



sommerfeltia

2

R. H. Økland & E. Bendiksen

The vegetation of the forest-alpine transition in
the Grunningsdalen area, Telemark, S. Norway.

1985



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This study is divided into two parts. The general part contains a review of theories of the nature of vegetation. It is concluded that present evidence points in the direction of species individuality and vegetational continuum as responses to continuous environmental gradients, on a regional, and mostly also on a local scale. Accordingly, a gradient approach to classification of the forest and alpine vegetation of the investigated area was designed as an alternative to traditional phytosociological classification. The importance of the concept of corresponding vegetation types in different regions is stressed. It is argued that four environmental gradients explain the major variation in Southern Norwegian forest and alpine vegetation. In the special part, the vegetation of the Grunningsdalen area is treated. Two gradients, the vertical gradient and the complex-gradient topographic moisture - snow cover, are considered sufficient to explain the major variation in forest and alpine vegetation in the area. The vegetation is classified into 16 site-types by division of the gradients into four zones (according to altitude) and four series (according to moisture - snow cover) by means of floristic criteria known to reflect particular ecological conditions. For each of the site-types a description of the vegetation and an extensive comparison with corresponding Fennoscandian vegetation is given. On the basis of results from the present study area regional variation in Southern Norwegian poor vegetation corresponding to the xeric, subxeric, and submesic series, and phytosociological classification in the forest-alpine transition are discussed. Various numerical classification and ordination methods are used in an analysis of the floristic composition of the site-types and the autecology of the species. The main phytosociological gradient in the investigated vegetation runs from dry and high altitude to wet and low altitude, most closely approaching the moisture gradient. Diversity relations are discussed. It is strongly emphasized that a hierarchic system is unable to give a consistent classification of a vegetation that must be regarded as a multidimensional network of variation along environmental gradients. Viewed in the light of the results of this study, a gradient approach to classification seems most suitable for a variety of Fennoscandian ecosystems.

Keywords: Alpine vegetation, Continuum, Diversity, Forest, Forest-alpine transition, Gradient reference frame, Norway, Numerical analysis, Regional variation, Site-types, Telemark.

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INTRODUCTION

The physiognomic limit between forested and unforested areas has been regarded as a main phytosociological borderline by most Fennoscandian phytosociologists. The alpine timberline has often been convenient for delimitation of study areas. Consequently, while much information has been accumulated on forest and alpine vegetation treated separately, few studies have taken particular interest in the nature of the forest-alpine transition.

It is often claimed that the distinct physiognomic borderline existing between the boreal and alpine zones is not followed by significant differences in most other characteristics of the vegetation. Thus Sjörs (1963) and Ahti et al. (1968) characterized the alpine forest limit as part of an ecotone. The similarity between the understory vegetation of the subalpine birch forests and the alpine heaths has led many authors to include the subalpine birch forests in accounts of alpine vegetation (e.g., T. Fries 1913, Samuelsson 1917a, Smith 1920, Tengwall 1920, Nordhagen 1928, 1937, 1943). In the same way the similarity of the subalpine belt to the boreal coniferous forests has been expressed by the inclusion of the birch forests in accounts of forest vegetation (e.g. Kielland-Lund 1967, 1973, 1981, Nihlgård 1980), and on the view that the subalpine birch belt forms part of the boreal zones (Sjörs 1963, 1965, 1967, Ahti et al. 1968). The concept of the "mountainous area" adopted by Du Rietz (1964) and Rune (1965), comprising all vegetation from the so-called "pre-alpine coniferous forest belt" upwards, effectively illustrates the high number of different opinions on the occurrence of distinct, natural borderlines in the forest-alpine transition.

Most Scandinavian phytosociological works have dealt with the vegetation of restricted areas, and regional variation has been considered by comparing local vegetation types with other areas. Detailed regional surveys exist for some vegetation types only, e.g. the account of Scandinavian snow-bed vegetation given by Gjærevoll (1956), and the treatment of forest vegetation of South-Eastern Norway by Kielland-Lund (1981). Less detailed regional surveys of alpine vegetation have been given by Nordhagen (1943, 1954a), Gjærevoll & Bringer (1965), Dahl et al. (1971) and Waldemarson Jensén (1980). Kielland-Lund (1971, 1973) and Nihlgård (1980) have given surveys of Scandinavian forest vegetation, while Du Rietz (1925b) and Sjörs (1965, 1967) have given general surveys of Scandinavian vegetation.

The importance of regional approaches to vegetation is emphasized in various contexts (e.g. Kalela 1960, Hämet-Ahti 1963, Morgan & Moss 1965, Ahti et al. 1968, Dickinson et al. 1971, Peet 1978b). An attempt to perform a division of Fennoscandia into vegetational zones (Ahti et al. 1968) met with increasing difficulties from Finland through Sweden to Norway, owing to insufficient knowledge of regional variation in Norwegian vegetation. Also from the point of view of nature conservation, the knowledge of regional variation in vegetation is important (cf. Nordiska ministerrådet 1977).

AIMS

The aims of the present investigation may be summarized briefly as follows:

(1) To evaluate the major theories of the nature of Scandinavian boreal and alpine vegetation on the basis of available literature sources.

(2) To use this assessment and current knowledge of major gradients in Southern Norwegian forest and alpine vegetation to construct a gradient reference frame for analysis of regional variation in such vegetation.

(3) To suggest an alternative system for classification and description of the vegetation in the Grunningsdalen area, Telemark, based on this gradient reference frame, and to compare the vegetation of this area with corresponding vegetation in other areas.

(4) To use the Grunningsdalen area as a starting point for an account of regional variation in Southern Norwegian forest and alpine vegetation.

(5) To evaluate the gradient-based classification system here adopted relative to different phytosociological and phytogeographical classifications of the forest-alpine transition.

(6) To investigate the nature of the forest-alpine transition in the Grunningsdalen area by means of numerical classification and ordination techniques and approaches involving diversity.

REALIZATION

The fieldwork was carried out during June to August 1980 with some supplementary visits to the area in 1981. The present study originated from an investigation of the area done for "Kontaktutvalget for Vassdragsreguleringer, University of Oslo" by the authors (Bendiksen & Halvorsen 1981). The rest of the work was carried out at the Botanical Garden and Museum, University of Oslo. Numerical analysis was done in 1982 by a SANYO CZ-2901 desk calculator, except for the ordination analyses, which were run on a UNIVAC computer at Norwegian Institute of Water Research (NIVA).

The first draft manuscript was written in 1981, and thoroughly revised in 1982. For various reasons publication was delayed until 1985. Owing to insufficient time a critical revision of the manuscript this year involved neither updating of literature (after 1982) nor incorporation of methodological developments in the field of multivariate analysis. The methods used are considered among the best available by the time the analysis was carried out. We are aware that the development of detrended correspondence analysis (DCA; Hill 1979, Hill & Gauch 1980) has opened the way for improved ordinations and estimates

of beta diversity, perhaps also for the construction of improved classification methods and homogeneity tests. However, we do not believe that the broad features of the results would be altered by use of alternative methods.

PREVIOUS BOTANICAL INVESTIGATIONS IN THE AREA

From Seljord parish some old floristic notes are available (H. Wille 1786, Lindblom 1839, N. Wille 1902). Some information from Seljord was also given by M. Blytt (1861) and A. Blytt (1874, 1876b). A phytogeographical investigation of mosses in Telemark was published by Størmer (1941). Aas (1970) has given an account of warmth-demanding vascular plant species with high upper limits in Seljord. At Telemark Distriktshøgskule in Bø, some theses have been worked out in areas bordering on Grunningsdalen. These, as well as other works from neighbouring areas, are listed in a botanical bibliography of Telemark (Vevle 1980). The vegetation of the whole Lifjell massif including the Grunningsdalen area was mapped (scale 1: 50.000) by Hofsten (1983).

NOMENCLATURE

The nomenclature of vascular plants follows Lid (1974), of mosses Koponen et al. (1977) with the following exceptions: The genera *Polytrichastrum* G. L. Smith and *Mniobryum* Limpr. are included in *Polytrichum* and *Pohlia*, respectively. *Racomitrium ericoides* is included in *R. canescens*. Liverworts follow Grolle (1976), and lichens Krog et al. (1980) with the exception that *Cladonia chlorophaea* is included in *C. pyxidata* coll.

GENERAL PART - COMMENTS ON THE LITERATURE

MAJOR PHYTOSOCIOLOGICAL APPROACHES APPLIED TO FENNOSCANDIAN FOREST AND ALPINE VEGETATION - BASIC CONCEPTS AND TERMINOLOGY

THE UPPSALA AND BRAUN-BLANQUET SCHOOLS

The Uppsala school - history and concepts

Outlines of the history and basic principles of the Uppsala school of phytosociology are given by Du Rietz (1921), R. Fries (1950), Hafsten (1958), Whittaker (1962), Shimwell (1971), and Trass & Malmer (1978).

Late 19th century Scandinavian phytosociology, using widely circumscribed formations based on life-forms of dominating species as units (e.g. Hult 1881, 1887), formed the origin of the North European phytosociological tradition. The physiognomic approach was introduced in the 20th century in the system of Nilsson (1902), who divided Swedish ecosystems into 4 "series" characterized by ecological conditions reflected by the general physiognomic appearance of the vegetation.

The 1910's saw the start of modern Scandinavian phytosociology. The fundamental unit of vegetation, the association, was defined by T. Fries (1913:47) as a vegetation-type with largely uniform physiognomy and floristic composition. The concept of the association was further developed by Du Rietz et al. (1918, 1920) and Du Rietz (1921, 1923), who redefined the association by replacing "floristic composition" with "having its own set of constants". A "constant" was defined as species occurring in more than 90 per cent of the sample plots assigned to an association (cf. Du Rietz et al. 1920). Nordhagen (1928) amended the definition again, emphasizing floristic-physiognomic uniformity as well as constant and dominant species.

Characteristic features of the Uppsala school were the use of five or more small sample plots per vegetation stand, delimitation of numerous, narrowly circumscribed units at the association level, and estimation of cover by the Hult-Sernander-Du Rietz scale (Du Rietz 1921). A phytosociological hierarchy was obtained by using life-forms of dominating species (mostly of upper strata) as a basis for discerning higher units, namely, formations (e.g., Sylvén 1904, T. Fries 1913, Samuelsson 1917a, Smith 1920, Nordhagen 1928).

The fundamental role of constants in the definition of the association, and the sharp distinction between constants and accidental species claimed by Du Rietz et al. (1920) and Du Rietz (1921), was strongly criticised by most other contemporary Scandinavian scientists as well as numerous non-Scandinavians (e.g. Nordhagen 1920, 1924, 1928 Arrhenius 1921, Braun-Blanquet 1921, 1925, Kylin 1923, 1926). This criticism

led Du Rietz (1930, 1932a, 1936) to shift to uniform dominance in each layer as the diagnostic feature of the fundamental unit, now renamed sociation. The sociation was largely equivalent to the old association of the Uppsala school.

Sociations have been widely applied in the description of mountain vegetation (e.g., Fægri 1934, Nordhagen 1937, 1943, Kalela 1939, Kalliola 1939, Gjærevoll 1949, 1950, 1956, Knaben 1952, Baadsvik 1974), but have failed to gain common usage for the description of forest vegetation (however, see Mork & Heiberg (1937), Arnborg (1943), and Malmström (1949)).

The Braun-Blanquet approach - history and concepts

Reviews of the history and basic principles of the Braun-Blanquet approach are given by Poore (1955a), Becking (1957), Whittaker (1962), Braun-Blanquet (1964), Shimwell (1971), Werger (1974), Maarel (1975), and Westhoff & Maarel (1978).

The principal concepts of the approach were developed between 1910 and 1920 by Braun-Blanquet and co-workers, and about 1925 the Braun-Blanquet approach had attained most of its present outline. The fundamental unit of classification is the association. Definitions of phytocoena involve floristic composition only, and are based upon diagnostic species of three types (cf. Westhoff & Maarel 1978): Character-species show preference for a given syntaxon; degree of restriction to the syntaxon is termed fidelity (Braun-Blanquet 1964). Differential-species prefer one among two or more compared syntaxa. Constant companions, or constants, occur in most sample plots belonging to a syntaxon.

Westhoff & Maarel (1978) defined the association as a phytocoenon having a characteristic species combination, including character-species, differential-species, and constant companions (cf. Braun-Blanquet 1921, Meijer Drees 1951, Becking 1957). The possession of character-species as an absolute constraint on the association has repeatedly been emphasized (Braun-Blanquet 1921, Meijer Drees 1951, Schwickerath 1954, 1968, Oberdorfer 1968, Dierschke 1971), while others have allowed associations to be defined by a characteristic species combination not including true character-species (e.g., Ellenberg 1954, Braun-Blanquet 1964, Werger & Gils 1976, Westhoff & Maarel 1978).

Associations form the basis of a formal hierarchy of syntaxa, the units of increasing rank above association being alliances, orders, and classes. Formal definitions of these units have not been agreed upon (cf. Pignatti 1968, Dierschke 1971, Westhoff & Maarel 1978). Usage of units of lower rank than association varies from author to author. A proposal for a rank order and definitions of subordinate syntaxa is given by Westhoff & Maarel (1978). Attempts to formalize the nomenclature of syntaxa have resulted in a "Code of phytosociological nomenclature" (Barkman et al. 1976).

Merging of the Uppsala and Braun-Blanquet schools

The hierarchy of the Braun-Blanquet approach, in particular the concept of the alliance, considered early on by the leading Scandinavian phytosociologists (Nordhagen 1924, 1928, Du Rietz 1932a, 1932b). However, owing to the poverty of species in the northern, formerly glaciated parts of Europe (Tengwall 1920, Nordhagen 1928, 1937, 1943, 1954a, Kalliola 1939, Dahl 1957.), an association-concept involving character-species seemed unsuitable for Scandinavian vegetation. The 6th Botanical Congress in 1935 paved the way for a merger of the two approaches (Du Rietz 1936). Sociations and associations were regarded as alternative basic units, both capable of being fitted into the hierarchy of higher units of the Braun-Blanquet school.

Nordhagen (1937), Kalela (1939), and Kalliola (1939) used the sociation as the basic unit for classification of mountain vegetation and grouped sociations into alliances and orders of the Braun-Blanquet system. Later on, sociations were combined with associations by means of differential and preferential species character-species in a very weak sense (e.g., Du Rietz 1942, Nordhagen 1943, 1954a, Gjærevoll 1949, 1950, 1956, Baadsvik 1974). The alliance has maintained its position as conceptually the most important among the higher units (Nordhagen 1937, 1943, 1954a, Kalliola 1937, Du Rietz 1942, Dahl 1957, Dahl et al. 1967, 1971, Kielland-Lund 1967, 1971, 1973, 1981, Aune 1973).

