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Vegetational Succession and Norway Spruce Development on a Rising Bothnian Coastline

Michelle Slaney

Supervisors: John Jeglum and Johan Svensson

Swedish University of Agricultural Sciences
Faculty of Forestry
Department of Forest Ecology
SE-901 83 UMEÅ

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Abstract

This paper elucidates the succession of Norway spruce (*Picea abies* L. Karst.) seedlings and trees in relation to elevation above sea level and ground age, field vegetation and ground cover, surface organic layer depth, and other tree species in five transects on rising coastlines of the Gulf of Bothnia near Umeå in northern Sweden. Five transects, 10-m^2 wide and variable lengths (28 to 59 m) were placed, extending from the first invasion of small alder ($\geq$50 cm tall) inland to the boundary between undisturbed communal and man-modified private forests, on coastlines that were exposed in varying degrees to the action of waves and ice drifting. A 1-m X 1-m coordinate grid was established in each transect, and seedlings and trees of all woody species were counted in each 1-m^2 quadrat. For the 1-m^2 quadrats along two, 1-m-wide strips within each transect, detailed measures were made for ground surface elevation relative to mean sea level, field vegetation and ground categories, 1-year-old seedlings of spruce, and the depth of surface organic layer. The transects spanned elevations from 26 to 222 cm, and ages from 31 to 261 years.

A two-way indicator species analysis (TWINSPAN) was used to classify field vegetation and ground layer. There were two main belts of vegetation, and two belts within each of these. The two main belts were: grass, herbs, low shrub, broadleaf litter, and other moss in the youngest stage of the coastline transects; and feathermoss, ericaceous species, hair-cap moss, and fine conifer litter in the older stages of the transects. The transitions between belts became progressively closer to the sea from highly exposed coastlines to those with lower exposures. The successional sequence of the seedling-size individuals (< 1.3 m) was alder, spruce, and rowan. The successional development of the tree-size individuals ($\geq$ 1.3 m) begins with alder followed by rowan and Norway spruce.

Seedling-seedbed relationships are important for understanding the germination and establishment of Norway spruce. A study of ingress of first-year seedlings in two sequential years revealed that they preferred feathermoss and conifer litter, in narrow openings in the spruce forest. This corresponded to the oldest parts of the transects, which are mainly closed but with smaller canopy gaps, and where fine conifer litter, hair-cap moss, feathermoss and ericaceous species are abundant.

Keywords: Gulf of Bothnia, competition, exposure, natural regeneration, organic layer, *Picea abies*, seedbed, seedling establishment, TWINSPAN

Agrovoc: Gulf of Bothnia, plant competition, natural regeneration, *Picea abies*, plant establishment

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1 Introduction

Norway spruce (*Picea abies* L. Karst.) is one of the main dominant tree species in Scandinavia, along with Scots Pine (*Pinus sylvestris* L.) and birch species (*Betula pendula* Roth and *B. pubescens* Ehrn[1]). Spruce is the most shade tolerant of these tree species, and in northern Sweden it replaces pine and birch during succession on upland, fresh to moist, morainal and lacustrine sites (*cf.* Kielland-Lund 1970). Norway spruce also occurs as a dominant species on wet peat sites that are intermediate to rich in nutrient status. The focus of this study is on Norway spruce development in relation to vegetation succession on rising morainal shores, with upland mineral soils, along the Gulf of Bothnia in northern Sweden near Umeå.

The ability of a species to reproduce under its own canopy is a feature of a climax tree species community (*e.g.* Hörnberg *et. al.* 1995). Gap disturbances create openings for natural regeneration to occur and contribute to the structural, functional, and species diversity (Kuuluvainen 1994). The gaps are filled by regeneration that continually establishes on the forest floor. This creates a cyclic successional pathway that is continually renewing the forest with developing stages of seedlings and young trees. The dynamics of old-growth boreal spruce forests are maintained by sufficient seed banks and canopy gap formations (Leemans 1991).

Recent research has been directed towards alternative silvicultural systems that use natural regeneration and advance growth to renew forests, alone or in combination with artificial regeneration methods (*e.g.,* Bamsay 1994; Laiho *et. al.* 1994). Current alternative management practices, such as 'continuous cover forestry' (Mason *et al.* 1999), follow the premise that natural regeneration is favored as a means of achieving greater species diversity and as an assurance that the species are suited to the site. This approach assumes that the use of processes such as natural regeneration is more sustainable than one based upon artificial regeneration and the creation of uniform stand structures of single species. However evidence for this assumption is generally lacking. Consequently, more detailed knowledge of naturally occurring advance reproduction is needed.

Little work has been done using detailed spatial transects to describe complete successional sequences from open, graminoid-dominated shorelines to fully closed mature spruce forests on the rising Bothnian shores (Ericson 1980). The aim of this paper is: (i) to describe and quantify the spatial distribution of naturally occurring Norway spruce in transects from the first woody plants to closed spruce forests; (ii) to relate spruce development to elevation above sea level, exposure, and steepness of the transect; and (iii) to determine the relationships of young seedlings to vegetation and ground cover, seedbed, and organic matter development.

[1] *Common and scientific names for all species mentioned in the text are given in Appendix 7. As well, species groups are defined and representative species are given.*

1.1 Background

Since the Weichselian glaciation, which ended about 10,000 years ago, the Fennoscandian (Norway, Sweden, Finland and Karelia) crust has been experiencing postglacial rebound. From the 3,000 m deep ice mass, the crust was depressed approximately 800 to 900 m below the present level. As the ice melted, the land began to rise. This uplift rate has varied substantially but is still continuing along the shores of the Gulf of Bothnia (Svensson and Jeglum 2000). As the land rises out of the sea, the newly exposed parent material experiences a primary succession of vegetation and forest, as well as soil development. This provides an excellent opportunity to study the ecological succession on a 'virgin' site.

The Fennoscandian forests have experienced human influence for a long period of time, directly by management regimes or indirectly by modified natural disturbance regimes and environmental factors (Hagner 1992a; Östlund 1993; Bernes 1994). Presently, old-growth spruce forests are not common in Sweden and successions to real, undisturbed climaxes are rare. However, some old-growth-like forests can be found along the coast in sites that are isolated or difficult to access for forestry or agriculture, or they are protected in community holdings. Development of ecologically sound and sustainable forest management strategies requires knowledge of succession, dynamics and the structural development of natural forests (*e.g.*, Lähde *et al.* 1991; Norokorpi *et al.* 1997).

The forests in which this study was conducted are well stocked and have developed within the last two to three centuries (Svensson 1998). They are situated on the rising Bothnian coastline in northern Sweden near Umeå, and provide an excellent opportunity to add new and important knowledge on the natural ecological processes of Norway spruce forests (Svensson and Jeglum 2000, 2001). In this area, it is possible to analyze the natural succession and dynamics of Norway spruce forests, in space and time, from the very beginning of the successional process.

1.2 Succession

Succession is defined as the change in the physiognomy, species composition, or proportion of species on a plot of ground over a moderate time interval (decades to a few centuries), normally following a disturbance (MacMahon 1981). Although there is general agreement as to the principles of succession, there is a surprising degree of variation of different successional pathways for various parts of the world, depending on the climatic, topographic, geologic, and biotic settings that prevail. The succession described in the present study must be set in the context of a boreal climate with boreal vegetation, glacially formed drumlin-shaped morainal deposits, and rising coastlines which develop rapidly on uplands into a Norway spruce/ feathermoss climax forest.

A key factor in succession is the vegetational gradient and how plant communities colonize and change in relation to abiotic factors. The spatial vegetation gradient observed on a specific shoreline is a representation of the course of succession at one point over time (Svensson and Jeglum 2000). Ericson (1980) concluded that the effect of land uplift on the vegetation sequence is largely a long-term phenomenon, which can be viewed for periods no shorter than a decade. He summarized the important factors that control the vegetation gradient on seashores: (1) shore slope; (2) inter- and intraspecific competition; (3) substrate and (4) fresh water versus salinity influence. Biotic factors such as (5) distance to seed source and (6) species composition of seed source (Schwank 1981) must be added to complete the picture (Svensson 2000). To fully understand primary succession one should take an ecological approach, examining not only vegetation but also soil development (Åström 2001).

1.3 Norway Spruce Regeneration

Natural regeneration has been defined as the "renewal of a tree crop by natural seeding, sprouting, suckering or layering" (*e.g.*, Groot *et. al.* 2001). It is well known that acceptable levels of natural regeneration can be achieved following disturbances such as fire, windthrow, and harvesting. Harvesting by clearcutting, although normally followed by artificial regeneration, may be accompanied by some levels of natural regeneration, including pre-existing advance regeneration, natural seedlings, and sprouting/suckering. It is possible to utilize natural regeneration with partial harvesting techniques.

Natural regeneration to satisfy management objectives may be categorized as 'unplanned regeneration' (that which was already present, or develops on a site after harvesting or other disturbance) and 'planned regeneration' (which involves regenerating a site using such harvesting systems as shelterwood, strip cutting, seed tree, and clearcutting) (*ibid.*). Each system has its own application methods and the success of the chosen system depends on the area and the species that are involved. In order to reach a desired management objective using one of the above regeneration techniques, knowledge about the ecology of the site and the silvics of the species is required. For the purpose of this study, I will focus on the silvical characteristics and regeneration dynamics of Norway spruce.

A key factor in understanding the primary succession and dynamics of Norway spruce is the time lag and transition between 'allochthonous' regeneration -- by seed migration and initial establishment, and its variability owing to distance to seed source, exposure, seedbed, and competition -- and 'autochthonous' regeneration in a closed forest where gap creation, local seedfall, and improved gap microclimates are the most important factors.

1.4 Silvics and Ecology of Norway Spruce

1.4.1 Mechanisms of reproduction

Sexual reproduction by seed is the predominant mechanism of regeneration of Norway spruce. Asexual, vegetative reproduction, much less common, can occur by layering (Svensson and Jeglum 2000). Layering is the phenomenon where low branches of a seedling or tree touch the ground, are covered by moss or litter, develop adventitious roots, and then turn up at the branch tips to form upright stems. The connection to the branch may become nonfunctional, and the layer then grows independently from the parent plant (*e.g.*, Natural Resources Canada 1995).

1.4.2 Shade tolerance and response to release

Norway spruce is intermediate in shade tolerance. In the youngest and smallest seedling classes, there is a continually 'changing seedling population', with continuous establishment and mortality occurring (*e.g.*, Paavilainen and Päivänen 1995). When trees blow down creating gaps, the seedlings that are present in the gaps respond and grow more rapidly in response to increased light, moisture and temperature. These conditions also favor new seedling regeneration. Norway spruce can regenerate in a large range of gap sizes (Hytteborn *et. al.* 1991). Size and spatial distribution of large trees has a strong effect on the understory seedlings and saplings (Kuuluvainen 1994). There are more seedlings and saplings in gaps and open areas. Often there are groups of seedlings or saplings of similar age or size, called 'cohorts', which reflect the reproduction or release of advance growth that occurs when a gap is created by windfall.

1.4.3 Frequency and quantity of seed crop

The size of seed crops can be forecast by observing flower development (Groot *et.al.* 2001). Seed crops can be reduced by adverse weather conditions, late spring frosts, or cone and seed insects. Low temperatures in northern Sweden are a limiting factor for flowering and heavy cone crops are stimulated by the occurrence of one or two warm, dry summers (Svensson and Jeglum 2000).

In the boreal forests of northern Sweden, spruce trees flower abundantly by the age of 40 to 50 years (Hannerz and Gemmel 1994), but probably flower much earlier with good growth in favorable sites. Large cone crops occur at variable intervals of 2 to 3 years up to 12 to 13 years (Svensson and Jeglum 2000). For example, the years 1995 and 1998 had particularly abundant cone crops in the coastal area near Umeå. Cone crops produce a high variation in seed, from 1 million and 10 million seeds per hectare every year, of which 100, 000 to 1 million are viable (Hannerz and Gemmel 1994).

