

# Spatio-temporal properties of tree-species belts during primary succession on rising Gulf of Bothnia coastlines

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This paper elucidates spatial and temporal pathways of tree-species colonization and forest development during 260 years of undisturbed primary succession on rising ground-moraine shorelines in the Norra Kvarken Archipelago, Gulf of Bothnia, northern Sweden. Four species — grey alder (*Alnus incana*), rowan (*Sorbus aucuparia*), juniper (*Juniperus communis*), and spruce (*Picea abies*) — occur commonly and form distinct belts. The earliest individuals ( $\geq 0.5$  m) of alder were found after 20 years of succession, of spruce after 40 years, of juniper after 50 years, and of rowan after 60 years. Because of the longer time required by spruce to become dominant, the order of belts from younger to older was: alder–rowan–juniper–spruce. The belt width decreased from alder to rowan to juniper, and with increasing shore slope. We identified six successional stages by occurrence and composition, from pure alder to pure spruce, and three stages by species dominance. Spruce became dominant after 160 years of succession and forms the climax forests on these sites.

Key words: coastal forest, land uplift, rising coastlines, succession, undisturbed forest, zonation

## Introduction

The post-glacial rebound of the Fennoscandian crust provides conditions for primary succession along the Gulf of Bothnia coastlines (Glenn-Lewin & van der Maarel 1992). Plants and communities are continually able to migrate downwards on the shore slope and colonize emerging ground (Cramer 1993, Rinkineva & Bader 1998, Svensson & Jeglum 2000). The ongoing land uplift provides a topographic sequence equivalent to a temporal sequence (chronosequence); the lower the elevation the younger the ground

with younger, pioneer communities, the higher the elevation the older the ground and the more mature the communities. The vegetation gradient from the shoreline and landwards reflects the actual course of succession (Ericson & Wallentinus 1979).

Several reports have been published on the geological and ecological significance of the Gulf of Bothnia land-uplift area, for instance by Ericson and Wallentinus (1979), Mörner (1980), Rinkineva and Bader (1998), Svensson and Jeglum (2000), and Fredén *et al.* (2001). It is evident that the coastlines provide exceptional

possibilities to study ecosystem succession, from original site emergence to the development of late-successional forest stages (Svensson & Jeglum 2001). It is also evident, however, that even though the successional sequences have been described in a general way, detailed quantitative studies are lacking. The route or routes towards late-successional, climax-like forest stages are to a large degree unknown, as concluded earlier by Ericson and Wallentinus (1979) and Ericson (1981a), and more recently in our review of successional work completed in the Gulf of Bothnia and elsewhere (Svensson & Jeglum 2000).

The temporal, successional sequence on the land-uplift coast can be constructed as a function of altitude (topography) and land-uplift rate. The known uplift rate (e.g. Bergsten 1954, Ekman 1993) provides the possibility to estimate the rate of ongoing terrestrial succession by measuring the ground-surface elevation above mean sea level and dividing by the rate of uplift. This method has been applied frequently in earlier studies for determining substrate age and interpreting ecological processes in land-uplift areas (Cramer 1985, Verwijst & Cramer 1986, Cramer & Hytteborn 1987, Carlsson *et al.* 1990, Starr 1991, Grégoire & Bégin 1993, von Mörs & Bégin 1993, Giles & Goudet 1997, Punning *et al.* 1998, Svensson & Jeglum 2003). In this study we use the above ground elevation, i.e. on top of the humus layer, and we refer to the estimated successional dating as 'ground age'.

The primary succession on rising ground-moraine shores terminates in Norway spruce (*Picea abies*) dominated communities (Appelroth 1948). Earlier (Svensson & Jeglum 2000), we have concluded that four distinct successional stages can be distinguished: (1) an open, early meadow-stage dominated by graminoids and low-growing shrubs; (2) a primary-forested stage dominated by broadleaf trees; (3) a secondary-forested, spruce-dominated stage; and (4) a climax-like, spruce-dominated stage, provided where there are long enough undisturbed sequences. Owing to the favorable climate in the Gulf of Bothnia region, the succession process may be rapid; a well-stocked, old-growth Norway spruce forest can develop within two to three centuries of succession (Svensson 1998).

Such sites present an excellent opportunity to examine natural succession and dynamics, and to classify stages of structural development (cf. Cramer 1985, Verwijst & Cramer 1986, Svensson & Jeglum 2001).

Many different factors influence the vegetation succession, e.g. exposure, fetch and location in the archipelago, shore slope, parent material, elevation relative to sea level changes, and site area and isolation (cf. Ericson & Wallentinus 1979, Svensson & Jeglum 2000). Pioneers and competition intolerant species colonize the initial stages (Ecke & Rydin 2000). Factors such as changing water levels, ice drifting, and strong winds, are important not only because of the overall disturbance, but also because of the erosive effect that makes new ground available for colonization. The ground close to the shoreline is less suitable for species that do not have the ability to tolerate such disturbances and to recover vegetatively (Ecke & Rydin 2000). On low-sloping shores, the width of newly-exposed ground is large, and regeneration by seeds is more successful. On steeply sloping shores on the other hand, the possibilities for regeneration by seeds are rather small owing to limited space and ground surface instability. Here, species that already are present and that are able to regenerate vegetatively are favored (Ericsson & Wallentinus 1979).

With increasing elevation and less disturbance, more competitive species are favored. Plants that inhabit the upper geolittoral (above mean water level) and landwards, i.e. mostly long-lived herbs, Ericaceae shrubs and other woody species, are influenced by water-level fluctuations and other seashore factors only to a slight degree (Ericson 1981a). Thus, in the upper geolittoral and landwards, the rate of downward migration by vegetation roughly coincides with the rate of land uplift (Ericson 1981a).

The objective of this paper is to elucidate the spatial and temporal relationships of tree-species belts, from early- to late-successional, along ground-moraine seashore gradients. A basic assumption was that the constant (over the viewed time period) and known land-uplift rate creates a temporal sequence (chronosequence) determined by the topographic slope, and that this provides a predictable successional gradient

of tree-species belts. We searched for patterns in tree-species performance and belt characteristics, and how these depended on the shore slope and on the spatial and temporal sequences available. These patterns may be related to the inherent properties of the species — e.g. regeneration traits, sensitivity to competition, phenotype, sensitivity to submergence and disturbance, seedbed requirements, and nutrient demand — relative to spatial and temporal aspects of succession.

## Material and methods

### Study area

The coastal area of Norra Kvarken (about 62°40′ to 64°10′ N and 19°10′ to 22°20′ E), the Gulf of Bothnia, belongs to the southern boreal zone which extends northwards in a narrow strip along the coast as a consequence of maritime influence (Rinkineva & Bader 1998). The seawater is brackish, with a salinity range from 0‰ to 5‰ (Ericsson & Wallentinus 1979). The tidal influence is very slight, less than 10 cm, but fluctuations in sea level owing to wind and air pressure changes are pronounced, normally 120 to 130 cm and in extreme cases 250 cm or more (Svensson 2002). The annual precipitation ranges between 400 and 550 mm, and the annual mean temperature is 3 to 4 °C. The duration of ice cover is 80 to 100 days, and the duration of snow cover about 150 days. The growth period is about 150 days (6 °C) (Ericsson & Wallentinus 1979, Ericson 1981a).

The coastal landscape is characterized by parallel upland drumlins, oval-shaped and low-altitude moraine ridges, with wetland swales between them. Islands and peninsulas are built up of moraine deposits and bedrock, mainly various kinds of granite, gneiss and acid igneous rocks (Fredén 1994). The coastline topography is gentle with numerous peninsulas, bays and islands, which results in substantial gain of land by the uplift process and rapid landscape changes within short times (Rinkineva & Bader 1998, Svensson 2002).