Recently, there has been a strong tendency to shift the emphasis from sociation to association as the basic unit (Nordhagen 1955, Dahl 1957, Bringer 1961, Hadač 1971, Kielland-Lund 1981). Many phytosociological classifications of Scandinavian forest vegetation have made use of the full hierarchy of the Braun-Blanquet school (Kielland-Lund 1962b, 1965a, 1965b, 1967, 1971, 1973, 1981, Dahl et al. 1967, Bjørnstad 1971, Aune 1973, Olsson 1974, Fremstad 1979, Bjørndalen 1980a, 1980b, 1980c, Odland 1981c). The inclusion of the Uppsala school in "the expanding sphere of the school of Braun-Blanquet" as stated by Trass & Malmer (1978) is at present nearly completed.

The Braun-Blanquet approach to regional variation in vegetation

Two major obstacles facing workers employing the Braun-Blanquet approach over wide geographical ranges are the intergradation of phytocoena along regional gradients and the lack of geographic consistence of species fidelity (cf. Braun-Blanquet 1921, Meijer Drees 1951, Werger & Gils 1976, Westhoff & Maarel 1978). Westhoff & Maarel (1978) recognized geographic character-species of three kinds: local character-species (fidelity restricted to a part of the total area of the syntaxon), regional character-species (fidelity in whole area of syntaxon, but distribution of the species exceeding that of the syntaxon), and general character-species (fidelity in whole area of syntaxon, areas of species and syntaxon coincident).

Two partly independent principles are applicable to the construction of a phytosociological hierarchy (e.g., Knapp 1948, Meijer Drees 1951, Westhoff & Maarel 1978): the horizontal classification with a geographic and the vertical classification with an edaphic-ecological basis. Most authors allow description of narrowly defined "regional" and "local" associations if they possess regional or general character-species (e.g., Meijer Drees 1951, Ellenberg 1954, 1956, Oberdorfer 1957, 1968, Passarge 1964, 1968, Passarge & Hofmann 1968, Westhoff & Maarel 1978). Local or regional associations occupying similar habitats in different areas are termed vicariant associations (Meijer Drees 1951, Fukarek 1964, Hartmann & Jahn 1967, Passarge 1968, Bjørnstad 1971, Aune 1973).

Geographic variation impossible to characterize by character-species is reflected in geographical races (Oberdorfer 1957, 1968, Kielland-Lund 1967, 1973, 1981). Braun-Blanquet (1928) and Meijer Drees (1951) restricted the use of variant to variation due to geographic causes, while the subassociation was reserved for use in vertical classification. Westhoff & Maarel (1978) preferred both horizontal and vertical classification at each level of the hierarchy.

Regional approaches to forest and alpine vegetation in Scandinavia

Du Rietz (1925b), in the first serious regional approach to Scandinavian vegetation, used a rough physiognomic division of vegetation as a basis for distinguishing regions. Sjörs (1967, 1971) combined the physiognomic approach with the series of Nilsson (1902) to describe Scandinavian vegetation. Nordhagen (1937, 1943) described geographic differentiation of Norwegian mountain vegetation partly as variants of sociations, partly as sociations with different distributions. In his account of Scandinavian snow-bed vegetation, Gjærevoll (1956) used the distribution of sociations (or higher units) to describe regional variation. He thus performed a horizontal and vertical classification at each hierarchic level. Such a principle has been adopted by most other Scandinavian phytosociologists with a regional approach.

Regional variation in forest vegetation has been described as vicariant associations in different climatic regions (Bjørnstad 1971, Aune 1973, Kielland-Lund 1967, 1973, 1981, Bjørndalen 1980a, 1980d, Blom 1980, Omberg 1980) or in different vertical zones (Fremstad 1979, Bjørndalen 1980b, Rodvelt & Sekse 1980, Kielland-Lund 1981). The concept of geographical race has been applied by Kielland-Lund (1967, 1973, 1981), who also introduced the term "elevation form" (Kielland-Lund 1973, 1981) for vertical variation.

THE FINNISH SCHOOL AND FOREST SITE-TYPES

History and concepts

Basic principles of the different forest site-type approaches are summarized by Malmström (1949), Whittaker (1962), and Frey (1978).

The Finnish school of forest site-types owes its origin to Cajander (1909, 1913, 1921a, 1922, 1923, 1926). The basic assumption of the approach is the value of the bottom and field layer species as indicators of site properties. Sites are classified into site-types, comprising all stands which at maturity have more or less identical floristic composition and ecologic-biological nature. (cf. Cajander 1926, Kalela 1954, Frey 1978). The site-types are thus independent of successional stage. Site-types are characterized by the use of dominant, constant, differential, and character-species (Cajander 1909, 1921a, 1926, Kalela 1939, 1954, 1960). Naming is based on dominants' names.

The forest site-types in the modern sense (e.g. of Kalela 1961) are narrow vegetation units corresponding to variants or subassociations in the Braun-Blanquet system (cf. Hämet-Ahti 1963, Kielland-Lund 1967, 1970, 1973, 1981, Ahti et al. 1968). Ecological relationships of the site-types have been expressed by arrangement of site-types in ecological series (Cajander 1903, Whittaker 1967, 1978b), ranging from dry-and-poor to wet-and-rich (Kalela 1961, Frey 1978). Site-types are grouped into site-type classes (Cajander 1921a, Frey 1978).

The site-type approach has been applied to Norwegian forest vegetation by Brantseg (1941) and Mork (1956), among others, but has not gained wide usage (cf. Kielland-Lund 1982).

A somewhat different approach evolved in Sweden (Eneroth 1931, 1934, 1937). Eneroth used combinations of synusia to make a classification not only of vegetation, but also of sites as indicated by vegetation. Forest site-types were presented in a two-dimensional co-ordinate system with axes of variation in moisture (5 classes) and nutrient status (4 classes). A third fundamental factor, temperature, was proposed by Eneroth (1937) to be included in the scheme as a vertical axis, but this was never practised. Further elaboration of the system was provided by Ronge (1936b), Arnborg (1940, 1943, 1945, 1964), Lindquist (1954), and Ebeling (1978).

Regional approaches by the Finnish school

The rationale of the Finnish approach to regional variation, and its terminological basis, were published explicitly by Cajander (1922), and later further developed by Kalela (1939, 1954, 1960), among others. The Finnish workers have put particular emphasis on the most frequently occurring vegetation-types in the areas investigated. Cajander (1921a) and Kalela (1939) distinguished between regional (climatic,

zonal) and local (edaphic, azonal) vegetation. Kujala (1936, 1938, 1945), Kalela (1954, 1960, 1961), Hämet-Ahti (1963), and Ahti et al. (1968) used regional vegetation as a basis for dividing into vegetation regions (Cajander 1922, Kalela 1939, 1954, 1960).

Lakari (1920) compared forest site-types in Northern and Southern Finland, using the term "corresponding forest site-types". Kujala (1929) described parallel sets of forest site-types in birch and coniferous forest regions of Northern Finland. Kujala (1936) compared ecological series of forest site-types from two regions to establish a vegetational borderline. Two of the most important contributions to regional studies were those of Kujala (1938, 1945), introducing the concept of vicariant site-types, i.e., types occupying ecologically equivalent sites in different regions. Series of vicariant site-types were termed parallel site-type series. Recent regional studies of Finnish forest vegetation have employed the parallel forest site-type series as a basis for distinguishing forest (or vegetation) regions (Kalela 1958, 1961, Kujala 1961, Hämet-Ahti 1963, Ahti et al. 1968, Kalliola 1973). Each region was characterized by one ecological series of forest site-types. The site-types of local vegetation have also been applied to the delimitation of vegetation regions, e.g., those of mire vegetation (Ruuhijärvi 1960, Eurola & Ruuhijärvi 1961, Eurola 1962).

THEORIES ON THE NATURE OF VEGETATION WITH PARTICULAR EMPHASIS ON IMPLICATIONS FOR REGIONAL APPROACHES TO VEGETATIONAL VARIATION

THEORIES ON THE NATURE OF VEGETATION

The nature of vegetation has been vigorously debated throughout this century.

The concept of the plant association as a concrete unit, a superorganism analogous to the species, was repeatedly put forward by a number of scientists in the 1920's (e.g., Clements 1916, 1928, Du Rietz et al. 1918, 1920, Du Rietz 1921, 1923). It was strongly criticized also by contemporary scientists (Nordhagen 1920, 1924, Kylin 1926, Kalela 1939, Whittaker 1962). Tuomikoski (1942) considered these topics as belonging to the past.

Two main concepts of the structure of vegetation are the most influential today (Whittaker 1962, 1978c, McIntosh 1967):

(1) Vegetation is a "*complex population pattern*" (Whittaker 1956, 1967, 1970, 1978b). Species are distributed individually (Gleason 1926, Ramensky 1930) with population centres scattered along vegetational gradients though affected by competition (Curtis & McIntosh 1951, Whittaker 1951, 1967, 1978b, McIntosh 1967). Vegetational variation along continuous environmental gradients is continuous ("the continuum concept of vegetation", Curtis & McIntosh 1951, McIntosh 1967), although some relative discontinuities are allowed to occur (Whittaker 1956, 1967, 1978b, 1978c). In a continuous vegetation, division lines are arbitrary with few exceptions. The mechanism responsible for the scattering of species distribution is the evolution of species towards reduced competition (Whittaker 1956, 1967, 1970, 1978b, Whittaker et al. 1973).

(2) The "*community-unit theory*" (Whittaker 1956, 1962). Natural groups of species with more or less coincident patterns of distribution occur (Du Rietz et al. 1920, Du Rietz 1921). More or less pronounced discontinuities occur between vegetation stands, and also along continuous environmental gradients (Cajander 1909, Du Rietz et al. 1918, 1920, Du Rietz 1921, Dahl 1957, etc.); thus vegetation is an objectively classifiable field of variation. The mechanism responsible for this pattern is a co-adaptation of plant species to environmental forces, eventually forming an integrated plant community (cf. Du Rietz et al. 1920).

These two concepts are extremes, allowing for the full series of intermediates. Views expressed by various scientists and phytosociological schools are reviewed by Whittaker (1962) and Trass & Malmer (1978).

EVIDENCE ON THEORIES, WITH SPECIAL REFERENCE TO SCANDINAVIA AND TO REGIONAL VARIATION

The evidence can be treated in two groups; (1) species distributions, and (2), similarity and continuity of vegetation stands.

(1) *Species distributions*. It is generally accepted that judged from their total distributions (or their distribution within a larger area, e.g., Scandinavia) the plant species are distributed individualistically, no pair of species having coincident distribution patterns (Hultén 1950, Sjörs 1967, Størmer 1969, Gjærevoll 1973). For these reasons, Fægri (1960) refused to carry out a division of Norwegian coast plants into elements, Berg (1963) emphasized the continuous series of distributional patterns among alpine plants in the Scandinavian mountain range from widespread to rare and disjunct, and Danielsen (1971) stated that a non-arbitrary delimitation of "mountain plants" is impossible.

On a local scale the available material is mostly biased by selective sampling. Opinions on these topics are, however, frequently expressed in the phytosociological literature (cf. Nordhagen 1920, Du Rietz 1925a, Dahl 1957, Kielland-Lund 1962a). Belt transects of alpine vegetation are provided by Gjærevoll (1956) and Dahl (1957). Apart from very few exceptions the distributional limits of the species do not coincide. A more or less regular, bell-shaped form of the distributional curves along the gradients, as claimed in works dealing with vegetation in other parts of the world (cf. Whittaker 1956, 1967, McIntosh 1967, Austin 1976, 1980), may be assumed for some species if the histograms are smooth. Truncated curves also occur frequently. We thus interpret transect data from alpine vegetation as pointing in favour of the principle of species individuality on a local scale.

Elven (1978) and Matthews (1978) provided species plexus diagrams from moraine vegetation. They showed loose, continuously intergrading groups of species in stable vegetation as well as in earlier successional stages. Species ordination in basiphilous pine forests (Bjørndalen 1981) and low alpine *Betula nana* heaths (Jonasson 1981) showed one cloud of species with almost uniform density in ordination space.

The dynamic interactions of plant species have not received sufficient attention. At present there seems to be increasing agreement in favour of the principle of niche differentiation among plant species (e.g., Whittaker 1956, 1962, 1965, 1969, 1977, Harper 1977, Pianka 1978, Watson 1980, Siack 1982).

(2) *Similarity and continuity of vegetation stands*. The individuality of species distributions on a regional scale implies that edaphically similar habitats are occupied by an increasingly different assemblage of species as the distance between the compared areas increases, a fact that is ascribed to differences in climate or vegetation history (Nordhagen 1943, Cain 1947, Meijer Drees 1951, Whittaker 1953, 1962, 1978c, Ellenberg 1954, Poore 1956). An example of a geographic continuum is the intergradation of edaphically corresponding forest site-types in Finland along a north-south gradient as documented by the studies of Kujala (1936, 1961), Kalela (1960,

1961), Hämet-Ahti (1963) and Ahti et al. (1968).

Nordhagen (1937, 1943, 1954a), in extensive comparisons between alpine vegetation stands from different parts of Scandinavia, particularly noticed the gradual change in species composition due to climatic conditions. Gimingham (1961, 1969, 1972) described the North Atlantic dwarf-shrub heath vegetation as an essentially continuous "network of variation", caused mainly by climatic factors.

An example of discontinuity between corresponding vegetation types in different regions was provided by Bjørndalen (1980a). He divided the basiphilous pine forests of disjoint calcareous areas of Scandinavia into 4 associations, and attributed the differences between them to the climatic differences and spatial separation between the areas.

In our opinion evidence from Fennoscandia thus unequivocally points towards the geographic expression of a vegetation continuum.

On a local scale evidence on the theories may be of two types, taking into account (1) the relative similarity of stands, and (2) the nature of the transitions between stands.