1.4.4 Distance of seed dispersal

The largest proportion of spruce seeds falls in late winter and early spring, when cone scales open owing to wetting and drying, and variations in temperature. Norway spruce seeds are winged and dispersed by the wind. The distance they are dispersed depends upon the size of the seed, the height of the tree, the wind speed and turbulence (Groot *et.al.* 2001). The majority of falling seeds remain close to the mother tree, with distances of one to several tree heights. However, according to Svensson and Jeglum (2000) Norway spruce seeds can be dispersed up to several kilometers when the snow surface is hard or crusty.

1.4.5 Windfirmness of seed trees

The degree to which a seed tree can withstand wind and exposure depends on the soil depth, soil type, tree height, tree age, root and stem decay, local climate, and topography (Groot *et.al.* 2001). Windfirmness varies among species and is an important consideration for Norway spruce on the Bothnian coastlines since they can be subject to a high degree of exposure. One of the main components of this study was to examine the regeneration in sites with different exposures. The sequences of spruce forests in our study transects are close to the shoreline, and have not been influenced by human activity. Hence, they are virgin-like and have developed gradually over long time-sequences up to around 260 years. The forests are well stocked, and there is not a high amount of windfall.

1.4.6 Seed germination and early seedling establishment

Seed germination and seedling establishment of Norway spruce are influenced by many factors: intrinsic seed quality, seedbed, degree of openness of sites which influences light, temperature and moisture, competition from vegetation, soil depth, sea water fluctuation and flooding, and physical disturbance by ice drifting in spring (*e.g.,* Svensson and Jeglum 2000). The most important atmospheric factors identified by Fleming *et. al.* (2001) are solar radiation, air temperature, relative humidity and wind speed. The most important soil conditions are texture, hydraulic conductance, water storage capacity, and the shape of the soil water retention function.

Rapid initial growth of roots and shoots is definitely an advantage in natural regeneration establishment and the best results are usually obtained where conditions of site and seedbed provide optimal conditions of soil temperature and soil moisture (*e.g.*, Lemans 1991; Fleming *et. al.* 2001). According to Fleming *et. al.* (2001) successful establishment depends on the soil surface remaining moist long enough for the seedling to develop a root system that is in soil layers with a more abundant and stable moisture supply.

1.4.7 Seedbed

Seedbed conditions are of primary importance to regeneration by seed, as they influence the relative moisture, temperature and nutrient conditions. Moisture and temperature are initially the most important to germination and establishment. After seedling establishment light and nutrient regime have increasing importance in addition to moisture and temperature. Seedbeds consist of both living and non-living types. Living ground mosses include feathermosses (includes *Pleurozium schreberi, Hylocomium splendens, and Ptilium crista-castrensis*), *Sphagnum*, Cladina and Cladonia spp., brown mosses (in wetlands), and pioneer mosses (on uplands, *e.g., Pohlia nutans*, *Ceratodon purpureus, Polytrichum* spp.). Usually only compact *Sphagnum*, and tight, low-growing pioneer mosses, which conserve moisture at the surface, are favorable seedbeds. *Cladina* and *Cladonia* species, more abundant in poor, open sites, are usually not good seedbeds.. Non-living seedbed materials include conifer litter, broadleaf litter, grass thatch close to the ground, rotting wood, various layers of surface organic (forest floor), and underlying mineral soil that may be exposed by windthrow, ice drifting, or active site preparation. Exposed mineral soil, or mineral soils with thin surface organic layers (*e.g.* 1 or 2 cm) are favorable seedbeds. Rotting wood can be favorable if it is moist enough. Compaction of mosses or of the organic layer, such as on trails and by human trampling, can improve the moisture holding characteristics of the substrate and increase seedling regeneration.

To the concept of receptive seedbed must be added the concept of receptive 'microsite' or 'microniche'. These are protected sites such as moist pockets beside stones, branches or logs, proximity to larger stems of *Alnus* or other woody species, and slightly drier mounds that elevate seedlings above flooding close to the coast. Such microsites provide modification of moisture regime, either towards moister or drier, that makes it more favorable to spruce seedling germination and establishment.

1.4.8 Susceptibility to damaging agents

Early regenerating spruce seedlings are more sensitive to damaging agents than established juvenile and mature spruces. On highly exposed coastlines, the main hazards are frost damage, ice drifting, high water levels, and browsing from animals such as moose, snowshoe hare and rodents. Our knowledge of the relative importance of these different factors is still fragmentary (Ericson 1980).

Insects can also be a cause of mortality to new germinants, but detailed information is lacking for Norway spruce. Fleming *et. al.* (2001) suggest that there is greater insect damage in shaded than in open areas, and on organic soil than on mineral soil seedbeds. The seedlings are often partially defoliated by insects thus predisposing them to other damaging agents that reduce their growth.

Fungi can also play a role as a damaging agent to new germinants. This phenomenon is most common in shaded, moist conditions and in less acidic and more fertile soils. Fungi may reduce the vitality of seedlings, and eventually may cause mortality. Some examples are root rots, needle rusts, and damping-off fungi (*ibid.*).

1.4.9 Interspecific competition

During primary succession, the majority of higher plant and tree species enter the succession as seeds. The seeds may arrive at any stage of the sere, but their entry, germination, and establishment may be either hindered or facilitated by the vegetation that is already present. First-year spruce seedlings are highly sensitive and it is estimated that only 2% of the viable seeds ever become seedlings (Fenner 1987; Hannerz and Gemmel 1994).

Fleming *et. al.* (2001) reported that slow-growing spruce seedlings do not compete very well with dense cover of grasses, herbs, shrubs, trees, and some rapidly growing, loose moss mats (*Sphagnum, Polytrichum commune*). There are 'allelopathic' species such as bilberry (*Vaccinium myrtillus*) that can interfere with seedling germination and growth through both physical and chemical interactions. Jäderlund *et.al.* (1996) reported that the inhibitory effects of bilberry leaves can delay the start of Norway spruce up to 10 days. They also concluded that Norway spruce seeds quickly absorbed toxins from the leaves, causing seed mortality before germination. In a similar study, Zackrisson *et.al.* (1995) found that crowberry (*Empetrum nigrum*) causes Norway spruce seedlings to establish less frequently. They suggested that this vegetation negatively influences mycorrhizal symbiosis and impairs N uptake.

2 Study Area

The study area is located on the shores of the Gulf of Bothnia ($63^0 50'$N, $20^0 45'$E), north of Umeå and close to Sävar in the province of Västerbotten, Northern Sweden. (Fig.1) The area is situated on the Fennoscandian crust which is still undergoing postglacial rebound since the Weichselian ice mass retreated some 10,000 years ago. It is close to the area of current highest land uplift rate in Fennoscandia. Since we know that the land in this area is uplifting at the rate of 8.5 mm per year, a measure of the elevation above sea level provides a basis to calculate the age of the ground (Svensson 1998).

Archipelagos found in the Gulf of Bothnia are mainly built up of moraine deposits, often boulder-strewn and wave-washed, and bedrock. The bedrock in the Umeå area is mainly pre-Cambrian peneplain that consists of various kinds of granite, gneiss and acid igneous rocks (Svensson and Jeglum 2000). The coastal area has been formed by glacial action, especially during the melting period, and the landscape is characterized by drumlins with the deepest accumulated till on the lee side (*ibid.*).

This area experiences a maritime climate with the seawater having a chilling effect during the spring and early summer, and a warming effect during the fall and early winter. The seawater has a salinity range from 2‰ – 5‰ and approaches zero in the bays and at the river mouths. The normal sea level fluctuation is from 120 to 130 cm as a result of wind and air pressure fluctuations, and according to Ericson (1980) this has an annual, regional and seasonal variation. The annual precipitation is approximately 400 to 550 mm and the mean annual temperature is 3 to 4 °C. The mean daily temperature for January is –5 to –7 °C, 0 to 1 °C for April, 15 °C for July, and 9 °C for September. The area is snow-covered for approximately 150 days and the duration of ice-cover is 80 to 100 days. In this area, the growth period is about 150 days (+ 6 °C) but cold spells can occur in early fall, affecting the life cycle for many seashore species (Svensson and Jeglum 2000). In this south to mid-boreal region, the forest growth is quite good.

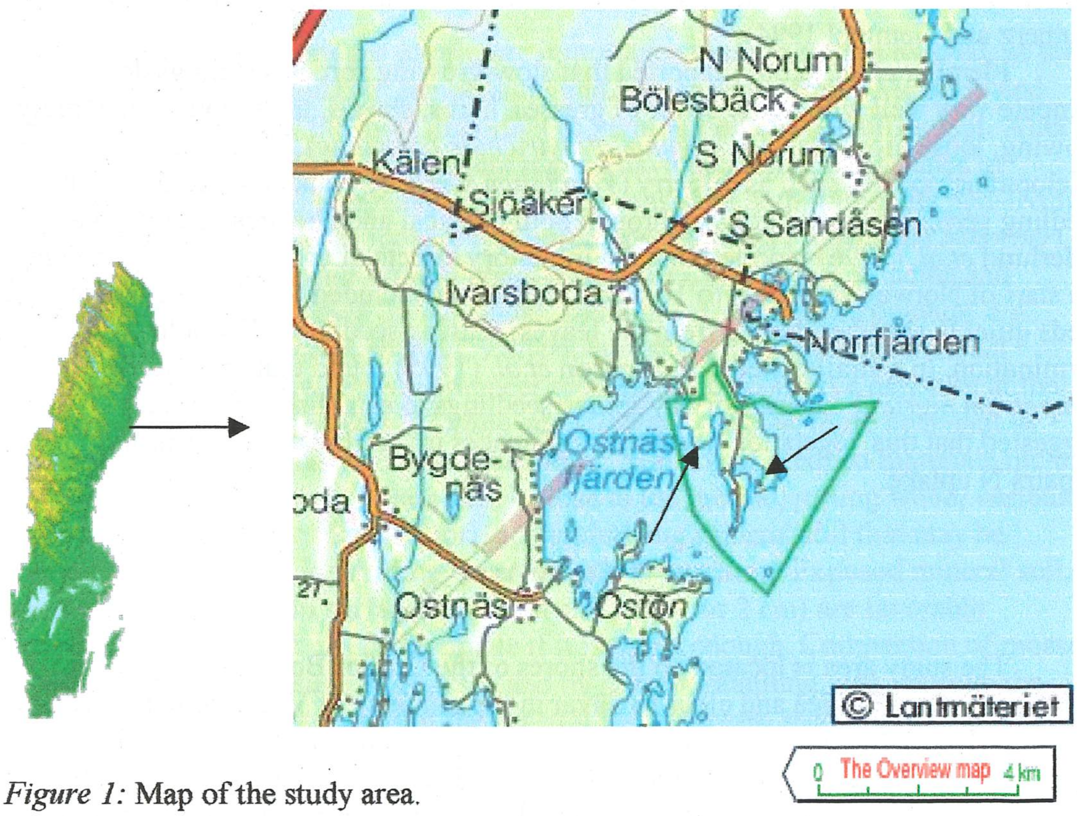


Figure 1: Map of the study area.

3 Methods

There were two main parts to this study. The first part of the study related older seedlings and trees of various species to ground age, surface organic layer depth, and field vegetation and ground cover, and elucidates the successional sequence along the rising shores of the Bothnian coastline using the downward migration of vegetation in relation to these other factors. Data on older seedlings and trees was collected before this project as part of a larger Ph.D. program (J. Svensson, Swedish University of Agricultural Sciences). The second part of the study involved an investigation of 1-year-old Norway spruce seedling establishment in relation to factors such as seedbed type, density of seeds, ground age, surface organic layer depth, site exposure and openings in the forest canopy (a strip cut treatment). It also involved a preliminary assessment of seedfall in the study area.

3.1 Study sites

Five sites with different degrees of exposure, from very exposed to the open sea and fetch to very sheltered in an enclosed bay, were chosen in order to sample the full range of conditions for Norway spruce succession. These sites were located within the Sladan Nature Reserve (63° 50'NN, 20° 45'NE), township of Ivarsboda, province of Västerbotten (Fig. 1). Two sites are on the Österstgrundet peninsula, one on the southern shore facing the open sea and one on the southwestern shore facing the small, semi-enclosed Bay of Sönnerstgrundsfjärden (Fig. 2). The remaining three sites are on the Lillgrundudden peninsula, all facing the large, semi-enclosed Bay of Ostnäs. The sites are on the south, southwest, and western shores respectively.

