Primary succession and dynamics of Norway spruce coastal forests on land-uplift ground moraine

JOHAN S. SVENSSON & JOHN K. JEGLUM

Department of Forest Ecology

'... it is the study of succession in the widest sense which has contributed and is contributing more than any other single line of investigation to the deeper knowledge alluded to (ecology).'
A.G. Tansley, 1935.

'An understanding of ecological succession provides a basis for resolving man's conflict with nature.'
E.P. Odum, 1969.

'Much of a forest manager's life is spent manipulating succession.'
J.P. Kimmins, 1997

Abstract

Svensson, J.S. & Jeglum, J.K. 2000. Primary succession and dynamics of Norway spruce coastal forests on land-uplift ground moraine. *Studia Forestalia Suecica* 209. 32 pp. ISSN 0039–3150. ISBN 91–576–5982–6.

This paper is an overview of primary succession on the rising coastlines of the Gulf of Bothnia, which emphasises Norway spruce succession and forest development and identifies topics for research. It is concluded that continuing postglacial rebound provides excellent successional sequences, and an exceptional opportunity to add new and important knowledge on original forest ecosystem development. First, long-term undisturbed forest seres, terminating in climax-like Norway spruce forest, exist. Secondly, a well-stocked, old-growth spruce forest can develop on the (generally) fairly productive mesic ground-moraine sites in a short ecological time. Thirdly, undisturbed successional sequences, which go back to original soil formation, permit reconstruction of ecosystems' developmental history. Fourthly, the relationship between ground elevation and land-uplift rate facilitates estimates of ground age, and consequently permits a four-dimensional study approach. Fifthly, in view of extensive anthropogenic influence in boreal Fennoscandian forests, the few remaining natural spruce forests should be recognised and carefully documented. From our review of the literature, we conclude that present knowledge of the succession of Norway spruce on emerging shorelines, and the part played by land uplift and other factors, is fragmentary. Attention should to be given to initial spruce seedling colonisation relative to factors such as sea-water level, exposure (winds, fetch), parent material, seedbed types, potential seed source (isolation), and island size. Possible multiple pathways of Norway spruce primary succession relative to temporal changes in exposure and other factors, have so far received little research effort. Attention also should to be paid to the response of spruce populations to site maturation, *i.e.* to increasing ground age based on land-uplift rate and elevation above sea level. Finally, attention should to be paid to autogenic processes in spruce-dominated stages developing towards climax-like, old-growth forests.

Key words: Literature review, Gulf of Bothnia, postglacial rebound, *Picea abies*, boreal, old-growth forest, natural forest, structure, Sweden.

Johan S. Svensson & John K. Jeglum. Dept. of Forest Ecology, SLU, SE-901 83 Umeå, Sweden
E-mail: Johan.Svensson@sek.slu.se

Contents

Introduction

Succession, the process of change in ecosystems over time, is one of the most fundamental concepts in ecology. Although it has been the subject of numerous theories and studies, it remains intriguing and is still in need of clarification and scientific inquiry. In particular, there is an increasing need for knowledge about succession and dynamics in forest ecosystems, to make it possible to develop sustainable forestry and ecosystem management strategies.

The Fennoscandian crust (*i.e.* Norway, Sweden, Finland and Karelia) is still rising following the melting of the Weichselian ice mass (Fig. 1). The phenomenon is termed postglacial land uplift or postglacial rebound (Ekman, 1993). A consequence of this is the continuous exposure of new ground along the shores of the Baltic Sea.

The primary succession (*cf.* Glenn-Lewin & van der Maarel, 1992) is continuous in space and time on this new ground as plants and communities colonise downwards. The ongoing land uplift provides a topographic sequence equivalent to a chronosequence: the lower the elevation the younger the land, with younger pioneer communities; the higher the elevation, the older the land and the more developed the communities. On any given shore, the vegetation gradient reflects the actual course of succession (Ericson & Wallentinus, 1979).
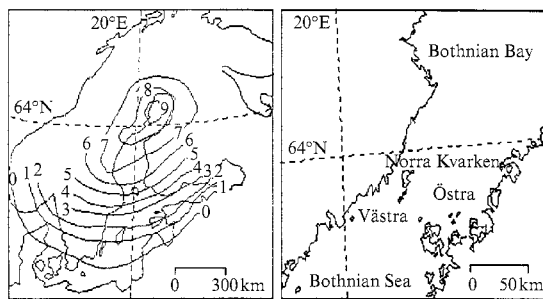

Fig. 1. Apparent land uplift in Fennoscandia 1890–1970 (mm yr^{-1}) according to Ekman (1993). The northern part of the Baltic Sea, *i.e.* N of the 5-mm uplift isoline (at *ca.* 60°N), is termed the Gulf of Bothnia. The Gulf of Bothnia is separated at Norra Kvarken (= Northern Strait, at *ca.* 64°N) at the 8-mm uplift isoline, into the Bothnian Bay in the N and the Bothnian Sea in the S. Norra Kvarken is separated into a W part (Västra Kvarken) on the Swedish side and an E part (Östra Kvarken) on the Finnish side.

The primary succession on rising ground-moraine shores along the Gulf of Bothnia terminates in Norway spruce (*Picea abies* (L.) Karst.) communities (*e.g.* Appelroth, 1948; Kielland-Lund, 1970). Figure 2 illustrates the normal ecological gradient. Four distinct successional stages can be distinguished: an open, early stage dominated by graminoids and low-growing shrubs; a primary forested stage dominated by broadleaves; secondary forested stage, dominated by Norway spruce; a fourth, climax-like Norway Spruce stage.

A reconnaissance in the Västra Kvarken Archipelago, in the Gulf of Bothnia (in prep.), has revealed that primary succession sequences of long duration, undisturbed by direct anthropogenic impact (tree-felling), can be found along the coastlines. The reconnaissance also identified common disturbances, such as firewood-cutting during World War II. This disturbance resulted in severe disruption of the forest structure, which still is easily detectable more than half a century later. Grazing and browsing by cattle, horses and sheep was also common in former agricultural management, as is browsing by elk (*Alces alces*) and roe deer (*Capreolus capreolus*) today. But 'to the degree that herbivores and plants have evolved together, it may be inappropriate to consider grazing as a disturbance' (Glenn-Lewin & van der Maarel, 1992). Wildfires probably are infrequent or absent from the coastline, resulting in development towards old-growth, climax-like forests (*cf.* Zackrisson, 1977; Sjöberg, 1994).

Owing to the favorable climate in the Bothnian region – even in its northernmost parts – the spruce communities on ground-moraine are fairly productive, with a rapid change from one seral stage to the next. A well-stocked, old-growth Norway spruce forest can develop within a short ecological time, two to three centuries (Svensson, 1998). Such forests present an excellent opportunity for examining natural succession and dynamics, and for classifying stages of structural development (*cf.* Cramer, 1985; Verwijst & Cramer, 1985; Svensson & Jeglum, in press). Despite the fact that the forests are relatively young, some have developed features characteristic of old-growth, such as consider-
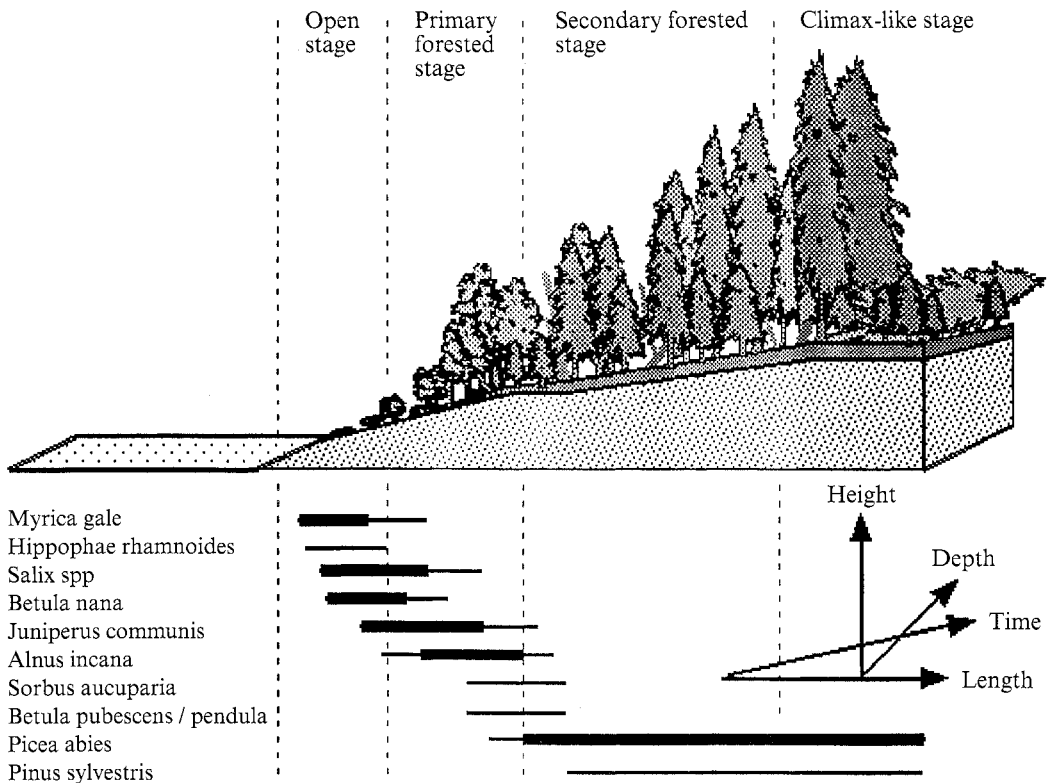
3

Fig. 2. The normal ecological gradient on an intermediate exposed ground-moraine shore on the Västra Kvarken coastline. The successional stages, with suggested terminology, the sequence of woody plants and the four-dimensional approach, are illustrated.

able amounts of coarse snags and fallen logs, uneven-aged and uneven-sized structures, and sometimes rare and threatened species (Suomi, Aarnivirta, Ahlroth, Huitu, Hyvärinen, Korkeamäki, Mattila, Niskanen, Päivinene, Rintala & Suhonen, 1997).

The main conclusion from the reconnaissance is that long-term, undisturbed primary succession sequences that terminate in old-growth Norway spruce forests can be found. Such sites are not abundant, however, whereas sequences to semi-mature, undisturbed spruce stages are fairly common. The inhabitants of coastal villages sometimes own the newly-elevated land in common, hence felling is not agreed upon. In other cases, the new land is in isolated places, on islands or far from settlements, or simply on private land where the owner has chosen not to harvest. Private land-ownership is common in the region.

The aim of the present paper is to review existing knowledge on primary succession, with emphasis on forests dominated by Norway spruce on the rising coastlines of the Gulf of Bothnia, and to identify the rationale for further research. The review emphasises vegetational and floristic changes, since we consider these to be the essence of succession (*cf.* Grime, 1979; Miles, 1979). Therefore, we do not go deeply into other process-related measures of eco-system succession, such as energy flows, biomass accumulation, nutrient cycling, *etc.* (*e.g.* Odum, 1969; Austin, 1981).

This paper derives from a doctoral project at the Department of Forest Ecology, SLU, Umeå, entitled 'Primary succession and dynamics in virgin Norway spruce coastal forests on land-uplift ground moraine', carried out in the Västra Kvarken Archipelago of the Gulf of Bothnia, in the county of Västerbotten, Northern Sweden. This is close to the area with the currently highest rate of land uplift in Fennoscandia (Fig. 1). The overall aim of the study is to provide basic information about primary succession, and in particular, about the dynamics and structural development of pristine Norway spruce forests.

The study is intended to be applied to the interpretation of successional trends and dynamic patterns in terms of sustainable ecosystem management and adaptive forestry principles. Details of research methods and outputs will be published elsewhere.

Natural forests

The concept of natural forests

In the Nordic countries, humans have greatly influenced forest land for a long period, directly by management or indirectly by controlling natural disturbances and environmental factors (Hagner, 1992a; Östlund, 1993; Bernes, 1994). There is at present no exact and objective information about the remaining area of natural forests; this depends partly on difficulties of definition and terminology (Anon., 1994). The Nordic Council of Ministers (Anon., 1994) defined natural forests as naturally regenerated forests where no systematic management regimes have been applied. Virgin forests are defined as being old, natural forests that have arisen from regeneration in natural forests. In virgin-like forests, some traces of human impact can be detected, even though the overall forest structure and continuity are maintained (Anon., 1994). The widely used term 'old-growth' may be regarded as synonymous with virgin-like forest (cf. Jones, 1945; Oliver & Larson, 1990).

Forests that have developed naturally, in the absence of disturbance for a long period, normally exhibit high species diversity. This is an effect of a higher diversity of habitats and niches, such as the presence of considerable amounts of dying and dead wood (Bartels, Bell, Knight & Schaefer, 1985; Samuelsson, Gustafsson & Ingelög, 1994), old and large trees (Esseen, Ehnström, Ericson & Sjöberg, 1992; Sjöberg & Ericson, 1992), and uneven-sized forest structure (Ingelög & Lennartsson, 1991). A significant proportion of the rare and threatened species can be found in forests containing such old-growth structures (Ingelög & Lennartsson, 1991; Anon., 1994; Bernes, 1994; Hörnberg, Ohlson & Zackrisson, 1995). As a result of the long-term, undisturbed development, complexity in food-webs and other ecological functions is high (Maser, Trappe & Nussbaun, 1978; Coleman, 1985; Perry, Amaranthus, Borchers, Borchers & Brainerd, 1989; Chapin, Torn & Tateno, 1996). Consequently, these forests are more sensitive to forestry and other disturbances (Pettersson, 1991; Ingham & Thies, 1996). But even in forests that today are classified as virgin or virgin-like, we frequently find traces of past human activities which, to a greater or lesser extent, have influenced the natural dynamics (Segerström, Bradshaw, Hörnberg & Bohlin, 1994).

From 1978 to 1981, the National Environmental Protection Agency and the National Board of Forestry in Sweden conducted a survey which revealed that ca. 33 000 ha (the northernmost province of Norrbotten and the alpine regions excluded) of virgin and virgin-like forests still remained in Sweden. It was concluded, however, that the majority of these forests were on low-productive sites (Bråkenhielm & Wallin, 1982). Moreover, forests with old trees are not very common; only ca. 7% of the productive forest land of northern Sweden consists of forests aged 140 years or older (Bernes, 1994). By comparison, Lähde, Laiho, Norokorpi & Saksa (1991) and Norokorpi, Lähde, Laiho & Saksa (1997) concluded that virgin forests – which they defined as uneven-aged stands entirely or for the most part undisturbed by humans – accounted for almost half and two-thirds of all Sweden's and Finland's forests, respectively, in the 1920s.

A common conclusion is that nearly all forests in the Nordic countries have been modified by human interaction, either directly or indirectly. True virgin forests are very rare, and can be found only close to the Scandinavian mountains (Anon., 1994).

Reference forests for ecosystem management

In the Nordic countries, clearfelling has been the dominant silvicultural method since World War II (Hagner, 1992a). Accordingly, research has emphasised artificial regeneration after clearfelling, and management of even-aged and even-sized monocultures. During the past decade or so, however, a paradigm shift in forest management has been taking place (e.g. Norokorpi et al., 1997; Hagner & Nyquist, 1998; Barnes, Zak, Denton & Spurr, 1998). The shift encompasses a range of alternative conceptual approaches to forest management, developed on a firm knowledge base of natural ecosystem

processes, and recognising multiple-use aspects (*e.g.* Hopwood, 1991; Hagner, 1992*b*; Grumbine, 1993; Lundqvist, 1993, 1994; Bernes, 1994; Franklin, 1989; Hånell & Ottosson-Löfvenius, 1994; O'Hara, 1998; Fries, Carlsson, Dahlin, Lämås & Sallnäs, 1998; Svensson & Jeglum in press).

The paradigm shift is fundamentally from rigid stand management to management with flexible targets; from single trees to landscapes (see conceptual reviews, *e.g.* by Boyce & Haney, 1997; O'Hara, 1998). The concept encompasses ideas of large- and small-scale structural heterogeneity, patches of old-growth with retention of coarse woody débris, maintenance or enhancement of structural and biological diversity, and long-term ecosystem sustainability. Franklin (1989) stated that the focus of New Forestry, '... a kinder and gentler forestry that better accommodates ecological values, while allowing for the extraction of commodities', is the maintenance of complex ecosystems. A sustainable ecosystem is '... one that, over the normal cycle of disturbance events, maintains its characteristic diversity of major functional groups; productivity, soil fertility, and rates of biochemical cycling.' (Chapin *et al.*, 1996). The sustainability of an ecosystem is thought to be closely linked to enhanced ecological variability, *i.e.* structural and biological diversity (*cf.* Magurran, 1988).