Elven (1978) investigated moraine vegetation in Central Norway by association-analysis (Williams & Lambert 1959, 1960). At all, including mature, stages of a successional series groups were interpretable in terms of environmental gradients, but they did not constitute discrete assemblage types. Matthews (1979a, 1979b) performed a detailed study of moraine vegetation using different sample sizes and numerical techniques. Different criteria for classification resulted in different classifications, and Matthews (1979b) concluded that vegetation types in climax stages attained some relative discreteness, but preferred to interpret the vegetation as "phytosociological gradients rather than discrete assemblage types". Jonasson (1981) ordinated a set of ecologically discrete *Betula nana* stands, each analysed by restricted random sampling. He obtained a relative discontinuity between the major sampling sites but continuous intergradation within sites. In our opinion the sparse unbiased evidence from Scandinavia is slightly in favour of relative continuity of vegetational stands.

Concerning the nature of transitions between stands Scandinavian phytosociological literature contains numerous observations a both discontinuities and continuities, and it is beyond doubt that both are present. Evidence for continuity or discontinuity must be searched for in transects along environmental gradients. Gjærevoll (1956) and Dahl (1957) both discussed transects from alpine vegetation with reference to zonation along the snow-cover gradient. Dahl (1957) pointed to the discreteness of zones in his transects, but a close reexamination reveals only a few species with coincident distributional limits, so that, when a zonation is observed in the field, it may be due to physiognomic differences among dominant species. Gjærevoll (1956) pointed to the lack of sharp zonations in the snow-beds, but in common with Nordhagen (1943), Gjærevoll (1949, 1956) emphasized the lower limit of *Vaccinium myrtillus* as astonishingly sharp. The *Vaccinium myrtillus* limit is, however, not generally followed by a parallel shift in the occurrence of other species (Gjærevoll

1956, Dahl 1957). The alliances *Loiseleurieto-Arctostaphylion* and *Phyllodoco-Myrtillion* in the systems of Kalliola (1939) and Nordhagen (1943) included the vegetation above the *Vaccinium myrtillus* limit. Both authors emphasized the coherent chain of intergrading communities formed by the alliances.

Fennoscandian forest vegetation been less subjected to detailed investigations providing evidence on the theories. Kielland-Lund (1962a, 1981) and Haug (1970) have commented on the relative discreteness of forest stands, while Bjørnstad (1971) interpreted the forest vegetation as a continuum. We interpret the sparse evidence on the nature of transitions between stands as giving indications of a mainly continuous intergradation.

ASSESSMENT

In our opinion the Scandinavian evidence relevant to theories on the nature of vegetation indicates a complex population pattern with prevailing continuity. The discontinuities mostly depend on environmental discontinuities (cf. Daubenmire 1966, McIntosh 1967, Beals 1969). From a geographical point of view vegetational continuity seems even more pronounced, and we consider vegetation as essentially continuously intergrading species populations along climatic gradients (cf. Whittaker 1962, 1967, 1978b, Matthews 1979b). This view is in accordance with current theories of evolution through natural selection (Whittaker 1969, 1972a, 1977, Harper 1977), as is evident from the conclusion of Harper (1977:748) on community structure: "There is nothing in the theory of evolution in natural selection that supposes any way in which "the species" reacts to or responds to events other than as the collective behaviour of its individuals. Moreover, there is nothing in the process of evolution that should lead us to imagine some community goal, nothing to suggest that the collective evolution of the populations in a community is towards some ideal - community structure, stability, diversity, productivity, efficiency, information content, entropic level."

IMPLICATIONS FOR LOCAL AND REGIONAL APPROACHES TO VARIATION IN THE COMPOSITION OF VEGETATION

The continuity of vegetation suggests that emphasis should be put on the multidimensional relationships of vegetation to the underlying environmental complex (Billings 1952, 1974), as stressed by numerous authors (e.g., Tuomikoski 1942, Sjörs 1948, Whittaker 1953, 1956, 1962, 1967, Goodall 1954, 1963, Kalela 1960, McIntosh 1967.) Its implications for studies of vegetation on a local (and subsequently on a regional) scale can be briefly summarized as follows:

(1) Numerous variables of the ecosystem (vegetational, environmental etc.) may be used to structure the observed vegetational variability (Whittaker 1962).

(2) The multidimensional pattern suggests ordination (Ramensky 1930, Goodall 1954, 1963, Whittaker 1967), the arrangement of observed vegetational characteristics in relation to gradients, but a classification is also possible, although it cannot be conceived as "natural" (Whittaker 1962, 1978c).

(3) The many non-parallel features of vegetation that may be used as basis for a structuring of data makes many different interpretations of a region's vegetation possible. No approach to vegetation can claim exclusive merit (Whittaker 1962).

(4) The application of more techniques to a particular problem, for instance a combination of ordination and classification approaches, seems profitable (D. Anderson 1965, McIntosh 1967, Whittaker 1967, 1972b, 1978a, Matthews 1979b, Halvorsen 1980, Gauch 1982a).

A GRADIENT REFERENCE FRAME FOR ANALYSIS OF REGIONAL VARIATION IN SOUTHERN NORWEGIAN FOREST AND ALPINE VEGETATION

TERMINOLOGY OF GRADIENTS

Single environmental gradients, changing more or less parallel in space, together form *complex-gradients* (Whittaker 1956, 1967, 1978b). Major directions of variation in vegetation are termed *coenoclines* (Whittaker 1960, 1967, 1978b, Maarel & Leertouwer 1967). The gradients of environment and vegetation mutually influence each other, and are thus not strictly "cause and effect" (Eneroth 1931, 1937, Cain 1944, 1947, Poore 1956, 1962, Whittaker 1962), although they approach such a concept (Whittaker 1962, Kellman 1974). A gradient of vegetation and environment is an *ecocline* (Whittaker 1960, 1962, 1967, 1978b).

Ahti et al. (1968), distinguished between two types of vegetational differentiation - *zonal* (caused by variation in climate) and *azonal* (caused by geological and geomorphological variation). These kinds of differentiation, *coenoclines*, are responses to complex-gradients of two kinds. In our terminology *zonal* variation equals regional *coenoclines*, and is due to *regional* complex-gradients; *azonal* variation equals local *coenoclines*, and is due to *local* complex gradients. The terms *regional* and *local* will be applied to environmental gradients, complex-gradients, *coenoclines*, and *ecoclines*.

The distinction between regional and local gradients is not always a sharp one; snow cover in winter is considered to be a local gradient, but is influenced by annual mean temperature and oceanicity of climate (regional gradients). In this account, gradients are classified as regional or local according to the scale on which they operate.

SOME COMMENTS ON CURRENT APPROACHES TO LOCAL AND REGIONAL VARIATION IN VEGETATION

Phytosociology takes vegetation as the only basis for classification; knowledge of variation in vegetation (*coenoclines*) precedes inference about ecological conditions (Dahl 1957). The prevalent approach to understanding the causes of vegetational variability is by comparison of phytosociological entities with environmental factors.

Correspondingly, Fennoscandian phytogeographers have delimited vegetation regions by vegetational and floristic criteria (e.g., Kalela 1939, 1958, Sjörs 1963, 1967, Ahti et al. 1968). In the opinion of Ahti et al. (1968) vegetation regions should be distinguished solely by vegetational criteria. Climatic characterization of vegetation regions has been a subsequent step, often considered of less importance (cf. Tuhkanen 1980).

Thus a distinct parallelism exists between the Fennoscandian approaches to phytosociology and vegetation geography. The approaches involve emphasis on classification of coenoclines (local or regional) without simultaneously drawing attention to the corresponding complex-gradients. In our opinion some much debated problems can be ascribed to the inconsistencies between the coenocline classification approach and the fact that vegetation is a more or less continuous function of environmental variation:

(1) Lengthy discussions on concrete classificatory questions (where to set the limit) are often met with in the literature.

(2) Different vegetational criteria are often used as a basis for division of one coenocline, and their suitability vigorously debated.

In our opinion neither of the problems has major ecological interest because in a continuous vegetation no classification can claim exclusive merit (Whittaker 1962, 1978a). Problem (2) often results from the presence of many non-parallel environmental gradients that may be used to structure the variation in vegetation. Generally the problems arise from isolated interest in vegetation itself. Ideally we should reach for an ecocline classification when classification is necessary.

Accumulation of ecological knowledge is a process of successive approximation (cf. Poore 1956, 1962). Initially, ecological knowledge accumulates through descriptions and observations, that is, through an inductive phase. Hypotheses regarding correlations between ecological parameters and vegetation emerge, and are to be tested in integrated studies. However, solving one problem mostly leads to formulation of new hypotheses, and so on. Conceptions of the major ecoclines will mostly emerge at a relatively early step in this process (in the inductive phase). Hypotheses about the physiological mechanisms by which the ecological factors act on the plant individuals, and thus on the vegetation itself, emerge from later phases of the successive refinement. Knowledge on this topic is sparse owing to the low number of integrated studies carried out so far.

A PROPOSAL FOR A REGIONAL APPROACH TO VARIATION IN SOUTHERN NORWEGIAN VEGETATION

We suggest a regional approach to variation in vegetation based on two major points:

(1) The extreme complexity in vegetation-environment relationships makes a simplification necessary. Compared to a study of vegetation on a local basis, a regional approach is considerably more complicated owing to the addition of regional gradients. The need for simplification involves two different aspects:

(a) It is necessary to concentrate on the quantitatively more important vegetation. A distinction between regional (climatic, zonal), the quantitatively most important, as opposed to local (edaphic, azonal) vegetation is often emphasized in connection with regional vegetation studies (cf. Schimper 1898, Cajander 1921a, Kalela 1939, 1954, 1960, Ahti et al. 1968.) This distinction cannot be a sharp one, and we have therefore refrained from using these terms. We consider it appropriate, for regional comparisons of Southern Norwegian vegetation, in the first place to use the normally occurring forest and alpine vegetation types for regional comparison.

(b) It is necessary to concentrate on describing variation along major regional ecoclines.

(2) Knowledge of local ecoclines must be at hand in order to perform a distinction between local and regional variation, and to make possible a conception of edaphic similarity between stands in compared regions. A practical classification of local ecoclines into a reticulate *local reference-frame* (cf. Tuomikoski 1942) makes recognition of *ecologically corresponding vegetation types* in different regions possible.

The gradient reference frame for Southern Norwegian forest and alpine vegetation to be presented is constructed after due consideration of available information. Ecological, vegetational, and floristic criteria are used to carry out division of the ecoclines.

REGIONAL GRADIENTS

Ahti et al. (1968) discussed the regional differentiation of Fennoscandian vegetation, and recognized two major regional gradients: a *zonal gradient* reflecting thermal variation and a *sectional gradient* reflecting oceanicity-continentality. These two gradients explain most of the variability caused by climatic factors (cf. Tuhkanen 1980).

The zonal gradient

The zonal ecocline of this work is caused by thermal conditions. Its coenocline counterpart is the zonal gradient of Ahti et al. (1968). The term *zone* is usually restricted to mean horizontal divisions (variation along the north - south (altitudinal) gradient), and the term *belt* is used for vertical (altitudinal) divisions (Flahault & Schröter 1910, Ahti et al. 1968). We use the term *zone* to mean divisions of the thermal coenocline, without indicating whether this refers to latitudinal or altitudinal differences, and we have not found it appropriate to use the prefix *oro-* to indicate vertical zones as proposed by Ahti et al. (1968). This is because (1) the latitudinal and altitudinal differentiations are due to the same thermal complex-gradient (Sjörs 1963, 1967, Ahti et al. 1968, Hämet-Ahti 1979, Tuhkanen 1980), and (2), the frequent occurrence of zones being simultaneously latitudinally and altitudinally based.

Important correlated climatic factors. Annual mean temperature is mentioned by Nordhagen (1943), Ahti et al. (1968), and Nihlgård (1980), summer temperature, temperature sum and length of the growing season by Nordhagen (1928, 1943), Dahl (1957), Kalela (1958), Ruuhijärvi (1960), Eurola (1962), Ebeling (1963), Sjörs (1963, 1965), Rune (1965), Ahti et al. (1968) and Tuhkanen (1980), and potential evapotranspiration by Hare (1954) and Tuhkanen (1980). In a comparative study Tuhkanen (1980) showed that length of the growing season, potential evapotranspiration, and effective temperature sum may all be used to distinguish satisfactorily between the boreal zones in parts of Fennoscandia.

A functional approach to the zonal gradient. A possible physiological mechanism for the effect of heat on plant growth, the respiration hypothesis, is proposed by Dahl & Mork (1959), later developed by Skre (1972, 1979a). Its fundamental assumption is that growth is restricted by temperature-dependent ATP production through dark respiration (Skre 1979a). When temperature increases above the level at which all ATP produced is used for maintenance, respiration increases exponentially with temperature. The ability to utilize high temperatures is expressed by the Q_{10} ratio (Skre 1972, 1979a, 1979b), the ratio between respirations at a given and at a 10° lower temperature. A respiration equivalent is the respiration in 30 days at 10°C (Skre 1972).

A comparison between current zonal divisions (e.g., that of Ahti et al. (1968)) and distribution maps of southern, warmth-demanding vascular plants (in the sense of Bendiksen & Halvorsen (1981)) shows high correspondence. Skre (1979b) has shown that the distribution of such species can be explained by assuming a poorer ability to utilize high temperatures (lower Q_{10}) than is found in the eastern species *Picea abies*, normally used for construction of maps with isolines for respiration equivalents. *Ulmus glabra*, a southern species, was found to have a $Q_{10}=2.0$ as contrasted with $Q_{10}=2.7$ in *Picea abies* (Skre 1979b). A map with isolines for respiration equivalents based on $Q_{10}=2.0$ is still not available, but will probably show a close correlation with maps of vegetation zones, e.g., the zonal division of Ahti et al. (1968).

Principles for division of the zonal gradient. In our opinion many of the differences between existing zone divisions can be ascribed to emphasis on different, not perfectly parallel climatic gradients making up the zonal complex-gradient. This suggests choice of one of these gradients as a basis for zonal division, and establishment of zonal borders over large areas by correlation with a map showing isolines for this gradient. The functional approach suggests future use of respiration equivalents based on a Q_{10} value of about 2.0 (Skre, in prep.) as the main climatic criterion for the ecocline division. At present adequate material for ecocline division is not available. Our present aim is therefore establishment of consistent zonal borderlines by choice of vegetational criteria assumed to reflect the climatic gradient.

Major division lines along the continuous zonal ecocline (an ecotone, cf. Ahti et al. 1968) have long been agreed upon. Thus there is general agreement that the proper boreal coniferous forests are bounded southwards by the northern limit

of naturally occurring *Quercus robur*, the "limes norrlandicus" (cf. M. Fries 1948, Sjörs 1948, 1950, 1963, 1965, 1967, Jalas 1957, Fransson 1965, 1972, Ahti et al. (1968). South of this limit the boreonemoral (Sjörs 1963, 1967) or hemiboreal zone (Ahti et al. 1968) represents the transition to the nemoral zone.