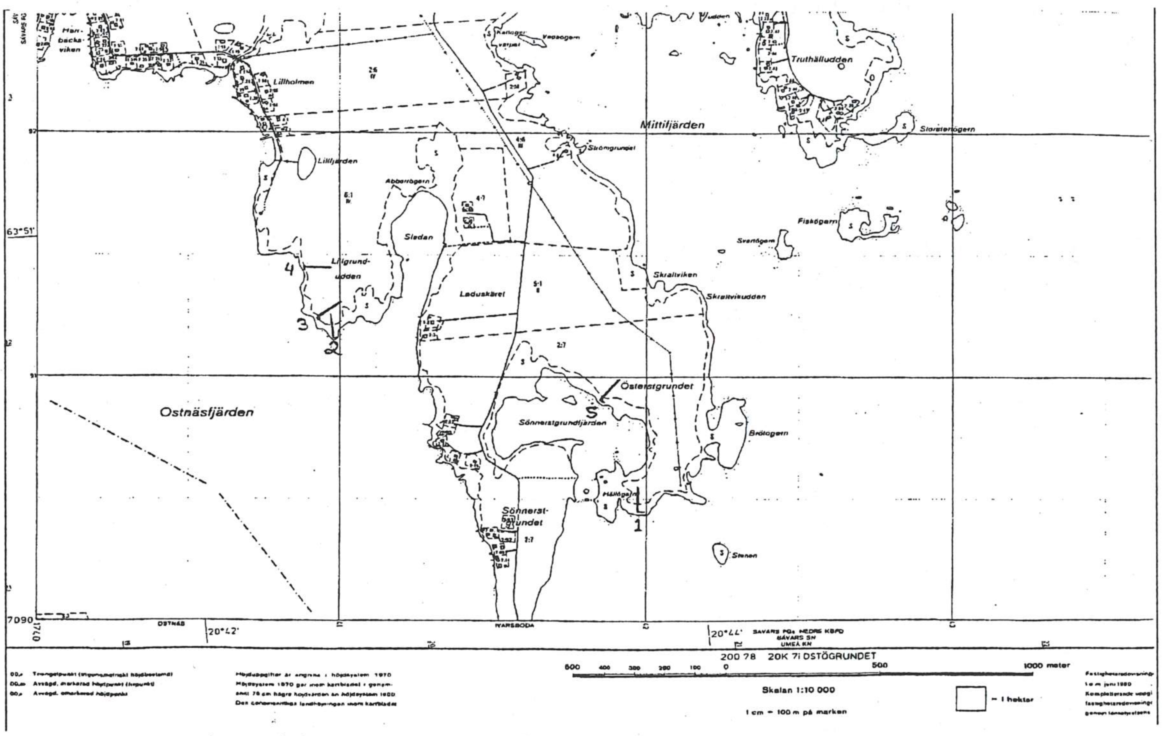


Figure 2: Location of the transects 1 to 5.

3.2 Transects and experimental design

A transect was established at each of the five sites, 10-m wide (X-axis) and variable lengths (Y-axis) from 28 to 59 m. The transects began with the most seaward occurring woody species $\geq$ 0.5 m, which was always *Alnus*, and ended at about the boundary between community-owned forest and private forest influenced by selection cutting (Fig. 3). These transects were marked and grided such that each $1m^2$-square quadrat was identified by X-Y coordinate numbers.

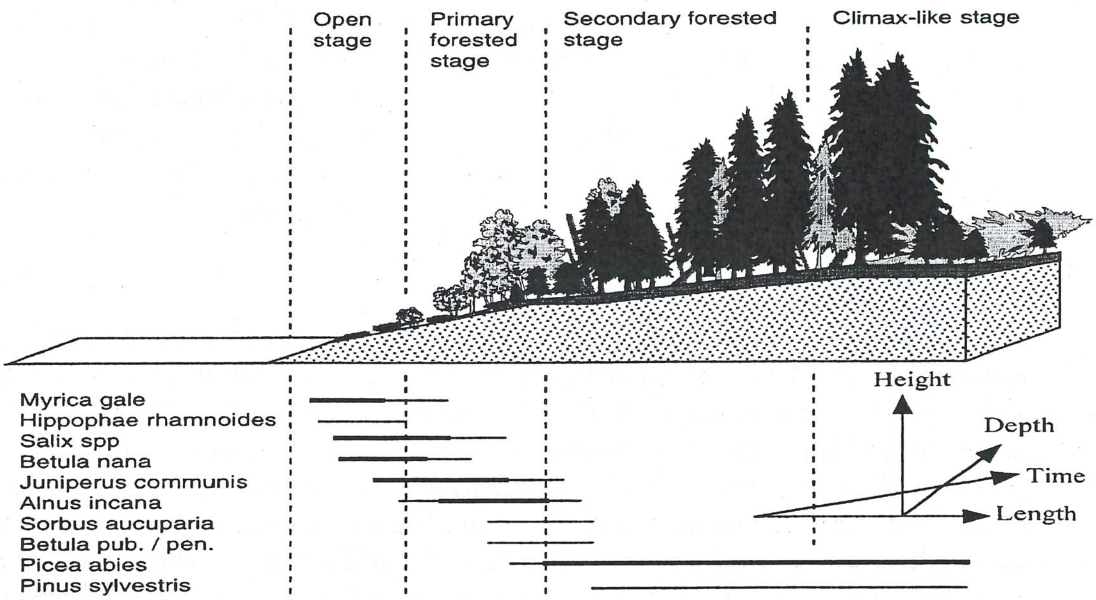


Figure 3: A view of the primary succession along the rising Bothnian coastlines (from Svensson and Jeglum 2000 with permission).

3.3 Experimental Design

In the spring of 1999, each transect was divided into four different treatment types associated with a harvesting experiment conducted by J. Svensson (Swedish University of Agricultural Sciences) (Fig. 4). Along the X-axis, the first 3 meters (0-3) were *undisturbed* and left in a natural condition, the next 2 meters (3-5) represented *overstory competition* with the understory removed (individuals < 1.3 m), the following two meters (5-7) were *clearcut* with the understory removed and the final three meters (7-10) represented *overstory* removed with the understory left in place.

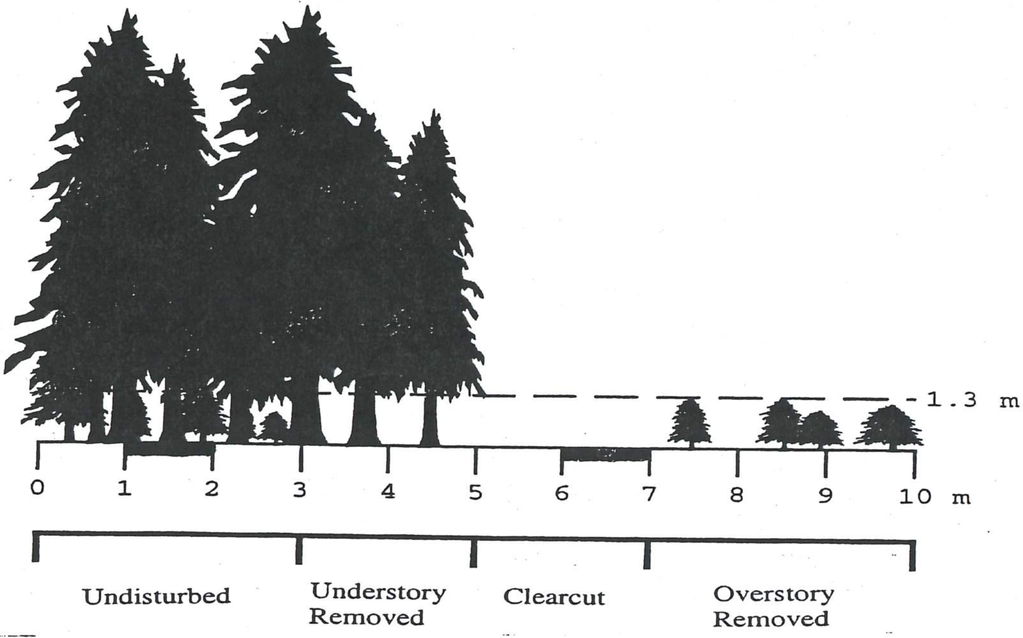


Figure 4: The experimental design for the five transects (as carried out by J. Svensson in 1999).

In order to sample several attributes in more detail, two 1-m-wide strips were established in each of the five transects. These were between X1 and 2, and X6 and 7, and continued along the Y axis for the whole length of each transect (see Fig. 4 and Appendix 2). The attributes measured in detail in each 1-m^2 quadrat along each strip were:

(1) Number of current year Norway spruce seedlings, recorded both in 1999 and 2000, and survivor seedlings from 1999 to 2000,
(2) Percentage cover of field vegetation and ground cover types,
(3) Elevation above mean sea level (MSL), and
(4) Depth of organic layer over mineral (DOL).

Within the 1-m-wide transects, a total of 450 square meter plots were used to investigate soil depth, elevation above MSL, percentage cover of field vegetation and ground cover, and *P. abies* current seedling data from 1999 and 2000.

3.4 Field measurements

3.4.1 Ground age

Elevation was measured in the same m^2 plots where soil depth was measured. One elevation reading was taken in the center of the plot. The average of the two treatment lines were taken by averaging the same quadrat number for the two parallel treatment lines, to obtain one measurement of elevation for each meter along the Y-axis of each transect.

Elevation was taken at each point using a theodolite and a 5-meter measuring-pole from which the readings were taken. Before taking the first elevation measurement, the theodolite was positioned in an area where the most consecutive readings could be taken. Then the first reading was taken at the edge of the water and the exact time of day recorded. Knowing the time of the first reading was crucial for making the appropriate adjustments in order to have accurate measurements, since all the readings taken had to be converted to mean sea level. Deviations from normal water level were corrected with data from the nearby Hydrological Station in Ratan (64°00'N, 20°55'E).

Steps necessary for adjusting Elevation readings:

(1) Base point (Bp) = t – h $\pm$ adjustment factor
(2) Elevation (E) = (h – e) + Bp

where *t* is the elevation at the edge of the water from the initial theodolite position, *h* is the height of the theodolite, and *e* is the elevation taken at the positions along the transect. (Note: The Base point value only has to be calculated once for each new transect, and the remaining elevation readings are converted using step 2.)

Formula for calculating Ground surface age:

$$\text{Ground age (years)} = \text{Elevation (m)} \times \frac{1 \text{ year}}{8.5 \text{ mm}} \times \frac{1000 \text{ mm}}{1 \text{ m}}$$

This formula provided an exact age value at the ground surface for each point where elevation was measured. In some analyses, the values were grouped into 10-year age classes and the median of that class was chosen to represent the age of that particular spot. As we progress upslope toward the climax Norway spruce community, the land becomes progressively older. In cases where there are depressions along the transects, the ground age becomes 'younger' temporarily.

3.4.2 Organic layer depth

The depth of surface organic layer was measured in the two, 1-m-wide subtransects within each of the five transects. Measurements were taken in each corner of every square meter along subtransects, using a steel soil measuring probe (Appendix 2). The mean value was obtained by taking the average for each 1-m^2 quadrat using the four corner values, then by averaging the same quadrat numbers along the Y axis for the two parallel treatment lines to obtain one value for each meter along the length of the transect (Appendix 2).

3.4.3 Field vegetation and ground cover

In determining which seedbed types facilitate and which hinder seedling establishment and development, it is important to know how much and what type of vegetative cover is surrounding the seedlings. In doing that, I established field layer vegetation types (above ground surface) and ground surface cover types (on the ground surface). The field layer was made up of low woody shrubs, herbs, and graminoids while the ground surface attributes consisted of feathermoss, hair-cap moss, 'other' mosses, sawdust, broadleaf litter, conifer litter (coarse and fine) and an 'other' category which included rocks, stumps, coarse woody debris, and ant mounds. The sawdust that was present in the transects was due to the harvesting in the small clearcut strips. Species or materials that were included in these categories are outlined in Appendix 1. In each m^2 quadrat, the covers of the field vegetation and ground cover types were estimated in percentage classes. The classes assigned were 1 (present to 0.9), 3 (1-4.9%), 10 (5-14.9%), 20 (15-24.9%), …, 90 (85-94.9%), 99 (95-100%).