Kuuluvainen, Syrjänen & Kalliola (1998) described the structure of a pristine Norway spruce forest in the southern boreal forest zone in Russia. They found that a smaller-scale structural heterogeneity and a larger-scale homogeneity characterised the forest. They suggested that '... the ecology and dynamics of extensive areas of natural boreal forests can be driven by small-scale disturbance.' This represents a swing away from the emphasis on the importance of periodic and large-scale disturbances, such as wildfire, on landscape patterning. They concluded that to develop an ecologically sound silviculture for the kinds of forests they studied, one should move away from a compartment and stand-level approach to one emphasising small-scale spatial heterogeneity and temporal variability. In other words, to maintain ecological diversity, one should adopt a selection system that mimics the natural small-scale disturbance patterns, thus maintaining a patchy forest cover with continuous presence of deadwood. In order to develop

ecologically sound and sustainable forest management strategies, there is a need for knowledge of dynamics and structural development of natural forests (Lähde *et al.*, 1991; Norokorpi *et al.*, 1997). Botkin (1990) emphasised this grand challenge as follows: 'We no longer have the luxury to believe that we can live in harmony with the environment without knowledge and understanding of natural systems.'

The lack of a clear and unambiguous definition of the virgin forest concept is evident (Norokorpi *et al.*, 1997; see above, p. 5). This confuses the overall picture, but still the trend is clear; there has been a marked decrease in natural forests in Fennoscandia, and at present, they are absent from vast areas. Thus, forests that could potentially be used as reference forests for understanding the long-term natural dynamics are not readily available. Consequently, forest ecologists have devoted considerable effort to finding the remaining virgin and virgin-like forests, and to studying their structure, dynamics and succession (*e.g.* Sirén, 1955; Hytteborn & Packham, 1987; Leemans & Prentice, 1987; Leemans, 1991; Lähde *et al.*, 1991; Quinghong & Hytteborn, 1991; Hofgaard, 1993*a* and 1993*b*; Hörnberg *et al.*, 1995; Norokorpi *et al.*, 1997; Linder, 1998).

Thus, the undisturbed, old-growth Norway spruce forests on the coastlines of the Gulf of Bothnia should be recognised and carefully documented, both for scientific investigation as potential natural reference forests and as records of natural forest development from initial site formation.

The Gulf of Bothnia

Post-glacial land uplift

At the maximum extension of the Weichselian ice sheet, 20 000–18 000 years B.P., the ice shield was *ca.* 3000 m thick at the centre. The heavy load pressed the Fennoscandian crust down 800–900 m below the present level (Fredén, 1994). As the ice began to melt, two processes started – the eustatic rise of the sea level, and the isostatic land uplift as the crust rebounded to its former position.

During initial stages of postglacial development, the sea-level rise could be substantial, as great as 1.5–2 m per century (Fredén, 1994), by

far exceeding the rate of land uplift. The highest sea level, denoted the highest shoreline, is still very obvious in many places. The level of this line above present sea level varies between 180 m in northern Sweden and 50 m in southern Sweden, with a maximum of 285 m in the central part. According to Fredén (1994) and Helmfrid (1994), the altitude differences depend on: (1) how far the crust was depressed; (2) the amount of sea-level rise; and (3) how long the area has been ice-free. Eventually, the land-uplift rate exceeded the sea-level rise; the net result is an increase in land area along the coasts. This is still an ongoing phenomenon along the shores of the Bothnian Sea, and in a few other places such as Hudson and James Bay, Canada (Ekman, 1993), and the White Sea, Russia (Kouznetsova, 1999*a*).

In 1835, Lyell was the first to conclude that the increase in land area depended on land uplift, rather than on a lowering of water levels (Ekman, 1993), the latter being the common interpretation at the time. The theory that uplift is a consequence of crustal rebound after deglaciation was first put forward a few decades later by Thomas Jamieson in 1865 (Ekman, 1993). Lyell used old mean sea-level marks on rocks along the Swedish and Finnish coasts. The oldest rock carving documentation of land uplift in Sweden dates back to 1491 (Ekman, 1993).

The oldest mareograph (automatic water-level meter) in Sweden was established in 1774 (Stockholm). In the late 19th century, several more were added (Fredén, 1994). Series of measurements from the mareographs, combined with levellings made at inland sites, make it possible to calculate the uplift rate and its geographical distribution. The present rate has been calculated on the basis of two survey levellings, with 65 years between, together with recordings from ten mareographs. The highest current rate of uplift in Fennoscandia, 9.2 mm yr^{-1}, is in the coastal area of northern Sweden, in the northern part of the county of Västerbotten and the southern part of the county of Norrbotten (Hela, 1953; Okko, 1967; Ekman, 1993; Fredén, 1994) (Fig. 1). The uplift rate decreases southwards to about zero, or even negative rates in the south Baltic area, where there is slight subsidence.

It should be pointed out that the maximum absolute rate of land uplift is at present 10.8 mm yr^{-1}. However, eustatic rise in sea-level and other factors reduce the apparent uplift (Ekman, 1993). The Bothnian Sea nevertheless loses *ca.* 10 million m^3 water annually because of land uplift (Sjöberg, 1994).

The total crustal rebound in Fennoscandia hitherto has been *ca.* 800 m; some 500 m during the glacial melting period and *ca.* 300 m subsequently, as expressed by the highest shore line (Ericsson & Wallentinus, 1979). The remaining uplift has been estimated at 50–120 m (Ekman, 1993). In a long-term historical perspective, the uplift rate and its geographical distribution have fluctuated substantially over the landscape.

The consequences of land uplift on the coastal landscape have been carefully documented (*e.g.* Skult (1956); Lisitzin, 1974; Alestalo, 1982; Lundqvist, 1982; Ericson, 1982). The effect of land uplift is generally more evident along gently-sloping coastlines and where the coast is broken up into peninsulas and bays. Owing to the accumulation of fine material in sheltered locations, and especially in the vicinity of river mouths, the net vertical gain of land may exceed the uplift rate substantially. Schwank (1982) reported that the bottom of a previously shallow bay on the northeast Finnish coast has risen 34 cm in 20 years.

Land uplift as a time sequence

One of the most intriguing challenges of ecological science is to understand the process of temporal change. There are several possible ways to obtain information about changes in plant communities: (1) to use permanent plots and records that span over a relevant time-period; (2) to use paleoecological, dendroecological and archeological reconstruction, including written documentation; and (3) to use study sites where a chronosequence is available. Because of the lack of permanent plot records spanning more than a century (Fastie, 1995), a permanent record of boreal forest development from pioneer to old-growth is not, to our knowledge, available. Paleoecological and archeological reconstruction have relatively low temporal and spatial resolution, and dendroecological methods provide no information about non-tree stages (Davis, 1989). The chronosequence approach implies the use of study sites with several stages of development available at the same location. For studies of succession in eco-

systems and plant communities, this is the classic approach (*e.g.* Cowles, 1899; Cooper, 1913).

A critical assumption in the chronosequence approach is that the older stages have developed through phases similar to the younger stages. Any change in environmental or other conditions relevant to ecosystem processes, over the time period considered, should thus be taken into account. Fastie (1995) pointed this out in his paper on multiple pathways of primary succession in the Glacier Bay study area; 'The juxtaposition in one putative chronosequence of pathways that differ in either developmental trajectory or rate can produce a misleading inference.'

For studies of primary succession on rising coastlines along the Gulf of Bothnia, the chronosequence is constructed as a function of altitude (topography) and land-uplift rate. It is assumed that the known rate provides the possibility to age any particular point, by measuring its elevation above normal sea level and dividing by the uplift rate. This method has been applied, *e.g.* by Cramer (1985), Verwijst & Cramer (1985) and Cramer & Hytteborn (1987), to determine the age structure of coastal *Alnus glutinosa* and other species; by Rydin & Borgegård (1988, 1991) to study species diversity changes on islands after lake lowering; by Carlsson, Elmquist, Wennström & Ericson (1990) to age host plants infected by pathogens; and by Starr (1991) to age soils along a 5000-year chronosequence on the Finnish side of the Gulf of Bothnia. A reverse approach, *i.e.*, to apply the downward migration rate of woody species to determine the land-uplift rate, has been used on the rising east coast of Hudson and James Bays, Canada (Bégin, Berube & Gregoire, 1992; Grégoire & Bégin, 1993; von Mörs & Bégin, 1993).

A common assumption is that ground age, *i.e.* site age since uplift emergence from the sea, and downward migration of plants on the shore, show a linear relationship. Ericson & Wallentinus (1979) concluded that the rate of downward spread of long-lived species roughly coincides with that of the actual land uplift. Carlsson *et al.* (1990) stated that the height above sea level of an island is correlated with age, and therefore with time since it was first colonised by plants. They found that for some species it was possible to calculate approximate

population ages. Cramer (1985) concluded that age of *Alnus glutinosa* and elevation were significantly correlated. Cramer & Hytteborn (1987) concluded that field layer (non-woody) vegetation changed with elevation at a rate consistent with the known land-uplift rate.

It is indicated, however, that the relative vertical position of species might influence the relationship. Verwijst & Cramer (1985) found that early-successional species on the lower part of the shore (*Alnus glutinosa, Fraxinus excelsior,* and *Hippophaë rhamnoides*) showed establishment rates in agreement with the rate of seashore displacement. The establishment rate of late-successional species on the upper part of the shore (*Picea abies*) also showed significant correlation with elevation above sea level, but with a different slope compared to the rate of sea-shore displacement (Verwijst & Cramer (1985); see Fig. 3).

The Västra Kvarken Archipelago

In their guidebook, Ericson & Wallentinus (1979) elucidated the climatic, geological and vegetational conditions along the shores of the Gulf of Bothnia. Also, Cramer (1993) provided a general description of dry coastal ecosystems of the Northern Baltic Sea. Here, some of the
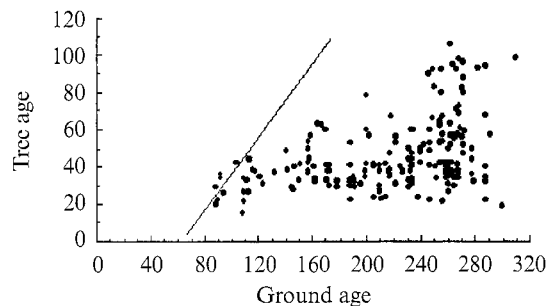
Fig. 3. Relationship between age of Norway spruce (cored at 0.25 m above ground) and ground age, based on topography and an uplift rate of 0.0085 m yr^{-1} (Lantmäteriet, 1989). The sample is from an undisturbed, old-growth Norway spruce forest on an island in the Bay of Sörfjärden (63°49′N, 20°41′E), Västra Kvarken Archipelago (n = 220). The line illustrates a 1 : 1 linear relationship (Tree age = Ground age + 65 years). The initial establishment level is equivalent to 0.5–0.6 m above normal sea level, which is close to the highest water level at this location. It is evident that that the age distribution of Norway spruce is lagged relative to the ground age sequence with a slope coefficient approaching 0.3 (from Svensson, in press).

basic features in the Västra Kvarken (Fig. 1) area will be briefly depicted.

The coastal area is transitional between the south-boreal zone that extends in a narrow strip along the coast, and the mid-boreal zone (*e.g.* Sjörs, 1967). The maritime influence on the climate is crucial. Seawater has a chilling effect during spring and early summer, and a warming effect during autumn and early winter. The seawater is brackish, with a salinity range from 2–5‰. At the river mouths, salinity approaches zero. The tidal influence is very slight. Instead, the fluctuations in sea level owing to wind and atmospheric pressure changes are pronounced, 120–130 cm according to Ericson (1980), and display regional, seasonal and year-to-year variations. The occurrence of high and low water years shows a cyclic periodicity of *ca.* 4–7 years. The normal pattern is that the highest mean water levels occur in January, but at that time, the ice cover has a moderating effect. The lowest levels usually occur in February to April, and low levels continue throughout May and June. In autumn and early winter, the levels rise, the amplitude increases and rapid changes can occur.

The bedrock is the pre-Cambrian peneplain that mainly consists of various kinds of granite, gneiss and acid igneous rocks. Archipelagos are found only in few places, as in the Norra Kvarken strait (Fig. 1). The islands are mainly built up of bedrock and morainal deposits, and are often boulder-strewn and wave-washed. The coastal area has been highly reworked by glacial action, especially during the melting period. The landscape is characterised by parallel drumlins – oval-shaped ridges formed beneath and parallel to an ice sheet as it moved over the terrain (Fredén, 1994) – with depressions between them. The most common drumlin in Västra Kvarken is the drumlinoid type, made up of a nucleus of bedrock with deepest accumulated till on the lee side (Fredén, 1994; see Fig. 4).

The annual precipitation is 450–500 mm. The mean temperature for the coastal area of Västra Kvarken is −5° to −7 °C in January, 0–1 °C in April, 15 °C in July, and 9 °C in September. The annual mean temperature is 3–4 °C. The duration of ice cover is 80–100 days, and the duration of snow cover *ca.* 150 days. The growing season lasts *ca.* 150 days (threshold + 6 °C; see also Ericson, 1980). Cold spells quite frequently occur in early autumn, and affect the life cycles of many seashore species.

Succession and dynamics

Central concepts and definitions

The literature dealing with forest succession and dynamics is extremely rich. It is evident, however, that there is confusion and vagueness in the use of terms, especially in literature dealing mainly with practical forestry applications of successional theory. This section therefore briefly reviews some central concepts and definitions. For more thorough conceptual reviews, the reader is referred to papers such as those by Miles (1987), Oliver & Larson (1990) and Glenn-Lewin, Peet & Veblen (1992).

Ecosystems are continuously changing in their structure, function, degree of complexity, and in the interactions between components (Botkin, 1990). The current composition of any ecosystem is merely a transitory assemblage (Chapin *et al.*, 1996). Kimmins (1997) recognised three major categories of ecosystem change: (1) long-term, slow and directional changes in the physical environment; (2) changes in the genetic constitution of the biota as a result of natural selection; and (3) temporal development and change in ecosystem structure and function. The last category is termed ecological succession, a term originally coined by Thoreau in 1863 (Kimmins, 1997).

Change is closely linked to the time scale addressed. Glenn-Lewin & van der Maarel (1992) suggested division of the time scale into: (1) short-term, the domain of fluctuations; (2) middle-range, the domain of succession; and (3) long-term, the domain of vegetation history. The time span for each category is a highly arbitrary measure; for the domain of succession, Glenn-Lewin & van der Maarel (1992) suggested a few decades to a few centuries, and Miles (1987) a decade to several millennia.

The process of change includes both the cause – the mechanism or mechanisms that induce the change, and the consequence – the virtual change that different components of the ecosystem undergo. Change can be induced by a variety of causes, both by intrinsic biotic and abiotic processes and by external factors. Jenny (1941) identified five independent state factors

that determine soil and ecosystem processes: (1) parent material, (2) climate, (3) topography, (4) biota, and (5) time. Chapin *et al.* (1996) introduced an extension of this approach by characterising four interactive controls: (1) regional climate, (2) soil resources, (3) functional groups and (4) disturbance regime. The interactive controls are constrained by the state factors and interact dynamically with ecosystem process and change (Chapin *et al.*, 1996).

A focal aspect to be acknowledged is that ecosystem change is a case of multiple determinism. If we eventually are able to understand fully the process of change in an ecosystem over time, then we are able to interpret the pathway; in other words, we are able to recreate the past and to determine the future on the basis of the present situation. Consequently, we are able to predict the kind and amount of response in the ecosystem, to the kind and amount of cause.

Kimmins (1997) defined successional pathway as the sequence of plant communities and changes in the ecosystem components (biotic and abiotic) over time. The distinction between pathway, on the one hand, and process, on the other, is ambiguous. Thus, the pathway is commonly denoted as the physical result of the processes. The process of succession can be described in an orderly, and often arbitrary, schematic outline of the progression along a sequence of stages, *e.g.* Clements' (1904, 1916) scheme: (1) nudation – creation of a bare area by disturbance; (2) migration – arrival of organisms; (3) ecesis – establishment of organisms; (4) competition – interaction of organisms; (5) reaction – modification of the abiotic condition by biotic interaction; and (6) stabilisation – development of climax. A more recent version, more strictly for forest development, was proposed by Oliver & Larson (1990): (1) initiation – new individuals and species appear after a major disturbance; (2) stem exclusion – self-thinning and species reduction; (3) understorey re-initiation – understorey individuals survive but are suppressed; and (4) old growth – overstorey trees die randomly and some understorey individuals begin to grow more rapidly.

In nature, however, neither the process of change nor the pathway follows an orderly sequence. Succession is a stochastic and variable process (Botkin, 1979), highly dependent on local conditions and chance (Glenn-Lewin &

van der Maarel, 1992). Vegetation and ecosystem processes always respond to many factors (Chapin *et al.*, 1996). Hence, a multiple pathway approach to succession (Olson, 1958), where both convergence and divergence can be observed (Glenn-Lewin & van der Maarel, 1992), is probably relevant in most cases.