Most authors seem to follow Ahti et al. (1968) dividing the boreal forests into three vegetation zones. The division of alpine areas into three zones is also well established (Vestergren 1902, Du Rietz 1928, 1964, Nordhagen 1928, 1943, Rune 1965, Sjörs 1967, Ahti et al. 1968). Thus it seems practical to divide the zonal ecocline of Fennoscandia into 8 zones; the nemoral zone, the hemiboreal (boreonemoral) zone, the lower (or southern) boreal zone, the middle boreal zone, the upper (or northern) boreal zone, the low alpine zone, the middle alpine zone, and the high alpine zone.

Three of the zonal limits have particular relevance to a study of the forest-alpine transition, and will be considered in some detail.

The MB-UB limit.

Sjörs (1950, 1963, 1965, 1967) recognized three coniferous and a sub-alpine birch forest sub-zone in Fennoscandia; Du Rietz (1964) increased the number of forest sub-zones to five like most Finnish authors (cf. Kalela 1958, 1959, 1961, Ruuhijärvi 1960, Eurola & Ruuhijärvi 1961, Eurola 1962). However, in the most recent attempt to carry out a zonal division of Fennoscandia, Ahti et al. (1968), following Zoller (1956), distinguish three boreal zones from "limes norrlandicus" to the forest limit.

Most authors who have performed a division of boreal vegetation into zones, recognize a sub-alpine birch forest zone (e.g., Sernander 1899, Du Rietz 1925b, 1928, 1930, 1932a, 1953, 1964, Holmboe 1925, Nordhagen 1928, 1937, 1943, Selander 1950, Sjörs 1950, 1963, 1965, 1967, Knaben 1952, Dahl 1957, Kalela 1958, 1959, 1961, Wistrand 1962, 1965, Hämet-Ahti 1963, Rune 1965). However, it is often emphasized that the vertical extension of the birch forests varies considerably and that it is positively correlated with climatic oceanicity (Regel 1952, Hare 1954, Zoller 1956, Hämet-Ahti 1963, Sjörs 1963, 1967, 1971, Ahti et al. 1968, Hämet-Ahti & Ahti 1969), even though areas with a continental climate may support a well-developed sub-alpine birch forest zone (cf. Kullman 1976). It is now common practice to include the birch forests in the broad concept of boreal forest zones (Zoller 1956, Sjörs 1963, 1965, 1967, Ahti et al. 1968, Vorren 1979a, 1979b) or to define a subalpine zone by other criteria (Hämet-Ahti 1963, Odland 1978, 1979, 1981a, Elven & Vorren 1980).

Bendixen & Halvorsen (1981) defined the limit between the middle and upper boreal zones (the MB-UB limit) for the Lifjell area, Telemark, by means of three criteria: (1) The upper limit of *Alnus incana*-dominated forests; often coincident with the upper limit of some warmth-demanding species (e.g., *Athyrium filix-femina*). (2) The lower limit of strictly alpine species (sensu Bendixen & Halvorsen 1981), e.g., *Alchemilla alpina* in natural habitats, *Phyllodoce caerulea*, *Arctostaphylos alpina*, *Loiseluria procumbens*, and *Juncus trifidus*. (3) The shift in dominance in tall-herb and fern vegetation from *Athyrium filix-*

femina to *A. distentifolium*.

The same set of criteria are used by Odland to distinguish between prealpine and subalpine forests in Røldal, Hordaland (Odland 1978, 1981c), Voss, Hordaland (Odland 1979), and Undredal, Sogn og Fjordane (Odland 1981a). Odland also puts emphasis on *Matteuccia struthiopteris* as an important prealpine differential species. Fredriksen (1978) delimited a subalpine zone in Eksingedal, Hordaland, by the same set of criteria.

Elven & Vorren (1980), following Fremstad & Øvstedal (1978), used the upper limit of *Alnus incana*-dominated forests to distinguish between the pre- and subalpine zones in Troms. All zone limits mentioned seem to be concordant also with respect to climatic characterization.

Hämet-Ahti (1963) distinguished subarctic and oceanic subzones of the birch zone in Northern Fennoscandia by means of the lower limit of alpine species and the upper limit of *Matteuccia struthiopteris*. Later on this limit was taken as the limit between middle and northern boreal zones by Ahti et al. (1968).

Corresponding limits in Northern Sweden are the limit between the central and pre-alpine conifer forest subregions of Du Rietz (1953, 1964) and the limit between the main and upper boreal sub-zones of Sjörs (1950, 1963, 1965), as evident from the occurrence of alpine species only in the latter zones.

Halvorsen & Bendiksen, the present paper	Kalela 1958, 1959, 1961, 1962,	Ahti et al. 1968	Ahti et al. 1968	Vorren 1979a	Odland 1978, 1979, 1981a, 1982, Elven & Vorren 1980	Du Rietz 1964	Sjörs 1963
Telemark, SE Norway	Finland	Finland	Finnmark, N Norway	N Norway	W + N Norway	N Sweden	N Sweden
Upper boreal zone	Forest zone of Fjeld-Lapland	(Oro)Hemi-arctic zone	(Oro)Hemi-arctic zone	Hemiarctic zone (HA)	Subalpine zone	Sub-alpine birch forest subregion	Woodland-Tundra sub-zone
	Forest zone of Forest-Lapland	Upper boreal zone	Upper (oro-)boreal zone	Northern boreal zone, northern part (NBn)		Pre-alpine conifer forest subregion	Sub-Arctic and Boreo-montane sub-zone + Sub-Alpine Birch Woodland belt
Middle boreal zone	Peräpohjola	Middle boreal zone	Middle (oro-)boreal zone	Northern boreal zone, southern part (NBs)	Prealpine zone	Central coniferous forest subregion	Main Boreal sub-zone
	Pohjanmaa		Middle boreal zone, northern part (MBn)	Middle boreal zone, northern part (MBn)		Myrica sub-region	

Fig. 1. Corresponding vegetation zones in different works from various parts of Fennoscandia.

In our opinion the MB-UB limit of Bendiksen & Halvorsen (1981) and corresponding limits of Ahti et al. (1968) between the middle and northern boreal zones in Northern Fennoscandia, do not correspond to the limit of Ahti et al. (1968) between the middle and northern boreal zones in Finland (Fig. 1). Ahti

et al. (1968) based their zonal division of Finland on Kalela's (1958, 1959, 1961) division of Finland into five zones. The three northernmost zones of Kalela (1958) were included in their northern boreal zone. In our opinion the MB-UB limit of Bendiksen & Halvorsen (1981) corresponds to the limit between the zones Peräpohjola and Forest-Lappland in Kalela's system, indicating that Peräpohjola should be regarded as part of the middle boreal zone. Arguments in favour of this view are:

(1) Vorren (1979a) and Eurola & Vorren (1980) use the terms northern boreal and middle boreal in a division of Northern Fennoscandia into mire vegetation zones, and state that zone names are chosen to indicate vegetational similarity with the mire zones of Finland (cf. Vorren 1979a: 16). Their maps (Vorren 1979a: Fig. 1, Eurola & Vorren 1980: Fig. 2) and the map of Ahti et al. (1968: Fig. 9) show coincident limits between the northern boreal (NB) and middle boreal (MB) zones in Finland. In Northern Norway, however, the zonal limits diverge by approximately one half zone; thus the MB-NB limit of Ahti et al. (1968) coincides with the NBs-NBn subzones limits of Vorren (1979a) and Eurola & Vorren (1980). Furthermore, the NBs-NBn limit of Eurola & Vorren (1980) in Finland corresponds to the limit between Peräpohjola and Forest-Lappland!

(2) Forests dominated by *Alnus incana* occur richly in Peräpohjola (cf. the "*Geranium-Dryopteris*-Typ" in Kalela (1961)), but are not reported from Forest-Lappland (cf. Kalela 1961).

(3) Most alpine species or species with their main distribution in the alpine zones, e.g., *Arctostaphylos alpina*, *Loiseleuria procumbens*, *Phyllodoce caerulea*, *Juncus trifidus*, and *Alectoria ochroleuca* do not appear until Forest-Lappland, (Kalela 1961, Kalliola 1973).

(4) Most thermophilous forest species characteristic of the southern boreal zone (cf. Ahti et al. 1968, Kalliola 1973) disappear in the zone of Pohjanmaa (considered middle boreal by Ahti et al.), and are hardly present in Peräpohjola (Kalela 1961). This loss of species is not immediately compensated for by the appearance of alpine species (Kalela 1961). The poverty of species in the middle boreal zone in the Grunningsdalen area (Bendiksen & Halvorsen 1981; this paper), the prealpine zone in the study of Elven & Vorren (1980), and in Peräpohjola (cf. Kalela 1961) indicates zonal correspondence.

In our opinion, the MB-UB limit of Bendiksen & Halvorsen (1981) and corresponding limits should be taken as the limit between a middle and an upper boreal zone. The various criteria for this limit deserve particular consideration.

(1) The upper limit of *Alnus incana*-forests. This criterion is emphasized in numerous Norwegian studies (e.g., Fremstad & Øvstedal 1978, Odland 1978, 1979, 1981a, 1981b, 1981c, Elven & Vorren 1980, Eurola & Vorren 1980, Bendiksen & Halvorsen 1981). Elven & Vorren stress this as an important criterion as it may be traced in climates differing widely in oceanicity. Ve (1930, 1940) and Knaben (1952) found dominance of *Alnus incana* to cease some 100-300 m below the forest limit in Sogn. In a few regional surveys of forest vegetation in Sweden *Alnus incana* is mentioned as an important component of forest up to the forest limit (Kilander 1955, 1965, Du Rietz 1964, Rune 1965). However, Samuelsson (1917a) and Nordhagen (1928) state

that *Alnus incana* stops far below the tree limit, and Kilander (1955) mentions that it is rare in the birch belt.

In oligotrophic areas, *Alnus incana*-forests are rare, and less useful as a zonal criterion (Bendiksen & Schumacher 1982, Bendiksen & Moss 1983).

This criterion seems to be completely dependent on a thermal factor, and should be taken as a basic criterion of the MB-UB limit.

(2) The upper limit of thermophilous species. The coincidence of the upper limits of *Matteuccia struthiopteris* and *Alnus incana*-forests is often mentioned (Hämet-Ahti 1963, Fremstad & Øvstedal 1978, Odland 1978, 1979, 1981a, 1981b, 1981c). Bjørndalen (1978, 1981c) and Fremstad (1979) hold the view that spruce forests with tall herb vegetation including *Matteuccia* have the same upper limit as the *Alnus incana*-forests. However, Sjörs (1950), Rune (1965), and Hultén (1971) report subalpine occurrences of *Matteuccia*. The general validity of these statements is doubtful, as Lid (1974) states, "scattered in both countries (Norway and Sweden) up to 600-700 m, Borgund in Sogn 940 m", thus indicating a species which avoids the upper boreal zone. The occurrence of the mophilous, often edaphically demanding species on south-facing slopes at high altitudes or at northerly latitudes is frequently reported (e.g., Du Rietz 1954, Nybø 1959, Gjærevoll 1966, Lundquist 1968, Aas 1970, 1972). Such stands indicate a particularly favourable microclimate and should be treated as extrazonal outliers of a lower zone (cf. Hämet-Ahti 1963). The occurrence of an element of thermophilous species in sites not particularly influenced by favourable microclimate, is probably due to the same limiting factor as that limiting the *Alnus incana*-forests. In particular, *Matteuccia struthiopteris* and dominance of *Athyrium filix-femina* seem to be useful as indicators of the zonal border.

(3) The lower limit of alpine plants. This is used as a criterion of the MB-UB limit by many authors, as has been noted. Records of alpine plant species like *Arctostaphylos alpina*, *Loiseleuria procumbens*, *Lycopodium alpinum*, *Phyllodoce caerulea*, *Pedicularis lapponica*, *Carex bigelowii*, and *Juncus trifidus* descending somewhat into open pine (or mixed) forests are frequent (cf. Sernander 1899, Samuelsson 1917a, Resvoll-Holmsen 1918, Selander 1950, Sjörs 1950, Wistrand 1962, Haug 1970, Moen 1978, Bendiksen & Schumacher 1982, Bendiksen & Moss 1983). Others emphasize the lower limit of dominance by *Athyrium distentifolium* in tall-herb and fern vegetation (Odland 1978, 1981c, Bendiksen & Halvorsen 1981). Records from mature birch forests in Central Sogn (Samuelsson 1938, Nordhagen 1954b) also indicate a lower limit of about 200 m below the forest limit for species like *Gnaphalium supinum*, *Phyllodoce caerulea*, *Salix herbacea*, and *Sibbaldia procumbens*.

Næss (1981), in a study of alpine plant species (in a wide sense, defined according to Danielsen 1971) in a coniferous forest area north of Oslo, shows that most of the possible indicators of the lower limit of the upper boreal zone are confined to rock crevices, roadsides, edges of paths and other habitats with low competition when they occur in the lowlands. A rich growth occurrence of alpine species along rivers, even at lower altitudes, is often reported (Wistrand 1962, Bendiksen

& Schumacher 1982, Bendiksen & Moss 1983). This is attributed to water-dispersal of diaspores.

However, this criterion does not seem to be correlated with criteria (1) and (2) in strongly oceanic or strongly continental areas. In outer Vestlandet suboceanic species penetrate the forest limit, and the alpine element in the flora is much impoverished (Samuelsson 1938, Nordhagen 1954b, Skogen 1976, Kummen 1977). Kummen (1977) tried in vain to use the presence of alpine species to indicate a subalpine zone in the birch forests of Outer Sogn, and concluded that it is no longer possible to keep the boreal zones separate in the extreme west. Odland (1981b) and Huseby & Odland (1981), also in investigations from Western Norway, have reached the same conclusion.

Hämet-Ahti (1963) notes the more frequent occurrence of alpine species in continental forest vegetation. This is also observed by Resvoll-Holmsen (1912), who reports alpine species in low altitude pine forests of continental Central Norway.

(4) Sjörs (1963) emphasizes the important correspondence between this limit and the "economic limit for artificial regeneration" used in forestry, and stresses that the corresponding lower growth rate, lower stature and increased spacing of trees ought to be used as a regional phytogeographic criterion.