3.4.4 Trees and seedlings

Information was recorded for all species of trees in these transects between 1996 and 1998 (J. Svensson, unpublished data). The woody species that occur in these areas include *Picea abies* (Norway spruce), *Pinus sylvestris* (Scots pine), *Alnus incana* (grey alder), *Sorbus aucuparia* (rowan), *Betula pubescens* (birch) and *Juniperus communis* (juniper). The X-Y coordinate position for tree-size individuals of woody species ($\geq$ 1.3 m) was recorded, along with height, diameter at breast height (dbh), and health status (live, declining, dead). This data was later transformed into number of stems per 1-m^2 quadrat for several height classes in the X-Y coordinate system. All seedlings of spruce <1.3 m were counted in each 1-m^2 quadrat. The spruce seedlings were further categorized into the following classes: <0.19 m, 0.20 to 0.49 m, and 0.50 to 1.29 m. Seedlings of other woody species were counted if $\geq$0.5 m to < 1.3 m. The data was expressed as numbers of all 'tree' size ($\geq$ 1.3 m) and 'seedling' size (<1.3 m) individuals in each 1-m^2 quadrat. The data on trees and seedlings of all woody species were based on observations from 2,150 square meter plots, using all 10 lines of 1-m^2 quadrats for each of the Y lengths of the five transects.

3.4.5 Seedling ingress and seedfall

For the two individual sample lines along the Y axis in the undisturbed (between X1-X2 m) and in the clearcut (between X6-X7 m) treatments, the number of current 1-year Norway spruce seedlings were recorded in autumn 1999 and marked by placing popsicle sticks around them. The seedbed type on which they were found was recorded These lines were re-assessed in autumn 2000 to determine survivor percentages for the marked 1999 seedlings, and to record the new crop of current year seedlings and seedbeds on which they occurred. The total number of 1-m2 quadrats assessed in both 1999 and 2000 were 430 (see Appendix 3).

An important factor influencing natural regeneration and seedling establishment is the occurrence of a seed crop. A good cone crop year occurred in summer of 1998. Therefore, in the winter of 1998-99, seed traps were placed in areas where there was the most and the least amount of exposure, transects 1 and 5 respectively. In each transect, 0.25 m^2 traps were placed in three different successional stages -- the open meadow stage, the primary forested stage, and the secondary forested stage (Svensson and Jeglum 2000). The traps were left for about 2 1/2 months (from mid-February to late-April) before they were collected and seeds counted. Data is presented in Appendix 4.

3.4.6 TWINSPAN analysis

The successional changes in the vegetation as the ground emerges from the sea can be viewed as a downward migration of vegetation (e.g., Ericson 1980). The changes in vegetation along transects are also indicative of the various 'belts' that accompany the downward migration of tree species. These 'belts' were analyzed using a multivariate analysis program called two-way indicator species analysis, TWINSPAN. In this program, data is arranged in an ordered two-way table by classification of the individual cover type attributes versus age groups as samples. This two-way classification makes possible a tabular matrix arrangement which orders and classifies both the attributes and the samples (Hill 1979).

Using this analysis, the 10-year age classes were assigned as synthetic 'samples' and the cover types were assigned as 'attributes'. The average of the two, 1-m^2 quadrats at each Y-distance was categorized into the appropriate 10-year age class sample for each meter along the transect. The cover type attributes were averaged within each of the 10-year age class samples, to provide mean cover values to characterize the samples. TWINSPAN was then run to obtain dichotomous divisions of samples into two different groups of samples at each division. In this program, I used 7 cut levels, which classified cover amounts, namely 0 (0-1%), 2 (2-4%), 5 (5-9%), 10 (10-24%), 25 (25-49%), 50 (50-74%) and 75 (75-100%). The attributes or cover types that were used in the analysis were low shrub, Ericaceae, herbs, grass, feathermoss, *Polytrichum*, other moss, fine conifer litter, and broadleaf litter.

The output consists of groupings of similar samples, and groupings of similar cover attributes. I chose two levels of division, yielding 4 groupings of samples, and I interpreted the dendrogram as four separate belts of vegetation. I performed this operation on each of the five transects separately. See Appendix 5 for an example of a dendrogram output.

4 Results

4.1 Transect profiles and ground age

The five transects encompassed different aspects, lengths, slopes, temporal slopes, and ranges of age (Table 1). The aspects (as one faces seaward from transect) ranged from S to W. The transects were of varying lengths from 28 to 59 meters.

Table 1*: Physical and age properties of the five transects in five areas, from the most exposed to the least exposed (transects 1-5)*

Transect-Exposure (yr/m)	Location	Aspect (Y)	Length (m)	Age (yr)	Slope (cm/m)	Temporal Slope
1	Österstgrundet	S	55	51-185	2.3	2.7
2	Lillgrundudden	S	59	43-261	3.4	4.0
3	Lillgrundudden	SW	32	49-238	5.8	6.9
4	Lillgrundudden	W	28	42-188	5.0	5.9
5	Österstgrundet	SW	41	31-238	4.9	5.7

Note: For the ranking, three parameters have been used: Exposure – the relative distance of open sea in front of the transect and relative protection from points or embayments; Aspect – general aspect standing at the transect and facing towards the sea.

Ground age is the independent variable used in most of the analyses. It is the baseline for comparing results among all transects and variables. Total ground age among transects varied from 31 to 261 years (Table 1). The years spanned within the transects were 134 (transect 1) to 218 yr (transect 2). The elevation, which was used to calculate ground age, allows us to compare the slope of each transect (Fig. 5). It presents clearly the difference in topography in each transect. The most gradual slope was on transect 1, the most exposed, whereas the steepest slope was on transect 3, an intermediate-exposed site.

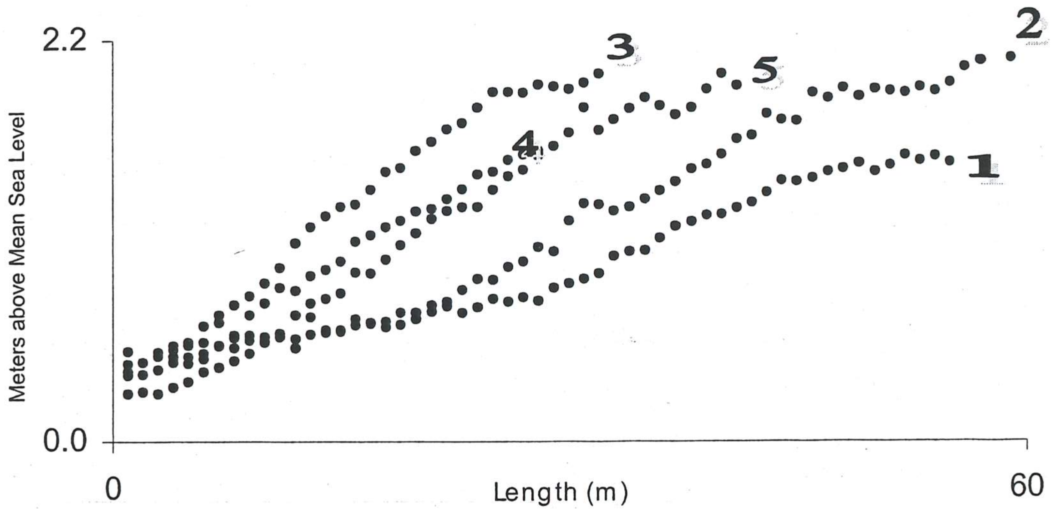


Figure 5: The topographic sequence showing slope for each of the transects.

4.2 Organic layer depth

The results for depth of organic matter were based on averages taken from 449 soil measurements in all 5 transects (see Appendix 2). As the age of the ground increases, so to does the depth of surface organic layer (Fig. 6). There was a linear relationship with a highly significant P value of 0.000.

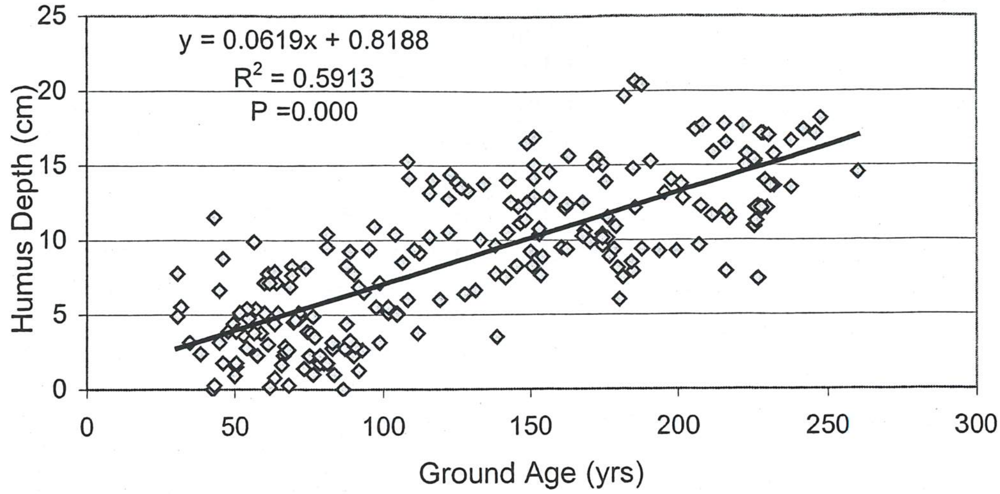


Figure 6: Relationship between organic layer depth and ground age, all 5 transects combined.

4.3 Field vegetation and ground cover

Table 2 presents an interpretation of where the field and ground types achieved high abundances in each transect. The types are organized in order of lowest to highest years of peaking. Usually grass is in the youngest locations, while fine conifer litter is in the oldest. Other categories achieve peaks in various locations along the transects, usually with a single peak (unimodal), but sometimes with a double peak (bimodal distribution). Transect 3 in particular achieves a number of bimodal peaks, indicating that the transect does not change uniformly in its development but instead varies along its length. In fact, one sees an early transition to Ericaceae, *Polytrichum*, and fine conifer litter at 115 m, a change to broadleaf litter, other moss and feathermoss at 145 to 195, and a change back again to Ericaceae, *Polytrichum*, and fine conifer litter at 195 to 235. There considerably more birch in transect 3 than in the other areas, which means that the undergrowth will be somewhat different, and it is also the transect with the highest slope.

Table 2: *Location of high abundances for field vegetation and ground cover types by age class intervals (the mid-points of 10-year interval; e.g 55 is the mid-point of 50 to 60 years). Transect 1 is the most exposed, transect 5 the least exposed.*

	1	**2**	**3**	**4**	**5**
Grass	55-105	45-75	46-65	45-95	35-55
Herbs	55-105	75-125	65-105	45-95	35-55
Low Shrub	105-125	45-75	65-105	45-95	55-95
Broadleaf Litter	105-125	75-125	145-195	95-105	55-95
Other Moss	105-125	125-175	145-195	95-105	55-95
Ericaceae	125-155	125-175	115-145,195-235	105-135	125-235
Feathermoss	125-155	175-235	145-195	135-185	125-235
Polytrichum	125-155	175-235	115-145,195-235	135-185	95-125
FineConif Litter	155-185	175-235	115-145,195-235	135-185	125-235

TWINSPAN was carried out on the data sets for each of the five transects. In the first division for all five runs, one group was characterized by grass, herbs, low shrubs, other moss, and broadleaf litter, while the other group was characterized by Ericaceous species, feathermoss, hair-cap moss (*Polytrichum*), and fine conifer litter. These two groups, called 2 and 3, were located closest to and furthest from the seashore, respectively. This first division occurred at 125 years in transect 1, the most exposed transect, and decreased progressively toward least exposed: 125, 105, 105, and 95 years in transects 2 to 5, respectively (Fig. 7).