Ivarsboda Municipality in the Norra Kvarken coastal area, northern Sweden, was subject in 1856 to estate legalization (Svensson 2002). A

border was set along the shoreline to enclose a strip of community-owned land seawards from the privately-owned land. According to Ristaniemi *et al.* (1997), this was a common procedure for Swedish and Finnish coastal villages in the past, to ensure public access to sea landings and to allocate the gain of land among the land holders in a just way. The strip of community-owned land has in some instances been left for natural development, and nowadays provides longer-term undisturbed succession sequences (Svensson & Jeglum 2000).

We selected five shoreline locations within the Sladan Nature Reserve (63°51′ N, 20°43′ E), Ivarsboda Municipality, and placed two transects (named A and B) at each site. The sites were chosen to: (1) represent a range of low to high coastal exposure; (2) have restricted ranges of compass aspects, south- (S) to west-facing (W); (3) consist of representative vegetation gradients; (4) have undisturbed successions; and (5) consist of as long-term undisturbed succession as possible.

Transects 1A and 1B (S-facing) represented the highest exposure, facing the open sea of Norra Kvarken on the tip of Österstgrundet Peninsula. Transects 2A and 2B (S) were on the tip of Lillgrundudden Peninsula close to the opening of the large Bay of Ostnäs. Transects 3A and 3B (SW) and 4A and 4B (W), on the west side of the peninsula facing the interior of the bay, represented successively less exposed shorelines. Finally, transects 5A and 5B (SW) were placed inside the semi-enclosed small Bay of Sönerstgrundsfärden, representing a sheltered location. A site map is provided in Svensson (2002).

### Data collection

Each transect was 10-m wide and extended landwards perpendicular to the shoreline, from a position on the shore where the outermost (earliest) tree-species individual was found. We define tree species as woody species that normally grow to heights of 1.3 m or more (*see* Table 2). Because of its frequent appearance, we included juniper (*Juniperus communis*) although it is a shrub species rather than a tree species. Transect

lengths varied with the width of undisturbed shoreline forest. Thus, their upper end usually coincided with the border between community-owned and privately-owned land.

All live tree species  $\geq 1.3$  m of height were mapped and positioned, with records on species, height, and diameter at 1.3 m. Individuals 0.5–1.3 m of height were counted in every square meter within the transects. Each transect can be viewed as a coordinate system of  $1 \times 1$  m square grid, with data on number per species for individuals 0.5–1.3 m in each square, on which mapped larger trees were overlaid. The  $x$ -axis in the coordinate system was set as the width (10 m) parallel to the shoreline, and the  $y$ -axis as the length (variable) perpendicular to the shoreline. The  $y$ -axis represents the spatial (distance) sequence.

Transect topography was measured with a theodolite. Elevation was measured on ground surface and compared with the current sea level. Adjustments to mean sea level were done according to records from the nearby Ratan Mareograph ( $64^{\circ}00'N$ ,  $20^{\circ}55'E$ ), provided by SMHI. In the five A-transects, i.e. one per site, we measured elevation at every meter along two lines,  $X = 1.5$  m and  $X = 6.5$  m starting at  $Y = 0.5$  m, and in each transect corner. In the five B-transects, we measured the elevation at every fifth meter plus at the transect end along the lines  $X = 0$  m,  $X = 5$  m and  $X = 10$  m, with the first measuring point at  $Y = 0$  m, and at every fifth meter along the lines  $X = 2.5$  m and  $X = 7.5$  m, starting at  $Y = 2.5$  m. The reason for the more careful treatment of the A-transects was that these were subject to more detailed studies of spruce seedlings, seedbed types, and non-woody vegetation. Results from these studies are presented in Svensson & Jeglum (2003).

## Analysis

The temporal sequence was constructed as a function of ground elevation above mean sea level and land-uplift rate. The uplift rate in the area is 0.0084 m/year (Topographic map Umeå 20K NO, Lantmäteriet 1989). Hence, 1 m of land uplift is equivalent to a 119 years ground-age sequence. Ehlert (1982) estimated the 95% confidence interval for the uplift rate to

$\pm 0.00049$  m/year, and Ekman (1993) the standard error to 0.0003 m/year.

The spatial (cm/m) and temporal (years/m) slopes were determined for each transect, as the regression coefficient from a linear regression of mean elevation points along the  $y$ -axis. Transects were ranked by slope according to this coefficient. A moving average trend line between two adjacent mean elevation points was used to illustrate the spatio-temporal profile of each transect (see Fig. 1). The spatio-temporal “window” covered by the ten transects was determined by calculating a regression model for straight lines that touched two upper and two lower profile points, respectively.

The spatial analysis concerned species density as the average of numbers in ten  $1\text{-m}^2$  squares in a row along the  $x$ -axis (named ‘ $10\text{-m}^2$  row’), i.e. for each meter along the  $y$ -axis. A tallest tree analysis, for individuals  $\geq 1.3$  m, was done for the tallest tree of each species in the  $10\text{-m}^2$  row.

Belt widths and ranges, population centers, and density modes were calculated based on species occurrence and density in the  $10\text{-m}^2$  rows, for individuals 0.5–1.3 m and for individuals  $\geq 1.3$  m, respectively. The population centers were calculated as the weighted average  $Y$  [meter] along the transect:

$$Y[\text{meter}] = \sum d_i Y_i / \sum d_i \quad (1)$$

where  $d_i$  was species density in the  $Y_i$ -meter from the transect start ( $Y = 0$ ). The density mode was located to the  $Y_i$ -meter in which the highest density was found. The spatial belt width of each species and its relationship with transect slope was analyzed based on Pearson’s correlation coefficient ( $r$ ).

The temporal analysis was done by 10-year ground-age classes, where ‘ground age’ is the estimated dating based on ground surface elevation above mean sea level and land-uplift rate. Ground age was determined as a mean of the measures for each  $10\text{-m}^2$  row. Because of uneven slope and slope differences among transects, the ground-age classes consisted of variable numbers of rows ( $n$ ). The ground-age classes are denoted by the mid-value, i.e. 25 for class 20 to 29 years, etc. Analysis was done on density of

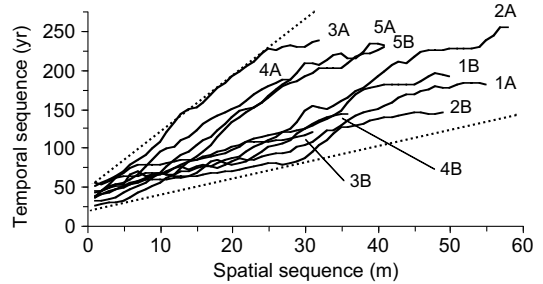
individuals and on tallest tree and average height for the different species. Density was determined for individuals 0.5–1.3 m and for individuals  $\geq 1.3$  m, respectively, as well as for the total population of each species. Tallest tree and average heights with standard errors were determined for individuals  $\geq 1.3$  m in occupied rows.

## Results

The ten transects represented a range of spatio-temporal properties (Table 1). The spatial sequences, i.e. transect lengths, varied from 28 (4A) to 59 (2A) meters. The temporal sequences ranged from 86 (3B) to 218 (2A) years of succession. Nine transects encompassed more than 100 years of succession, and three transects more than 200 years. Taking the transects together, sequences from 24 (5B) to 261 (2A) years of succession was covered.

The spatial and temporal shoreline slopes varied almost threefold, from 2.0 to 5.8 cm per meter, and from 2.4 to 6.9 years per meter. The transects were ranked based on increasing slope from transect 2B to 3A. The linear regressions used for slope calculations gave coefficients of determination ( $r^2$ ) that ranged from 0.934 (2B) to 0.993 (4A).