(5) Dahl (1979) uses the upper limit of permanent agriculture as a criterion of the MB-UB limit in Norway.

(6) The presence of a species-poor zone below the limit is documented by Elven & Vorren (1980), and can be traced in Finland (cf. Kalela 1961, Kalliola 1973).

It seems possible to make a consistent division of Fennoscandia into a middle and an upper boreal zone by means of the upper limit of *Alnus incana*-forests and thermophilous species. These criteria are supposed to show close correspondence with isolines for respiration equivalents of *Ulmus glabra* ($Q_{10}=2.0$). Additional criteria may have local or regional importance. Criteria (4) and (5) should be subjected to more detailed investigations.

The UB-LA limit. Sjörs (1963) distinguishes a hemiarctic subzone containing the transition between closed forests and the upper occurrences of birch outliers. Ahti et al. (1968) similarly defines an orohemiarctic zone. Many different limits have been defined in this "timberline ecotone" (cf. T. Fries 1917, Smith 1920, Tengwall 1920, Kilander 1965, Aas 1969, Kullman 1979). The vertical extent of this ecotone varies from below 50 m at most stations in the Southern Swedish scandes (Kilander 1965, Kullman 1979) to more than 100 m in Western Norway (Ve 1940, Knaben 1952). Owing to the possibility of giving a precise definition of the forest limit, and the fact that this criterion is probably due to the same set of climatic factors throughout Fennoscandia (cf. Hämet-Ahti 1979), we reject the hemialpine zone as a zone on its own.

The UB-LA limit is here defined as the forest limit, in Kullman's (1979) meaning of the term: The line connecting the uppermost occurrences of tree stands minimum 5 x 5 m in diameter, consisting of at least 15 trees with a height of 2 m. This corresponds to the upper and the climatic timberlines of Aas (1969).

The LA-MA limit. The existence of a transition zone in the alpine vegetation where dwarf-shrub heaths, mires and willow shrubs give way to dry-grass heaths and unstable earth, can be traced back to Vestergren (1902). Except for a few investigations disregarding this limit (T. Fries 1913, 1917, Smith 1920, Tengwall 1920), it is usually recognized although its sharpness varies from area to area and has been much debated (cf. Nordhagen 1928, 1943, Dahl 1957).

Two different criteria of this limit have been widely applied: (1) The upper limit of *Vaccinium myrtillus*-heaths, that is, where *Vaccinium myrtillus* no longer forms closed vegetation and dominance is taken over by heaths dominated by *Juncus trifidus* (cf. Vestergren 1902, Samuelsson 1917a, 1917b, Resvoll-Holmsen 1920, Du Rietz 1925b, 1928, Nordhagen 1928, 1937, 1943, Dahl 1975, Gjærevoll 1950, 1956, Knaben 1952, Poore & McVean 1957, Gjærevoll & Bringer 1965, Sjörs 1967, Odland 1979, 1981a, Bendiksen & Schumacher 1982, and Halvorsen & Salvesen 1983). (2) The absolute upper limit of *Vaccinium myrtillus* as proposed by Du Rietz (1942) and later used by Kilander (1950, 1955, 1965), Du Rietz (1953, 1964), Dahl (1957), and Rune (1965).

The two ways of performing the division do not produce similar results. Nordhagen (1943) reports the absolute limit to be situated 100-150 metres above the physiognomic limit in Jotunheimen, but according to R. Jørgensen (1932) the upper limit of *Vaccinium myrtillus* in Jotunheimen is 1700 m, indicating that the difference between the limits may locally be even greater. In Fana, Western Norway, *Vaccinium myrtillus* ascends to the highest point, 981 m, while the physiognomic limit lies at approximately 750-800 m (Naustdal 1951). In Lifjell, the physiognomic limit lies at 1250 - 1280 m (Aas 1970, Bendiksen & Halvorsen 1981), while *Vaccinium myrtillus* reaches the summit of Målefjell, 1415 m, and it is reported from 1500 m at Gausta some 40 km farther north by R. Jørgensen (1932).

Kilander (1950, 1955) stresses the sharpness of the *Vaccinium myrtillus* limit, and emphasizes the correspondence of this limit with upper limits of *Solidago virgaurea*, *Athyrium distentifolium*, and *Alchemilla alpina*.

Bendiksen & Halvorsen (1981) stress the sharpness of criterion (1) as the shift in dominance from *Vaccinium myrtillus* to *Juncus trifidus* normally occurs within a 50 m vertical range.

However, even if criterion (2) is more exact, it suffers from important weaknesses: It is monothetic (Goodall 1978b, Orlóci 1978), and as such vulnerable to chance fluctuations. Thus it defines a low alpine zone of highly variable vertical extent, although this will most often be 400-500 m (cf. Nordhagen 1943, Kilander 1950, Dahl 1957). Compared to the boreal zones, criterion (2) results in a far more extensive range along the zonal gradient. Consequently, its practical value seems small. The quoted examples support our choice of the physiognomic criterion as a zonal limit. In calcareous areas, where *Vaccinium myrtillus* plays a minor part in the vegetation, neither of the above mentioned criteria seems to be useful for a division of the alpine region (Selander 1950, Hedberg 1952). Other species that may serve the purpose are

proposed by Hedberg (1952). The correlation of criterion (1) with the upper limit of willow shrubs and mires gives useful additional criteria that may have particular importance in calcareous areas.

The sectional gradient

The sectional ecocline of this work corresponds to the sectional gradient of Ahti et al. (1968), caused by differences in the oceanicity of the climate. This gradient is emphasized in numerous Fennoscandian vegetation studies (e.g., Nordhagen 1928, 1937, 1943, Knaben 1952, Malmer 1962, Hämet-Ahti 1963, Sonesson 1967, 1970, Rodvelt & Sekse 1980).

Important correlated climatic factors and division of the sectional gradient. Ahti et al. (1968) intended to provide a consistent division of Fennoscandia into oceanicity sections, and reviewed earlier attempts. They divided Fennoscandia into 5 sections, ranging from O₃ (euoceanic) via OC (indifferent) to C₁ (slightly continental).

Attempts to characterize steps along the gradient by climatic indices are reviewed by Tuhkanen (1980). Ahti et al. (1968) emphasized temperature amplitude (e.g., difference in monthly mean temperature between warmest and coldest month), hygric values (annual or growth season precipitation or relative humidity), and combined indices of oceanicity.

Tuhkanen (1980) tested the correlation between each of 5 different climatic indices and the sections of Ahti et al. (1968). Conrad's index of continentality (Conrad 1946) performed best, but no index was found completely satisfactory. Tuhkanen (1980) ascribed this to the crudeness of the original division into sections, and the complexity of the gradient.

The effect of oceanicity on the vegetation is complex. The complex-gradient is made up of more climatic gradients known to have direct effect on plant distribution. For instance, Fægri (1958) attributes the eastern limit of many western species to low tolerance for cold winters and Lye (1967, 1970) suggests low resistance to drought as a limiting factor for some strongly western species. Winter temperature, temperature amplitude, and hygric factors are only in part correlated, and give rise to different sectional classifications. More insight into the oceanicity ecocline is needed until an acceptable sectional subdivision can be made.

LOCAL COMPLEX-GRADIENTS

Examination of Fennoscandian literature dealing with forest and alpine vegetation has revealed the existence of two complex-gradients holding a key position in determining the major variation in vegetation on a local scale. These may be termed "complex-gradient nutrient status" and "complex-gradient topographic moisture - snow cover", respectively. The latter is the more complex. However, it seems convenient to consider snow cover and topographic moisture as members of a single

factor complex as there is considerable correlation between them. Studies in alpine vegetation considering these two complex-gradients as the most important include Nordhagen (1928, 1943), Gjærevoll (1956), Sjörs (1967, 1971), Dahl (1957), and Waldemarson Jensen (1980). Similarly, Eneroth (1931, 1934, 1937), Arnborg (1943, 1960, 1964), Sjörs (1967, 1971), Kielland-Lund (1973, 1981), and Ebeling (1978) ascribed major variation in forest vegetation to them. Two additional gradients may locally be important, viz. a soil drainage gradient (cf. Gjærevoll 1956, Dahl 1957, 1975, Kielland-Lund 1981, Bendiksen & Salvesen 1985), and in the mountains a soil stability gradient (cf. Dahl 1957). However, these are considered subordinate for description of large-scale variation of vegetation.

The complex-gradient nutrient status

This coenocline is reflected in the distinction between the "heath" and "meadow" series in the system of Nilsson (1902). Later on the concepts of "poor" and "rich" were employed to mean the complex-gradient, the coenocline or the ecocline (cf. Sjörs 1967, 1971, Fransson 1972), and the term "lime-rich" is repeatedly applied to areas including certain indicator species or vegetation types (Smith 1920, Tengwall 1925, T. Fries 1925a, Knaben 1952, Gjærevoll 1956).

Important correlated chemical parameters.

It is practical to maintain a distinction between primary and secondary ecological factors (cf. T. Fries 1925b, Dahl et al. 1967). Primary factors depend on the bedrock, weathering or leaching of soils, and supply from precipitation (Dahl et al. 1967). Ca^{2+} is often considered the major determinant of the coenocline (cf. Hedberg 1952, Sjörs 1967, Dahl et al. 1967, Dahl 1975. Positive correlations with the vegetational gradient are shown by Baadsvik (1974) and Wielgolaski et al. (1975) in alpine vegetation and Kielland-Lund (1981) in forest vegetation. However, most studies do not show a simple positive correlation between vegetation and Ca^{2+} concentrations (Dahl et al. 1967, Bjørnstad 1971, Aune 1973, Kielland-Lund 1981). A somewhat better correlation may be reached by measuring Ca^{2+} as a fraction of humus content (cf. Kielland-Lund 1981).

pH takes a position between the primary and secondary ecological factors. It is often claimed to be the most important single chemical parameter correlated with the poor-rich variation in vegetation (Sjörs 1967, Baadsvik 1974), and correlations with vegetational differences have repeatedly been established.

Secondary ecological factors are results of processes in the ecosystem (Dahl et al. 1967). Among factors correlated with this coenocline the following have been mentioned: base saturation percentage (Gorham 1953, Malmer & Sjörs 1955, Dahl et al. 1967), ash content, *N* content in per cent of loss on ignition (Dahl et al. 1967), *C/N* ratio, and soil profile.

A functional approach to the complex-gradient nutrient status. Dahl et al. (1967) emphasized the importance of divalent ions such as Ca^{2+} and gave an outline of a mechanism of their action. They assume that divalent ions increase the

nitrogen turnover and influence the accessibility of nitrogen for growth. The lack of direct correlation between the vegetational gradient and calcium concentration does not invalidate the hypothesis, as the accessibility of Ca^{2+} is in turn often assumed to be correlated with pH (Sjörs 1967).

Division of the gradient in nutrient status. Alpine vegetation types have often been divided into two main categories along this complex-gradient (e.g., Tengwall 1925, Gjærevoll 1956, Sjörs 1967, Hesjedal 1973, Waldemarson Jensén 1980). As regards forest vegetation, the picture is more complicated. Nihlgård (1980) presented a diagram showing Fennoscandian forest vegetation types occupying overlapping positions along the poor-rich gradient, but maintained a division into two "series" according to Nilsson (1902). The forest site-type system of Eneroth (1931, 1937), Arnborg (1943, 1964) and Ebeling (1978) used 4 steps along the gradient.

So far no common usage has been established for division of this gradient in forest and alpine areas, and the essentially continuous variation in vegetation makes many different methods of division possible.

The established practice of dividing mire vegetation into 4 to 6 groups along this gradient (cf. Sjörs 1948, 1967, Du Rietz 1949, Fransson 1972, Moen 1984) indicates that a division into 4 groups may be preferable.

The complex-gradient topographic moisture-snow cover

The alpine zones. The fundamental position of snow cover as determinant of major variation in mountain vegetation has been well known since the pioneer work of Vestergren (1902).

Important factors correlated with snow cover. The uneven distribution of snow cover is primarily ascribed to variation in topography and exposure to winds (cf. Vestergren 1902, Nordhagen 1928, Kalliola 1939, Dahl 1957, Matthews 1979b). Above the snow beds (in the sense of Nordhagen 1943; below the maximum snow cover endurable by *Vaccinium myrtillus*), snow cover is paralleled by soil moisture content, as pointed out by Smith (1920), Tengwall (1920), Nordhagen (1928, 1943, 1954a) and shown by measurements (Tengwall 1925, Jonasson 1981). Transpiration due to winds, shorter duration of snow cover and frost in itself have the effect of reducing soil moisture in this part of the gradient. In the snow beds, however, moisture conditions vary from seasonally wet to permanently irrigated (T. Fries 1913, Samuelsson 1920, Nordhagen 1943, Hedberg 1952, Gjærevoll 1956, Dahl 1957, 1975, Sjörs 1967). Gjærevoll (1950, 1956) divided the snow bed vegetation into a series of seasonally wet vegetation types poor in hygrophiles and a series of more or less permanently irrigated vegetation types rich in hygrophiles. These two series are also emphasized by Waldemarson Jensén (1980). The occurrence of tall fern and tall herb vegetation is due to supply of moving water rich in oxygen (T. Fries 1913, Samuelsson 1917a, Nordhagen 1928, 1943, M. Fries 1949, Dahl 1957, Sjörs 1967.) This is damp flushing in the sense of Dahl (1957). The requirement for a stable snow cover is well documented (e.g., Nordhagen 1943, Baadsvik 1974), but vegetation of this type does not correspond directly to a

specific level in the snow cover zonation. Gradients in soil depth (Dahl 1957, Jonasson 1981), soil texture (Dahl 1975) and to a lesser degree pH (Nordhagen 1943, Jonasson 1981) run parallel with the snow cover gradient above the lower limit of *Vaccinium myrtillus*.

Functional effects of snow cover. The effect of snow cover on vegetation is direct and well known. The most important effect is probably the shortening of the growing season caused by long duration of snow cover, as pointed out by A. Blytt (1869), Norman (1895, 1901), Vestergren (1902), Braun-Blanquet (1913), and T. Fries (1913), as well as Dahl (1957) and other recent investigators. Resvoll (1917) described the adaptations of plants to the short summer of the late snow beds. Some further effects of snow cover are of major importance: A stable snow cover during winter and spring is an effective protection against low temperatures (T. Fries 1913, Helland-Hansen 1915, Keränen 1920, Tengwall 1925, Gjærevoll 1956, Dahl 1957, Baadsvik 1971), and also protects against wind abrasion and desiccation during these parts of the year (Tengwall 1925, Kalliola 1939, Nordhagen 1943, Hedberg 1952, Knaben 1952, Dahl 1957, Baadsvik 1971, 1974, Thannheiser 1975).