TWINSPAN analysis further separated each of the first two groups into two more groups. Group 2 was divided into groups 4 and 5, and group 3 was divided into groups 6 and 7 (Appendix 5, Fig. 7). These divisions are arranged in sequences of groups 4 - 5 - 6 - 7, from closest to the seashore to furthest inland. The four vegetative cover groups were broadly similar, but did vary somewhat from one transect to the other.

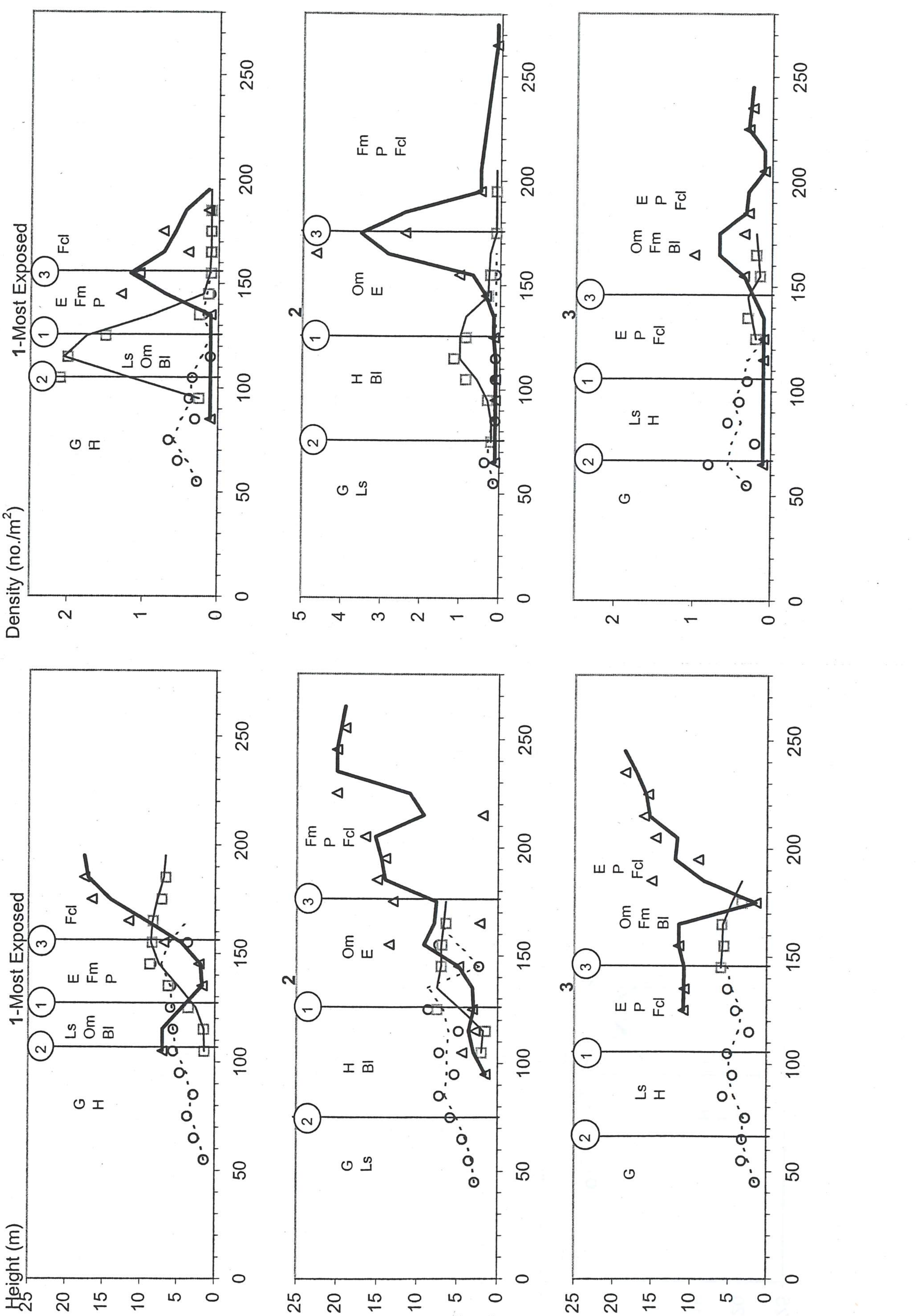
Transect 4 was different from the sequences in the other transects. Its group widths were more narrow, similar to those of transect 1. Also, its division 2 was located quite far from the sea, similar to that in transect 1. The narrowness of the belts may be explained by the fact that these transects encompassed the smallest ranges of ages, and were the youngest of the five transects at their furthest ends, 185 and 188 years, respectively. Hence, their vegetation zones were compressed into the narrowest belts among all the transects.

4.4 Succession of all woody species

Figure 7 illustrates where the tallest trees of alder, rowan, and Norway spruce, and the seedlings for these three species, occur in relation to the groups of field vegetation and ground cover. The first group (4), typified by grass dominance, was characterized by tree-size alder, and seedlings of alder, spruce and rowan The second group (5) usually contained all three species as seedlings and trees, except for transect 3 which did not contain tree-size spruce or rowan, and transect 5 which did not contain tree-size rowan. (Recall that transect 3 had high amounts of birch, and the steepest slope of all the transects.) The third group (6) contained the tree-size of all species in all transects; however, for the seedling-size the alder drops out. In the fourth group (7) there are tree-size spruce, and tree-size rowan in all but one transect. Seedling size spruce are always present, but rowan is missing in the two least exposed transects 4 and 5.

Alder always begins in belt one (group 4) and peaks within the first two belts (between 35 to 125 years). Rowan begins in the transitions between belts one and two (group 5) (between 65-95 years) and usually peaks in the transition between belts two and three (group 6) (between 95-145 years). Spruce always begins in belt one (55-85 years), peaks in belt four (group 7) or the transition between three and four (between 150-200 years), and then decreases towards the ends of the transects. Transect three showed a slightly different pattern for spruce seedlings and vegetative cover belts.

When one examines seedling (≥0.5 to <1.3 m) distribution, the order of appearance is alder (35 years), spruce (55 years), and rowan (65 years) (Fig. 7). Alder seedlings are most abundant at the beginning, than decrease and drop out after 155 years. Rowan begins low, peaks at about 125, then decreases and drops out after 195 years. Spruce begins with low densities, reaches a peak at about 165 to 175 years, and then falls to lower values to the end of the transects, but does not disappear from this older old-growth-like stage.


1-Most Exposed
Height (m)
Density (no./m²)
G
H
Ls
Om
Bl
E
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Fcl
1
2
3
0
50
100
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200
250
5
10
15
20
25

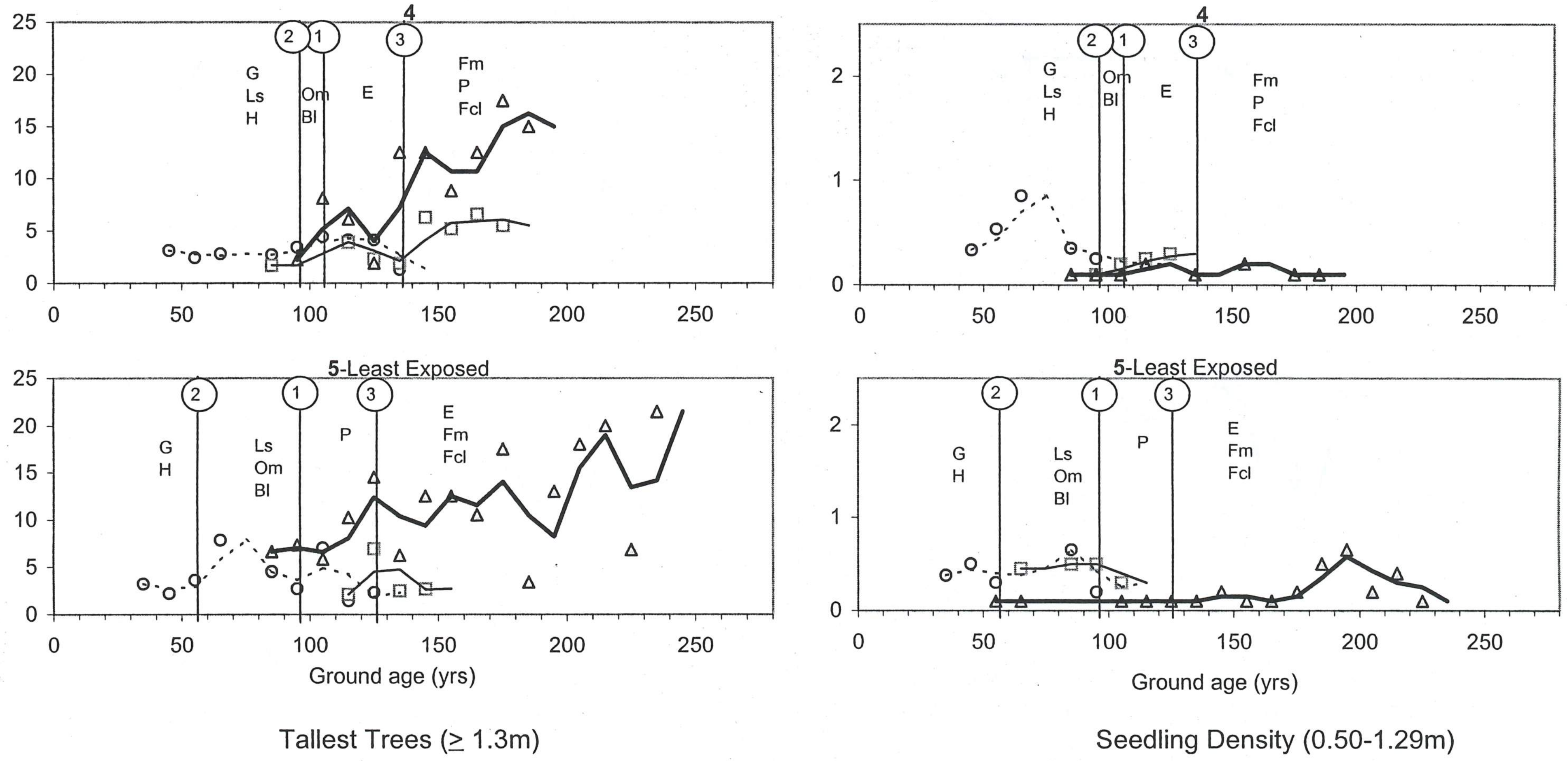

Figure 7: Distribution and density of all woody species, seedlings and tallest trees in each transect, and across vegetation belts.

*The vegetation cover types are as follows: G-grass, H-herbs, Ls-low shrubs, Om-other moss, Bl-broadleaf litter, P-haircap moss, E-ericaceous species, Fm-feather moss, Fcl-fine conifer litter. Note the difference in scale in the seedling density figures on the right, there are two different scales. * For all figures, the circle and broken line represents alder, the square and solid line represents rowan and the triangle with a bold line represents spruce. The trend line is the moving average of each observation.

*The divisions in each transect are represented by the circled numbers (eg. (1) indicates the location of the first division of each TWINSPAN.)

4.5 Succession of Norway spruce

4.5.1 Established seedlings and trees

Tree-size individuals (≥ 1.3 m) are found as early as 35 years for alder, after which it rises to peak values at 65 years and then tapers off gradually (Fig.8A). Spruce and rowan begin low at 85 years. Rowan increases to a plateau, which it maintains until dropping out after 185. Spruce trees also increase to a level density, which is maintained until 245. (The drop in 265 should not be emphasized since it is based on a single stand.)

For seedlings ≥ 0.50 m to 1.29 m, alder comes in earliest, followed by spruce and then rowan (Fig. 8B). Alder has its modal occurrence at about 60 years, rowan at 120 years, and spruce at 170 years. Seedlings of alder and rowan drop out at 160 and 190 years, whereas spruce continues into the old-growth-like forest and does not drop out.