As to definition of the term ecological succession, numerous versions have been presented. Clements (1916) defined it as the sequence of plant community development from lower to higher life forms; and Gleason (1927) defined it as all vegetation change in time, covering the range from fluctuations to fundamental changes in the plant association. Odum (1969) defined ecological succession in terms of three parameters: (1) it is an orderly process of community development that is reasonably directional and therefore predictable; (2) it results from modification of the physical environment by the community, *i.e.* community-controlled but environmentally determined; and (3) it culminates in a stabilised ecosystem with homeostatic properties (see also McIntosh, 1981). McNaughton & Wolf (1979) stressed the directional change and Colinvaux (1986) the successive change in populations. Kimmins (1997) noted that the term can be used in two ways: (1) it can refer to the sequence of plant, animal and microbial communities that successively occupy an area over a period of time – the pathway; and (2) it can refer to the process of change by which biotic communities replace each other and by which the physical environment becomes altered. When the term is used in the latter sense, the entire sequence of community and ecosystem change is called a sere, and each discernible stage is called a seral stage (Tansley, 1935).

A primary succession is vegetation development on newly-formed or exposed raw parent material, with no seedbank or organic matter derived from prior biota (*e.g.* Glenn-Lewin & van der Maarel, 1992). The substrate has not yet been altered in any way by living organisms (*e.g.* Kimmins, 1997). Pianka (1988) stressed pedogenesis as the initiation of a primary succession. In the general sense, a major disturbance can initiate a primary succession. The absence of disturbance, defined as a direct disruption of the biotic organisation (Glenn-Lewin & van der Maarel, 1992) during the

succession sequence is, however, another fundamental requirement in denoting a primary succession.

When succession begins in an environment that has already been more or less modified by a period of occupancy by living organisms, it is termed secondary succession; *e.g.*, as in forest development after clearfelling, or old-field succession. Egler (1954) very early distinguished two main processes, 'initial floristic composition', *cf.* secondary succession, and 'relay floristics', *cf.* primary succession, although he preferred the term vegetation development to succession. The distinction between the terms is ambiguous; 'Primary succession seems easy to recognise, leaving all else to a very broad secondary succession concept, but in nature primary and secondary succession probably form a continuum' (Glenn-Lewin & van der Maarel, 1992).

For a specific sequence, classifications can be made according to initial moisture condition, *i.e.* xerarch (xeroseres), mesarch (mesoseres) and hydrarch (hydroseres) successions, and to initial fertility status, *i.e.* oligotrophic, mesotrophic and eutrophic successions. Although the starting point defines the original conditions of moisture or fertility, these may change during the sere, depending on how the biota modify the parent material (*cf.* Sjörs, 1983).

Based upon the mechanisms that cause the change and that have an impact on the direction of the process, succession may also be classified as autogenic or allogenic. Autogenic succession is vegetation change caused by intrinsic forces of biotic interactions and biotic modification of the environment, while allogenic succession is caused by environmental conditions and environmental change (*e.g.* Tansley, 1935; Glenn-Lewin & van der Maarel, 1992). Autogenic successions often render the site less optimal for the organisms producing the change, and more optimal for the organisms that replace them. A third class that may be recognised is biogenic succession (Kimmins, 1997). Here, the mechanisms include insect epidemics, diseases and invasion by non-native species, where a living organism interferes with an autogenic or an allogenic succession or both, and becomes the major agent of change.

The term dynamics, or vegetation dynamics, has been used more or less synonymously to succession. Oliver & Larson (1990) defined dynamics as the study of changes in forest structure over time, and included forest development during and after disturbances. Glenn-Lewin *et al.* (1992) defined it more broadly, as the study of plant succession and regeneration dynamics. In the literature, it is evident that a very common definition of the term is autogenic, small-scale and community-internal succession, following the shifting mosaic concept of ecosystem change proposed by Watt (1947). For example, Hörnberg *et al.* (1995) suggested in a paper on an old-growth Norway spruce forest in northern Sweden, that the internal dynamics, caused by single-tree mortality in combination with sexual reproduction and local factors, are the driving forces in self-perpetuating forests in the short term.

Another term that must be mentioned is the climax, or climax community. A climax is an indefinitely prolonged stage of a sere, where community development and change become exceedingly slow and where the composition of the biota remains approximately constant for a long period of time (Kimmins, 1997). According to this, succession can be termed progressional – towards a climax condition, and retrogressional – referring to the effects of disturbance (*e.g.* wildfire; rising water table) – in moving the seral condition back to an earlier stage (*cf.* Odum, 1969).

Convergence towards the regional climax, in equilibrium with the regional climate (climatic climax), was the theoretical foundation for the first theory of succession, the mono-climax theory of the Danish botanist E. Warming in the late 19th century (Clements, 1936). The regional climax was considered as a predictable end-point of a succession for a specific area, and analogous to a supra-organism. This theory was subsequently modified to a second major theory of succession, the poly-climax theory (Tansley, 1935), which stated that many factors may intervene to prevent an area from reaching the climatic climax condition. Thus, the theory states that succession in a region does not lead toward a single climax, but toward a mosaic of different climax communities determined by the mosaic of habitats. The interaction between the biota and their environment maintains or amplifies habitat variation in space and time (Watt, 1947). Watt further elaborated on a 'phasic equilib-

rium' (phasic climax), a definite proportion between the constituent biotic phases, as a result of a constant environment. Jones (1945) wrote a few years earlier: "It is conceivable that 'climax forest' is a concept only, never existing in practice either because of catastrophic initiation of fresh seres, or because of the time lag ... in the adjustment of the vegetation cover to an ever-changing environment." Watt agreed: '... phasic equilibrium may rarely be achieved even though the tendency is always in that direction'. Along this route, a third theory of succession, the climax pattern hypothesis (Whittaker, 1953), suggested that vegetation forms a continuum in which species are distributed and replace each other, independent of association (community), along environmental gradients.

These contrasting views of succession; orderly–predictable (*e.g.* Clements, 1916; Odum, 1969) versus disorderly–unpredictable (*e.g.* Gleason, 1917; Drury & Nisbet, 1973), are fundamental for encouraging the development of knowledge on the topic of ecological succession. Thus, the concept of succession is undergoing intense reconsideration. Much of this reconsideration addresses the regularity and directionality of processes, and the causal mechanisms underlying change in community structure (*e.g.* Gorham, Vitousek & Reiners, 1979). Processes include, for instance, chemical regulation, carbon accumulation and productivity rates, and casual mechanisms such as climate change, atmospheric pollution and drastic disturbances by insects.

Overview of literature on primary succession

Primary succession occurs on many different substrates, such as river deltas, floodplains, elevating sea shores, volcanic deposits, sand dunes, glacier forelands, landslips, granite outcrops, coal and mine waste tips, abandoned quarries, excavated peat surfaces, reefs, *etc.* (*cf.* Glenn-Lewin & van der Maarel, 1992). The literature reveals that some of these substrates have been more frequently studied, for example, glacier forelands (*e.g.* studies from Norway, Canada, Alaska, Chile and New Zealand), floodplains (*e.g.* Peru and Alaska), and lava fields (*e.g.* Iceland, Italy, USA, Reunion Island, New Hebrides, Japan, Hawaii, Papua-New Guinea, New Zealand). To give a few examples: soil

development and nutrient cycling have been studied by Clein & Schimel (1995) and Emmer & Sevink (1994); mechanisms of primary succession following deglaciation by Chapin, Walker, Fastie & Sharman (1994) and Vetaas (1994); vegetational processes following volcanic eruptions by Heath (1967), Matson (1990) and Shiro & del Moral (1995); successional patterns in rain forests by Aplet & Vitousek (1994) and Whittaker & Bush (1993); and primary successions on floodplains and sandbanks by Walker & Chapin (1986).

For boreal conditions, a few research areas are of especial interest. There is an excellent literature available on floodplain primary succession, especially from studies in North America, Alaska in particular: *e.g.* Viereck (1970) on forest succession and soil development; van Cleve, Viereck & Schlentner (1971) on nitrogen accumulation in alder ecosystems; Yarie (1983) on environmental and successional relationships; McClanahan (1986) on the successional influence of seed source; Walker, Zasada & Chapin (1986) on life history processes; Krasny, Vogt & Zasada (1988) on Salicaceae species ecology; Yarie (1993) on the effects of selected forest management practices on environmental parameters related to successional development; Mann, Fastie, Rowland & Bigelow (1995) on spruce succession, disturbance and geomorphology; and Binkley, Suarez, Stottlemyer & Caldwell (1997) on terrace dynamics. It is generally concluded that floodplain vegetation succession is controlled by river reallocation of inorganic matter, by soil chemistry and nutrient cycling, and by permafrost build-up and collapse (van Cleve, Chapin, Flanagan, Viereck & Dyrness, 1986).

More recently, interest has developed regarding the impact of herbivores on the vegetation succession on floodplains. Since browsers prefer willow species, in Alaska especially *Salix alaxensis*, hare and moose population sizes influence the shift from the early-successional willow stage to the later-successional alder stage (Collins & Helm, 1997; Kielland, Bryant & Ruess, 1997; Kielland & Bryant, 1998). Helm & Collins (1997) argued that browsing can cause multiple successional pathways on river plains.

Primary succession on glacier forelands has long been an area of documentation and research (*e.g.* Lawrence, 1958). Since Cooper's ex-

peditions in the 1920s and 1930s (*e.g.* Cooper, 1923), the glacier retreat at Glacier Bay, Alaska, and the subsequent primary succession, has been one of the best-documented successional pathways. A few more studies from this specific location may be mentioned: nitrogen fixation by *Dryas drummondii* by Schoenike (1958); plant diversity by Reiners, Worley & Lawrence (1971); *Sphagnum* invasion and paludification at the end of the chronosequence by Noble, Lawrence and Streveler (1984); and changes in productivity and distribution of nutrients by Bormann & Sidle (1990). In an attempt to reconstruct the invasion history of woody plants, Fastie (1995) emphasised causes and consequences of multiple pathways. He suggested that texture, lithology of soil parent material, and proximity to seed source, are important initial conditions that influence the pathway. Other locations, such as Exit Glacier on the Kenai Peninsula, Alaska, have been carefully studied. On the Exit Glacier foreland, Helm & Allen (1995) identified seven stages of vasular plant communities along the chronosequence, and Helm, Allen & Trappe (1996) reported on time requirements for mycorrhiza formation.

For coastal areas, some research has dealt with colonisation of sand dunes by vegetation. Emmer, Hulshoff & Breij (1991) and Emmer & Sevink (1994) reported on the effect of *Pinus sylvestris* plantations on humus build-up and humus profile development. Fanta (1986) reported on the development of *Pinus sylvestris* stands, litter and humus layer build-up, and plant association formation in similar environments. Walker, Thompson, Fergus & Tunstall (1981) illustrated the ultimate dependence of terrestrial biological systems on soil fertility, and the tendency for coastal sand dune ecosystems to lose nutrients and decrease in fertility over long time periods. They suggested that in the long term, and indeed in the short term for some nutrient-poor systems subject to intensive land use, the assumption of a self-perpetuating forest climax seems biologically and geochemically untenable. Gorham *et al.* (1979) summarised ecosystem processes in relation to biogeochemical cycling in developing ecosystems, including inputs, hydrological processes influencing inputs, and biological processes affecting the balance of inputs and outputs. The concepts of progressive and retrogressive forest succession can be related to biogeochemical processes and nutrient gains or losses over time.

Reported studies on primary succession on rising coastlines outside Fennoscandia are not common in the literature. Bliss & Gold (1994) report on plant colonisation, successional sequences, and plant association development on a rising high-arctic coastline on Devon Island, Canada. The rising coastlines along Hudson Bay, Canada, offer excellent opportunities for studying primary succession (Sims, Wickware & Cowell, 1987), both concerning wetland successions and successions on mesic and drier sites. The response of littoral shrub populations (*Salix* spp, *Alnus rugosa*) to land emergence, as well as conifer (*Larix laricina* and *Picea mariana*) population response and community development, have been carefully documented for the east shore of James Bay and Hudson Bay (Bégin *et al.*, 1992; Grégoire & Bégin, 1993; von Mörs & Bégin, 1993; Lescop-Sinclair & Payette, 1995). Kouznetsova (1999*a* and *b*) studied soil evolution from marsh to upland podzols and back to peat soils along 4000-year transects on the Karelian White Sea shore in Russia. The rate of land uplift in this area varies from 2 mm yr^{-1} to $5-6 \text{ mm yr}^{-1}$. Kouznetsova concluded that soil transitions are polygenetic: development towards upland, mineral types; directly towards organic peat soils; or to upland mineral and then back towards organic peat soils, owing to secondary paludification. Studies on land-uplift primary succession along the Gulf of Bothnia are reviewed below (pp. 14–19).

Succession that occurs on exposed open pits or mine tailings, abandoned gravel and sandpits and cutaway peat deposits offers exposed raw parent materials. These successions may be considered as primary or secondary, depending on the depth of extraction relative to the depth of weathering and pedogenesis, and on whether any viable seeds or spores still are present (Curran & MacNaeidhe, 1986; Salonen, 1987; Smart, Wheeler & Willis, 1989; Salonen, 1990). The succession is rapid in the initial stages (*e.g.* Jukola-Sulonen, 1983; Huston & Smith, 1987) and, in the case of primary succession, totally dependent on immigration of seeds and spores from a neighboring source (*cf.* Miles, 1987; Glenn-Lewin & van der Maarel, 1992).

During the course of many terrestial seres, the majority of higher plant species enter the suc-

cession as seeds (Fenner, 1987). Wind is probably the main agent for distribution in most cases. The effectiveness of seed dispersal depends, according to van der Valk (1992), on five factors: (1) seed production, (2) vector of seed transport, (3) timing of seed release, (4) distance of dispersal and (5) fate of dispersed seeds. There is a logarithmic decrease in propagule density with distance (Sjörs, 1971). Sjörs observed that in the Swedish flora *Epilobium angustifolium* has the slowest-falling seeds, and thus the greatest potential for long-distance dispersal. The distance, species composition, and fertility of the seed source are important to the success of colonisation, but also important are the surface structure and the physical and chemical conditions of the ground (Horn, 1981; Sousa, 1984; Salonen, 1990). In general, high densities of propagules reach an open, bare surface, but only a small proportion becomes established (Wheeler & Shaw, 1995). Species with light seeds adapted to long-distance transport by wind, and with adhesive capacity, are the most successful.

Primary succession on Bothnian coastlines

Overview of the literature

The primary succession on the rising ground-moraine shores along the Gulf of Bothnia terminates in Norway spruce (*Picea abies*) communities (Fig. 2). According to Ericson & Wallentinus (1979), not much research has been done on the moraine shores. There is, in fact, a significant lack of studies that deal specifically with the spruce succession sequence, community dynamics and structural development. Ericson (1980) concluded that our present knowledge of the colonisation of Norway spruce on the emergent shores, and the role played by the land uplift and other factors, is only fragmentary. In general, the literature dealing with the Finnish coast is rich and comprehensive, while the literature dealing with the Swedish coast is limited (Ericson & Wallentinus, 1979).

Some conceptual transect analyses were made by Appelroth (1948, 1981) who emphasised productivity, forest site type development, regeneration features, and silvicultural aspects of coastal Norway spruce forests in the region.

Appelroth (1948) hypothesised that natural primary succession on ground-moraine will continue beyond the Norway spruce stage into a Scots pine (*Pinus sylvestris*) stage. Owing to a falling groundwater table as uplift goes on, the site would develop into a poor ecosystem with a natural setback of spruce and natural establishment of the more drought-tolerant pine. The general impression from the reconnaissance mentioned in the Introduction is that the pine forests found result either from disturbances (past clearfelling, fire, over-grazing) or from a different successional pathway. Pine sometimes forms stands on the neck of an island or a peninsula, where the soil normally is shallow. We suggest that the occasional pine forests are stationary phenomena that reflect particular site conditions, which are not part of the normal primary succession on the deeper morainal shore slopes (Fig. 4). In a very long-term perspective, however, spruce may also enter the pine sites.

The ecology of broadleaves along the coast has been well documented. For instance, Tapper (1993) reported on the replacement of *Alnus glutinosa* by *Fraxinus excelsior* with increasing elevation above sea level on an island in the Stockholm Archipelago; Ericson (1972) gave a general description of broadleaves along the coast of the Gulf of Bothnia; and Cramer (1985) and Verwijst & Cramer (1985) studied the age structure of several woody species on a rising seashore in northern parts of the province of Uppland, Central Sweden (for the ecology of specific woody species, see below, pp. 17–19). The mires along the Bothnian coast have also been well studied as, for example, the classification and development of open mire vegetation by Elveland (1976, 1981, 1984a), and forested and open wetland complexes by Sjöberg & Ericson (1992). Also well documented are the coastal and river-shore meadows (Elveland, 1984b, 1985; Schwank, 1974, 1981), and the downward migration of seashore non-woody plants (Vartiainen, 1980; Ericson, 1980, 1981; Cramer & Hytteborn, 1987).