Division of the topographic moisture-snow cover gradient in the alpine zones. Topographically induced variation in snow cover often gives rise to beautiful zonation complexes, and the full range of vegetation types from those of wind-swept ridges to extreme snow beds may be present within a short distance. Figures showing zonation of vegetation according to the snow cover gradient are frequently encountered in the literature (e.g., T. Fries 1913, Tengwall 1925, Nordhagen 1928, 1943, Gjærevoll 1949, 1956, Hedberg 1952, Knaben 1952, Dahl 1957, Baadsvik 1974, Waldemarson Jensén 1980, Bendiksen & Schumacher 1982). They are highly concordant, and Waldemarson Jensén (1980) considered the possibility of dividing mountain vegetation into zonation complexes. Most of the cited works encountering the whole range of vegetation types recognize 6 major zones in typical sites (Tab. 1). Different zonation complexes have been described from poor and rich sites (Gjærevoll 1950, 1956, Waldemarson Jensén 1980), but only poor vegetation poor in hygrophiles has been included, as this represents the most frequently encountered zonation complex in Fennoscandian alpine vegetation. Some important ecological reference points along the gradient may be noted. The limit between zones 1 and 2 roughly corresponds to the limit between vegetation without and with stable snow cover in winter, respectively (Vestergren 1902, Du Rietz 1942, Nordhagen 1943, Dahl 1957). According to Gjærevoll (1956), the lower limit for *Vaccinium myrtillus*, corresponding to the transition between zones 3 and 4 in Table 1, is the most marked limit in alpine vegetation. This is frequently used to indicate the upper limit of snow beds (Nordhagen 1937, 1943, Gjærevoll 1949, 1956). Dahl (1957), however, preferred to include all distinctly chionophilous vegetation in the snow beds, using an upper limit of snow beds roughly coinciding with the limit between zones 2 and 3. A third way of demarcating the snow beds is proposed by Vestergren (1902) and Du Rietz (1942), using the limit between zones 4 and 5 to indicate the upper limit of snow beds. Gjærevoll (1956) emphasized the important biological limit at

Tab. 1. Examples in literature of zonations along the snow cover gradient. All zonations refer to normally occurring vegetation types on poor soils without permanent irrigation.

Author	Locality/zone	1	2	3	4	5	6
Nordhagen 1928	S.Norway, Sylane/LA	Flechtenreiche Loiseleuria-Ass.	Flechtenreiche Empetrum-Ass.	Flechtenreiche Vaccinium myrtillus-Ass.	Alpine Nardus-Ass.	Moosreiche Salix herbacea-Ass.	Anthelia juratzkana-Ass.
Tengwall 1925	N.Sweden, Sarek/LA	Flechtenreiche Diapensia-Loiseleuria-Heide	Moosreiche Betula-nana-Gebüsch	Flechtenreiche Vaccinium myrtillus-Heide	Anthoxanthum odoratum-Grasheide	Salix herbacea-Schneeboden	Moos-Schneeboden
Samuelsson 1917a	Sweden, Dalarne/LA	Cetraria nivalis-Heide	Empetrumreiche Cladonia-Heide	Vaccinium myrtillusreiche Moosheide	Lycopodium alpinum-reiche Moosheide	Salix herbacea-reiche Moosheide	
Samuelsson 1917b	W.Norway, Hardangervidda/MA	Juncus trifidus-reiche Flechtenheiden		Lycopodium alpinum-reiche Flechtenheide	Anthoxanthum odoratum- and Carex rigida-Wiese	Salix herbacea-reiche Moosheide	Cesia-Heide
Knaben 1952	W.Norway, Middle Sogn/LA	Loiseleuria-heaths	Empetrum heath	Vaccinium myrtillus heath	Deschampsia flexuosa-Ant-hoxanthum heath/Nardus stricta heath	Salix herbacea snow-bed	Moss snow-bed
Gjærevoll 1956	Scandinavia, synopsis of alliances/LA				Deschampsio-Anthoxanthion	Herbaceon	Polytrichion norvegici
Dahl 1957	S.Norway, Rondane/LA	Cetrarietum nivalis typicum	Cladonietum alpestris	Myrtilletum	Deschampsieto-Dicranetum fuscae/Chiono-Juncetum trifidi/Nardetum	Lophozieto-Salicetum herbaceae	
Sjörs 1967	Scandinavia, synopsis/LA	Diapensia-Loiseleuria-hed	Empetrum hermaphroditum-Betula nana-hed	Vaccinium myrtillus-hed	Deschampsia flexuosa-Ant-hoxanthum-hed	Salix herbacea-hed	Nåstan kärlväxtfri veg. av snölege-mossor

the transition between zones 5 and 6, where vascular plants are no longer able to survive owing to the shortening of the growing-season.

The boreal zones. Apart from the complex-gradient nutrient status the most important environmental factors of boreal forests may be grouped into a topographic moisture complex. Ecological series of vegetation types along this complex-gradient are frequently encountered in the literature, and the importance of moisture conditions is emphasized by Cajander (1921a), Ilvessalo (1921, 1922) and subsequently by most proponents of the forest site-type system, as well as other phytosociologists. American investigators of forest vegetation have considered the topographic moisture gradient of major importance (e.g., Brown & Curtis 1952, Whittaker 1956, 1960, 1967, Curtis 1959, Loucks 1962, Whittaker & Niering 1965, Mowbray & Oosting 1968, Peet & Loucks 1977, Morale & A. Watson 1978, Peet 1978a, 1978b, 1981).

Important factors correlated with topographic moisture. In the subalpine birch forests strong winds often cause uneven distribution of snow cover (Lie 1919, Smith 1920, Nordhagen 1928). Smith (1920) found a distinct parallelism between the series of forest vegetation types along the topographic moisture gradient, snow depth, and duration of snow cover. Kielland-Lund (1981) also mentioned snow cover as a factor influencing xeric forest vegetation in lower zones.

The importance of micro- and macrotopography (and the associated variables slope and aspect) for the soil moisture status, is repeatedly emphasized. Hägglund & Lundmark (1977) used *subsoil water table* as an indicator of position along the gradient. Tall herb and fern vegetation of the boreal zones depends on a high, sloping ground water table supplying water rich in oxygen (Samuelsson 1917a, Nordhagen 1928, 1943, M. Fries 1949, Malmström 1949, Kielland-Lund 1962b, 1981, Dahl et al. 1967, Sjörs 1967, Bjørndalen 1978, 1980b). Other correlated factors are *soil particle size* (Cajander 1913, Arnborg 1943, Malmström 1949, Kielland-Lund 1962b), and *soil depth* (Kielland-Lund 1962b). *pH* and *ash content* increase slightly along the topographic moisture gradient (Kielland-Lund 1962b, 1981, Dahl et al. 1967, Aune 1973). This is an indication of more favourable nutrient conditions in the more mesic vegetation types (cf. Kielland-Lund 1962a, 1962b, 1970, 1973, 1981, Dahl et al. 1967, Sjörs 1967). However, there is by no means a direct parallelism between the two complex-gradients (Eneroth 1931, 1937, Arnborg 1943 etc.) and in a reference frame of local gradients it seems convenient to consider vegetation types with edaphic differences due to moisture conditions as having the same position along the complex-gradient nutrient status.

Division of the topographic moisture-snow cover gradient in the boreal zones. Sharp zonations are rather infrequent in the boreal forests. However, this complex-gradient has been used for describing parallel site-type series in Finland (Kujala 1938, 1945, Kalela 1961, 1962, Hämet-Ahti 1963, Kalliola 1973). Hämet-Ahti (1963) divided Finnish forest site-types into groups of vicariant types, four of which constitute a series from xeric to mesic poor sites, the three closest to the xeric end of the scale being "dry heath forests with lichens", "dry heath

forests with mosses" and "fresh heath forests". The "forests with tall ferns" may be considered the fourth, and mesic end of the series. Kalela (1961) and Kalliola (1973) separated four groups of vicariant forest site-types corresponding to the three most xeric groups of Hämet-Ahti (1963) and added a mesic type. Kielland-Lund (1973) paralleled his forest phytocoena from Norway with corresponding forest site-types from Finland, and indicated a division of the coenocline into four groups along this gradient. At high altitudes (with a humid climate) or in oceanic climates lichen-dominated vegetation drops out, and the coenocline reduces to three groups (cf. Aune 1973, Kielland-Lund 1973).

Correspondence between vegetation types along the complex gradient topographic moisture-snow cover. Correspondence between alpine and boreal vegetation types has often been noted. In an account of the vegetation in the central, continental parts of Southern Norway, Resvoll-Holmsen (1912) pointed out the high similarity between the field and bottom layers of the alpine lichen heaths and the pine forests of high altitudes. Similarly, Samuelsson (1917a) considered the *Calluna*-dominated alpine heaths to be essentially identical with the understory vegetation of *Calluna*-*Pinus* forests and called attention to the parallelism of high altitude lichen-rich pine forests with *Cetraria nivalis* on exposed ridges and *Cetraria nivalis*-heaths above the tree limit. Kalliola (1939) made a detailed comparison between alpine heath vegetation types and the subalpine birch forest site-types described by Kujala (1929), and found each of the major alpine sociations to have its counterpart in the understory of the birch belt. Nordhagen (1943) stressed the similarity between types of low alpine dwarf shrub heaths and the birch, pine or spruce forests at lower altitudes, and also pointed out the correspondence between snow cover and ground water table as ecological factors. He also emphasized the parallelism between *Empetrum*-dominated vegetation in the low alpine and subalpine zones. Sjörs (1967, 1971) emphasized the small floristic difference between corresponding forest and alpine vegetation types in general. Recently, Odland (1979, 1981a), Rodvelt & Sekse (1980) and Huseby & Odland (1981) commented on the small floristic differences between *Vaccinium myrtillus*-dominated vegetation of the boreal and alpine zones. Correspondence between tall fern and herb vegetation described from different zones from the lower boreal to the low alpine is emphasized by Holmen (1965), Bjørndalen (1978, 1980b), and Odland (1981b, 1981c).

Ecologically corresponding vegetation types in alpine and boreal zones. The vertical correspondence between forest and alpine vegetation types of different vegetation zones belonging to the same oceanicity section is evident from the studies cited above. However, when vegetation types are compared along the sectional gradient, an important complication arises. An increased difference in climatic oceanicity makes sites of similar topographic position increasingly different as regards soil moisture and local climatic conditions. This difference is reflected in vegetation, as expressed in the geo-ecological law of plant distribution (Boyko 1947, H. Walter & E. Walter 1953, Peet 1978b, Whittaker 1978b): a plant species will occupy

sites with similar habitat conditions in different regions, thus tending to have their local distributions displaced against the xeric end of a local topographic-moisture complex-gradient in the more oceanic area. A shift of positions in nomograms of vegetation types in different areas along an oceanicity-continentality gradient is shown by Peet (1978b). Observations of shifts in plant distributions along the sectional gradient are frequent also in Norwegian literature (Nordhagen 1943, Naustdal 1951, Malme 1971, Aune 1973). Observations by Nordhagen (1943), Kielland-Lund (1967, 1973, 1981, Bjørnstad (1971), and Aune (1973) seem to indicate a larger shift in bottom layer composition than in the composition of the field layer along the sectional gradient due to the higher sensitivity of mosses and lichens to differences in macro- and microclimate than to changes in soil moisture (Størmer 1969).

The fact that variation along regional gradients is not followed by strictly parallel changes in all features of vegetation renders choice among these features necessary when correspondence is to be defined. It seems that a combination of field and bottom layers, with particular emphasis on the first, may yield a useful result.

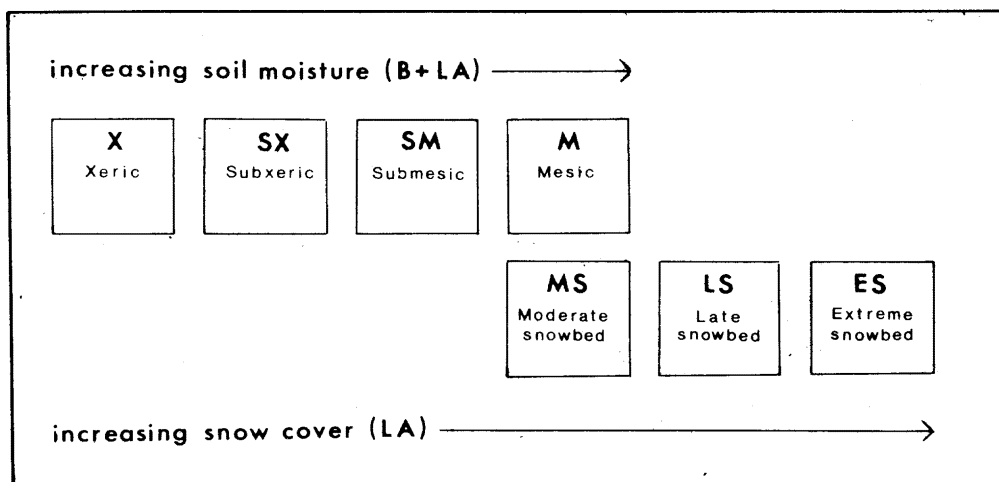


Fig. 2. Subdivision of the complex-gradient topographic moisture-snow cover into series in the boreal zones (B) and the low-alpine zone (LA).

A division of the complex-gradient topographic moisture-snow cover is shown in Fig. 2. The position of the most frequently encountered phytocoenon names is shown in Tab. 2. The basic part of the reference frame is the coenocline ranging from xeric, lichen-dominated heaths to mesic, tall fern stands, including four series. The xeric series is represented

Tab. 2. Provisional grouping of boreal and alpine plant communities on poor soil along the complex-gradient topographic moisture-snow cover.

