds 2001). This has been shown for both natural and anthropogenic disturbance regimes. While intense local disturbance, such as frost heave, can trigger high rates of germination, mortality can be so great that net recruitment is kept to a minimum (Nielsen 1997). Experimental removal of successive field layers in a more stable understorey vegetation, dominated by *Vaccinium myrtillus* and *V. vitis-idaea*, indicated that relatively strong mechanical disturbance is needed to enhance sexual reproduction (Hautala et al. 2001). Taken together, these findings suggest that the patches of bare ground resulting from heavy trampling in the Nordic mountain birch heath and meadow understorey vegetation may present opportunities for colonization from seed, provided that frost heave, soil compaction, or soil erosion are not too severe.

14.3 Rates of Regeneration

Once disturbed, natural regeneration of even lightly or moderately trampled vegetation and soils can be a very slow process, although this depends in part on factors like substrate slope, temperature, moisture, nutrient status, and the latitude of the site. In a review (Forbes et al. 2001), similarly created high arctic patches were indeed found to return more slowly toward the productivity and physiognomy of their respective control communities than they did in subarctic mountain birch forests and in low arctic regions. On all but the wettest sites, after two or more decades, disturbed patches remained distinct from adjacent undisturbed ground in terms of vegetation composition, cover, and certain edaphic parameters (e.g. soil pH, temperature, thaw depth, etc.). Close to the tree line in Norway tractor tracks more than 50 years old often seem to be less than 5 years old based on their appearance (Wielgolaski 1997).

In the short term, studies in subarctic Fennoscandian mountain birch forest and heaths have reported hiking tracks becoming visible after as little as 25 (Tolvanen et al. 2001) to 70 trampling passes (Gellatly et al. 1986b) in heath vegetation. 'Delayed action' responses in heath and dwarf-shrub communities have been observed by Bayfield (1979b) and Gellatly et al. (1986b), in which plants continued to die for up to 1 year after the initial impact at levels of 70 or more passes. This is similar to the situation observed close to the mountain birch tree line at Kilpisjärvi, Finnish Lapland, where plants of *Empetrum nigrum* continued to die 1 year, and *Betula nana* well into the second year, after one-time experimental trampling treatments (Forbes et al., unpubl.).

At the population level, three groups of plants clearly differed in their response to trampling in the Nordic mountain birch zone study in Finland by Tolvanen et al. (2001). The most tolerant species were *Carex bigelowii* and the group of three forbs in which the population density was the same as in the

control even in the most intense trampling treatment. *Vaccinium myrtillus* and *V. vitis-idaea* were intermediate in their tolerance, since old tillers suffered from trampling, but the resilience was high even after 1 year. These species were therefore expected to rapidly achieve full recovery within the trampled area. The most vulnerable species were *Dryas octopetala* (Wielgolaski 1998), *B. nana*, and *E. nigrum*, in which resilience decreased with increasing trampling intensity. Old branches from which branching occurred in *D. octopetala*, *B. nana*, and *E. nigrum* were dramatically damaged, indicating low resistance in these species.

Emanuelsson (1984) reported on natural regeneration after 2 years in similar vegetation types in northern Sweden. Although his sampling protocol makes his results not directly comparable with those from the Cole and Bayfield (1993) experimental method, he observed significant recovery in both *Empetrum* heath and *V. myrtillus* heath. Nonetheless, he estimated that damage from more than 50–150 passes per year, depending on vegetation type, would still be visible after 35–50 years.

Monz (2002) followed regeneration in two vegetation types in experimentally trampled tundra in northern Alaska. Although different from the vegetation types currently under investigation in the Nordic mountain birch forest (Tolvanen et al. 2001; Forbes et al., unpubl.), it is worth noting that he observed a distinct threshold between the low–moderate and high levels of impact. Five hundred passes resulted in an immediate loss of approximately 50% cover in dwarf shrub tundra dominated by *Dryas octopetala* and 70% cover loss in cottongrass tundra dominated by *Eriophorum angustifolium*. After 4 years impact was still evident in plots subjected to 200 and 500 passes, but vegetation cover and height had more or less returned to pre-disturbance levels in plots subject to 25 and 75 passes.

Arnesen (1999) experimentally trampled several vegetation types in central Norway, making 300 passes annually over a period of 5 years. In his results from the 'damp heath' vegetation, *V. myrtillus* displayed rather high resistance (sensu Cole and Bayfield 1993) and was able to maintain a relatively stable presence in the paths for the first 4 years, before eventually decreasing to 50% of its original cover. This appears to be greater resistance than that measured by Tolvanen et al. (2001) and may be related to the relative moisture of the pre-disturbance habitats, since the *V. myrtillus* heath investigated by the latter occurred on fairly dry, nutrient-poor soils.

There is little published information on rates of regeneration for periods longer than 5 years, at least in Fennoscandia. The literature contains only a couple of studies, and these have necessarily relied on data from uncontrolled trampling plots. Coker et al. (1998) measured resilience over a 22-year period in four montane habitats in central Norway and reported relatively rapid recovery of *Salix herbacea* snowbed and *Vaccinium myrtillus* heath vegetation compared to *Betula nana* and lichen heath. Even a 'low level' of trampling was clearly visible after two decades in the latter two vegetation types. Wielgolaski

(1998) also followed 22 years of natural regeneration in Norwegian arctic-alpine tundra within three vegetation types following 'severe' uncontrolled trampling over a period of 5 years. In the lichen heath, ground cover of all life forms combined remained below 25 % for nearly a decade. It was only after two decades that total cover approached 100 %, with about 85 % of this provided by bryophytes (*Polytrichum* spp.) and lichens (*Cladonia* spp., *Cetraria* spp., and, especially, *Ochrolechia frigida*). Compared to untrampled ground, the vegetation composition still differed significantly even after 22 years. He estimated the 'under-representation' of vascular plants on trampled ground to be more than 50 %.

14.4 Conclusion

In the controlled trampling experiments in the understory of Nordic mountain birch forests reviewed in this chapter, relatively low levels of trampling were applied compared with the amount of trampling pressure occurring under normal conditions in recreational areas in the mountain birch zone in Fennoscandia (see Chap. 15). Hence, the experiments provide important information primarily on the initial vegetation and soil responses during pedestrian trampling or following the cessation of short-term trampling. In reality, however, hiking trails can be subject to tens of thousands of passes during their lifetime, and the pressure may persist for decades. Long-term observations on the vegetation connected with concrete data on the earlier trampling pressures (by, e.g., visitor counts) are needed in order to provide a more realistic understanding of the regeneration rates occurring under ongoing disturbance.

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