The main ecological factors

Recently emerged islands consist of bedrock or boulders and stones, usually rock and coarse material at the top and finer material on the shoulders. The process of colonisation is charac-
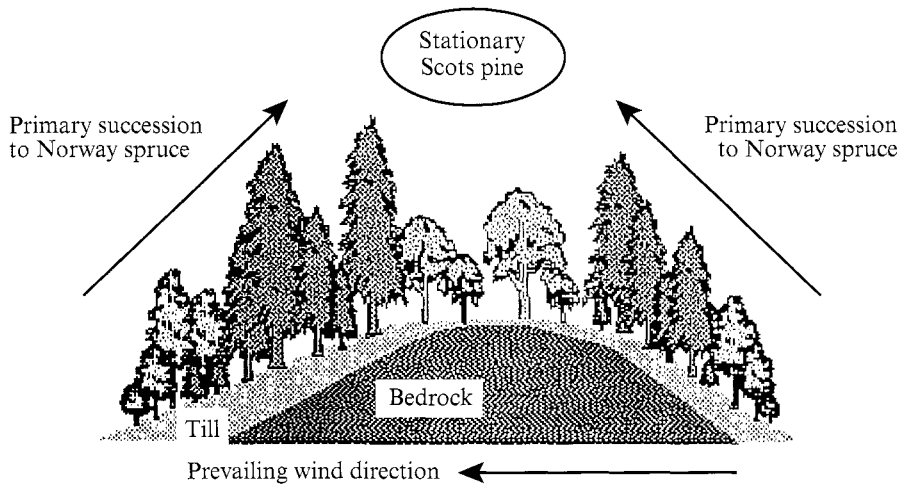
Fig. 4. An illustration of drumlin build-up relative to prevailing wind direction and main forest types. A stationary Scots pine forest, not involved in the general primary succession, sometimes occurs on shallow soil on the drumlin neck. The pine forest may be a result of a different successional pathway, in combination with past clearfelling, over-grazing or wildfire disturbance.

terised by migration onto ground previously without vegetation. Wind disperses propagules from other islands or from the headlands nearby, plants colonise, and humus and soil profiles begin to develop. In addition, propagule dispersal by seawater, by animals or both, occurs, as well as vegetative regeneration. In places, aquatic deposits, consisting of mineral and organic matter, build up, both in shallow waters and as ridges on the shore.

As the community matures and changes, the importance of allochthonous plant colonisation decreases, while the importance of autochthonous resurgence increases. Furthermore, it may be assumed that early-succession processes are primarily under abiotic control, while biotic factors take on greater importance later in the sequence (Viereck, Dyrness & Foote, 1993; Kielland & Bryant, 1998). As long as no major disturbance interferes, the primary succession continues progressively towards the regional climax for each ecosite type.

In more sheltered locations, in the inner archipelago and in bays and lagoons, there is less influence of wave-wash and ice-drift. This allows the accumulation of finer deposits of silt and clay, also of organic deposits originating from aquatic and submerged vegetation. Here, the term primary succession is more questionable, since organic substrates are involved to some extent in the original site formation.

The spatial vegetational gradient observed on a specific shoreline reflects the actual course of succession (Ericson & Wallentinus, 1979). In the initial stages, pioneers and competition-intolerant species are able to colonise. Changing water levels are of importance, because of the associated erosive effect that creates new, bare ground available for establishment at low water levels. With increasing elevation and less disturbance, more competitive species are favoured. On gently-sloping shores, the width of the exposed ground is great, and generative establishment by fruits or seeds is more successful. On steeply-sloping shores, on the other hand, the opportunities for generative establishment are rather small, owing to the lack of a stable surface and limited area. Here, species that are able to regenerate vegetatively are favoured (Ericson & Wallentinus, 1979).

Ericson (1980) concluded that the consequence of land uplift on the succession is largely a long-term phenomenon. For species occupying the lower geolittoral (see below, pp. 17–18) and seawards, succession should be observed for periods of ten years and more. For shorter periods, the effects of annual and seasonal fluctuation in sea level are more important to the composition of shore vegetation, strongly influencing germination and seedling survival (Ericson, 1980). Most seashore species germinate in the early summer, *i.e.* the time of the most pronounced

15

and stable low water-level period. During a year with pronounced low water levels, rapid seedling colonisation takes place, and species can successfully occupy new areas (Ericson, 1980). The rate of seaward colonisation can in such situations substantially exceed the land-uplift rate (Ericson, 1980; Schwank, 1981; Alestalo, 1982). During years with pronounced high water levels, however, established plants are set back, and seedling colonisation is inhibited. Accordingly, species that are able to regenerate vegetatively are better adapted to such fluctuations (Ericson & Wallentinus, 1979).

Ericson (1981) summarised the important factors that control the vegetational gradient on seashores: (1) shore slope, (2) interspecific competition, (3) substrate and (4) influence of freshwater *versus* salinity. Salinity shows striking seasonal variation, with low values in spring and early summer, owing to the influx of fresh surface water. The effect of salinity decreases upwards on the shore. Moreover, 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.

Several of these factors are primarily related to the exposure, *i.e.* the relative location in the archipelago and the aspect of a specific shore relative to prevailing winds and fetch (*cf.* van Cleve & Viereck, 1981). Ericson & Wallentinus (1979) pointed out the existence of a gradient, from the outermost to the innermost archipelago, expressed by decreases in salinity, degree of wave-action and duration of sunshine, and increases in amount of sedimentation, duration and thickness of ice cover and amount of precipitation. This salinity-exposure-climate gradient influences the vegetation on the shores. For example, vernal species tend to disappear seawards, and extensive birch woodlands tend to occur in the outer archipelago (Ericson & Wallentinus, 1979).

The more exposed the shoreline, the more influenced is the vegetation sequence by factors related to the salinity-exposure-climate gradient. As islands and peninsulas continue to rise seawards through time, however, the exposure of a specific shore may decrease because of increasing relative shelter. This may modify the succession by causing a deviation or maintain a continuous divergence in the pathway, and interfere in the chronosequence by improving seedling establishment conditions on lower sea-

shore levels (Svensson, in press). Improved seedling establishment conditions include both improved intrinsic abiotic stability and maturation, and improved biotic conditions, such as decreased distance to allogenic seed sources and increased autogenic seed source.

As the archipelago develops as a result of postglacial land uplift, establishment conditions on a specific shoreline may have improved substantially on lower shore levels compared to higher shore levels; this allows plants to establish at successively lower levels (Fig. 5). Such effects will become clear within a time-span of two to three centuries, which is equivalent to the development of a climax-like Norway spruce forest from the initiation of succession (Svensson, 1998; Svensson & Jeglum, in press). Hence, the influence of multiple successional pathways (*cf.* Fastie, 1995; Helm & Collins, 1997), as well as disruptions in the presumed chronosequence, should be taken into consideration at any specific location.

Ecological gradients

Seashores often show an obvious vegetational gradient, owing to edaphic and climatic conditions. The littoral can be divided into the fol-
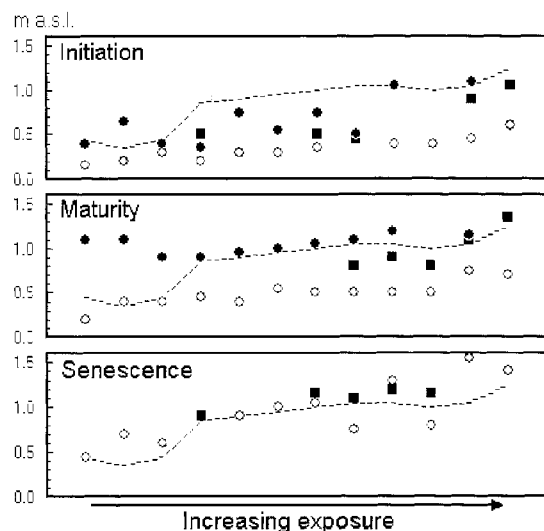
Fig. 5. Initiation-, maturity- and senescence-level above normal sea level for *Picea abies* (●), *Alnus incana* (○) and *Sorbus aucuparia* (■), relative to highest water level (dashed line), inferred from jetsam on the shore and adjusted according to sea-level records from the Ratan hydrological station (64°00′N, 20°55′E) for 1968. Sample from 12 sites in the Västra Kvarken Archipelago, arranged from low to high exposure (after Ericson, 1972).

16

lowing belts from wetter to drier, according to Ericson & Wallentinus (1979): (1) sublittoral, the permanently submerged belt; (2) eulittoral, the amphibious area between the extreme high and low water levels; and (3) epilittoral, the terrestial belt which never is submerged. The eulittoral can be further divided into: (2a) geolittoral, above the mean water level; and (2b) hydrolittoral, below the mean water level (Fig. 2 illustrates belts 2 and 3).

Ericsson & Wallentinus (1979) prefer the term 'ecological gradient', instead of 'zonation', since the vegetation belt undergoes spatial displacement. They defined the following stages of communities along the gradient of decreasing moisture (roughly): (1) aquatic vegetation, (2) epilithic algal vegetation, (3) vegetation on soft bottoms, (4) vegetation on fine-grained shores, (4a) exposed shores subject to wave action, and (4b) sheltered shores, (5) saline vegetation; (6) vegetation of shore drift, (6a) spring flood drift, (6b) early autumn drift, and (6c) late autumn–winter drift, (7) vegetation of coastal sand deposits, (8) lichen vegetation, (9) deciduous vegetation and (10) conifer vegetation. The diversity of habitats provides a high species diversity. Schwank (1981) found, e.g., 130 vascular plant species in the Larsmo Archipelago of NE Finland.

The vegetational gradient for a rather sheltered bay (Sörfjärden 63°49′N, 20°41′E) exhibited a marked salinity gradient (2.8 to 3.9‰ for the off-shore water) and a development towards more sheltered conditions (Ericson, 1980): *Chara aspera–Potamogeton filiformis–Scirpus tabernaemontani, Eleocharis uniglumis, Deschampsia bottnica, Agrostis stolonifera* var. *bottnica–Calamagrostis neglecta, Juncus gerardi–Carex nigra, Carex pulchella, Molinia caerulea–Filipendula ulmaria–Rubus arcticus, Myrica gale, Alnus incana–Agrostis tenuis, Alnus incana.* The initial occurrence of some woody species was reported: *Betula pubescens,* mean water level +20 cm; *Myrica gale, Salix phylicifolia, S. pentandra,* +25 cm; *Alnus incana,* +30 cm; *Picea abies,* +40 cm; *Sorbus aucuparia,* +45 cm.

Schwank (1981) gave quite different values for initial establishment of *A. incana* (mean water level +50 cm) and *P. abies* (+120 cm) for the Larsmo Archipelago, NE Finland. Verwijst & Cramer (1985) showed that *P. abies* establishes at *ca.* 100 cm, 50 cm and 70 cm for ex-

posed, intermediate and sheltered locations, respectively, for a central Swedish seashore. Ericson (1972) reported on increasing level of initial establishment of *P. abies* (+35 to +110 cm) on a sequence of 12 sites from low to high exposure in Västra Kvarken (Fig. 5).

Plants that inhabit the upper geolittoral and landwards, i.e. mostly long-lived herbs, ericaceous shrubs and woody species, are influenced by water-level fluctuations only to a slight extent, and the importance of vegetative growth also diminishes (Ericson, 1980). At this level, however, exposure is still a key factor influencing the vegetational gradient, but the salinity gradient is not as important (cf. Ericson, 1981). Thus, in the upper geolittoral and landwards, the rate of downward spread roughly coincides with the actual land uplift (Ericson, 1980).

Ecology of the main woody species

Not many woody species are present in the coastal area of Västra Kvarken. *Alnus glutinosa* has reached its northern limit, and occurs only as scattered trees on the outermost, exposed headlands or on river floodplains. Instead, *Alnus incana* forms extensive, continuous thickets in the upper geolittoral and lower epilittoral (e.g. Pekkari, 1957; Appelroth, 1981) (Fig. 2). Svenonius (1945) observed, partly in contrast to this, that *A. incana* occurred in the eulittoral but not in the epilittoral. *A. incana* does not normally grow taller than 8–10 m at most, and individual trees usually die off at an early age – *ca.* 45 years of age, according to Schwank (1981). Ericsson & Wallentinus (1979) pointed out that *A. incana* readily coppices, but is unable to reproduce by seed. By comparison, Cramer (1985) observed that *A. glutinosa* regenerates from seed seawards and vegetatively landwards. At exposed locations in the the Västra Kvarken Archipelago the ground-moraine shores are strongly wave-washed, and boulders and stones dominate the substrate. A humus layer is usually absent. Here, *A. incana* is normally prevented from forming a dense, clonal thicket, which allows other tree species, such as *Sorbus aucuparia* and *Betula pubescens,* to establish and sometimes to dominate.

S. aucuparia is very desirable to browsing elk and roe deer. Since populations of elk and roe deer presently are high, they have a large impact on the abundance and distribution of *S. aucuparia.* Skye (1965) observed that *S. aucuparia* ap-

pears to be very tolerant to high exposure, hence normally prevails in the outermost archipelago (Fig. 5) and on relatively small and isolated islands.

On more sheltered shores, *A. incana* is fringed by *Salix phylicifolia* thickets, sometimes mixed with *S. pentandra* and other *Salix* spp on the seaward side, and with *Betula pubescens* on the landward side. *Salix* spp, *Myrica gale* and *Betula nana*, are usually the first woody colonisers on the shores (Fig. 2).

Betula pubescens and *S. aucuparia* sometimes form an intermediate stage between *A. incana* and *Picea abies* (Fig. 2 and 5). *Betula pendula* is sometimes also present. Extensive birch woodlands tend to occur in the outer archipelago. It has been suggested that birch is dominant owing to better tolerance of extreme coastal climatic conditions (high exposure), compared to pine and spruce (Ericson & Wallentinus, 1979), but past agricultural management towards improved grazing and hay-making, and more effective dispersal of lighter birch seeds, are probably also part of the explanation.

Hippophaë rhamnoides is an early pioneer species that occasionally forms quite extensive but usually low-grown thickets (a few decimetres tall) in the upper hydrolittoral and lower geolittoral, in front of the *A. incana* border (*e.g.* Enkola, 1940; Salo, 1989; see Fig. 3). *H. rhamnoides* is, together with *Alnus* spp. and *Myrica gale*, a nitrogen-fixing species. Verwijst & Cramer (1985) found for a Central Swedish seashore that the establishment rate of *H. rhamnoides* coincides with the rate of seashore displacement. It has been suggested by Schwank (1981) that past agricultural management – grazing and hay-making – favoured *H. rhamnoides* over *A. incana* and *P. abies*. The stage used for this purpose was the nitrogen-enriched landward side of the alder fringe, which was converted into a quite extensive and rich meadow with scattered trees. In undisturbed conditions, however, *H. rhamnoides* is unable to compete successfully with *A. incana*. Closed thickets begin to degenerate at relatively young ages, giving space at their centres to herbs or larger woody plants. Several factors may contribute to the degeneration. Vouristo & Rousi (1976) suggested fungal infection, excessive water (paludification), mechanical effects of ice, and browsing as possible mechanisms. From Norra Kvarken and northwards, extensive *H. rhamnoides* thick-

ets can only be found on the outermost, strongly wave-washed, and exposed south-facing shores, where *A. incana* colonisation is delayed. However, Vouristo & Rousi (1976) observed that *H. rhamnoides* does not inhabit bare granite rocks, but rather shallow shores consisting of pebbles, moraine or finer material. Dispersal by birds explains the common occurrence of *H. rhamnoides* and *S. aucuparia* in isolated localities.

Juniperus communis occurs scattered along the coast. It usually enters the succession just seawards of the *A. incana* border, but fails to stand the competition of other woody plants landwards. In places, where domestic grazing or hay-making in the past has been of major importance and duration, rather large and tall thickets have developed and are able to persist.

Pinus sylvestris usually occurs in more open conditions or on less fertile and dry parent material, or both (Schwank, 1981), with shallow soil cover. Skye (1965) observed that *P. sylvestris* tends to be more sensitive to high exposure, *i.e.* wind, than *Picea abies*.

Picea abies initially establishes above the highest water level, at *ca.* 0.6–0.7 m above normal sea level in the Västra Kvarken area. On steeply-sloping shores, the transition from alder to spruce generally is sudden, but on gently-sloping shores a prolonged mixed transitional zone can occur (*cf.* Svenonius, 1945), usually with *Sorbus aucuparia* and *Betula* spp intermixed (Fig. 2; Plates 1 and 2). *P. abies* tends to colonise gradually. This can probably be explained to a large extent by the coincidence between a good seed crop and good establishment conditions – mainly low water levels and absence of late-summer frost (*cf.* Ericson & Wallentinus, 1979; Ericson, 1980 and 1981). Several other factors influence when and where *P. abies* invades, such as N availability, soil moisture, ice drifting (mechanical), and low salinity (Ericson & Wallentinus, 1979). However, our present knowledge of how different factors influence establishment is still fragmentary (Ericson, 1980).