Author	Locality/zone	Xeric (X)	Subxeric (SX)	Submesic (SM)	Mesic (M)
Kujala 1961	S.Finland/LB	ClT	CT, VT	MT	FT
Kielland-Lund 1967, 1973, 1981b	E.Norway/LB	Cladonio-Pinetum p.p.,	Cladonio-Pinetum p.p., Vaccinio- Pinetum	Eu-Piceetum myr- tilletosum	Eu-Piceetum athy- rietosum
Aune 1973	M.Norway:Hemne/LB		Bazzanio-Pinetum	Corno-Betuletum myrtilletosum	Corno-Betuletum athyrietosum
Kaløla 1961	M.Finland:Pohjanmaa/MB	ClT	ECT, EVT	VMT, DeMT	FT
Hämet-Ahti 1963	N.Norway:Finnmark/MB (sub- maritime subzone of birch zone)		ET	CoMT	
Kielland-Lund 1967, 1973, 1981b	E.Norway/MB-UB	Cladonio-Pinetum p.p	Barbilophozio- Pinetum	Eu-Piceetum myr- tilletosum	Eu-Piceetum athy- rietosum
Hämet-Ahti 1963	N.Finland/UB (continental subalpine subzone of birch zone)	sELiT	sELiT, sEMT p.p.	sEMT p.p.	
Nordhagen 1943	S.Norway:Jotunheimen/LA	Loiseleurieto- Arctostaphylion p.p.	Loiseleurieto- Arctostaphylion p.p., Phyllodoco- Vaccinion p.p.	Phyllodoco-Vacci- nion p.p	Lactucion alpinae p.p.
Dahl 1957	S.Norway:Rondane/LA	Cetrarietum nivalis typicum	Cladonietum alpes- tris	Myrtilletum	Athyrietum alpes- tris
Dahl 1957	S.Norway:Rondane/MA	Cetrarietum nivalis trifidetosum	Cladonietum alpes- tris	Phyllodoco-Junce- tum trifidi p.p.	

by lichen-dominated, wind-exposed mountain ridges (zone 1 in Tab. 1) and its lowland counterparts, roughly corresponding to the ClT of Finnish authors (e.g., Kujala 1929, 1961, Kalela 1961) and the drier parts of Cladonio-Pinetum of Kielland-Lund (1967, 1973, 1981). The subxeric series comprises the *Empetrum*- or *Calluna*-dominated vegetation types occurring in sites intermediate between the xeric and the submesic, the latter defined as typical *Vaccinium myrtillus*-dominated vegetation (cf. Rodvelt & Sekse 1980). The mesic series is defined by dominance of tall ferns and/or tall herbs. Snow-beds (zones 4 to 6 in Tab. 1) are included in the reference frame, but depend on another set of ecological factors. The three zones 4 to 6 in Tab. 1 are termed moderate, late and extreme snow-beds, and constitute one series each. Division of snow-bed series into subseries according to moisture conditions as done by Gjærevoll (1950, 1956) is not considered here, but may be built into the reference frame.

SPECIAL PART - THE FOREST-ALPINE TRANSITION IN THE GRUNNINGSDALEN AREA

THE INVESTIGATION AREA

DELIMITATION

The Grunningsdalen area is situated within the municipalities Bø, Hjartdal, Notodden and Seljord in the county of Telemark, Southern Norway (Fig. 3). The most important names of the Grunningsdalen area are shown in Fig. 4.

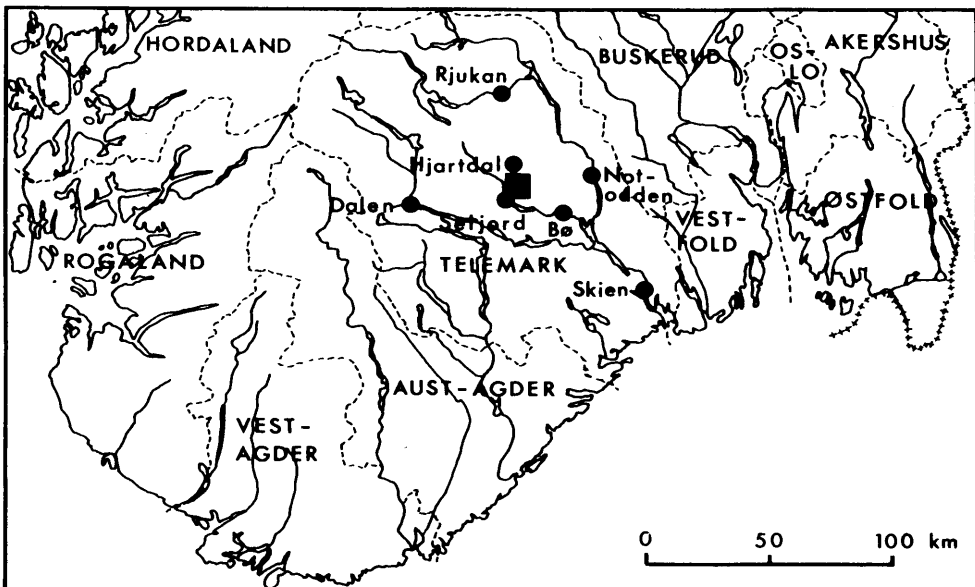


Fig. 3. The position of the Grunningsdalen area relative to the counties of Southern Norway and some towns and villages of Telemark.

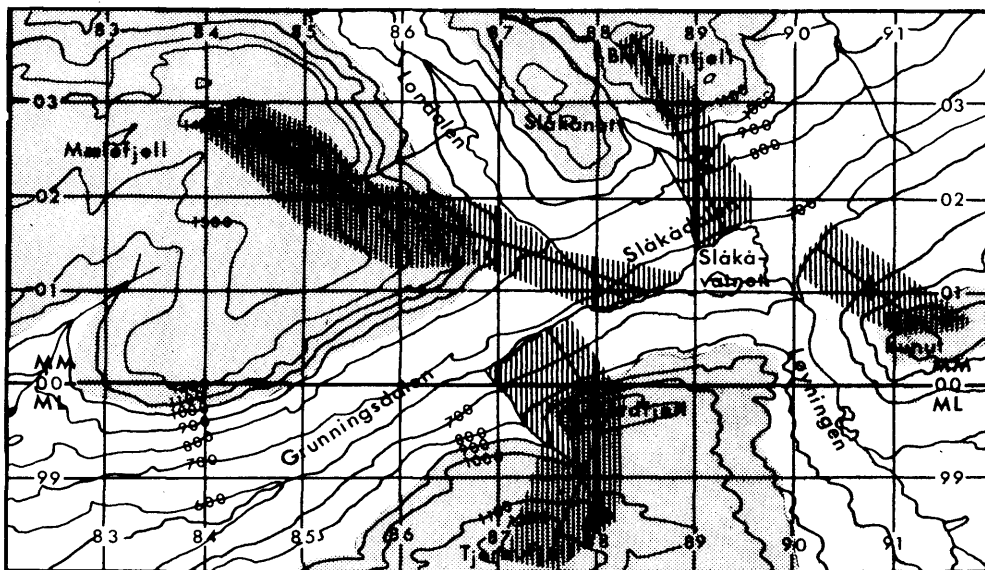


Fig. 4. The investigation area. Important names, alpine zones (dotted), and intensively investigated transects T1-T4 (hatched) are indicated. UTM reference grid (zone 32 W) is drawn in. Contour interval 100 m.

GEOLOGY

Descriptions are based on Werenskiöld (1909), Dons (1960) and Dons & Jorde (1978). The Grunningsdalen area is located within the Precambrian of Southern Norway. The main bedrock is quartzite belonging to the Seljord group, a part of the Telemark suite. After deposition as horizontal sediments of sand and gravel in shallow ocean bays, the layers have later been exposed to folding, metamorphosis and erosion. The rocks are acid with a quartz content up to 99.9%. Basic dikes of amphibolite occur locally, but have not been observed within the studied area. A belt of conglomerate stretches the whole length of Grunningsdalen from Flatdal to Sauland.

In many places the bedrock has a high degree of foliation, often with a strong fall. Grunningsdalen has been exposed to strong pressure and stretching in the east-west direction. Benching with moderate fall to the south can easily be seen from many positions in the valley. Structurally the quartzite occupies downfolded sites in the large area of Telemark granites.

Quaternary deposits are represented mostly as shallow moraine. North-west of Slåkåvatnet moraine deposits shaped as low, rounded cones have been observed.

TOPOGRAPHY

In accordance with the relief types of Rudberg (1968), two morphological relief types are represented. Mountainous relief of the type *fjell in general*, with rounded forms and slopes of medium height, is the dominant one. *The alpine relief type* is restricted to the highest isolated mountains.

The following descriptions are partly taken from Werenskiold (1909), partly based on our own observations. From the Hjartdal Valley the terrain slopes evenly to a plateau edge at 600-700 m. Southward from this, there is a weaker ascendance. This is interrupted locally by high mountains. Målefjell, 1415 m, consists of a large boulder field plateau with several isolated tops and narrow valleys. Grunningsdalen, situated south of Målefjell, stretches from Flatdal to Sauland. Around the watershed located north of Lake Slåkåvatnet it has a flat bottom with extensive mires. From here the river Mjella flows northwards to Hjartdal. The rivers Londøla and Uppdøla, draining into Slåkåvatnet from west and east, respectively, are the most extensive watercourses of the area. The main river, Grunnåi, drains from Slåkåvatnet through Grunningsdalen to Flatdal.

The lowest point of the investigated area is Lake Slåkåvatnet, 690 m, while Målefjell at 1415 m is the highest point. Nordfjell-Tjorbuffjell and Sigurdbunut, located south of Grunningsdalen, reach altitudes of 1291 m and 1078 m, respectively.

CLIMATE

Precipitation

No meteorological station is situated within the investigated area. A summary of precipitation data from five nearby stations is given in Tab. 3. All these stations are within 30 km of Grunningsdalen.

The table clearly shows an increase in precipitation with increased altitude. According to Førland (1979), precipitation is expected to increase by ca. 56 mm/year.100 m in the Sørlandet region, of which the Grunningsdalen area is a part. On the basis of the nearby meteorological stations, annual precipitation is calculated to be about 1150 mm at 700 m (in the bottom of the Grunningsdalen valley) and about 1550 mm at the top of Målefjell, 1415 m.

Tab. 3. Monthly and annual mean precipitation (mm) 1931-1960 for five meteorological stations close to the investigation area (from Norske Meteorologiske Institutt, unpubl.)

Station	M.a.s.l.	J	F	M	A	M	J	J	A	S	O	N	D	Year
Gvarv	26	49	32	22	37	42	62	89	99	84	79	78	62	735
Kviteseid-Moen	77	51	39	28	37	45	66	88	103	80	83	78	67	765
Hjartdal	162	52	38	28	41	52	74	102	117	92	88	81	70	835
Lifjell	354	74	56	40	56	59	84	113	124	110	103	114	91	1024
Gaustatoppen	1828	153	129	94	109	79	103	122	125	108	118	171	198	1509

Temperature

A summary of temperature data for the two nearby stations is given in Tab. 4. Recent works of Laaksonen (1976a, 1976b, 1976c, 1977, 1979), made an estimate of temperatures at different altitudes in the investigation area possible. The effect of lakes (Laaksonen 1977) and urban environments (Laaksonen 1976c) was considered negligible. Calculations are based on data from station Gvarv, some 25 km south-east of Grunningsdalen. The estimated annual mean temperature varies from about 1.5°C at 700 m in the bottom of the Grunningsdalen Valley to approximately -2.0°C at the top of Mælefjell, and correlates well with data from Gaustatoppen. However, the estimates for January (ca. -9.5°C at 700 m, ca. -12.5°C at 1400 m) and July (ca. 13.5°C at 700 m, ca. 9°C at 1400 m) mean temperatures seemed to be less exact owing to deviations from observed values at Gaustatoppen.

Tab. 4. Monthly and annual mean temperatures ($^{\circ}\text{C}$) 1931-1960 for two meteorological stations close to the investigation area (from Bruun 1967).

Station	M.a.s.l.	J	F	M	A	M	J	J	A	S	O	N	D	Year
Gvarv	26	-6,5	-5,4	-1,1	4,6	10,3	14,4	16,8	15,3	10,6	5,3	0,7	-3,2	5,2
Gaustatoppen	1828	-11,5	-11,7	-9,8	-7,1	-2,1	2,2	4,9	4,1	0,3	-3,8	-7,1	-9,5	-4,3

Humidity

Climatic humidity is a function of precipitation and temperature. Increased precipitation implies greater humidity, lowered temperatures, and cause decreased evaporation, and in turn an increase in humidity (Sjörs 1948). Consequently, climatic humidity is expected to increase with increasing altitude.

The Martonne index of humidity (Martonne 1926) is estimated to be $H=100$ at 700 m and $H=200$ at 1400 m. Index values higher than $H=60$ are characteristic of a superhumid climate according to the climatic classification of Hesselman (1932).

Oceanicity

Oceanicity and continentality are functions of temperature and humidity. According to Tuhkanen (1980), an oceanic climate is characterized by a small difference between the mean temperatures of the warmest and the coldest months of the year. Tuhkanen (1980) used Conrad's index of continentality as a measure of climatic oceanicity. Based on observations from Gvarv and Gaustatoppen, respectively, Conrad's index decreases from 29 to 16 within the study area, indicating a strong increase in climatic oceanicity at higher altitudes.

Wind

Fig. 5 shows the dominant seasonal wind directions in Gvarv (data from Werner Johannessen 1960). Apart from winter and spring, when south and north-westerly winds are almost equally frequent, southerly winds prevail in summer and autumn. This pattern is characteristic for central Telemark (Werner Johannessen 1977).

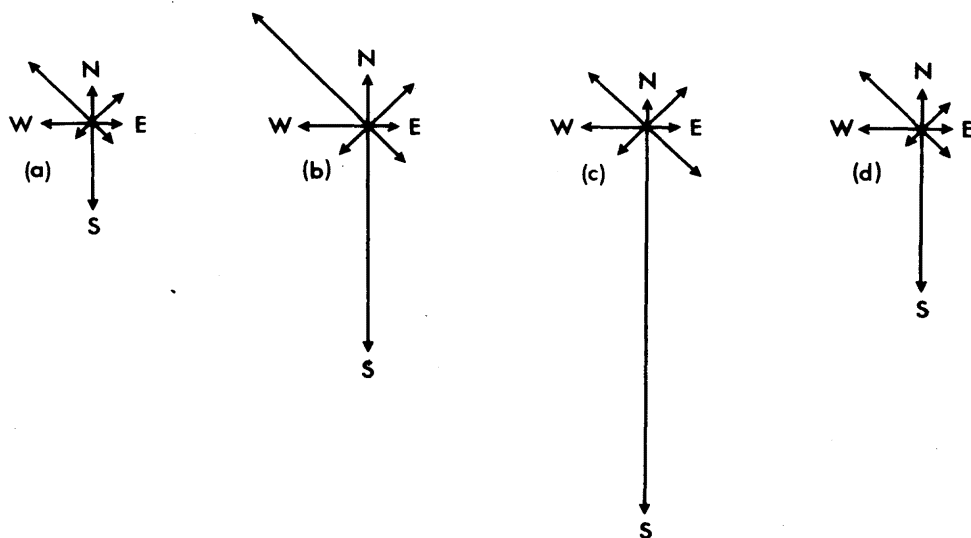


Fig. 5. Prevailing wind directions at Gvarv according to Werner Johannessen (1960). Length of arrows expresses relative frequency of the directions, (a) winter, (b) spring, (c) summer, (d) autumn.