Transect pairs 1A and 1B, and 5A and 5B, showed similar ground-surface profiles, but the other three pairs of transects did not (Fig. 1). The  $\alpha$  values (y-axis intercept at  $X = 0$ , i.e. at



**Fig. 1.** Ground-surface profiles for the ten transects. The profiles of the ten transects are represented by a moving average line between mean elevation points. The dotted lines enclose the spatio-temporal “window” covered by the ten transects.

transect origin) from the linear regression on mean elevation points, varied between transects from 5 (5B) to 46 (4B) cm above mean sea level, corresponding to 6 and 54 ground-age years. The dotted lines in Fig. 1 enclose the spatio-temporal “window” covered by the ten transects. The slopes of these lines are 2 and 7 cm (3 and 9 years) per meter for lower and upper lines, respectively. The  $\alpha$  values were 19 cm (23 years) for the lower line, and 46 cm (54 years) for the upper line.

A total of seven taxonomic groups of tree species 0.5 m tall or more were found within the ten transects. Table 2 summarizes the numbers of individuals in two height classes and totals over the 4220 m<sup>2</sup> inventoried. Birch (*Betula* spp.) includes *B. pendula* and *B. pubescens*, and

**Table 1.** Spatio-temporal properties and slope rank for the ten transects. Spatial sequence = transect length. Temporal sequence = ground age dating at transect start and end. Spatial and temporal slopes are based on linear regressions of mean elevation points at each meter along the y-axes. Transect slopes are ranked from less to more steep shore slope.

Transect	Spatial sequence (m)	Temporal sequence (yr)	Spatial slope (cm m <sup>-1</sup> )	Temporal slope (yr m <sup>-1</sup> )	Slope rank
1A	55	134 (51–185)	2.3	2.7	3
1B	50	157 (38–195)	3.0	3.5	5
2A	59	218 (43–261)	3.4	4.0	6
2B	49	113 (32–145)	2.0	2.4	1
3A	32	189 (49–238)	5.8	6.9	10
3B	31	86 (33–119)	2.5	2.9	4
4A	28	146 (42–188)	5.0	5.9	9
4B	36	111 (31–142)	2.3	2.7	2
5A	41	207 (31–238)	4.9	5.7	7
5B	41	205 (24–229)	4.9	5.8	8

willow (*Salix* spp.) includes *S. phylicifolia* and *S. myrsinifolia* types. A total of 4108 individuals 0.5 m tall or more were sampled, which is close to one per m<sup>2</sup> on average.

Four species occurred commonly in the transects: grey alder (*Alnus incana*), Norway spruce, rowan (*Sorbus aucuparia*) and juniper. Birch, Scots pine (*Pinus sylvestris*) and willow were found only occasionally. Transect 3A, which had the steepest slope among the ten transects (Table 1), harbored half or more of the sampled individuals of these occasional species.

Alder was generally found at the start, or very close to the start, of the transects (Table 3). The general species sequence for the height class 0.5–1.3 m was from alder to spruce to rowan to juniper. Rowan appeared earlier than spruce in one transect (1B), and as late as or later than juniper in two transects (5A and 5B). A common but not absolute trend was that individuals which belonged to the smaller height class (0.5–1.3 m) were found before individuals which belonged to the larger height class ( $\geq 1.3$  m). For the larger height class, spruce tended to appear as late as or later than rowan. Here, the general order of appearance was from alder to rowan to spruce.

Hence, the order between rowan and spruce was reversed as compared with the smaller height class. Because height development is not a significant measure for juniper, all individuals of this species were sorted into the smaller height class.

Alder was the first species to become extinct, followed by juniper and rowan. Since spruce is the terminal species in these successions, with a distribution that continues beyond the transects, its upper belt range was set equal to the upper end of the transects in Table 3.

The belt width generally decreased from alder to rowan to juniper. The belt width also generally decreased with increasing shore slope, from transect 2B (gentle slope) to transect 3A (steep slope). The belt width for spruce is added in Table 3 to provide a reference measure.

The position of population centers (weighted average of density) and density modes (highest density) showed that alder followed by rowan dominated in early successional stages. The alder population center was earlier than for the other species in all ten transects. The rowan population center was the second earliest in nine out of ten transects. Likewise, the alder density mode was earlier than for the other species in all

**Table 2.** Number of recorded individuals in two height classes, 0.5–1.3 m and  $\geq 1.3$  m, and total for both classes.

Species	Class	1A	1B	2A	2B	3A	3B	4A	4B	5A	5B	Total
Alder	0.5–1.3 m	135	63	46	122	40	44	59	82	63	50	704
	$\geq 1.3$ m	245	99	126	147	60	141	76	173	55	54	1176
	Total	380	162	172	269	100	185	135	255	118	104	1880
Spruce	0.5–1.3 m	122	26	201	65	46	95	12	60	46	22	695
	$\geq 1.3$ m	49	34	80	92	58	22	34	54	80	54	557
	Total	171	60	281	157	104	117	46	114	126	76	1252
Rowan	0.5–1.3 m	135	61	78	23	10	80	11	26	32	17	473
	$\geq 1.3$ m	79	29	27	9	5	34	11	17	9	9	229
	Total	214	90	105	32	15	114	22	43	41	26	702
Juniper	0.5–1.3 m	60	22	22	5	8	1	0	0	27	22	167
	$\geq 1.3$ m	2	17	2	1	15	0	2	1	3	3	46
	Total	62	39	24	6	23	1	2	1	30	25	213
Birch	0.5–1.3 m	0	0	0	0	21	0	0	9	2	0	32
	$\geq 1.3$ m	1	0	0	0	2	0	0	4	0	1	8
	Total	1	0	0	0	23	0	0	13	2	1	40
Pine	0.5–1.3 m	1	0	0	0	6	0	0	0	0	1	8
	$\geq 1.3$ m	1	1	1	1	1	0	0	0	2	0	7
	Total	2	1	1	1	7	0	0	0	2	1	15
Willow	0.5–1.3 m	0	0	0	1	3	0	2	0	0	0	6
	$\geq 1.3$ m	0	0	0	0	0	0	0	0	0	0	0
	Total	0	0	0	1	3	0	2	0	0	0	6
Total		830	352	583	466	275	417	207	426	319	233	4108