The initial colonisation of recently emerged islands by *P. abies* depends on long-distance dispersal of seeds by wind. The distance to the seed source and the prevailing wind direction are of the utmost importance. Several studies, for example by Hesselman (1919) on *P. abies* in
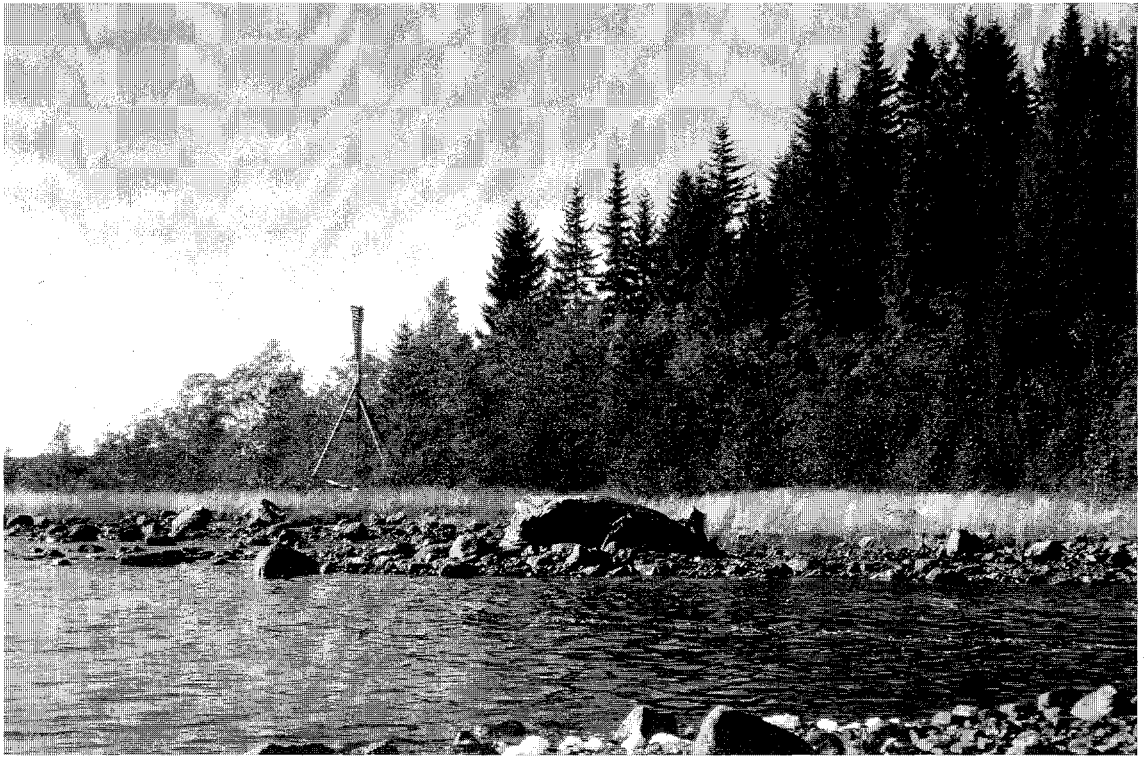
Plate 1. Österstgrundet peninsula, Västra Kvarken. Exposed location. The transition along the ecological gradient is gradual, from an early open stage (graminoid and sedge dominated), through a primary forested stage (alder dominated), to a secondary forested stage (spruce dominated). Photo J.K. Jeglum, May 1998.

NE Sweden and by Ritchie & MacDonald (1986) on *P. glauca* in central Canada, have revealed that conifer seeds can be dispersed over distances of several kilometres when the surface is frozen or snow-covered. *P. abies* normally regenerates from seed, but clonal regeneration by layering also occurs.

Structure and dynamics of coastal Norway spruce forests

Norway spruce forest development

When Norway spruce eventually becomes the dominant tree species on an island in the Bothnian Archipelago, it might be expected that regeneration would largely be by seeding from mature trees on that island. There is, however, a considerable delay between the time at which spruce initially becomes established, and the development of cones and subsequent autochthonous regeneration. Lindgren, Ekberg & Eriksson (1977) concluded that the juvenile period of

Norway spruce may sometimes last 40–50 years. One might expect, however, that the maritime conditions along the coast would reduce the interval substantially. The extension of the time-lag between initial establishment and prevailing autochthonous regeneration, compared to allochthonous seed immigration, and its variability owing to exposure, island size and distance to seed source, are key questions to address for understanding the primary succession and dynamics of Norway spruce.

Owing to the cyclic nature of cone production by Norway spruce, large cone crops and seedfall occur irregularly (*e.g.* Tirén, 1935; Andersson, 1965). In the boreal zone of northern Sweden, large cone crops occur at variable intervals of two to three years and up to 12–13 years (Sarvas, 1968; Koski & Tallqvist, 1978; Leikola, Raulo & Pukkala, 1982; Wennström, 1994). Heavy cone crops are stimulated by the occurrence of one or two warm and dry summers; thus low temperature is a limiting factor for flowering in the northern parts of the range of spruce (*e.g.* Tirén, 1935). A good seed year is

19

Plate 2. Bay of Mittifjärden, Västra Kvarken. Intermediate exposed location. The transition from the primary forested to the secondary forested stage is sudden, associated with a rapid decline of alder, considerable amounts of dead wood and large amounts of spruce seedlings and saplings. Photo J.K. Jeglum, May 1998.

usually followed by several poor seed years (Leikola *et al.*, 1982). This can be ascribed to the morphology of the shoot system of spruce, whereby prolific flowering reduces the number of buds capable of vegetative development, and subsequently the ability to initiate floral primordia (*e.g.* Sarvas, 1968; Eriksson, Lindgren & Werner, 1975). Factors such as tree age and size, crown exposure and edaphic conditions also affect the periodicity of cone and seed production (Lindgren *et al.*, 1977).

Seed germination and seedling establishment of Norway spruce are influenced by many factors, from intrinsic seed quality to seed–seedling–seedbed relationships and environmental factors (*e.g.* Yli-Vakkuri, 1961; Ohlson & Zackrisson, 1992; Zackrisson & Nilsson, 1992; Wennström, 1994, 1995; Steijlen, Nilsson & Zackrisson, 1995). According to viability predictions for spruce seed by Wennström (1994, 1995), very high viability of Norway spruce seeds is to be expected in coastal areas, even at high latitudes.

Depending on a range of factors – island size, isolation, exposure, seed crop, water level, *etc.*, – the sequence of spruce succession towards dominance and forest maturation may vary substantially in space and time, from slow-growing, sparsely stocked stands with abundant layering regeneration and late maturation, to fast-growing, dense stands with severe self-thinning and early maturation. Hypothetically, a time difference of a century and more between these two extremes may be expected. Eventually, over time and in the absence of disturbances, a climax-like Norway spruce forest develops. The route (or routes) by which this stage is reached is, however, still largely unknown (*e.g.* Ericson & Wallentinus, 1979; Ericson, 1980). Nonetheless, a great amount of knowledge has accumulated on the outline of the natural dynamics of Norway spruce forests; this is also applicable to the dynamics and structural development of the climax-like, coastal spruce forest. It is generally agreed that the ecology and dynamics of extensive areas of natural Norway

spruce forest are driven by small-scale disturbance (e.g. Kuuluvainen et al., 1998) and not by periodic and large-scale disturbances.

Norway spruce patch dynamics

The concept of gap dynamics (e.g. Doyle, 1981; Pickett & White, 1985) or patch dynamics (Hytteborn & Packham, 1987; Hytteborn, Packham & Verwijst, 1987; Quinghong & Hytteborn, 1991), i.e. autogenic succession, in climax or climax-like forests, can be characterised as 'a steady state of repeated short-term cyclic variations in the composition of small patches of vegetation around a mean community condition' (Kimmins, 1997). The concept mainly derives from the classic paper by Watt, 'Pattern and process in the plant community' (Watt, 1947). Watt concluded that a fundamental requirement for understanding the ecology of plant communities is to move away from individual plants to aggregates of individuals and of species, which form different kinds of patch. The orderly tendency of a community is a result of the persistence of the patchy pattern. 'But there are also departures from this inherent tendency to orderliness caused by fortuitous obstacles to the normal time sequence'. And Watt continues, 'At any given time, therefore, structure is the resultant of causes which make for order and those that tend to upset it'.

The regeneration dynamics of Norway spruce forests has been widely studied (e.g. Sirén, 1948, 1955; Kielland-Lund, 1963; Steijlen & Zackrisson, 1987; Junttila & Skaret, 1990; Lundqvist, 1991, 1994; Hofgaard, 1993a,b; Zackrisson, Nilsson, Steijlen & Hörnberg, 1995). Owing to their moderate shade tolerance, Norway spruce seedlings can develop under shade, but grow better in openings and gaps. Because of this, in the absence of tending and thinning, spruce forests tend to develop naturally into all-sized, all-aged, multi-layered forests (e.g. Lähde, Laiho, Norokorpi & Saksa, 1992; Norokorpi, 1992).

Typically, the size distribution of individuals in a natural, late-successional forest forms a reverse-J shaped curve, i.e. a Poisson or negative exponential distribution (Greig-Smith, 1964; see Fig. 6). The literature supporting this view is extensive: e.g. for Norway spruce, Sirén (1955); Hytteborn et al. (1987); Leemans & Prentice (1987); Lähde et al. (1991); and Lundqvist
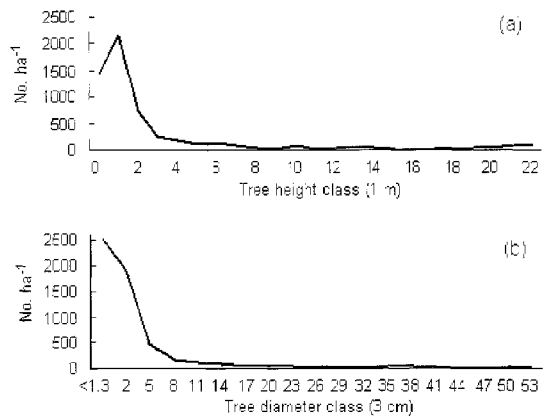

Fig. 6. An example of reverse-J distribution of Norway spruce height (A) and diameter (B). The sample is from an undisturbed, old-growth Norway spruce forest on an island in the Bay of Sörfjärden (63°49′N, 20°41′E), the Västra Kvarken Archipelago, expressed as number ha^{-1} for live, declining and recently dead spruce (n = 904) (from Svensson & Jeglum, in press).

(1993), and for other species, e.g. Newton & Smith (1988) for Black spruce (Picea mariana) and Balsam fir (Abies balsamea); Battles, Johnson, Siccama, Friedland & Miller (1992) for Red spruce (Picea rubens); O'Hara (1996, 1998) for Ponderosa pine (Pinus ponderosa); McCarthy & Bailey (1996) for mixed hardwood forest (Quercus rubra, etc.); and Goodburn & Lorimer (1999) for northern hardwood forests (Acer saccharum, etc.).

Sirén (1955) concluded that undisturbed Norway spruce stands in northern Finland go through repeated cycles of build-up and destruction, and display a multi-storied, reverse-J shaped structure only during parts of this cycle. More recent studies (cf. Lundqvist, 1993) revealed that this structure can be maintained for extended periods. Hörnberg et al. (1995) claimed that the reverse-J shaped structure is a climax structure, which is an effect of a stable balance between recruitment and mortality.

Owing to intense competition for light, successful Norway spruce regeneration requires canopy gaps. Lundqvist (1994) argued that the mortality of seedlings less than 0.1 m tall is very high in uneven-sized forests where the foliage is well distributed vertically, as a result of light competition. Small-scale disturbances, caused mainly by the fall of single trees, make it possible for younger and suppressed trees to develop (e.g. Hytteborn & Packham, 1987; Skarpe,

Hytteborn & Cramer, 1989). Skarpe *et al.* (1989) re-analysed a transect in a 250–300 year old coastal spruce forest studied by Sernander 50 years earlier. They concluded that the spruce age structure was determined not by the original primary succession following land uplift, but rather by gap-phase regeneration in windfall openings created in 1830 and 1885.

The aggregation of saplings and sub-canopy trees is a normal structural pattern in natural Norway spruce forests (Leemans, 1991). The fallen and decomposing logs and root plates form suitable establishment microsites for natural regeneration (*e.g.* Hofgaard, 1993*a*,*b*; Kuuluvainen, 1994; Linder, 1998). Because of competition above- and belowground, seedlings are unable to establish outside the gap (Watt, 1947). Watt used the metaphor 'microcosm' to describe the gap, from which the seedling is '... unable to spread, but it may develop.' The ability of species to reproduce under their own canopy is a feature of a climax community (*e.g.* Hörnberg *et al.*, 1995), where gap disturbances contribute to the structural, functional, and species diversity (Kuuluvainen, 1994).

Structure and the relative maturity of forests

A classification is an abstraction of reality into a limited number of diagnostic characteristics (Zonneveld, 1988*a*), a tool for understanding the processes presently prevailing and for determining the possible pathway of future change. Classical classifications of plant communities are based on their structure, their floristic composition, or a combination of structural and floristic systems (Küchler, 1988). An 'accurate enough' classification of structure at a specific stage of ecosystem development forms the basis for all process-related ecological analysis (Küchler & Zonneveld, 1988), and the subsequent potential for forestry practice (Moeur, 1993).

A major challenge has been – and still is – to provide guidelines for such 'accurate enough' classifications. One such guideline has to do with the approach to structural attributes in a forest. The structure of a forest can be characterised by several attributes, *e.g.* horizontal spacing, vertical stratification, size, age, and species. Independent of the attribute or attributes used,

a structural classification is a characterisation of potential ecological diversity and accordingly an indicator of ecosystem viability (*cf.* Magurran, 1988). According to Norokorpi *et al.* (1997), natural stands show a spatial arrangement of the trees that is variable both vertically and horizontally. Furthermore, they argued that the stock of trees in a forest plays a central role in the formation of habitats and thus for the biodiversity of the ecosystem. They concluded that natural stands are very close to fulfilling the best requirements of biodiversity.

The spatial (three-dimensional) structure of forests has long been a focus of interest for ecologists (*cf.* Moeur, 1993). Richards *et al.* (1939), for instance, argued that vegetation primarily should be characterised by its own features. Smith (1972) concluded that spatial heterogeneity tends to reduce the intensity of competition and thus have a stabilising effect on the ecosystem. He argued that both stability and diversity are primarily products of spatial heterogeneity: 'The patterns of change in stand structure are simply the result of interactions of plants and are emergent properties of tree interaction' (Oliver & Larson, 1990). The structural complexity of forests often seems to be a good predictor of overall species diversity (Begon, Harper & Townsend, 1986). Leps (1990) and Smith (1972) argued, however, that pattern analysis serves mainly to suggest hypotheses about underlying mechanisms; mechanisms can be suggested, but not tested, by pattern analysis.

A current concept is that spatial analysis, based on structural stratification in vertical layers, and density within strata, have significance for ecological interpretations of forest dynamics (Zonneveld, 1988*b*; Moeur, 1993; Parker, 1995; Kuuluvainen, Penttinen, Leinonen & Nygren, 1996). Moeur (1993) concluded that analysis of spatial patterns within and between groups of trees allows reconstruction of past stand structure and interpretations of ecological processes. Especially in a heterogeneous forest, the spatial vegetation structure and the distribution and proportion of free space are of ultimate importance for an understanding of the role of competition and internal dynamics (*cf.* Richards, 1983; Grime, 1987).

Interest is currently directed towards indices that encompass three-dimensional forest struc-

tural variability, *e.g.* the 'Canopy closure index' (Lieberman, Lieberman & Peralta, 1989) and the 'Dissimilarity coefficient' (Hagner & Nyquist, 1998). Of greatest interest is the possibility to explore the use of indices and classifications for analysis of spatial change and the relative maturity of a certain developmental stage.

An important aspect of spatial change is the continual recruitment, competition and turnover among individual trees. This offers the possibility to interpret dynamics *via* successional stages of tree health, from vigorous living to dead and decaying. For instance, Maser, Anderson, Cormack, Williams & Martin (1979) and Bartels *et al.* (1985) classified successional stages of decomposition of conifer logs and snags into nine and five classes, respectively, and Rouvinen & Kuuluvainen (1997) emphasised the role of crown form development and decline in this sense.