For spruce seedlings of all size classes, the most seaward seedlings occur at 35 years, and smallest seedlings (<0.20 m) achieve a broad peak at 105 to 195 (Fig. 8C). The early occurrence of Norway spruce seedlings shows they can establish and survive on ground that is below the highest sea levels, which can reach 0.6-0.7 m above mean sea level. The next two size classes 0.2 to 0.49, and 0.5 to 1.29 m, achieve peaks around 155 to 195 years.

Figure 9 displays how spruce seedlings (< 1.3 m) and mature spruce trees (≥ 1.3 m) are distributed along the five transects. There is an obvious trend progressing from youngest to oldest. For four transects there is definite unimodal, sometimes bimodal, peaking, first of seedlings, then of trees. However, transect 5 has the lowest density of seedlings and trees, and they are present on all ages in low numbers. We do not have a good explanation for this difference. Seedlings occurred quite far down initially, at 35 to 45 years, in transects 2 to 5, below the maximum sea level. However, in the most exposed transect 1 seedlings occurred initially at 65, which was at about the maximum sea level.

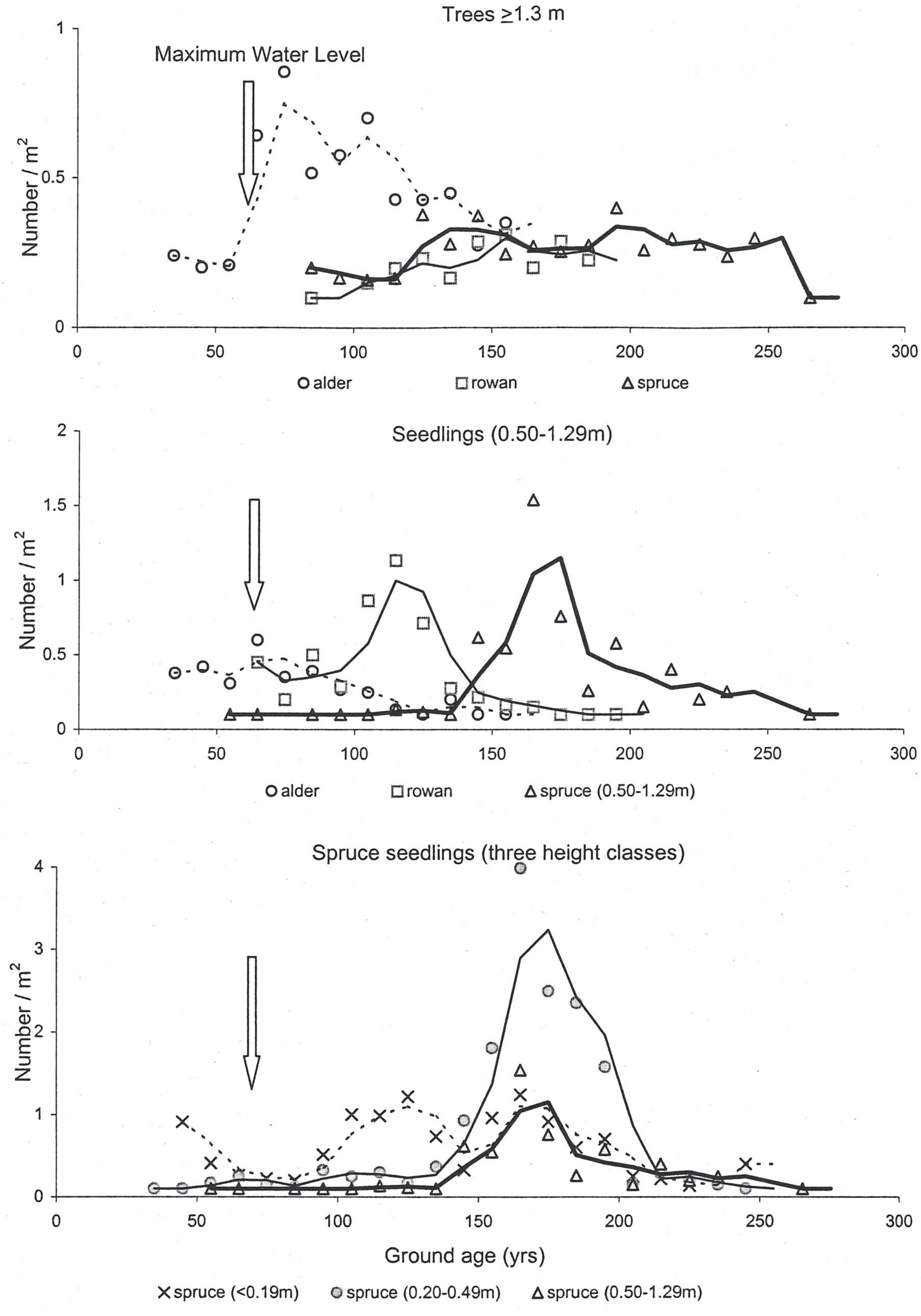

Figure 8: Density of all species of trees and saplings in a all five transects. Top: Tree-size, ≥1.3m, three species; Middle: Seedlings, 0.5-1.29m, three species; Bottom: Spruce seedlings, all < 1.3 m. *Note the difference in scale on the Y-axis of each figure.

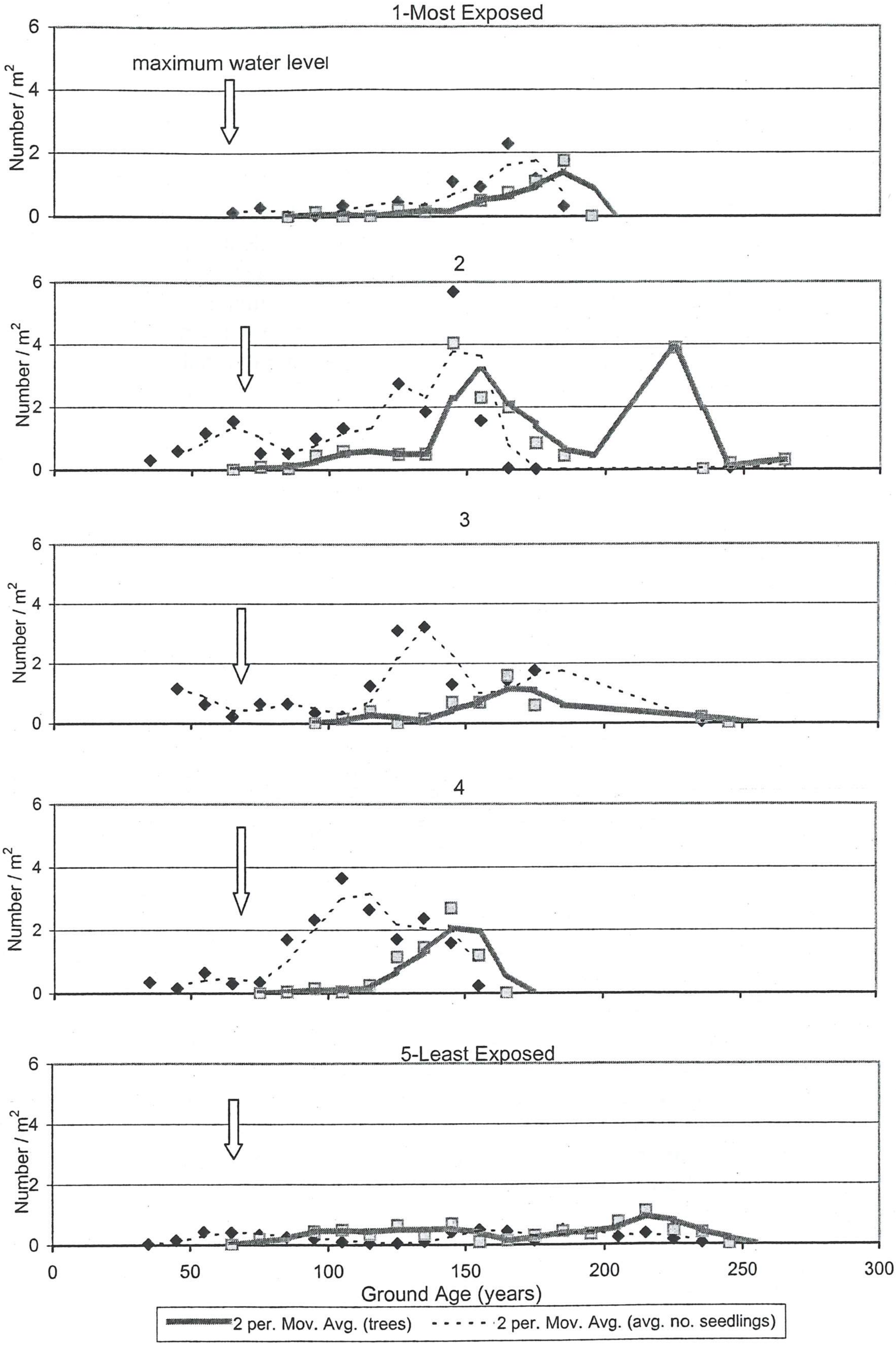

Figure 9: Distribution and average density (for 10 square meters) of spruce seedlings(<1.3m) and tallest trees (≥1.3 m) per 10-year classes in all transects. *Moving average is an analysis tool that allows one to smooth fluctuations in data.

4.5.2 Norway spruce current-year seedlings

The number of current seedlings arising in 1999 and 2000, shows a steady increase with increasing ground age (Fig. 10). It is evident that seedling ingress and establishment occurs on young ground, between 35 – 45 years old, which is only some 0.3 – 0.4 m above mean sea level. Hence, some ingress occurs in the zone of high sea water flooding (geo-littoral), although it is not known what proportion of these will actually survive. It is important to keep in mind that these results are based only on observations during two sequential years, and a rather small data set (n = 63).

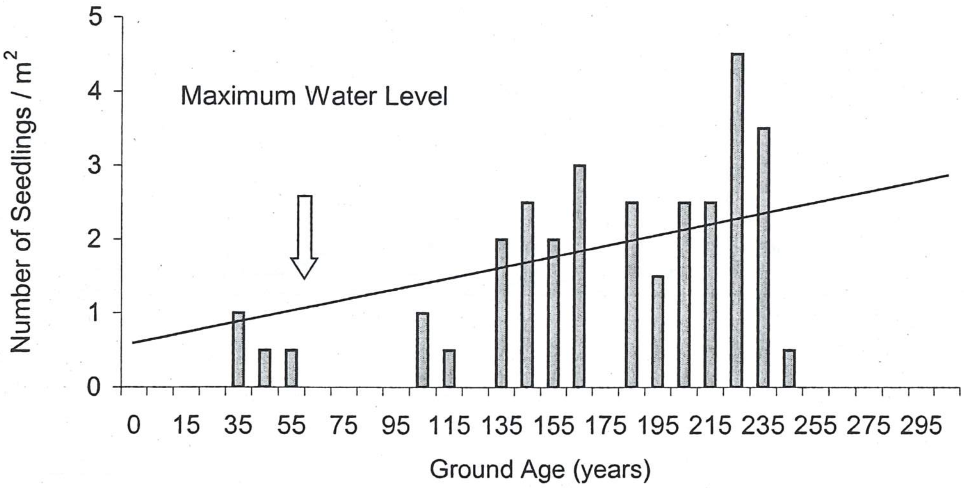

Figure 10: The age-class frequency distribution of spruce seedlings (current and 1-year-old) in transects 1-5, based on total seedlings arising in both 1999 and 2000 combined. The arrow illustrates the maximum point to which water level rises.

However, the above relationship is supported by the larger data set, which included all the established Norway spruce seedlings (< 1.3 m) (Figs. 8, 9). When current-year seedlings were identified and recorded in 1999 and 2000, the seedbed type in which they occurred was recorded. Most seedlings established on conifer litter and mosses (all moss types combined) (Fig. 11), which are most frequent in areas of higher elevation in the enclosed Norway spruce belt.