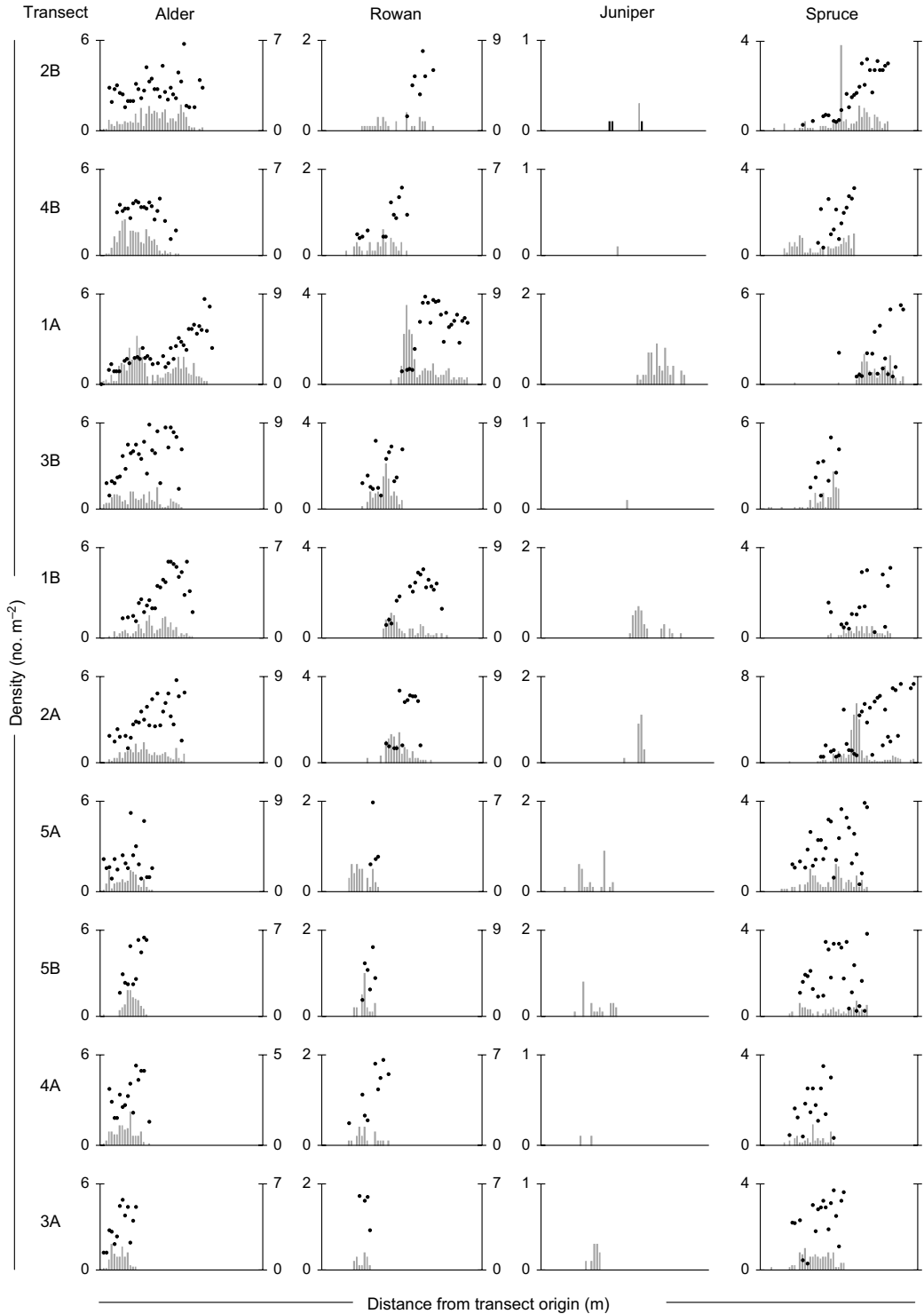


ten transects, and the rowan density mode was the second earliest in eight of the ten transects. These measures were calculated for the two height classes combined, to portray the total

population patterns. The population centers and density modes for spruce should be viewed as reference measures for the other species. The highest densities found were 5.5 m<sup>-2</sup> (spruce),

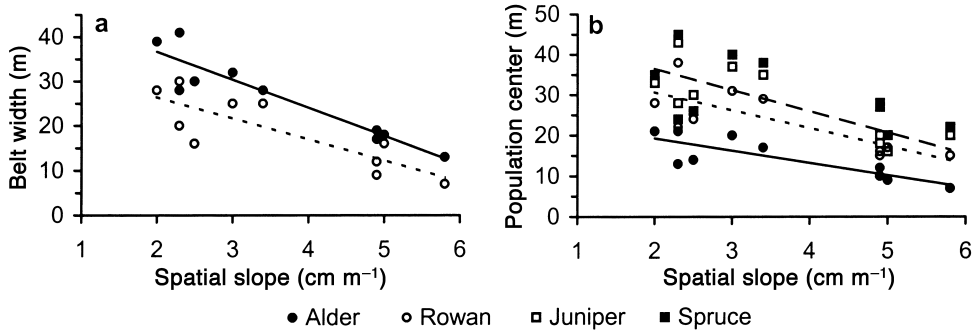
**Table 3.** Spatial belt range and width for alder, rowan, juniper and spruce in two height classes (one class for juniper), and population centers and density modes for the height classes combined. Transects are arranged from low to high slope (Table 1), and species after the position of the population centers. The belt range is displayed as the position in meters from transect start of the occurrence of the first and last individuals. The belt width is the spatial distance of the species range. The upper belt range for spruce is set equal to the upper end of the transects. The positions of population centers and density modes are in meters from transect start. The density mode can occur at one meter (one value given), two meters (two values), or more than two meters (range given).

Transect	Species	Belt range (m)		Belt width (m)		Population center (m)	Density mode	
		0.5–1.3 m	≥ 1.3 m	0.5–1.3 m	≥ 1.3 m		(m)	(no. m <sup>-2</sup> )
2B: 49 m	Alder	1–35	3–38	35	36	21	30	1.7
	Rowan	15–37	32–42	23	11	28	32	0.4
	Juniper	25–37		13		33	36	0.3
	Spruce	5–49	16–49	45	34	35	31	3.8
4B: 36 m	Alder	2–29	6–28	28	23	13	9	2.5
	Rowan	13–32	13–32	20	20	22	23	0.6
	Juniper	28		1		28	28	0.1
	Spruce	9–36	22–36	28	15	24	36	1.0
1A: 55 m	Alder	1–38	1–41	38	41	21	14	3.2
	Rowan	26–55	30–55	30	26	38	32	3.5
	Juniper	35–52		18		43	42	0.9
	Spruce	13–55	30–55	43	26	45	40	2.0
3B: 31 m	Alder	1–29	2–30	29	29	14	21	1.5
	Rowan	17–30	15–30	14	16	24	24	2.1
	Juniper	30		1		30	30	0.1
	Spruce	3–31	19–31	29	13	26	28	2.6
1B: 50 m	Alder	3–32	8–34	30	27	20	18	1.5
	Rowan	23–47	24–45	25	22	31	26	1.4
	Juniper	31–49		19		37	34	0.7
	Spruce	30–50	26–50	21	25	40	37–43	0.5
2A: 59 m	Alder	4–31	3–31	28	29	17	16	1.4
	Rowan	17–41	24–37	25	14	29	29	1.4
	Juniper	29–36		8		35	34	0.9
	Spruce	11–59	23–59	49	37	38	37	5.5
5A: 41 m	Alder	2–17	1–19	16	19	10	3,11	1.4
	Rowan	10–17	18–21	8	4	15	11,13	0.6
	Juniper	8–18		11		18	22	0.9
	Spruce	8–41	12–41	34	30	27	29	1.2
5B: 41 m	Alder	1–15	7–17	15	11	12	10,11	1.8
	Rowan	12–20	15–20	9	6	16	16	1.0
	Juniper	12–27		16		20	15	0.8
	Spruce	11–41	15–41	31	27	28	37	0.7
4A: 28 m	Alder	1–14	3–18	14	16	9	11	2.2
	Rowan	11–16	10–25	6	16	17	14,16	0.4
	Juniper	14–18		5		16	14,18	0.1
	Spruce	9–28	11–28	20	18	20	20	0.9
3A: 32 m	Alder	3–12	1–13	10	13	7	4	1.8
	Rowan	12–17	14–18	6	5	15	16	0.4
	Juniper	16–21		6		20	19,20	0.3
	Spruce	4–32	12–32	29	21	22	17	1.0



**Fig. 2.** Spatial distribution of species density and tallest tree. Transects are arranged vertically from low to high slope (Table 1). The x-axes are drawn from 0 to 60 m in all cases. The left y-axes display mean density (bars) for each 10-m<sup>2</sup> row. The right y-axes display the tallest tree (≥ 1.3 m) (dots) for each 10-m<sup>2</sup> row. No height values are given for juniper.





**Fig. 3.** — a: Belt width for alder (solid regression line) and rowan (dashed regression line). Spatial slope of the ten transects according to Table 1. — b: Population center positions in meters from transect start for alder, rowan, juniper (broken regression line) and spruce (no regression line).

3.5 m<sup>-2</sup> (rowan), 3.2 m<sup>-2</sup> (alder), and 0.9 m<sup>-2</sup> (juniper). These values indicate good establishment and survival conditions at these positions.