One approach to defining the relative maturity of a forest is the change in diversity. The general trend is an immediate increase in diversity in early seral stages after disturbance, followed by a decrease as the succession approaches its later stages (*e.g.* Jukola-Sulonen, 1983; Ekstam & Forshed, 1992). A further approach is *via* the structural development and the presence of late-stage forest (old-growth) attributes (Kuuluvainen *et al.*, 1998; Leppäniemi, Hallikainen, Mikola, Puoskari & Sepponen, 1998). Hörnberg *et al.* (1995), for example, listed the following old-growth attributes: multi-layered tree canopy; large amounts of snags; dead wood and large fallen stems; undisturbed hydrology; stable moisture conditions; and high biological diversity.

A functional approach to characterising the relative maturity of seral stages in a succession is to look at the processes of carbon sequestration and element cycling. Odum (1969) emphasised bioenergetics, and suggested that in the early stages of succession there was a Photosynthesis : Respiration ratio > 1, whereas in later stages the ratio decreased to < 1. The energy fixed tends to be balanced by the energy cost of maintenance in the mature (climax) community. The P/R ratio, he argued, is an excellent functional index of the relative maturity of the successional sequence.

Vitousek & Reiners (1975) compared the pattern of change in net ecosystem production during primary and secondary succession of terrestial sites. They argued that in the course of primary succession, initially element output is relatively high, approximately equal to input. As net ecosystem production increases to a maximum, output falls to a minimum, because elements accumulate in biomass and detritus. Eventually, productivity levels off and then declines. This is followed by a rise in output rates, until they approximately equal input. In late stages of succession, net ecosystem production approaches zero.

Identified research needs

Terms such as 'ecosystem biodiversity' and 'sustainable forestry' are presently in use worldwide to describe an emerging paradigm for a new, adaptive forest management concept (*e.g.* the review by O'Hara, 1998). Measures of biodiversity and sustainability must be derived from a firm knowledge of natural ecosystem processes. Furthermore, analyses of natural ecological processes need to be derived from an identification and description, in time and space, of a starting point from which the processes originate; or as Watt (1947) ended his paper: 'What I want to say is what T. S. Eliot said of Shakespeare's work: we must know all of it in order to know any of it.'

From this point of view, the primary succession of plant communities dominated by Norway spruce on the rising coastlines along the Gulf of Bothnia, provides an excellent opportunity for adding new and important knowledge about the development of spruce forests – from original site formation. This statement is based on the following facts: First, long-term natural forest seres, undisturbed by forestry and terminating in a climax-like Norway spruce forest, can be found (Svensson, 1998; Svensson & Jeglum, in press). Secondly, the mesic ground-moraine sites are generally quite productive; a well-stocked, old-growth spruce forest can develop within a short ecological time. Thirdly, the undisturbed successional sequence, going back to original soil formation, provides an excellent opportunity for reconstructing the history of site development.

Fourthly, the relationship between ground elevation and land-uplift rate facilitates estimates of ground age and consequently, allows a four-dimensional study approach. Fifthly, in view of the extensive anthropogenic influence in boreal Fennoscandia, the few remaining natural spruce forests should be recognised and carefully documented. Even though nature reserves and other preservation measures are frequent in the coastal areas (e.g. Bråkenhielm & Wallin, 1982), more attention needs to be given to these areas (Anon., 1994).

Coastal conditions differ substantially from inland conditions. Thus, in order to understand the dynamics and succession of seashore plant communities, the climatic and edaphic factors must be acknowledged in any rigorous scientific exploration. Consequently, the research approach should take into account both the biotic and the abiotic component. The abiotic conditions influence and direct changes in the vegetation over time. Attention should be given both to the main active edaphic and environmental factors, and to how their relative importance changes over time, i.e. with increasing distance from, and elevation above, sea-level, and with changes in forest structure. The biotic component encompasses the succession of vegetation along the topographic time-sequence gradient, and the dynamics of the Norway spruce plant community. Here, the term 'dynamics' refers to internal structural changes over time, i.e. recruitment, invasion and decline of species and cohorts, and establishment, growth and death of individuals. An understanding of natural dynamics is fundamental to the development and validation of ecologically sound forest management concepts.

From our review of the literature, we conclude that present knowledge of the succession of Norway spruce on the emergent shores, and the part played by land uplift and other factors, is only fragmentary. Attention should be paid to initial seedling colonisation on emerging shores, relative to factors such as sea-water level, degree of exposure (winds, fetch), parent material, seedbed types, potential seed source (isolation), and island size. Possible multiple pathways of Norway spruce primary succession relative to spatial and temporal changes in exposure and other factors, have so far received little research effort. Attention also should to be given to the response of the spruce population to ground age as a function of land-uplift rate and topography. How does the age distribution of Norway spruce relate to ground age along undisturbed primary-succession sequences? Finally, attention should to be paid to autogenic processes in spruce-dominated stages developing towards climax-like, old-growth forests.

Literature cited

Alestalo, J. 1982. Morfologisk succession vid Österbottniska landhöjningskuster. In: Högskolan i Luleå, Sveriges Geologiska Undersökning och Luleå kommun. Landhöjning och kustbygdsförändring. p. 85–94. *Nordiskt symposium. Luleå 2–4 juni 1982. Symposiepublikation Vol. I.* (Swe.).

Andersson, E. 1965. Cone and seed studies in Norway spruce (*Picea abies* (L.) Karst.). *Studia Forestalia Suecica 23*, 214 pp.

Anon. 1994. *Nord 1994:7. Nordiska ministerrådet, Nordiska rådet.* Naturskogar i Norden. 100 pp. (Swe., Eng. summary).

Aplet, G.H. & Vitousek, P.M. 1994. An age-altitude matrix analysis of Hawaiian rain-forest succession. *Journal of Ecology 82(1)*, 137–147.

Appelroth, E. 1948. Några av landhöjningen betingade skogliga särdrag inom den Österbottniska skärgården. In: *Nordenskiöld-samfundet. Skärgården*, 292–304. (Swe.).

Appelroth, E. 1981. Till belysande av gråalens roll i den av landhöjningen betingade synkroniserade landskaps- bonitets och trädslagsdynamiken. *Svenska Skogsvårdsförbundets Tidskrift 6*, 83–92. (Swe.).

Austin, M.P. 1981. Permanent quadrats. An interface for theory and practice. *Vegetatio 46*, 1–10.

Barnes, B.V., Zak, D.R.; Denton, S.R. & Spurr, S.H. 1998. *Forest Ecology.* 4th edition. John Wiley & Sons, New York. 774 pp.

Bartels, R., Bell, J.D., Knight, R.L. & Schaefer, G. 1985. Dead and down woody material. In: Brown, E.R. (Ed.). *Management of wildlife and fish habitat in forests of Oregon and Washington.* p. 171–186. U.S. Government Printing Office, Washington D.C.

Battles, J.J., Johnson, A.H., Siccama, T.G., Friedland, A.J. & Miller, E.K. 1992. Red spruce death: Effects on forest composition and structure on Whiteface Mountains, New York. *Bulletin of the Torrey Botanical Club 119(4)*, 418–430.

Bégin, Y., Berube, D. & Grégoire, M. 1992. Downward migration of coastal conifers as a response to recent land emergence in eastern Hudson Bay, Quebec. *Quarternary Research 40*, 81–88.

Begon, M., Harper, J.L. & Townsend, C.R. 1986. *Ecology. Individuals, populations and communities.* Blackwell Scientific Publications, Oxford. 876 pp.

Bernes, C. (Ed.). 1994. *Naturvårdsverket. Monitor 14.* Biologisk mångfald i Sverige. En landstudie. 267 pp. (Swe., Eng. summary).

Binkley, D., Suarez, F., Stottlemyer, R. & Caldwell, B. 1997. Ecosystem development on terraces along the Kugururok River, northwest Alaska. *Ecoscience 4(3)*, 311–318.

Bliss, L.C. & Gold, W.G. 1994. The patterning of plant communities and edaphic factors along a high arctic coastline: Implications for succession. *Canadian Journal of Botany 72*, 1095–1107.

Bormann, B.T. & Sidle, R.C. 1990. Changes in productivety and distribution of nutrients in a chronosequence at Glacier Bay National Park, Alaska. *Journal of Ecology 78*, 561–578.

Botkin, D.B. 1979. A grandfather clock down the staircase: Stability and disturbance in natural ecosystems. In: Waring, R.H. *Forests: Fresh perspectives from ecosystem analysis.* p. 1–10. Corvallis, Oregon State University Press.

Botkin, D.B. 1990. *Discordant harmonies. A new ecology for the twenty-first century.* Oxford University Press, New York. 241 pp.

Boyce, M.S. & Haney, A. 1997. *Ecosystem management. Applications for sustainable forest and wildlife resources.* Yale University Press. New Haven & London. 361 pp.

Bråkenhielm, S. & Wallin, B. 1982. *Urskogar. Inventering av urskogsartade områden i Sverige. 1. Allmän del.* Naturvårdsverket och Skogsstyrelsen. 72 pp. (Swe.).

Carlsson, U., Elmqvist, T., Wennström, A. & Ericson, L. 1990. Infection by pathogens and population age of host plants. *Journal of Ecology 78*, 1094–1105.

Chapin, F.S. III, Walker, L.R., Fastie, C.L. & Sharman, L.C. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs 64(2)*, 149–175.

Chapin, F.S. III, Torn, M.S. & Tateno, M. 1996. Principles of ecosystem sustainability. *The American Naturalist 148(6)*, 1016–1037.

Clein, J.S. & Schimel, J.P. 1995. Nitrogen turnover and availability during succession from alder to poplar in Alaskan taiga forests. *Soil Biology and Biochemistry 27(6)*, 743–752.

Clements, F.E. 1904. The development and structure of vegetation. *Botanical Survey of Nebraska 7.* The Botanical Seminar, Lincoln, Nebraska.

Clements, F.E. 1916. Plant succession. An analysis of the development of vegetation. *Carnegie Institute Washington, Publication 615.* 512 pp.

Clements, F.E. 1936. Nature and structure of the climax. *Journal of Ecology 24*, 252–284.

Coleman, D.C. 1985. Through a ped darkly: An ecological assessment of root-soil-microbial-faunal interactions. In: Fitter, A.H., Atkinson, D., Read, D.J. & Usher, M.B. (Eds.). *Ecological interactions in soil.* p. 1–21. Blackwell Scientific Publications, Oxford.

Colinvaux, P. 1986. *Ecology.* Ohio State University. John Wiley & Sons, New York. 876 pp.

Collins, W.B. & Helm, D.T. 1997. Moose, *Alces alces*, habitat relative to riparian succession in the boreal forest, Susitna River, Alaska. *Canadian Field-Naturalist 111(4)*, 567–574.

Cooper, W.S., 1913. The climax forest of Isle Royale, Lake Superior, and its development. *Botanical Gazette 55(4)*, 1–45; 11–140; 189–235.

Cooper, W.S. 1923. The recent ecological history of Glacier Bay, Alaska. I. The interglacial forests of Glacier Bay. *Ecology 4*, 93–128.

Cooper, W.S. 1923. The recent ecological history of Glacier Bay, Alaska. II. The present vegetation cycle. *Ecology 4*, 223–246.

Cowles, H.C. 1899. The ecological relationships of the vegetation on the sand dunes of Lake Michigan. *Botanical Gazette 27*, 95–391.

Cramer, W. 1985. The effect of sea shore displacement on population age structure of coastal *Alnus glutinosa* (L.) Gaertn. *Holarctic Ecology 8*, 265–272.

Cramer, W. 1993. Dry coastal ecosystems of the Northern Baltic Sea. In: van der Maarel, E. (Ed.). 1993. *Ecosystems of the World 2A, Dry coastal ecosystems, polar regions and Europe.* p. 95–107. Elsevier. 600 pp.

Cramer, W. & Hytteborn, H. 1987. The separation of fluctuation and long-term change in vegetation dynamics of a rising seashore. *Vegetatio 69*, 157–167.

Curran, P.L. & Macnaeidhe, F.S. 1985. Weed invasion of milled-over bog. *Weed Research 26*, 45–50.

Davis, M.B. 1989. Retrospective studies. In: Likens, G.E. (Ed.) *Long-term studies in ecology. Approaches and alternatives.* p. 71–89. Springer Verlag, New York.

Doyle, T.W. 1981. The role of disturbance in the gap dynamics of a montane rain forest: An application of a tropical forest succession model. In: West, D.C., Shugart H.H., Botkin, D.B. (Eds.) *Forest succession. Concepts and applications.* p. 56–73. Springer Verlag, New York. 517 pp.

Drury, W.H. & Nisbet, I.C.T. 1973. Succession. *Journal of the. Arnold Arboretum, Harvard University 54*, 331–368.

Egler, F.E. 1954. Vegetation science concepts. I. Initial floristic composition, a factor in old-field vegetation development. *Vegetatio 4*, 412–418.

Ekman, M. 1993. Postglacial rebound and sea level phenonema, with special reference to Fennoscandia and the Baltic Sea. Nordic Geodetic Comission. In: Kakkuri (Ed.). *Geodesy and Geophysics. Publications of the Finnish Geodetic Institute 115*, 35–60.

Ekstam, U. & Forshed, N. 1992. Om hävden upphör. Kärlväxter som indikatorer i ängs- och hagmarker. *Naturvårdsverket*, p. 18–29. (Swe., Eng. summary).

Elveland, J. 1976. Myrar på Storön vid Norrbottenskusten. *Wahlenbergia 3.* 274 pp. (Swe., Eng. summary).

Elveland, J. 1981. Vegetational changes in seashore fens at Storön, Norrbotten, N. Sweden, during the period 1970–1980. *Wahlenbergia 7*, 17–31. (Swe., Eng. summary).

Elveland, J. 1984a. Vegetationsinvandring på blottad torv i ett rikkärr vid norrbottenskusten. *Svensk Botanisk Tidskrift 78*, 177–186. (Swe., Eng. summary).

Elveland, J. 1984b. Degeneration hos våtslåttervegetationen orsakad av vattendränkning av liestubben. *Svensk Botanisk Tidskrift 78*, 45–58. (Swe., Eng. summary).

Elveland, J. 1985. Några graminiders reaktion på slåtter och träda på en strandäng vid Torne älv. *Svensk Botanisk Tidskrift 79*, 187–203. (Swe., Eng. summary).

Emmer, I.M., Hulshoff, R.M. & Breij, V. 1991. Soil development during a primary succession of *Pinus sylvestris*. *Geografish Tijdschrift 25(4)*, 354–362.

Emmer, I.M. & Sevink, J. 1994. Temporal and vertical changes in the humus form profile during a primary succession of *Pinus sylvestris*. *Plant and Soil 167*, 281–295.

Enkola, K. 1940. Der Sanddorn (*Hippophaë rhamnoides* L.) im schärenbezirk von Rauma. *Silva Fennica 53*, 25–26. (Finn., Eng. summary).

Ericson, L. 1972. Lövvegetationen vid norrlandskusten. *Norrlandica 6*, 227–255. (Swe.).

Ericson, L. 1980. The downward migration of plants on a rising Bothnian sea-shore. *Acta Phytogeographica Suecica 68*, 61–72.

Ericson, L. 1981. Aspects of shore vegetation of the Gulf of Bothnia. *Wahlenbergia 7*, 45–60.

Ericson, L. 1982. Landhöjningens betydelse för vegetationens utveckling. In: Högskolan i Luleå, Sveriges Geologiska Undersökning och Luleå kommun. Landhöjning och kustbygdsförändring. p. 133–143. *Nordiskt symposium. Luleå 2–4 juni 1982. Symposiepublikation Vol. I*. (Swe.).

Ericson, L. & Wallentinus, H.G. 1979. Sea-shore vegetation along the Gulf of Bothnia. *Wahlenbergia 5*, 142 pp.

Eriksson, G., Lindgren, K. & Werner, M. 1975. The flowering biology of Norway spruce an obstacle to a rational program for tree breeding. *Sveriges Skogsvårdsförbunds Tidskift 5*, 413–426. (Swe., Eng. summary).

Esseen, P.-A., Ehnström, B. Ericson, L. & Sjöberg, K. 1992. Boreal forests – The focal habitats of Fennoscandia. Applications in temporal and boreal environments. In: Hansson, L. (Ed.). 1992. *Ecological principles of nature conservation*. Elsevier, London. 436 pp.

Fanta, L. 1986. Primary forest succession on blown-out areas in the Dutch drift sands. In: Fanta, J. (Ed.). *Forest dynamics research in Western and Central Europe*. p. 164–169. PUDOC, Wageningen, The Netherlands.

Fastie, C.L. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology 76(6)*, 1899–1916.

Fenner, M. 1987. Seed characteristics in relation to succession. In: Gray, A.J., Crawley, M.J. & Edwards, P.J. (Eds.). Colonization, succession and stability. p. 103–114. *26th Symposium of the British Ecological Society*. Blackwell Scientific Publications, Oxford.

Franklin, J.F. 1989. Toward a New Forestry. *American Forests. November/December 1989*, 37–40.

Fredén, C. (Ed.) 1994. *National Atlas of Sweden. Geology*. SNA. 208 p. ISBN 91-87760-28-2.