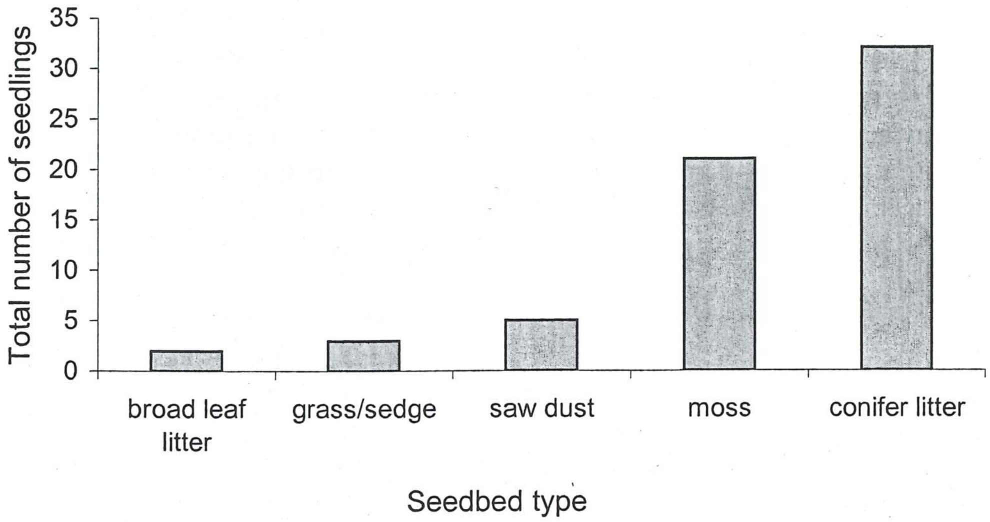

Figure 11: Preferred seedbed types of Norway spruce seedlings (current and 1-year-old), from 1999 and 2000 combined, in transects 1–5.

*Note: The sawdust is an artificial seedbed as a result of the harvesting operation.

4.5.3 Seedfall

It is clear from the data in Appendix 4 that seeds were falling in this area. The numbers of seeds trapped was least in the open stage (11 to 14 m^2), increased into the primary forested stage (29 to 30 m^2), and was greatest in the secondary forested stage (103 to 58 m^2, numbers for most exposed and least exposed transects, respectively).

5 Discussion

5.1 Organic layer depth

In Figure 6, we can see that surface organic layer depth increases with increasing ground age. This is logical since the successional pattern includes more vegetative cover and trees as the transects become older and as old-growth features develop. It is noteworthy that 15 to 20 cm of surface organic layer accumulated between about 110 and 250 years. To obtain true ground age, one should probably subtract the depth of surface organic layer from the elevation above mean sea level, and then determine age of the mineral soil, morainal surface. However, we may divide the surface organic layer depth by surface age, to obtain a rough estimate of accumulation rate. The regression line suggests about 0.7 mm of accumulation organic layer per year on average. Of course, these are unconsolidated depths of surface organic layer.

5.2 Field vegetation and ground cover

It could be hypothesized that the steeper the slope, the narrower the belts of vegetation. On steeply sloping shores the transitions from belt to belt are reported to be generally sudden, but on low sloping shores, a prolonged mixed zone can exist. According to Ericson and Wallentinus 1979, on steep sloping shores the possibility for generative establishment is rather small, owing to the lack of stable surface and limited area. In these areas, species that are able to regenerate vegetatively are favored.

However, there was no evidence in this study to support the hypothesis of steep slope influence. From Figure 5, we can see that with respect to slope, transects range from 3, 4, 5, 2, 1, in order of decreasing slope. Table 1 showed that the transects with the narrowest belts, transect 1 and 4, had quite different ground surface slopes of 2.3 to 5.0 cm/m. In fact, all of the slopes were rather gently sloping, from 2.3 cm/m to 5.9 cm/m. A much larger sample of transects would have been required to demonstrate relationships of vegetational belt width to steepness of slope.

I hypothesize that the narrow belts in transects 1 and 4 were more related to the low maximum age of these two transects, 185 and 188 years. The low ages are reflected in the lower maximum tree heights in this transects, about 18 m, in comparison to 20 to 22 in the other transects. The shorter time spans would have artificially 'forced' narrower belts to be created in the TWINSPAN in which there were always derived four classsification groups.

The vegetation sequence in transect 3 is quite irregular and doesn't fit the patterns shown by the other transects. There are several possible reasons for this difference. First, It is evident that this transect has the steepest slope of all the transects (Fig. 5). Secondly, it contains more birch than any other transect, and it also contains pine and has other mosses mixed with feathermoss. Thirdly, it seems to demonstrate irregular patterns of alternating field and ground types (Table 2) that may relate to varying parent material, or to the mixture of the birch with conifer in irregular pulses. This is the only transect where this occurs and hence suggests that there is something unusual about this transect.

It is important to remember that the results presented here on vegetation gradients are based on measures taken in the fall of the year when vegetation had browned and was reduced in density. Undoubtedly, the vegetational belts could be clarified with more information on species and using line intercept cover. It would be a more complete picture if this were a long-term study with several years of data collection.

5.3 Succession of all woody species

Upon investigating where all seedlings of woody species occur within the vegetative belts, there were general relationships (Fig. 7). Seedlings came into the first and second belts, and peaked in the second to fourth. Among trees, individuals ≥1.3 m, the sequence is alder, rowan and spruce from the seashore to the climax forest. It is also interesting to see how the seedlings show the same sequences, but offset closer to the sea. Of course spruce is the longest lasting species in both seedlings and trees. The decrease in spruce seedlings is owing to increasing size of spruce trees in later stages. The decrease in spruce trees in later stages is probably owing to the increasing spacing of larger trees and decreasing frequency. There are fewer trees because they are farther apart and less frequent but their size and canopy coverage is high.

5.4 Succession of Norway spruce

In forest conditions, owing to intense light competition, successful Norway spruce regeneration requires canopy gaps. With respect to moderate shade tolerance, Norway spruce seedlings can develop under moderate shade, but grow better in openings and gaps. This is evident when comparing treatment types to see which best supports seedling ingress. It is clear that small openings are more suitable for regeneration. From the data based on the 63 seedlings from 1999 and 2000, 80% of them were found in the clearcut strips while 20% were found beneath the overstory of undisturbed forest canopy (See Appendix 5). From Figures 10 and 11, we can see that most of these seedlings occurred on ground between 205 to 235 years of age and preferred conifer litter and moss (predominantly feathermoss) as a seedbed type. In other studies it has been noted that feathermoss is not normally a good seedbed, but in those studies there has also been site preparation to produce exposed mineral soil, a much superior seedbed (Jeglum and Kennington 1993).

It is well known that seedlings are in constant flux, with establishment and mortality happening continually. This is referred to as a 'changing seedling population' (Paavilainen and Päivänen 1995). Seeds may germinate soon after falling to the ground if they land on favorable seedbeds or in sheltered microsites with favorable moisture conditions (Leemans 1991). However, many of the seedlings will not survive long enough to become saplings. In the present study, 65% of the 1999 seedlings were dead in the 2000 assessment. Some of the seedlings that occur in the first vegetational belts are eventually out competed by grasses, small herbs and other vegetation that are in competition for water, light and nutrients. Seedlings can also be buried by fallen litter and debris which cuts off light and smothers them (Hannerz and Gemmel 1994). These factors probably explain why so few seedlings were observed, even in a year after a heavy cone crop when there should have been high numbers of germinants.

When considering the established spruce seedlings (< 1.3 m) in all five transects, it is evident that most of them appear on ground between 155 to 205 years of age. In all transects, this corresponds to belt 4, which includes fine conifer litter and sometimes ericaceous species and feathermoss. This suggests that the younger 1-year-old seedlings seem to occupy the older portions of the transects which are closer to the climax spruce forest and the seed bank in the crowns. First year seedlings probably have a lower establishment and high mortality rate on younger ground age where there is more competition and more extreme conditions of fluctuating water levels and exposure to drying.

5.5 Site aspect and exposure

In this study, the transects were purposely chose to represent aspects from S to W. This was done to reduce the variation among sites. Hence, there were not enough transects to permit any comparisons regarding aspect. The transects were also selected purposely to represent a range of exposures. This study shows that exposure does have an effect on succession. The field vegetation and ground cover groups from TWINSPAN occurred as higher belts in the exposed and lower in the sheltered locations. There is some evidence also that site exposure has an impact on seedling ingress and establishment. In the four least exposed transects 2 to 5, seedlings established initially at about the same level, 35 to 45 years, but in the most exposed did not establish until 65 years. In addition, seedlings achieved their modal occurrences at lowest elevations in one of the less exposed transects (4) and at highest elevations in the most exposed transect (1). This shift of modal occurrence of seedlings landward was related to a similar shift of the vegetation zones landwards, reflecting the important influence of both seedlings and vegetation to the influences of exposure, in particular the action of waves and ice drifting during high water levels.

6 Conclusions

From this and other studies, it is clear that old-growth forests can develop on these rising shorelines within a short ecological time frame (*cf.*, Svensson and Jeglum 2000, 2001). This area presents ample opportunity to study succession at its finest where land rises from the sea and becomes colonized and ultimately reaches a climax forest in a mere 200 to 300 years. It is fair to say that natural regeneration in this area of primary succession is a very viable means of regenerating the site.

As seen in this study, the downward migration eventually declines with increasing elevation above mean sea level (*cf.* Ericson 1980). This is true for all species of trees, seedling and for vegetation species. The rate at which this downward migration declines and where vegetation stabilizes into a mature spruce forest is at about 1.27 to 1.96 m above mean sea level or 150 to 230 years, depending on exposure and possibly slope. When the mature forest is established, the original factors of succession and downward migration are taken over by internal dynamics of the spruce-dominated forest. Then gap creation, intra-species competition, and understory regeneration dominate the internal dynamics.

This paper demonstrates that the regeneration potential of naturally developed forests is high. The full utilization of the undergrowth in managed stands has the ability to minimize the need for artificial regeneration, shorten the rotation, enhance yield and increase the internal biodiversity of stands (Laiho *et. al.* 1994). Since our knowledge in the area of emerging coastlines is so fragmentary, I suggest that a more intensive and longer-term study of the vegetation gradients and survival rates of initial spruce seedling regeneration should be undertaken. Spatial and temporal changes occur more frequently for vegetation and the changing seedling populations on the shorelines than could be measured over several years. As well seed supply, seedfall, and seedling-seedbed relationships are of critical importance.

7 Acknowledgements

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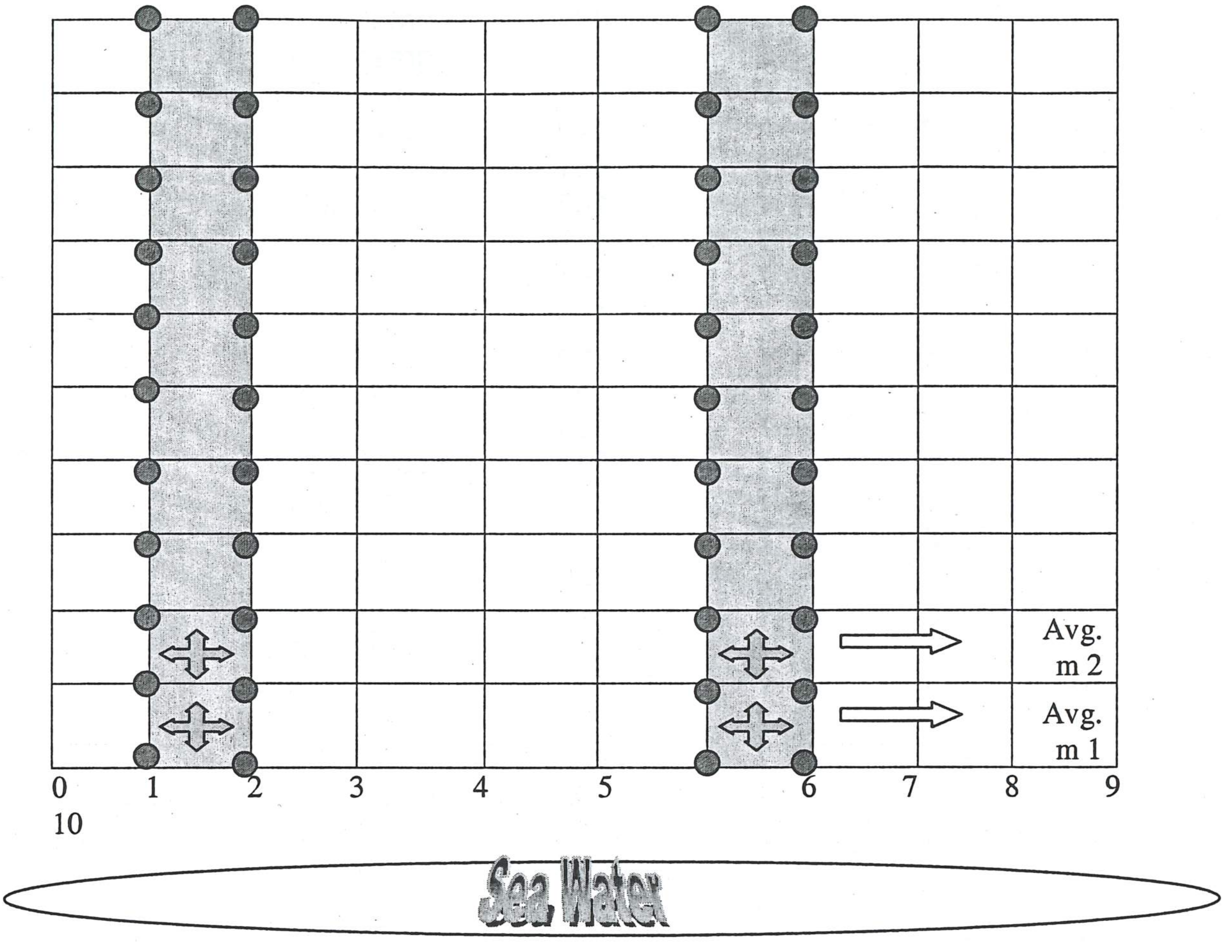
List of Appendices