The position of population centers and density modes along the transects seldom coincided. A density mode earlier than the population center would indicate a positively skewed distribution and a more prolonged extinction phase as compared with colonization phase. Conversely, a center earlier than the mode would indicate a negatively skewed distribution and a more prolonged colonization phase. The positions of modes and centers were too variable among transects, however, to yield strong conclusions with respect to these distributions.

There were no common trends in how the species densities (height classes combined) were distributed along the spatial sequences (Fig. 2). The patterns varied from ordered to disordered; from unimodal mesokurtic (e.g. alder 5B and 4A), platykurtic (e.g. alder 5A and juniper 1A), and leptokurtic (e.g. rowan 5B and spruce 2A), to bimodal (e.g. alder 1A and spruce 1A) and to multimodal (e.g. alder 1B and spruce 5A). Negative and positive skewness were as common as symmetric distributions. Compared with the other species, spruce tended to show distributions with more obvious tails towards the earlier stages of succession (negatively skewed, e.g. 3B), which indicates a more prolonged process of colonization.

The species occupied successive phases along the spatial sequence. Alder was the first species to appear and normally reached high mean densities, one individual per m<sup>2</sup> and more, quite early. Then rowan followed by juniper occupied intermediate phases, before spruce eventually

became dominant. Juniper was not as significant as the other species were.

The height development, represented as the tallest tree per meter, normally peaked later than the density mode. For alder and rowan it is also indicated that the height decreased towards the upper range of their occurrence range, whereas the reverse was true for spruce.

Figure 3a displays a trend of decreasing belt width with increasing shore slope for the alder and rowan populations. A linear trend was more evident for alder ( $r^2 = 0.870$ ) than for rowan ( $r^2 = 0.683$ ). The correlation coefficient ( $r$ ) between the alder and rowan belt widths was 0.927. This correlation was largely owing to similarities in the occurrence range of small-sized individuals (0.5–1.3 m,  $r = 0.928$ ) rather than in larger-sized individuals. The alder belts were generally wider than the rowan belts, but the difference tended to decrease with increasing shore slope (from 14 m to 2 m).

The positions of population centers showed a tendency to become closer to the shoreline with increasing shore slope (Fig. 3b);  $r^2$  values for the included regression lines are 0.681 (alder), 0.664 (juniper), and 0.623 (rowan). Spruce population centers are included as reference points. Transects 1A and 1B, and 5A and 5B, showed similar locations of population centers, but the other three pairs of transects did not (not displayed in the figure). The positions of population centers correlated to a high degree between species, from  $r = 0.888$  between spruce and juniper to  $r = 0.978$  between rowan and juniper. The correlation coefficients among alder, rowan and juniper population centers were all above 0.9,

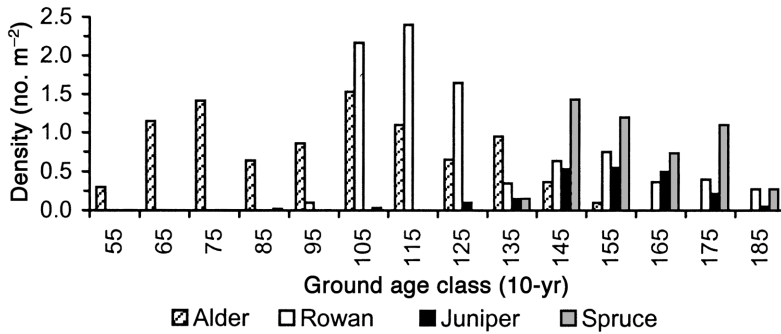


Fig. 4. Temporal sequence of tree-species belts for transect 1A.

while coefficients between population centers for spruce and other species were below 0.9.

The temporal sequences of the tree-species belts gave more distinct trends as compared with the spatial sequences displayed in Fig. 2. An example is given in Fig. 4 for Transect 1A. The bimodal distribution of alder along the spatial sequence became less pronounced along the temporal sequence. In 1A, alder occurred during 110 years of succession from the 55-year to the 155-year ground-age class. Spruce occurred from the 85-year class, rowan from the 95-year class, and juniper from the 125-year class. Rowan had the highest density ( $2.4 \text{ m}^{-2}$ ) and showed a positively skewed distribution. All species except alder continued throughout the transect.

Among the 10 transects, alder was first found between the 25-year and the 55-year ground-age classes, spruce from the 45-year to the 105-year classes, rowan from the 65-year to the 125-year classes, and juniper from the 55-year to the 155-year classes. Alder became extinct from the 95-year to the 155-year ground-age classes, rowan from the 125-year to the 175-year classes, and juniper from the 125-year to the 195-year classes. Juniper occurred during 10 to 120 years of succession, rowan during 60 to 100 years, and alder during 80 to 120 years.

The temporal sequence of averaged density modes for the species among all ten transects combined progressed from younger to older ground-age classes as follows (Fig. 5): alder (75-year class,  $1.1 \text{ m}^{-2}$ ), rowan (105-year,  $0.9 \text{ m}^{-2}$ ), juniper (155- to 165-year,  $0.3 \text{ m}^{-2}$ ), and spruce (165-year,  $1.3 \text{ m}^{-2}$ ). Likewise, the order of population centers revealed the same species sequence: alder (85-year class), rowan (125-year), juniper (135-year), and spruce (155-year). It should be

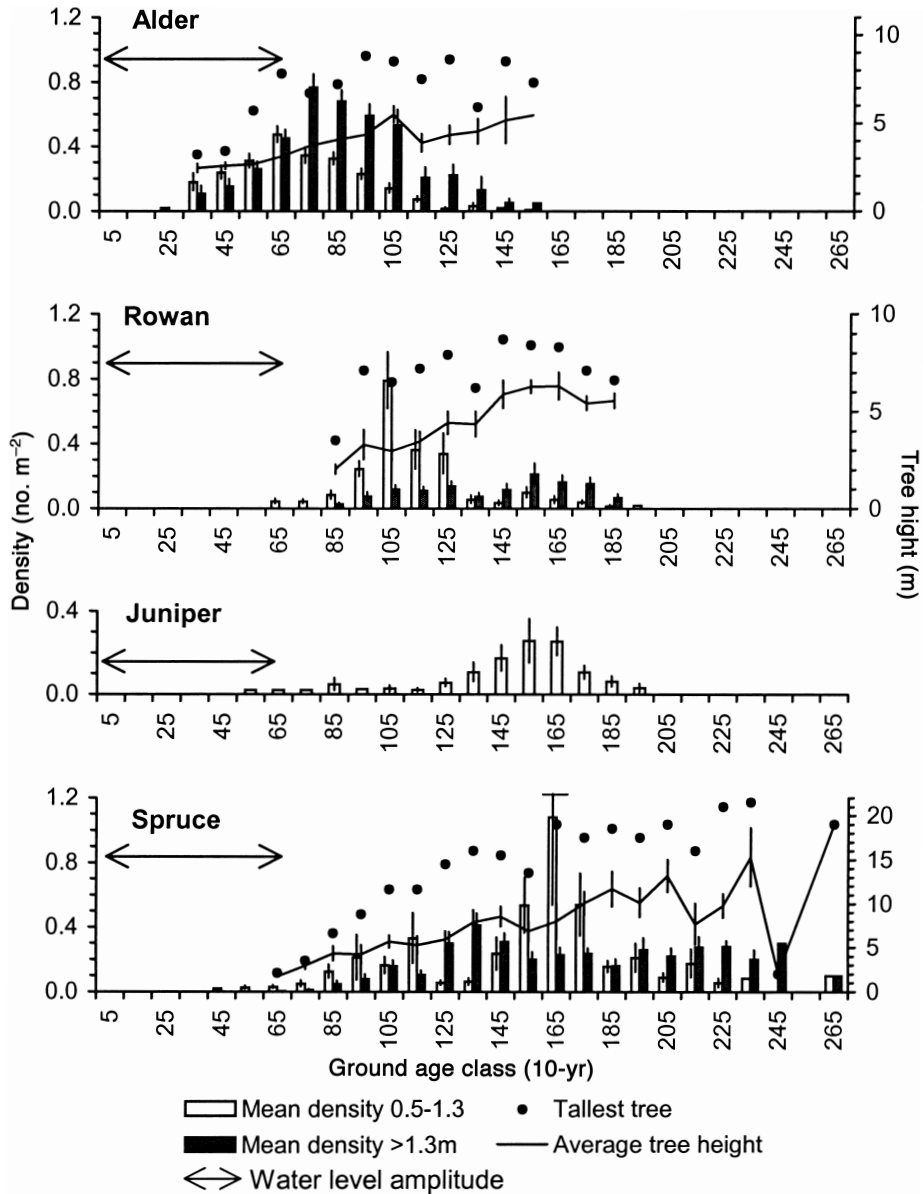
noted that all species were found within a zone that can be submerged at normal high-water-level amplitudes, i.e. up to the 75-year ground-age class, as indicated by the included arrow.