Fries, C., Carlsson, M., Dahlin, B., Lämås, T. & Sallnäs, O. 1998. A review of conceptual landscape planning models for multiobjective forestry in Sweden. *Canadian Journal of Forest Research 28*, 159–167.

Gleason, H.A. 1917. The structure and development of the plant association. *Bulletin of the Torrey Botanical Club 44*, 463–481.

Gleason, H.A. 1927. Further views on the succession concept. *Ecology 8*, 299–326.

Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T. (Eds.). 1992. *Plant succession. Theory and prediction*. Chapman & Hall, London. 345 pp.

Glenn-Lewin, D.C. & van der Maarel, E. 1992. Patterns and process of vegetation dynamics. In: Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T. (Eds.). *Plant succession. Theory and prediction*. p. 11–44. Chapman & Hall, London. 345 pp.

Goodburn, J.M. & Lorimer, C.G. 1999. Population structure in old-growth and managed northern hardwoods: an examination of the balanced diameter distribution concept. *Forest Ecology & Management 118*, 11–29.

Gorham, E., Vitousek, P.M. & Reiners, W.A. 1979. The regulation of chemical budgets over the course of terrestial ecosystem succession. *Annual Review of Ecology & Systematics 10*, 53–84.

Grégoire, M. & Bégin, Y. 1993. The recent development of a mixed shrub and conifer community on a rapidly emerging coast (eastern Hudson Bay, subarctic Quebec, Canada). *Journal of Coastal Research 9(4)*, 924–933.

Greig-Smith, P. 1964. *Quantitative plant ecology*. 2nd edition. Butterworth, London. 256 pp.

Grime, J.P. 1979. *Plant strategies and vegetation processes*. Wiley & Sons, Chichester. 222 pp.

Grime, J.P. 1987. Dominant and subordinate components of plant communities: Implications for succession, stability and diversity. In: Gray, A.J., Crawley, M.J. & Edwards, P.J. (Eds.), Colonization, succession and stability. p. 413–428. *26th symposium of the British Ecological Society*. Blackwell Scientific Publishers, Oxford.

Grumbine, R.E. 1993. What is Ecosystem Management? *Conservation Biology 8(1)*, 27–38.

Hagner, M. 1992a. Basic ideas behind the new trends in Swedish Forestry. In: Hagner, M. (Ed.). Silvicultural alternatives: *Proceedings from an Internordic workshop, June 22–25, 1992. SLU, Department of Silviculture. Umeå. Report 35*, 97 pp.

Hagner, M. 1992b. Methods to enable enrichment planting without scarification. Field tests with different types of physical shelters meant to protect coniferous seedlings from attacks by Hylobius abi-

etus. In: Hagner, M. (Ed.). Silvicultural alternatives: *Proceedings from an Internordic workshop, June 22–25, 1992. SLU, Department of Silviculture, Umeå, Report 35.* 97 pp.

Hagner, M. & Nyquist, H. 1998. A coefficient for describing size variation among neighbouring trees. *Journal of Agricultural, Biological & Environmental Statistics 3(1)*, 62–74.

Heath, J.P. 1967. Primary conifer succession, Lasses volcanic National Park. *Ecology 48(2)*, 270–275.

Hela, I. 1953. A study of land upheaval at the Finnish coast. *Fennia 76(5)*. 36 pp.

Helm, D.J. & Allen, E.B. 1995. Vegetation chronosequence near Exit Glacier, Kenai Fjords National Park, Alaska, U.S.A. *Arctic and Alpine Research 27(3)*, 246–257.

Helm, D.J., Allen, E.B. & Trappe, J.M. 1996. Mycorrhizal chronosequence near Exit Glacier, Alaska. *Canadian Journal of Botany 74*, 1496–1506.

Helm, D.T. & Collins, W.B. 1997. Vegetation succession and disturbance on a boreal forest floodplain, Susitna River, Alaska. *Canadian Field-Naturalist 111(4)*, 553–566.

Helmfrid, S. (Ed.). 1994. *National Atlas of Sweden. The Geography of Sweden.* SNA. 176 pp. ISBN 91–87760–39–8.

Hesselman, H. 1919. Iakttagelser över skogsträdens spridningsförmåga. *Meddelanden från Statens Skogsförsöksanstalt 16(2–3)*, 27–53. (Swe.).

Hofgaard, A. 1993a. Structure and regeneration patterns in a virgin *Picea abies* forest in northern Sweden. *Journal of Vegetation Science 4*, 601–608.

Hofgaard, A. 1993b. Fifty years of arboreal regeneration and mortality in boreal old-growth *Picea abies* (L.) Karst. forest, northern Sweden. *Journal of Vegetation Science 4*, 773–782.

Hopwood, D. 1991. Principles and practices of new forestry. A guide for British Columbians. *BC Ministry of Forests. Land Management. Report 71.* 95 pp. ISSN 0702–9861

Horn, H.S. 1981. Some causes of variety in patterns of secondary succession. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.). *Forest succession. Concepts and Applications*, p. 24–35. Springer Verlag, New York. 517 pp.

Huston, M. & Smith, T. 1987. Plant succession: life history and competition. *American Naturalist 130*, 168–198.

Hytteborn, H. & Packham, J.R. 1987. Decay rate of *Picea abies* logs and the storm gap theory: A re-examination of Sernander plot III, Fiby urskog, central Sweden. *Arboricultural Journal 11*, 299–311.

Hytteborn, H., Packham, J.R. & Verwijst, T. 1987. Tree population dynamics, stand structure and species composition in the montane virgin forest of Vallibäcken, northern Sweden. *Vegetatio 72*, 3–19.

Hånell, B. & Ottosson-Löfvenius, M. 1994. Windthrow after shelterwood cutting in *Picea abies* peatland forests. *Scandinavian Journal of Forest Research 9*, 261–269.

Hörnberg, G., Ohlson, M. & Zackrisson, O. 1995. Stand dynamics, regeneration patterns and long-term continuity in boreal old-growth *Picea abies* swamp forest. *Journal of Vegetation Science 6*, 291–298.

Ingelög, T. & Lennartsson, T. 1991. *Åtgärder för att stärka biologisk mångfald i odlings- och skogslandskap. Idékatalog för beslutsfattare.* SLU Info, Uppsala. ISBN 91–576–4513–2. (Swe.).

Ingham, E.R. & Thies, W. 1996. Soil foodweb responses following disturbance: Effects of clearcutting and application of chloropicrin to Douglas-fir stumps. *Applied Soil Ecology 3(1)*, 35–47.

Jenny, H. 1941. *Factors of soil formation. A system of quantitative pedology.* McGraw-Hill, New York. 218 pp.

Jones, E.W. 1945. The structure and reproduction of the virgin forest of the north temperate zone. *New Phytologist 44*, 130–148.

Jukola-Sulonen, E.-L. 1983. Vegetation succession of abandoned hay-fields in central Finland. A quantitative approach. *Communicationes Instituti Forestalis Fenniae 112.* 85 pp.

Junttila, O. & Skaret, G. 1990. Growth and survival of seedlings of various *Picea* species under northern climatic conditions. *Scandinavian Journal of Forest Research 5*, 69–81.

Kielland, K. & Bryant, J.P. 1998. Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. *Oikos 82*, 377–383.

Kielland, K., Bryant, J.P. & Ruess, R.W. 1997. Moose herbivory and carbon turnover of early successional stands in interior Alaska. *Oikos 80*, 25–30.

Kielland-Lund, J. 1963. Some factors affecting germination of spruce. *Tidskrift for Skogbruk 1*, 58–70. (Norw., Eng. summary).

Kielland-Lund, J. 1970. Vegetation succession in the forest. *Tidskrift for Skogbruk 78(2)*, 209–220. (Norw., Eng. summary).

Kimmins, J.P. 1997. *Forest Ecology.* Temporal changes in ecosystem structure and function., p. 397–472 2nd edition. University of British Columbia. 596 pp.

Koski, V. & Tallqvist, R. 1978. Results of long-time measurements of the quantity of flowering and seed crop of forest trees. *Metsäntutkimuslaitos. Institutum Forestale Fenniae 364.* 32 pp. (Finn., Eng. summary).

Kouznetsova, A.M. 1999a. Succession soil line on White Sea Keret island. *Docuchaev's lectures–99. Soil, Ecology, Society.* Sankt-Peterburg, 1999, pp. 30–31.

Kouznetsova, A.M. 1999b: Holocene succession: from marsh to peatland. *Abstracts of International Peat Symposium 'Chemical, physical and biological processes in peat soils'*, p. 28–29.

Krasny, M.E., Vogt, K.E. & Zasada, J.C. 1988. Establishment of four Salicaceae species on river bars in interior Alaska. *Holarctic Ecology 11*, 210–219.

Kuuluvainen, T. 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland. A review. *Annales Zoologici Fennici 31*, 35–61.

Kuuluvainen, T., Penttinen, A., Leinonen, K. & Nygren, M. 1996. Statistical opportunities for comparing stand structural heterogeneity in managed and primeval forests: An example from boreal spruce forest in southern Finland. *Silva Fennica 30(2)*, 315–328.

Kuuluvainen, T., Syrjänen, K. & Kalliola, R. 1998. Structure of a pristine *Picea abies* forest in north eastern Europe. *Journal of Vegetation Science 9*, 563–574.

Küchler, A.W. 1988. The classification of vegetation. In: Küchler, A.W., Zonneveld, I.S. (Eds.) *Vegetation mapping. Handbook of Vegetation Science 10*. p. 67–80. Kluwer Academic Publishers, Dordrecht, The Netherlands. 587 pp.

Küchler, A.W. & Zonneveld, I.S. (Eds.) *Vegetation mapping. Handbook of Vegetation Science 10*. Kluwer Academic Publishers, Dordrecht, The Netherlands. 587 pp.

Lantmäteriet 1989. 1:50000 topographic map. 2nd edition. Umeå 20KNO.

Lawrence, D.B. 1958. Glaciers and vegetation in South-eastern Alaska. *American Scientist. June 1958*, 89–122.

Leemans, R. 1991. Canopy gaps and establishment patterns of spruce (*Picea abies* (L.) Karst.) in two old growth coniferous forests in central Sweden. *Vegetatio 93*, 157–165.

Leemans, R. & Prentice, I.C. 1987. Description and simulation of tree-layer composition and size distribution in a primaeval *Picea-Pinus* forest. *Vegetatio 69*, 147–156.

Leikola, M., Raulo, J. & Pukkala, T. 1982. Prediction of the variations of the seed crop of Scots Pine and Norway Spruce. *Metsäntutkimuslaitos. Institutum Forestale Fenniae 537*. 32 pp. (Finn., Eng. summary).

Leppäniemi, P., Hallikainen, V., Mikkola, K., Puoskari, J. & Sepponen, P. 1998. Forest structure classes in central Finnish Lapland. *Scandinavian Journal of Forest Research 13*, 442–450.

Leps, J. 1990. Can underlying mechanisms be deduced from observed patterns. In: Krahulec, F., Agnew, A.D.Q., Agnew, S., Willems J.H. (Eds.). *Spatial processes in plant communities*, p. 1–11. SPB Academic Publishing bv, The Hague, The Netherlands. 259 pp.

Lescop-Sinclair, K. & Payette, S. 1995. Recent advance of the arctic treeline along the eastern coast of Hudson Bay. *Journal of Ecology 83*, 929–936.

Lieberman, M., Lieberman, D. & Peralta, R. 1989. Forests are not just swiss cheese: Canopy stereogeometry of non-gaps in tropical forests. *Ecology 70(3)*, 550–552.

Linder, P., 1998. Structural changes in two virgin boreal forest stands in central Sweden over 72 years. *Scandinavian Journal of Forest Research 13(4)*, 451–461.

Lindgren, K., Ekberg, I. & Eriksson, G. 1977. External factors infuencing female flowering in *Picea abies* (L.) Karst. *Studia Forestalia Suecica 142*. 51 pp.

Lisitzin, E. 1974. Den vandrande strandlinjen. In:

Nordenskiöld-samfundet. Skärgård i omvandling. 73–78. (Swe.).

Lundqvist, J. 1982. Landhöjningen och landskapets omvandling. In: *Högskolan i Luleå, Sveriges Geologiska Undersökning och Luleå kommun. Landhöjning och kustbygdsförändring. Nordiskt symposium. Luleå 2–4 juni 1982. Symposiepublikation I*, 9–15. (Swe.).

Lundqvist, L. 1991. Some notes on the regeneration of Norway spruce on six permanent plots managed with single-tree selection. *Forest Ecology and Management 46*, 49–57.

Lundqvist, L. 1993. Changes in stand structure in permanent *Picea abies* plots managed with single-tree selection. *Scandinavian Journal of Forest Research 8*, 510–517.

Lundqvist, L. 1994. Growth and competition in partially cut sub-alpine Norway spruce forests in northern Sweden. *Forest Ecology and Management 65*, 115–122.

Lähde, E., Laiho, O., Norokorpi, Y. & Saksa, T. 1991. The structure of advanced virgin forests in Finland. *Scandinavian Journal of Forest Research 6*, 527–537.

Lähde, E., Laiho, O., Norokorpi, Y. & Saksa, T. 1992. Stand structure of thinning and mature conifer-dominated forests in boreal zone. In: Hagner, M. (Ed.). Silvicultural alternatives: p. 58–65. *Proceedings from an Internordic workshop, June 22–25, 1992. SLU, Department of Silviculture, Umeå. Report 35*.

Magurran, A.E., 1988. *Ecological diversity and its measurement*. Chapman & Hall. University Press, Cambridge. 179 pp.

Mann, D.H., Fastie, C.L., Rowland, E.L. & Bigelow, N.H. 1995. Spruce succession, disturbance and geomorphology on the Tanana River floodplain, Alaska. *Ecoscience 2(2)*, 184–199.

Maser, C., Trappe, J.M. & Nussbaun, R.A. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology 59*, 799–809.

Maser, C., Anderson, R.G., Cormack, K. Jr., Williams, J.T. & Martin, R.E. 1979. Dead and down woody material. In: Thomas, J.W. (Ed.). Wildlife habitats in managed forests–the Blue Mountains of Oregon and Washington. p. 78–95. *Agriculture handbook no 553. Washington D.C. U.S. Department of Agriculture Forest Service*.

Matson, P. 1990. Plant-soil interactions in primary succession at Hawaii Volcanoes National Park. *Oecologia 85*, 241–246.

McCarthy, B.C. & Bailey, D.R. 1996. Composition, structure and disturbance history of Crabtree Woods: an old-growth forest of western Maryland. *Bulletin of the Torrey Botanical Club 123(4)*, 350–365.

McClanahan, T.R. 1986. The effect of a seed source on primary succession in a forest ecosystem. *Vegetatio 65(3)*, 175–178.

McIntosh, R.P. 1981. Succession and ecological theory. In: West; D.C., Shugart, H.H., Botkin, D.B

(Eds.). *Forest succession. Concepts and applications.* p. 10–23. Springer Verlag, New York. 517 pp.

McNaughton, S.J. & Wolf, L.L. 1979. *General Ecology.* Syracuse University, 2nd edition. Holt, Rinehart & Winston, New York.

Miles, J. 1987. Vegetation succession: Past and present perceptions. In: Gray, A.J., Crawley, M.J., Edwards, P.J. (Eds.) *Colonization, succession and stability. 26th symposium of the British Ecological Society.* p. 1–29. Blackwell Scientific Publications, Oxford.

Miles. J. 1979. *Vegetation dynamics.* Chapman & Hall, London. 80 pp.

Newton, P.F. & Smith, V.G. 1988. Diameter distributional trends within mixed Black spruce/Balsam fir and pure Black spruce stand types. *Forest Ecology & Management 25*, 123–138.

Noble, M.G., Lawrence, D.B. & Streveler, G.P. 1984. Sphagnum invasion beneath an evergreen forest canopy in southeastern Alaska. *The Bryologist 87(2),* 119–127.

Norokorpi, Y. 1992. Natural strucure and development of forests as the basis for alternative silvicultural methods in northern Finland. In: Hagner, M. (Ed.). Silvicultural alternatives. *Proceedings from an Internordic workshop, June 22–25, 1992. SLU, Department of Silviculture, Umeå. Report 35*, 78–85.

Norokorpi, Y., Lähde, E., Laiho, O. & Saksa, T. 1997. Stand structure, dynamics and diversity of virgin forests on northern peatlands. In: Trettin, C.C., Jurgensen, M.F., Grigal, D.F., Gale, M.R., Jeglum, J.K. (Eds.). *Northern forested wetlands. Ecology and management.* p. 73–87. Lewis publishers. New York.

Odum, E.P. 1969. The strategy of ecosystem development. *Science 164*, 262–270.

O'Hara, K.L. 1996. Dynamics and stocking-level relationships of multi-aged Ponderosa pine stands. *Forest Science Monograph 33, Vol. 42(4)*, 1–34.