Appendix 1: Species that are included in the ground surface and field layer vegetation categories.

Vegetation Layer Species	Category	Included
Ground Surface Layer	Feathermoss	*Hylocomium splendens* *Pleurozium schreberi* *Ptilium crista-castrensis* Dicranum spp.
	Polytrichum	*Polytrichum spp.*
	Sphagnum	*Sphagnum spp.*
	Other mosses	(all others that are not listed above)
	Lichens	*Cladina* and *Cladonia spp.*
	Sawdust	(from the clearcut transects)
	Fine conifer litter	(needles, fine litter material and twigs < 1 cm)
	Coarse conifer litter	(twigs >1 cm, branches, cones and scales)
	Broadleaf litter	(mostly leaves, some small twigs and very small hardwood seedlings)
	Other	(rocks, stumps, coarse wood, animal scat, ant mounds or anything not listed in other categories)
Field Layer	Low shrub (shrubs < 0.5 m with woody stems)	*Hippophae rhamnoides* *Myrica gale* *Juniperus commune*
	Ericaceous sp.	*Vaccinium spp.* *Empetrum spp.*
	Herbs, Pteridophytes	*Oxalis* *Equisetum* *Lycopodium*
	Grass, Sedge	*Carex spp., Gramineae*

Appendix 2: Experimental Design of the Transects



As described in the text, this is the experimental design of the transects. Every block represents a square meter and every grey block represents where the sampling was carried out. The black dots represent points where soil depth and elevation were measured. The four-point arrows (✣) in the center of the squares represent the average of the four points that were used to calculate the average value for that square meter.

After a mean value was assigned to each quadrat, using the four corner points, the average of the two quadrats along the X- axis (→) was calculated and used as the value for that specific meter along the Y- axis (↑). The forward arrow ⇨) gives the average for the two square meters that were sampled along the X- axis to get a single value for each meter along the length of the Transects (eg. 1, 2, 3, etc. along the Y-axis).

** Note: This figure is just a sample of the first 11 meters of the transects.*

Appendix 3: Distribution of 1-year old seedlings in relation to treatment, ground age and seedbed type. In both 1999 and 2000, 430, 1-m2 quadrats were assessed.

From the 1999 inventory

Seedling	Transect	Treatment	Ground Age	Seedbed Type
1	1	2	55	grass/sedge
2	1*	2	131	grass/sedge
3	1*	7	168	conifer litter
4	2*	2	149	conifer litter
5	2*	2	151	conifer litter
6	2*	7	185	sawdust
7	2	7	149	conifer litter
8	2	7	151	moss
9	2	7	168	moss
10	2	7	168	moss
11	2	7	185	sawdust
12	2	7	185	moss
13	2	7	222	conifer litter
14	2	7	222	conifer litter
15	2	7	226	conifer litter
16	2	7	226	conifer litter
17	2	7	225	conifer litter
18	2	7	246	conifer litter
19	3	7	49	grass/sedge
20	3*	7	206	conifer litter
21	3*	7	206	conifer litter
22	4	2	106	broadleaf litter
23	4	2	106	broadleaf litter
24	4	7	133	moss
25	5	2	35	moss
26	5	7	32	moss
27	5	7	134	sawdust
28	5*	7	151	moss

* Note: The * indicates seedlings that were missed in 1999 but noted in 2000, treatment 2 represents the undisturbed transect and treatment 7 represents the clearcut transects.

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From the 2000 inventory

Seedling	Transect	Treatment	Ground Age	Seedbed Type
29	1	7	168	moss
30	1	7	168	moss
31	1	7	184	moss
32	2	7	149	conifer litter
33	2	7	207	conifer litter
34	2	7	228	conifer litter
35	2	7	226	conifer litter
36	2	7	225	conifer litter
37	2	7	232	conifer litter
38	3	2	225	conifer litter
39	3	2	231	conifer litter
40	3	7	194	conifer litter
41	3	7	202	conifer litter
42	3	7	202	moss
43	3	7	216	conifer litter
44	3	7	228	moss
45	3	7	238	moss
46	3	7	238	conifer litter
47	4	2	182	moss
48	4	7	133	sawdust
49	4	7	150	sawdust
50	4	7	163	moss
51	5	2	191	conifer litter
52	5	2	199	conifer litter
53	5	2	238	conifer litter
54	5	7	117	moss
55	5	7	144	conifer litter
56	5	7	149	conifer litter
57	5	7	151	moss
58	5	7	215	conifer litter
59	5	7	215	conifer litter
60	5	7	217	conifer litter
61	5	7	211	moss
62	5	7	238	moss
63	5	7	238	moss

Survivorship of 1-year-old seedlings between 1999 and 2000 seedling inventory.

Transect		Seedlings 1999	Survivors In 2000	Overlooked seedlings(99)	Seedlings 2000
1		1	0	2	3
2		12	8	3	6
3		1	1	2	9
4		3	1	0	4
5		3	1	1	13
	Total	20	11	8	35

Appendix 4: Seedling density for the seed traps in each stage of the most and least exposed transects.

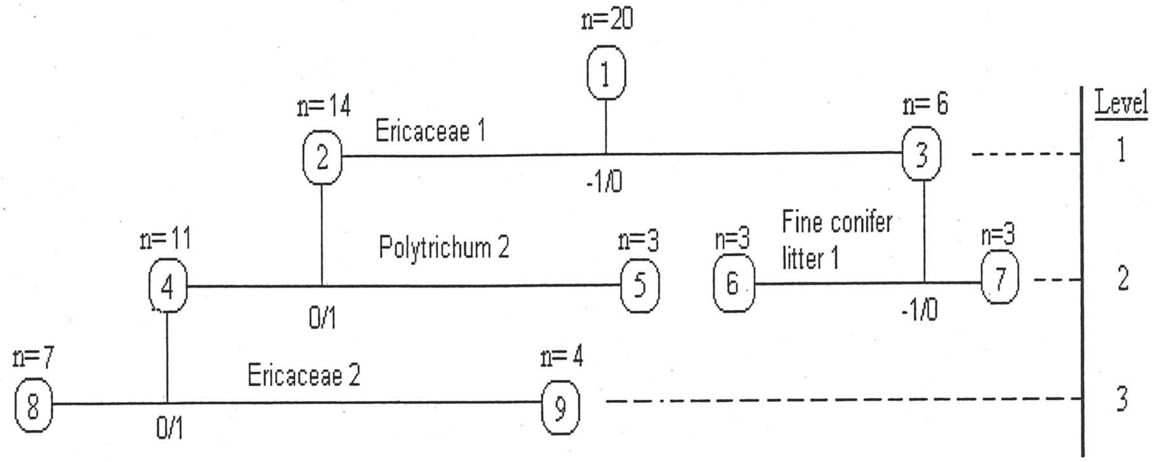
Transect	*1 – Most Exposed*	*5 – Least Exposed*
Open stage (4 seed traps)	11 / m^2	14 / m^2
Primary Forested Stage (3 seed traps)	30 / m^2	29 / m^2
Secondary Forested Stage (3 seed traps)	103 / m^2	58 / m^2

* Note: The open meadow stage contained 4, 0.25-m^2 traps and the primary and secondary forested stages contained 3, 0.25-m^2 traps. It is important to remember that these numbers are based on a one–year study.

The number of seeds in each trap was counted in 2000 and seed density was determined. Since each trap represented ¼ of a square meter, the density of seeds / m^2 was determined using this formula:

$$\text{Density} = \frac{\text{total number of seeds}}{0.75\ m^2 \text{ (for three traps) or } 1.0\ m^2 \text{ (for four traps)}} = \text{number of seeds} / m^2$$

Appendix 5: An example of a classification dendrogram (e.g., transect 5) produced by the TWINSPAN analysis showing the rules and species used to create the three divisions.



Samples (Age Classes)
1= 35
2= 45
3= 55
4= 65
5= 75
6= 85
7= 95
8= 105
9 = 115
10= 125
11= 135
12= 145
13= 155
14= 165
15= 175
16= 185
17= 195
18= 205
19= 215
20= 225

Cut Levels (% ground coverage)
1= 0 (0 - 1%)
2= 2 (2 - 4%)
3= 5 (5 - 9%)
4= 10 (10 - 24%)
5= 25 (25 - 49%)
6= 50 (50 - 74%)
7= 75 (75 - 100%)

From the figure above, *n* = the number of samples, the species names followed by a number (eg. *Ericaceae)* represents the cut level number and species by which the division rule was determined and the *levels* indicate the number of divisions used in the classification.

Appendix 6: The distance of the transects from their starting point to the water level.

Transect	Distance (m)
1	8
2	18
3	5
4	3
5	12

* Note: All distances were measured from the middle of the transects (from meter 5 along the X-axis) August 18^{th}, 2001 and may change slightly during the year. The distances given here represent the point at which the start of the water level occurred however, in some cases there was a lot of vegetation or terrain that extended much further toward the sea before being completely submerged. The transects where this was most obvious were 2 and 5. Transect 2 extended for approximately another 40 meters before there were waves with no visible vegetation, and in transect 5 there was a mire that extended to the bay for approximately 15 meters past the point where I measured the first visible water level.

Appendix 7: Common and scientific names of all species mentioned in thesis.

Scientific Name	Common Name
Alnus incana	grey alder
Betula pendula	pendulous birch
Betula pubescens	pubescent birch
Carex spp.	sedge
Ceratodon purpureus	fire moss
Cladina spp.	reindeer lichen
Cladonia spp.	cup and club lichen
Dicranum spp.	broom moss
Empetrum nigrum	crowberry
Equisetum spp.	horsetail
Gramineae	grass
Hippophae rhamnoides	sea buckthorn
Hylocomium splendens	stair-step moss
Juniperus communis	juniper
Lycopodium	club moss
Myrica gale	sweet gale
Oxalis spp.	wood sorrel
Picea abies	Norway spruce
Pinus sylvestris	Scots Pine
Pleurozium schreberi	shrebers moss
Pohlia nutans	copper wire moss
Polytrichum commune	common hair-cap moss
Ptilium crista-castrensis	plume moss
Sorbus aucuparia	rowan
Sphagnum spp.	sphagnum moss
Vaccinium myrtilloides	blueberry
Vaccinium myrtillus	bilberry
Vaccinium vitis-ideae	lingonberry