Alders 0.5–1.3 m were found at earliest in the 25-year ground-age class, and alders  $\geq 1.3$  m in the 35-year class. The density mode of the smaller height class was in the 65-year ground-age class ( $0.5 \text{ m}^{-2}$ ), and of the larger height class in the 75-year class ( $0.8 \text{ m}^{-2}$ ). The distribution patterns were symmetric for both height classes, during a total occurrence range of 140 years. The tallest alder found was 8.8 m in the 95-year ground-age class. The height development indicated a slight height decrease towards the end of the occurrence range. The average height mode, 5.5 m, was found in the 105-year class, after which the average height curve leveled off.

Rowans 0.5–1.3 m were found at earliest in the 65-year ground-age class, with the density mode in the 105-year class ( $0.8 \text{ m}^{-2}$ ), and with a positively skewed distribution pattern. Individuals  $\geq 1.3$  m were more evenly distributed and less frequent, occurring from the 85-year to the 195-year class, with the density mode in the 155-year class ( $0.2 \text{ m}^{-2}$ ). Just as for alder, rowan had a total occurrence range of 140 years. The tallest rowan found was 8.7 m, in the 145-year ground-age class. The average height mode, 6.3 m, was in the 165-year class, and just as for alder, rowan had a similar decreasing height trend towards older ground-age classes.

Juniper distribution was negatively skewed, occurring from the 55-year to the 195-year ground-age class. Its total occurrence range was 150 years.

Spruce was the second species to establish, with individuals 0.5–1.3 m first occurring in the



**Fig. 5.** Temporal sequences of density and tree height. Mean density per ground-age class for height classes 0.5–1.3 m and  $\geq 1.3$  m (combined for juniper), and tallest tree and average height for alder, rowan and spruce. Vertical line indicates standard error, calculated if  $n \geq 3$ . The error line for spruce 0.5–1.3 m, 165-year class, is interrupted. The included arrow indicates the zone that can be submerged at high-water-level amplitudes within normal amplitude.

45-year ground-age class. Its density mode was in the 165-year class ( $1.1 \text{ m}^{-2}$ ). A closer look reveals a bimodal distribution pattern, with a smaller mode in the 115-year class. Individuals  $\geq 1.3$  m were less frequent and showed a more even distribution from the 65-year class and onwards, with a density mode of  $0.4 \text{ m}^{-2}$ . The

tallest spruce found was 21.5 m, in the 235-year class. The tallest tree curve showed a close to linear increase up to the 135-year class. Half of the height of the tallest tree (11.0 m) was reached as early as in the 105-year class. The average height development increased to a peak value of 15.0 m in the 235-year ground-age class.

All species had their average height and tallest tree modes beyond their population modes and centers. Alder was the dominant species, based on average height, up to the 85-year ground-age class, and based on the tallest tree up to the 95-year class, before spruce became the dominant.

## Discussion

### Spatio-temporal properties

The ten transects taken together covered a temporal sequence of close to 240 years of succession, from about 20 to about 260 years of ground age (Table 1 and Fig. 1). The temporal sequence applied is a function of elevation above mean sea level, determined from ground surface level on top of the humus layer, and land-uplift rate. It can be questioned if it would be more accurate to use the elevation of the underlying moraine surface, by subtracting depth of the humus layer from the ground surface elevation. There are many uncertainties, however, to take into account, both methodological and regarding insufficient knowledge of processes that influence shoreline topography and elevation.

Shore slopes vary and the surface is uneven with boulders and stones, and with local convexities and concavities, and this affects accumulation rates of organic matter and mineral soil. Factors like erosion, reallocation, damage by waves, ice-drifting and wind, type of vegetation, richness of parent material, etc., also need to be taken into account. It may be assumed that mineral soil accumulates above the moraine surface and adds to the elevation, probably more in sheltered localities and less in exposed localities. Moreover, the rate of land-uplift decreases slightly with time. Estimates vary between 1% and 3% per century (Svensson 2002), and this influences dating also over sequences 200 to 300 years long. In Svensson and Jeglum (2003) we showed that humus depth increases asymptotically with increasing distance from shoreline and altitude towards a maximum after approximately 220 years of succession, and then stays stable or indicates a slight decrease in depth. Subtracting the depth of humus according to this model would decrease the oldest ground age

in the temporal sequence by approximately 20 years.

Dating successional time on the land uplift coast with precision is an arduous problem that requires further investigation. It is our conviction that the most appropriate and repeatable method, based on present knowledge, is to estimate ground age from the elevation of the top of the humus layer. As compared with dating based on the elevation of the underlying moraine surface, it may overestimate successional time by 10% at the most.

The transects started from different topographic levels, from 19 to 46 cm above mean sea level, corresponding to 23 to 54 years of ground age. Since the transects started where the earliest tree species (0.5 m tall or more) was found, these figures indicate the range of initial tree-species establishment in these successions. It is clear that tree species colonize and survive close to the mean water level, and far (40 to 50 cm) below the highest water level within the normal fluctuation amplitude.

Four tree species occurred commonly in our transects: grey alder, Norway spruce, rowan, and juniper (Table 2). Juniper is a shrub species rather than a tree species, although heights up to 2.1 m were recorded. Alder, rowan, and juniper tended to have many stems from ground level, which made it difficult to distinguish between individuals during the inventory. The standard procedure was to record separate individuals in unclear cases. Thus, the numbers of individuals of these species may be overestimated as compared with the number of spruce individuals. Birch, pine, and willow were present, but in insignificant numbers. Other tree species should not be expected to any extent (Skye 1965, Vuoristo & Rousi 1976, Schwank 1981, Svensson & Jeglum 2000). Black alder (*Alnus glutinosa*), for instance, is near its northern distribution limit and can be found only occasionally, and aspen (*Populus tremula*) is more common on the Finnish side of Norra Kvarken (Rinkineva & Bader 1998).

Alder and the common shrubs *Hippophaë rhamnoides* and *Myrica gale* are nitrogen-fixing species. The presence of nitrogen fixers and other facilitative pioneer species is a common phenomenon in early stages of primary suc-

cession (e.g. Bégin *et al.* 1993, Chapin *et al.* 1994). Many studies of primary succession have demonstrated, however, that late-successional species may colonize early stages, although they may not form dominant populations (belts) until later in the sequence (e.g. Fastie 1995, Helm & Allen 1995). Lawrence (1958), for instance, found young Sitka spruce (*Picea sitchensis*) migrating out onto recently exposed salt-strands of the Glacier Bay mouth, Alaska, and Lichter (1998) found that symbiotic nitrogen fixation did not contribute significantly to the development of forest ecosystems during primary succession on Lake Michigan sand dunes.