O'Hara, K.L. 1998. Silviculture for structural diversity. A new look at multiaged systems. *Journal of forestry. July 1998*, 4–10.

Ohlson, M. & Zackrisson, O. 1992. Tree establishment and microsite realtionships in north Swedish peatlands. *Canadian Journal of Forest Research 22*, 1869–1877.

Okko, M. 1967. The relation between raised shores and present land uplift in Finland during the past 8000 years. *Annales Academiae Scientarium Fennicae. Series A. III. Geologica-Geographica 93.* 59 pp.

Oliver, C.D. & Larson, B.C. 1990. *Forest stand dynamics.* McGraw-Hill, NY. 467 pp.

Olson, J.S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. *Botanical Gazette 199*, 125–170.

Östlund, L. 1993. Exploitation and structural changes in the north Swedish boreal forest 1800–1992. *Thesis. SLU, Umeå. Department of Forest Vegetation Ecology. Dissertation 4.* ISBN 91–576–4754–2.

Parker, G.G. 1995. Structure and microclimate of forest canopies. In: Lowman, M.D., Nadkarni, N.M.

(Eds.), 1995. *Forest canopies.* p. 73–98. Academic Press, London. 624 pp.

Pekkari, A. 1957. De nordligaste förekomsterna av *Alnus glutinosa* i Sverige. *Svensk Botanisk Tidskrift 51*, 344–346. (Swe.).

Perry, D.A., Amarathus, M.P., Borchers, J.G., Borchers, S.L. & Brainerd, R.D. 1989. Bootstrapping in ecosystems. *BioScience 39*, 230–237.

Pettersson, B. 1991. Bevarande av faunans och florans mångfald vid skogsbruk. Rapport från skogsstyrelsens arbetsgrupp för översyn av föreskrifteroch allmänna råd till 21§ skogsvårdslagen. *Skogsstyrelsen*, Jönköping. 23 pp. (Swe.).

Pianka, E.R. 1988. *Evolutionary Ecology.* 4th edition. Harper & Row, New York. 468 pp.

Pickett, S.T.R. & White, P.S. (Eds.) 1985. *The ecology of natural disturbance and patch dynamics.* Academic Press, Orlando, Florida. 472 pp.

Quinghong, L. & Hytteborn, H. 1991. Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. *Journal of Vegetation Science 2*, 391–402.

Reiners, W.A, Worley, J.A. & Lawrence, D.B. 1971. Plant diversity in a chronosequence at Glacier Bay, Alaska. *Ecology 52(1)*, 55–69.

Richards, P.W. 1983. The three-dimensional structure of tropical rain forest. In: Sutton, S.L., Whitmore, T.C., Chadwick, A.C. (Eds.), Tropical rain forest: Ecology and management. p. 3–10. *The British Ecological Society, Tropical Group No. 2.* Leeds Symposium on tropical rain forest ecology and resource management 1982. Blackwell Scientific Publications, Oxford.

Ritchie, J.C. & MacDonald, G.M. 1986. The patterns of post-glacial spread of White spruce. *Journal of Biogeography 13*, 527–540.

Rouvinen, S. & Kuuluvainen, T. 1997. Structure and asymmetry of tree crowns in relation to local competition in a natural mature Scots pine forest. *Canadian Journal of Forest Research 27*, 890–902.

Rydin, H. & Borgegård, S.-O. 1988. Plant species richness on islands over a century of primary succession: Lake Hjälmaren. *Ecology 69(4)*, 916–927.

Rydin, H. & Borgegård, S.-O. 1991. Plant characteristics over a century of primary succession on islands: Lake Hjälmaren. *Ecology 72(3)*, 1089–1101.

Salo, K. 1989. The site requirements of sea buckthorn (*Hippophaë rhamnoides*) on some islands in the Gulf of Bothnia, Finland. *Luonnon Tutkija 93*, 40–45. (Finn., Eng. summary).

Salonen, V. 1987. Relationship between the seed rain and the establishment of vegetation in two areas abandoned after peat harvesting. *Holarctic Ecology 10*, 171–174.

Salonen, V. 1990. Early plant succession in two abandoned cut-over peatland areas. *Holarctic Ecology 13*, 217–223.

Samuelsson, J., Gustafsson, L. & Ingelög, T. 1994. Dying and dead trees. A review of their importance

for biodiversity. *Swedish Threatened Species Unit, SLU Uppsala.* 86 pp. ISBN 91–88506–03–7.

Sarvas, R. 1968. Investigations on the flowering and seed crop of *Picea abies. Communicationes Instituti Forestalis Fenniae 67(5),* 76 pp.

Schoenike, R.E. 1958. Inflence of Mountain Avens (*Dryas drummondii*) on growth of young Cottonwood (*Populus trichocarpa*) at Glacier Bay, Alaska. *The Minnesota Academy of Science. Proceedings. Vol. XXV–XXVI,* 1957–1958.

Schwank, B. 1974. Vegetationens förändring på de framväxande skären. In: *Nordenskiöld-samfundet. Skärgård i omvandling,* 79–85. (Swe.).

Schwank, B. 1981. Landhöjningen och floran. In: Anon., 1981. *Societas Scientiarum Fennica. Finska Vetenskaps Societeten Årsbok,* p. 157–163. (Swe.).

Schwank, B. 1982. Strändernas floradynamik på flacka kuster med maximal landhöjning. Landhöjning och kartbygdsförändring. *Nordiskt symposium i Luleå, 2 till 4 juni 1982.* (Swe.).

Segerström, U., Bradshaw, R., Hörnberg, G. & Bohlin, E. 1994. Disturbance history of a swamp forest refuge in northern Sweden. *Biological conservation 68,* 189–196.

Shiro, T. & del Moral, R. 1995. Species attributes in early primary succession on volcanoes. *Journal of Vegetation Science 6,* 517–522.

Sims, R.A., Wickware, G.M. & Cowell, D.W. 1987. A study of coastal vegetation at a site on Hudson Bay near Winsk, Ontario. *The Canadian Field-Naturalist 101,* 335–345.

Sirén, G. 1948. Ett bidrag till frågan om tall- och granplantors konkurrensförmåga under första vegetationsperioden. *Skogsbruket,* 295–301. (Swe.).

Sirén, G. 1955. The development of spruce forests on raw humus sites in northern Finland and its ecology. *Acta Forestalia Fennica 62(4),* 1–408.

Sjöberg, B. (Ed.). 1994. *National Atlas of Sweden. Hav och Kust.* SNA. ISBN 91–87760–16–9.

Sjöberg, K. & Ericson, L. 1992. Forested and open wetland complexes. Applications in temperate and boreal environments. In: Hansson, L. (Ed.). *Ecological principles of nature conservation.* p. 326–351. Elsevier, London. 436 pp.

Sjörs, H. 1967. *Nordisk växtgeografi.* 2nd edition. Svenska Bokförlaget Bonnier, Stockholm. 240 pp. (Swe.).

Sjörs, H. 1971. *Ekologisk Botanik. Biologi 10.* Almqvist & Wiksell, Stockholm. 296 pp. (Swe.).

Sjörs, H. 1983. Mires of Sweden. In: Gore, A.J.P. (Ed.). *Ecosystems of the world 4B. Mires: swamp, bog, fen and moor. Regional studies.* p. 69–94. Elsevier, New York.

Skarpe, C., Hytteborn, H. & Cramer, W. 1989. Fifty years of forest development at Granskär, northern Uppland. *Svensk Botanisk Tidskrift 83,* 177–185. (Swe., Eng. summary).

Skult, H. 1956. Skogsbotaniska studier i skärgårdshavet. Med speciell hänsyn till förhållandena i Korpo utskär. *Acta Botanica Fennica 57.* 244 pp. (Swe., Eng. summary).

Skye, E. Glimpses of the Bothnian coast. *Acta Phytogeographica Suecica 50,* 176–179.

Smart, P.J., Wheeler, B.D. & Willis, A.J. 1989. Revegetation of peat excavations in a derelict raised bog. *New Phytologist 111,* 733–748.

Smith, F.E. 1972. Spatial heterogeneity, stability, and diversity in ecosystems. In: Deevey, E.S. (Ed.) *Growth by intussusception. Ecological essays in honor of G. Evelyn Hutchinson.* Vol. 44, 309–335. The Connecticut Academy of Arts and Sciences, New Haven, Connecticut. 443 pp.

Sousa, W.P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology & Systematics 15,* 353–391.

Starr, M. 1991. Soil formation and fertility along a 5000 year chronosequence. *Geological Survey of Finland, Special Paper 9,* 99–104.

Steijlen, I., Nilsson, M.-C. & Zackrisson, O. 1995. Seed regeneration of Scots pine in boreal stands dominated by lichen and feather moss. *Canadian Journal of Forest Research 25,* 713–723.

Steijlen, I. & Zackrisson, O. 1987. Long-term regeneration dynamics and successional trends in a northern Swedish coniferous stand. *Canadian Journal of Botany 65,* 839–848.

Suomi, T., Aarnivirta, A., Ahlroth, P., Huitu, O., Hyvärinen, E., Korkeamäki, E., Mattila, J., Niskanen, K., Päivinen, J., Rintala, T. & Suhonen, J. 1997. Biodiversiteten i Norra Kvarkens gamla skogar. *Kvarkenrådets publikationer 6.* 46pp. (Swe., Eng. summary).

Svenonius, H. 1945. Gråalen som strandväxt vid Bottniska viken. *Botaniska notiser 1945,* p. 166–169. (Swe.).

Svensson, J.S. 1998. Structure and dynamics of an old-growth conifer forest on the rising boreal coastline. *Proceedings from an Nordic symposium on new stand types in boreal forests-ecological features and silvicultural consequences, Vaasa February 10–11 1998,* 55–61.

Svensson, J.S. Long-term chronosequences of Norway spruce primary succession on the rising Gulf of Bothnia coastlines. *IUFRO XXI World Congress Proceedings. 7–12 August 2000, Kuala Lumpur, Malaysia.* (In press.)

Svensson, J.S. & Jeglum, J.K. Structure and dynamics of an undisturbed old-growth Norway spruce forest on the rising Bothnian coastline. *Forest Ecology and Management.* (In press.)

Tansley, A.G. 1935. The use and abuse of vegetational concepts and terms. *Ecology 16,* 284–307.

Tapper, P.G. 1993. The replacement of *Alnus glutinosa* by *Fraxinus excelsior* during succession related to regenerative differences. *Ecography 16(3),* 212–218.

Tirén, L. 1935. Om granens kottsättning, dess periodicitet och samband med temperatur och nederbörd. *Meddelanden från Statens Skogsförsöksanstalt 28,* 413–524. (Swe., Eng. summary).

Walker, J., Thompson, C.H., Fergus, I.F. & Tunstall, B.R. 1981. Plant succession and soil development in coastal sand dunes of subtropical eastern Australia. In: West, D.C., Shugart, H.H., Botkin,

D.B. (Eds.). *Forest succession: concepts and applications.* p. 107–131. Springer Verlag, New York.

Walker, L.R., Zasada, J.C. & Chapin, F.S III. 1986. The role of life history processes in primary succession on an Alaskan floodplain. *Ecology 67(5),* 1243–1253.

Walker, L.R. & Chapin, F.S. III. 1986. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. *Ecology 67(6),* 1508–1523.

van Cleve, K., Chapin, F.S. III, Flanagan, P.W., Viereck, L.A. & Dyrness, C.T. (Eds.). 1986. *Forest ecosystems in the Alaskan Taiga.* Springer Verlag, New York . 225 pp.

van Cleve, K. & Viereck, L.A. 1981. Forest succession in relation to nutrient cycling in the boreal forest of Alaska. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.). *Forest succession: concepts and applications.* p. 185–211. Springer Verlag, New York. 517 pp.

van Cleve, K., Viereck, L.A. & Schlentner, R.L. 1971. Accumulation of nitrogen in Alder *(Alnus)* ecosystems near Fairbanks, Alaska. *Arctic and Alpine Research 13(2),* 101–114.

van der Valk, A.G. 1992. Establishment, colonization and persistence. In: Glenn-Lewin, D.C., Peet, R.K., Veblen, T.T. (Eds.). 1992. *Plant succession. Theory and prediction.* p. 60–92. Chapman & Hall, London. 345 pp.

Vartiainen, T. 1980. Succession of island vegetation in the land uplift area of the northernmost Gulf of Bothnia, Finland. *Acta Botanica Fennica 115.* 105 pp.

Watt, A.S. 1947. Pattern and process in the plant community. *Journal of Ecology 35,* 1–22.

Wennström, U. 1994. Kottförekomst och frökvalitet frömognadsåret 1994. *Skogforsk Resultat 22.* 4 pp. (Swe.).

Wennström, U. 1995. Kottförekomst och frökvalitet frömognadsåret 1995. *Skogforsk Resultat 25.* 7 pp. (Swe.).

Verwijst, T. & Cramer, W. 1985. Age structure of woody species in primary succession on a rising Bothnian sea-shore. In: Fanta, J. (Ed.) *Forest dynamics research in western and central Europe.* p. 145–163. PUDOC, Wageningen, The Netherlands.

Vetaas, O.R. 1994. Primary succession of plant assemblages on a glacier foreland – Bodalsbreen, southern Norway. *Journal of Biogeography 21,* 297–308.

Wheeler, B.D. & Shaw, S.C. 1995. Restoration of damaged peatlands, with particular reference to lowland raised bogs affected by peat extraction. Department of the Environment. *HMSO.* London. 211 pp.

Whittaker, R.H. 1953. A consideration of climax theory: the climax as a population and pattern. *Ecological Monographs 23,* 41–78.

Whittaker, R.J. & Bush, M.B. 1993. Dispersal and establishment of tropical forest assemblages, Krakatoa, Indonesia. *Special Publication of the British Ecological Society.* p. 147–160. Blackwell Scientific Publications, Oxford.

Viereck, L.A. 1970 Forest succession and soil development adjacent to the Chena River in interior Alaska. *Arctic and Alpine Research 2(1),* 1–26.

Viereck, L.A., Dyrness, C.T. & Foote, M.J. 1993. An overview of the vegetation and soils of the floodplain ecosystems of the Tanana river, interior Alaska. *Canadian Journal of Forest Research 23(5),* 889–898.

Vitousek, P.M. & Reiners, W.A. 1975. Ecosystem succession and nutrient retention: a hypothesis. *BioScience 25,* 376–381.

von Mörs, I. & Bégin, Y. 1993. Shoreline shrub population extension in response to recent isostatic rebound in eastern Hudson Bay, Quebec, Canada. *Arctic and Alpine Research 25(1),* 15–23.

Vuoristo, A. & Rousi, A. 1976. Changes during 35 years in the range of *Hippophaë rhamnoides* in the Archipelago of Rauma on the Gulf of Bothnia coast. *Aquilo Serie Botanica 14,* 1–5.

Yarie, J. 1983. Environmental and successional relationships of the forest communities of the Porcupine River drainage, interior Alaska. *Canadian Journal of Forest Research 13(5),* 721–728.

Yarie, J. 1993. Effects of selected forest management practices on environmental parameters related to successional development on the Tanana River floodplain, interior Alaska. *Canadian Journal of Forest Research 23,* 1001–1014.

Yli-Vakkuri, P. 1961. Experimental studies on the emergence and initial development of tree seedlings in spruce and pine stands. *Acta Forestalia Fennica 75.* 122 pp.

Zackrisson, O. 1977. Influence of forest fires on the north Swedish boreal forest. *Oikos 29,* 22–32.

Zackrisson, O. & Nilsson, M.-C. 1992. Allelopathic effects by *Empetrum hermaphroditum* on seed germination of two boreal tree species. *Canadian Journal of Forest Research 22,* 1310–1319.

Zackrisson, O., Nilsson, M.-C., Steijlen, I. & Hörnberg, G. 1995. Regeneration pulses and climate-vegetation interactions in non-pyrogenic boreal Scots pine stands. *Journal of Ecology 83,* 469–483.

Zonneveld, I.S. 1988a. Establishing a floristic classification. In: Küchler, A.W., Zonneveld, I.S. (Eds.) *Vegetation mapping. Handbook of Vegetation Science 10.* p. 81–88. Kluwer Academic Publishers, Dordrecht, The Netherlands. 587 pp.

Zonneveld, I.S. 1988b. Composition and structure of vegetation. In: Küchler, A.W., Zonneveld, I.S. (Eds.) *Vegetation mapping. Handbook of Vegetation Science 10.* p. 25–35. Kluwer Academic Publishers, Dordrecht, The Netherlands. 587 pp.

Unpublished reference

Sjöberg, K. 1994. Biodiversitetsaspekter i det uthålliga skogsbruket. In: Mattsson, L., Sjöberg, K. Uthållig skogsanvändning mot bakgrund av den nya skogspolitiken. *Institutionen för Skogsekonomi, SLU Umeå. Arbetsrapport 190.* (Swe., Eng. summary).

Acknowledgements