Alder, rowan, juniper, and spruce formed distinct belts (Table 3, Figs. 2 and 5). The initial colonization sequence was from alder to spruce to rowan to juniper. As the species populations develop, with reference to both density and height, the order changed to: alder–rowan–juniper–spruce. This species sequence was evident for the belt ranges and for the position of population centers and density modes along the spatial and temporal sequences. Junipers were found in lower numbers as compared with the other species (Table 1), and are not as significant in the succession as the other three species are. Species distributions were highly variable along the spatial sequence, but more distinct along the temporal sequence (compare Fig. 2 with Figs. 4 and 5).

Differences in shore slope explain differences in belt widths. The belt width generally decreased from alder to rowan to juniper (Table 3). Alder and rowan belt widths correlated significantly, and the width decreased in a linear fashion with increasing shore slope (Fig. 3). Alder consistently had wider belts than rowan, but the differences tended to decrease with increasing slope. The positions of species population centers correlated significantly, and tended to become closer to the shoreline with increasing shore slope.

Alder, rowan, juniper and spruce were all found to establish in the geolittoral, i.e. in the zone between mean and highest water level, and persist into the epilittoral, above the highest water level (Fig. 5). The earliest individuals of these species were found within 20 to 70 years of ground age, corresponding to 17 to 60 cm above mean sea level.

Alder was found from the 25-year ground-

age class to the 155-year class, during a period of 140 years (Fig. 5). The decline in alder was associated with the transition from geolittoral to epilittoral. It is reasonable to assume that its ability to recover vegetatively (Ericsson & Wallentinus 1979, Ecke & Rydin 2000) from disturbances caused by a fluctuating water table and other seashore factors is advantageous at lower elevations and also on steeper shore slopes. Ericson (1972) reported from a study in the Norra Kvarken Archipelago that alder establish at 30 to 60 cm above mean sea level, and become extinct at 45 to 155 cm. His figures indicate an occurrence range of 35 to 130 years. Later, Ericson (1981a) reported initial alder establishment at 30 cm from Sörfjärden, Norra Kvarken. Schwank (1981) gave 50 cm for Larsmo archipelago, northeast Finland.

Rowan appeared in an intermediate stage between alder and spruce, as a transitory assemblage (*sensu* Chapin *et al.* 1996), from the 65-year to the 195-year ground-age class, just as alder during a period of 140 years (Fig. 5). Ericson and Wallentinus (1979) noted that alder normally does not form dense thickets at exposed locations with strongly wave-washed shores. Other tree species, like rowan and birch, can then dominate. Skye (1965) observed that rowan seems to be very tolerant to high exposure, and hence normally prevails in the outermost archipelago and on relatively small and isolated islands. Ericson (1981a) reported initial colonization of rowan at 45 cm from Sörfjärden, Norra Kvarken.

Rowan was found in significant numbers (Table 2) with a higher density mode (3.5 individuals  $m^{-2}$ ) than alder (3.2), but not as high as spruce (5.5) (Table 3). Rowan is very palatable to browsing mammals (Danell *et al.* 1991, Ball *et al.* 2000). With the present high population densities of browsing mammals in the Kvarken Region (Ball *et al.* 2001) it would have been reasonable to expect a less significant occurrence. Mammal browsing is recognized as an important influence during succession (e.g. Russow *et al.* 1997). Several studies have shown that the shift from early- to late-successional species may be influenced by browsing (e.g. Binkley *et al.* 1997, Collins & Helm 1997, Kielland *et al.* 1997, Kielland & Bryant 1998). Helm and Collins (1997)



argued that browsing can cause multiple successional pathways during primary succession on river floodplains in Alaska. Because of browsing, the rowan population may be reduced in our study sites, but it is still a significant species in these successional sequences.

Juniper occurs scattered along the Bothnian coast. In places where domestic grazing or mowing in the past has been of major importance and duration, rather large thickets have developed and are able to persist (Svensson & Jeglum 2000). We found juniper from the 55-year to the 195-year ground-age class, over a 150-year period (Fig. 5).

Spruce was initially found in the 45-year ground-age class (Fig. 5), which is 20 years after alder, 20 years before rowan and 10 years before juniper. Spruce had a more prolonged establishment phase as compared with the other species, with its population centers and density modes approximately where alder becomes extinct, i.e. at the transition from geolittoral to epilittoral. Svenonius (1945) noted that the transition from alder to spruce generally is sudden on steep-sloping shores, but more prolonged with a mixed transitional zone of rowan and birch on low-sloping shores. Spruce tends to colonize in periodic pulses. The pulses can probably be explained by the coincidence between a good seed crop and good establishment conditions (Ericson & Wallentinus 1979, Ericson 1981a, 1981b, Svensson & Jeglum 2000), but information on these processes is scanty.

The establishment level of spruce as compared with the mean sea level has been touched on in a few earlier studies. Ericson (1972) reported on increasing level of initial establishment of spruce, 35 to 110 cm on a sequence of 12 sites from low to high exposure for Norra Kvarken. Later, Ericson (1981a) reported 30 cm from Sörfjärden, Norra Kvarken. Schwank (1981) gave quite different values, 120 cm for Larsmo archipelago, northeast Finland. Vervijst and Cramer (1986) showed that spruce establishes at about 100 cm, 50 cm, and 70 cm above water level for exposed, intermediate and sheltered locations respectively, for a central Swedish seashore.

## Tree-species belts and succession

Identification of species belts and interpretations of the processes producing them has been a main line of research on ecological succession from the earliest to the most recent studies (e.g. Cowles 1899, Cooper 1913, Miles 1987, Ecke & Rydin 2000, Lichter 2000). Walker *et al.* (1986) identified four tree-species stages during primary succession on the Tanana River floodplains (interior Alaska): willow (*Salix alaxensis*) – alder (*Alnus tenuifolia*) – poplar (*Populus balsamifera*) – white spruce (*Picea glauca*). They concluded that the successional patterns largely result from interactions between stochastic events and life history traits. Light seeds and rapid growth rates of willow and poplar resulted in high abundance at early stages, whereas heavier alder and spruce seeds were less widely distributed and mainly found in later stages. A combination of short life span, herbivory, and shade intolerance eliminated willow during mid-succession, while differences in longevity explained the change from alder to poplar to spruce during later stages. Properties like availability of receptive seedbeds, seed germination, seedling establishment, and competition also need to be taken into consideration to interpret ecological causes underlying belt characteristics (Walker *et al.* 1986, Tapper 1993).

Viereck *et al.* (1993), Mann *et al.* (1995), and several others have reported on the temporal patterns on the Tanana River floodplain successions. Willow colonizes within 5 years, and alder follows after another 5 years. Then an open forest of balsam poplar develops and becomes closed after several decades before white spruce invades after some 40 years. White spruce becomes dominant after approximately 175 years. The terminal successional stage is a climax black spruce (*Picea mariana*) – *Sphagnum* community (e.g. Viereck 1970, Viereck *et al.* 1986).

Helm and Allen (1995) reported that the initial establishment of tree species might last as long as 30 years at the retreating Exit Glacier foreland, Kenai Peninsula, Alaska. They studied six terminal moraines dating from 1825 to 1951, and identified five tree-species stages:

alder (*Alnus sinuata*) – cottonwood (*Populus trichocarpa*) – cottonwood and Sitka spruce (*Picea sitchensis*) – Sitka spruce and hemlock (*Tsuga mertensiana*).

Chapin *et al.* (1994) identified three successional tree-species stages at the retreating Glacier Bay foreland: willow (*Salix* spp.) and cottonwood during 20 to 50 years after deglaciation, alder (*Alnus sinuata*) during 50 to 100 years, and Sitka spruce from 100 years and onwards. There the succession terminates in a *Sphagnum*-dominated muskeg after thousands of years (Chapin *et al.* 1994, Lawrence 1958).

The east coast of Hudson Bay, Canada, experiences land uplift primary succession processes. The arctic climate in the region provides, however, much more severe establishment and growth conditions as compared with the climate of the Gulf of Bothnia region. Tree-species belts occur only occasionally, with a shrub mat before the conifers. The shrub mat generally consists of low growing *Salix candida*, *Myrica gale*, *Salix glauca*, *Betula glandulosa*, and *Alnus crispa*, in a sequence from seashore and landwards. Conifers are tamarack (*Larix laricina*), white spruce and black spruce (Bégin *et al.* 1993, Grégoire & Bégin 1993, von Mörs & Bégin 1993).

There are many similarities between the succession sequence on Gulf of Bothnia rising coastlines and the examples reviewed above. There are usually two main broadleaf species, of which one is an alder, before a spruce species. The spruce species is alone, or together with other conifers, the terminal species developing a climax forest community. White spruce invades after 40 years on the Tanana River floodplains, and Norway spruce after 40 to 50 years as reported here (Fig. 5). Sitka spruce dominates from 100 years after deglaciation at Glacier Bay, and Norway spruce from 80 to 100 years in our case. *Alnus sinuata* persists until 170 years after ice-melt at Glacier Bay (Lawrence 1958), which is not too different from the 140 years reported for grey alder in this study.

Many studies on primary succession have pointed out distance from seed source as a key factor. Fastie (1995) concluded that distance to seed source was a main factor explaining

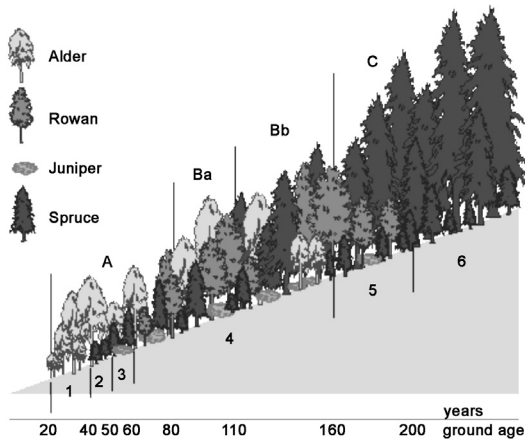
multiple pathways of species change during succession at the Glacier Bay foreland. There, large areas are being exposed owing to the rapid glacial withdrawal, 30 to 40 km per century (Lawrence 1979, Fastie 1995). Lawrence (1958) and Chapin *et al.* (1994) pointed out that Sitka spruce requires only 5 years for successful germination and establishment on the foreland if seed sources are close. Distance from seed source and seed dispersal characteristics are important to rates of seedling establishment, population densities, competition amongst species, and establishment of tree-species belts, but is probably not a critical factor in the successional sequences presented in this study. Table 3, and Figs. 4 and 5 clearly illustrate that regeneration is continuous within the area occupied by a particular species. Undoubtedly, however, distance from seed source and seed characteristics are more critical concerning the plant migration to and establishment on emerging archipelago islands.

## Forest development

Alder and rowan heights decreased towards the upper ranges of their occurrence, whereas this was not the case for spruce (Figs. 2 and 5). For both alder and rowan it is assumed that this is a consequence of competition from the rapidly developing spruce population (cf. Chapin *et al.* 1994) which causes taller broadleaves to die. Alder and rowan reached about the same top height, close to 9 m, whereas spruce reached 21.5 m (Fig. 5) within the transects. This is close to the top height reported by Svensson and Jeglum (2001), 22.0 m, from a nearby study site on an undisturbed old-growth Norway spruce island. This height is not impressive, however. The low height growth is thought to be a consequence of the coastal conditions, where factors such as strong winds, snow, and ice are limiting factors (cf. Rouse 1991, Kumler 1997, Stainforth *et al.* 1998, Karlsson 2000).

From the tree-height point of view, alder was found to be the dominant up to 80 to 100 years of succession, before spruce reached taller heights. An alder forest developed within 60 to





**Fig. 6.** Successional stages of tree species belts on moraine shores in the Norra Kvarken Archipelago, the Gulf of Bothnia. Stages 1 to 6 are based on occurrence and composition of tree species: (1) Alder, 20 to 40 years; (2) Alder and spruce, 40 to 50 years; (3) Alder, spruce and juniper, 50 to 60 years; (4) Alder, spruce, juniper and rowan, 60 to 160 years; (5) Spruce, juniper and rowan, 160 to 200 years; and (6) Spruce alone, from 200 years of ground age and onwards. Stages A to C are based on dominance: (A) Alder stage, 20 to 80 years; (Ba) Mixed stage with increasing rowan and juniper, 80 to 110 years; (Bb) Mixed stage with decreasing rowan and juniper, 110 to 160 years; and (C) Spruce stage, 160 years and onwards.

70 years, based on the location of density mode of individuals  $\geq 1.3$  m (Fig. 5). The average alder height was 3.1 m at this stage, and increased up to a peak average of 5.5 m some 40 years later. A spruce forest developed within 130 to 140 years. At this stage, the average spruce height was 7.9 m, and the tallest spruce 16.0 m.

In comparison, Lichter (1998) reported that development of forest ecosystems requires about 300 years on average, on primary succession on Lake Michigan sand dunes. Such habitats are probably more limiting to successional development in terms of nutrient and moisture regime, and other ecological factors. Lawrence (1958) compared time for forest establishment between the Glacier Bay and Juneau Ice Field forelands, and reported that it took 50 to 100 years at the Glacier Bay site as compared with only 5 to 10 years at the Juneau site. The more rapid development at the Juneau Ice Field was found to be a result of the short distance to mature vegetation, i.e. seed sources, and of a much more limited area of newly exposed ground.

## Successional stages of tree-species belts

Tree-belt stages along the Norra Kvarken rising coastlines can be identified in several ways. We have identified belts based on occurrence and composition of species and based on species dominance (Fig. 6). The former way revealed the following successional stages: (1) Alder, 20 to 40 years; (2) Alder and spruce, 40 to 50 years; (3) Alder, spruce and juniper, 50 to 60 years; (4) Alder, spruce, juniper and rowan, 60 to 160 years; (5) Spruce, juniper and rowan, 160 to 200 years; and (6) Spruce alone, from 200 years of ground age and onwards. The latter way revealed three main stages: (A) Alder stage, 20 to 80 years; (B) Mixed stage with decreasing alder, increasing and then decreasing rowan and juniper, and increasing spruce, 80 to 160 years; and (C) Spruce stage, 160 years and onwards. To define dominance we used the rule that one single species should have more than half of the total number of individuals. The second stage can be divided into (Ba) with increasing rowan and juniper taken together, 80 to 110 years; and (Bb) with decreasing rowan and juniper, 110–160 years. The division between (Ba) and (Bb) marks the tree-species diversity mode.

It is reasonable to assume that the successional pathway illustrated in Fig. 6 is valid on intermediately exposed and non-isolated ground-moraine, mesic shores in mid or inner parts of the Norra Kvarken Archipelago. The successional pathway in the outer archipelago and on isolated islands may be different both in terms of establishment levels (later), successional rates (delayed), and species composition. Ericson and Wallentinus (1979) indicated that birch and rowan are more common in the outer archipelago. A more frequent appearance of aspen on the Finnish side of Norra Kvarken (Rinkineva & Bader 1998) may influence the pathway. More frequent appearance of Scots pine should generally be expected on xeric and sandy sites, as well as lower successional rates. Moist and flat sites may display different composition of tree-belt stages — birch, mainly *B. pubescens*, sometimes dominates in the transitional stage between alder and spruce — and/or may develop towards a paludifying community with dominance of *Polytrichum* and *Sphagnum* mosses on the ground.

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