Snow cover

Kravtsova (1972) has mapped maximum mean monthly snow depth 1901-30 in Norway and gave rough estimates of altitudinal gradients of snow cover. The estimated maximum snow cover increases by about 5 cm/100 m in the investigation area, and maximal snow depth figures of 60 cm at 700 m (bottom of the Grunningsdalen valley) and 90 cm at 1400 m are assumed. The snow melts early, and on July 20th, 1980, snow was totally absent from the investigation area. However, it should be emphasized that these are only rough estimates and that the snow cover shows strong local variation. The snow cover is characterized as "stable" (Nordiska Ministerrådet 1977).

SOIL

The morainic soil in the area is mostly formed from resistant rocks and therefore rich in boulders.

Organic soils are widely distributed. Because of high humidity there is a marked tendency to mire formation. In many northerly exposed slopes, e.g., Sigurd bunut, peat has been formed over most of the area because of the rich supply of slowly moving water to the soil close to the surface. Organic soil is also well developed in drier sites. Because of slow decomposition of organic matter at higher altitudes, the soil most often consists of raw humus. A thin layer of mineral soil may be observed between the raw humus and bedrock layers.

Where the soil is deep enough for development of a soil profile, podsolization dominates in the dry and moderately moist sites. This is true for the boreal zones and also partly for the low alpine zone. Higher up in the mountains soil formation is poor and the soil azonal (lithosol). Tendencies to a zone of eluviation may be seen locally. Brown soil may be developed in sites dominated by tall ferns and herbs.

FLORISTIC PHYTOGEOGRAPHY

Species with characteristic distributional patterns in Southern Norway are classified to phytogeographic elements according to Bendiksen & Halvorsen (1981) by use of data from Hultén (1971), E. Jørgensen (1934), Størmer (1941, 1969), Nyholm (1954-69), Arnell (1956), Dahl & Krog (1973), and Krog et al. (1980). Bryophytes and lichens are provided with sparse and incomplete distributional records. Lists of cryptogams are consequently incomplete and the phytogeographical classification of such organisms provisional.

The western element

The western element is divided into four species groups. The group of slightly western species occur in a broad coastal belt from Gran (Oppland) and Aurskog (Akershus) to Troms. This group is represented by three species:

Juncus squarrosus
Narthecium ossifragum
Kurzia trichoclados

The group partly conforms with the atlantic or oceanic elements mentioned by other authors (cf. Dahl 1950, Lye 1967 and Gjærevoll 1973).

Winter temperature is known to be the limiting factor of most phanerogams with a western distribution (Dahl 1967). This does not seem to be the case for the two phanerogamous species occurring in this area, as they are found at high altitudes with a January mean temperature of -8 - -9°C or lower (sheltered by a stable snow cover). According to Fægri (1958), the occurrence of such species may be explained by dependence on high humidity and snow cover. High humidity is also the common explanation of such distributional patterns among bryophytes and lichens (Dahl 1967). This explanation is supported by the fact that many species have both a lower and a higher altitudinal limit in more continental areas, indicating dependence on high humidity (high precipitation and low temperature) at the lower limit and a need for a growing season of definite length or a certain amount of heat at the upper limit.

The group of widely distributed species with a western tendency is represented by five species:

Blechnum spicant
Leucobryum glaucum
Plagiothecium undulatum
Rhytidiadelphus loreus
Sphagnum molle

Humidity seems to be the limiting factor for these species as well. *Blechnum spicant*, *Plagiothecium undulatum* and *Rhytidiadelphus loreus* all have a lower and a higher altitudinal limit in South-Eastern Norway (cf. Fægri 1958, Størmer 1969). *Leucobryum glaucum* is transitional to the southern element.

Warmth-demanding elements

Two elements, the southern and the south-eastern, include warmth-demanding species. Each element is divided into four species groups. Only one group, widely distributed species with a southern tendency, is represented. These species typically reach their altitudinal limit about the border between the middle and upper boreal zones. 17 species are noted:

Agrostis canina
Anemone nemorosa
Carex leporina
Drosera anglica
D. rotundifolia
Oxalis acetosella
Pteridium aquilinum
Stellaria alsine
Atrichum undulatum
Barbilophozia barbata
Brachythecium populeum
Dicranum polysetum
Lophocolea heterophylla
Mnium hornum
Plagiomnium affine
P. cuspidatum
Polytrichum formosum

Southern species require mild winters and moderately warm summers. *Mnium hornum* most often occurs below 200 m (Størmer 1969). At lower altitudes, e.g., in Seljord, the flora contains more than one hundred southern and south-eastern species (Bendiksen & Halvorsen 1981).

The eastern element

The eastern element is divided into two species groups. One species in the area belongs to the group of markedly eastern species:

Carex globularis

The group of slightly eastern species includes three species:

Picea abies
Scheuchzeria palustris
Plagiothecium piliferum

Lye (1967) summarized possible factors responsible for an eastern distributional pattern.

The alpine element

The alpine element is divided into three species groups. The group of pronounced alpine species, rarely descending into the middle boreal zone, contains 31 species:

Arctostaphylos alpina
Athyrium distentifolium
Carex bigelowii

C. lachenalii
Cassiope hypnoides
Cerastium cerastoides
Cryptogramma crispa
Epilobium anagallidifolium
Gnaphalium supinum
Hieracium alpinum coll.
Juncus trifidus
Loiseleuria procumbens
Lycopodium alpinum
Phyllodoce caerulea
Salix herbacea
Saxifraga stellaris
Sibbaldia procumbens
Anthelia juratzkana
Aplodon wormskjoldii
Gymnomitrium concinnatum
Kiaeria starkei
Lophozia opacifolia
Marsupella brevissima
Moerckia blyttii
Nardia breidleri
Pleuroclada albescens
Polytrichum sexangulare
Alectoria nigricans
Cladonia ecmocyna
Cornicularia divergens
Pseudephebe minuscula

The area has a poor alpine flora, mainly owing to the extremely poor bedrock. Besides the pteridophyte and ericaceous species (except *Cassiope hypnoides*), only two species are common. These are *Carex bigelowii* and *Juncus trifidus*. Most of the alpine bryophytes are restricted to late and extreme snow-beds.

The area is situated at the edge of the Southern Norwegian mountain ridge, and some species which are common in large parts of the mountain ridge are missing, probably owing to obstacles to immigration.

The group of boreal-alpine species have their main distribution in the mountains, but with high frequency also in the boreal zones. Species in this group extend southwards to the limit between the lower boreal and hemiboreal zones. 14 species occur in the area:

Epilobium hornemannii
Gentiana purpurea
Gnaphalium norvegicum
Lactuca alpina
Phleum commutatum
Ranunculus platanifolius
Salix glauca
S. lapponum
Lescuraea radicata

Pohlia wahlenbergii var. *glacialis*
Alectoria ochroleuca
Cetraria cucullata
Cladonia macrophyllodes
Solorina crocea

The group of hemiboreal - alpine species have their main distribution in the boreal and alpine zones, but extend southwards into the hemiboreal zone. Their frequency is normally lower in the hemiboreal than in the boreal zones. 28 species occur in the area:

Betula nana
Calamagrostis purpurea
Carex brunnescens
C. vaginata
Selaginella selaginoides
Barbilophozia floerkei
B. lycopodioides
Bryum weigelii
Calliergon sarmentosum
Diplophyllum taxifolium
Harpanthus flotowianus
Jungermannia sphaerocarpa
Lescuraea incurvata
Philonotis seriata
Polytrichum alpinum
Rhizomnium pseudopunctatum
Cladonia bellidiflora
Nephroma arcticum

The importance of the elements

The alpine element is dominant in the area (Tab. 5). Most of the species occurring in the boreal zones are ubiquitous. Because of the poor bedrock and high altitude, the Grunningsdalen area lacks a lot of species which occur elsewhere in the surrounding Liffjell mountain massif (cf. Bendiksen & Halvorsen 1981). A total of 17 western and 30 eastern species have been observed in the latter (Bendiksen & Halvorsen 1981). Accordingly, the area contains both oceanic and continental floristic elements. In the larger area 89 alpine species have been observed.

HUMAN INFLUENCE

Human influence is insignificant in the area. There is no trace of intensive forestry. From older times, however, the area has been used for grazing (Gravir 1922). Some mountain pastures, no longer in use, are located in the area around Lake Slåkåvatnet. The bottom of the Grunningsdalen valley was in 1981 still grazed by cows, and small herds of sheep were observed in all of the analysed mountain areas during the

Tab. 5. Number of species belonging to the different phytogeographic elements in the Grunningsdalen area.

Phytogeographical element	Number of species
Western	10
Southern	5
South Eastern	0
Eastern	5
Alpine	66

summers 1980 and 1981. The grazing pressure was low, and has probably not influenced the vegetation markedly.

PRINCIPLES OF CLASSIFICATION IN THIS WORK

THE DIRECT GRADIENT APPROACH

In the general part we discussed theories on the nature of vegetation and gave reasons for our support for the population pattern theory. The method we have chosen to describe the vegetation, direct gradient analysis (Whittaker 1967, 1978a), has been widely used by supporters of this theory, particularly in the U.S.A. Its major principles are as follows: It is assumed that the major coenoclines and their underlying complex-gradients are known. The task is then to describe the variation in vegetation along these coenoclines. A corollary of the population pattern theory is the continuity of vegetation, suggesting a stepless display of variation in vegetation, such as the mosaic chart (cf. Whittaker 1956, 1960, 1967, 1978b, Whittaker & Niering 1965, Peet 1978b, 1981). However, a multidimensional pattern may be converted into discrete units by dividing the gradient axes, providing a reticulate, non-hierarchic classification (cf. Tuomikoski 1942, Webb 1954). Approaches to classification of vegetation through a division of ecoclines are encountered in studies of Fennoscandian mire vegetation (Sjörs 1948, Du Rietz 1949, 1954, Malmer 1962, 1968, Fransson 1972), and in the ordering of Finnish forest site-types in site-type series (Cajander 1921a, Ilvessalo 1921, 1929, Kujala 1938, 1945, 1961, Kalela 1961, Hämet-Ahti 1963). An early venture in gradient analysis of Swedish forest vegetation is the system of site-types proposed by Eneroth (1931, 1934, 1937; see also Arnborg 1940, 1943, 1945, 1964, Ebeling 1978), where vegetation and environment are classified together into site-types, making up square pieces in a two-dimensional system of major environmental gradients.

The direct gradient approach has frequently been used in ecological studies of forest and alpine vegetation in other parts of the world. Simultaneous applications to elevation and topographic moisture gradients are encountered in the studies of Whittaker (1956, 1960), Whittaker & Niering (1965, 1968) and Peet (1978b, 1981). A similar approach to forest and alpine vegetation in Northern Finland was made by Kärenlampi & Kauhanen (1972). Variation of vegetation along a vertical gradient was treated by Mark (1963), Scott et al. (1964), Wells & Mark (1966), and Beals (1969), while the topographic moisture gradient was subjected to direct gradient analysis by Maycock & Curtis (1960), Loucks (1962), Waring & Major (1964), Mowbray & Oosting (1968), Walker & Coupland (1968), Wali & Krajina (1973), and Wikum & Wali (1974).

Our reasons for choosing the direct gradient approach are: (1) The approach is in accordance with our opinion on the nature of vegetation. (2) Construction of a gradient reference frame, a reticulate, non-hierarchic classification, seems optimal for regional comparison of vegetation. (3) Most works dealing with Fennoscandian forest and alpine vegetation have used phytosociological methods for description of vegetation. This direct gradient approach offers a good opportunity to

compare the relative merits of the two approaches.

GRADIENTS IN FOREST AND ALPINE VEGETATION OF THE INVESTIGATED AREA

Two gradients out of the four included in the gradient reference frame are necessary to describe the main variation encountered in forest and alpine vegetation in the Grunningsdalen area. These are the zonal gradient, a regional gradient, and the complex-gradient topographic moisture-snow cover, a local gradient. There are no significant differences in oceanicity within the studied area; variation in nutrient status is caused by differences in moisture conditions. All vegetation is thus considered as poor.

A DIRECT GRADIENT APPROACH TO FOREST AND ALPINE VEGETATION IN THE GRUNNINGSDALEN AREA

A division of ecoclines should take advantage of both environmental and vegetational criteria. The zonal gradient may be approached by division into zones with given amplitude (Whittaker 1956, Peet 1981). The topographic moisture-snow cover complex-gradient is far more complex, and no accepted method exists for quantifying positions along it (cf. T. Fries 1913, Tengwall 1925, Maycock & Curtis 1960, Sjörs 1967, Whittaker 1967, 1978b, Peet 1978a, 1978b, 1981). Subjective estimation of moisture by slope and exposure is used by Whittaker (1956, 1960) and Whittaker & Niering (1965, 1968), while calculation of site indices by a combination of moisture-related measures is used by Loucks (1962), Walker & Coupland (1968), Kärenlampi & Kauhanen (1972) and Peet (1981), among others. There are considerable difficulties in adopting terrain form as a direct indication of soil moisture in Fennoscandia (see however Hägglund & Lundmark 1977), mainly due to the broken microtopography. Another major weakness of an approach through environmental factors alone is the danger of erecting groups differing widely in beta diversity. We performed a division of the ecoclines by vegetational characteristics based on knowledge of relationships between vegetation and environment. This is due to (1) the complication arising from division by measurement of environmental factors, and (2) the intimate co-variation of vegetation and environment (cf. Eneroth 1931, Cain 1947, Poore 1956, 1962, Whittaker 1962, Kellman 1974).

The units distinguished are called *site-types*. The vegetational criteria used to define them are local, strictly applicable to the investigation area only. To promote comparability with other studies, the zonal gradient was divided into vegetation zones and the complex-gradient topographic moisture-snow cover was divided into units corresponding to major zones in the zonations recognized in

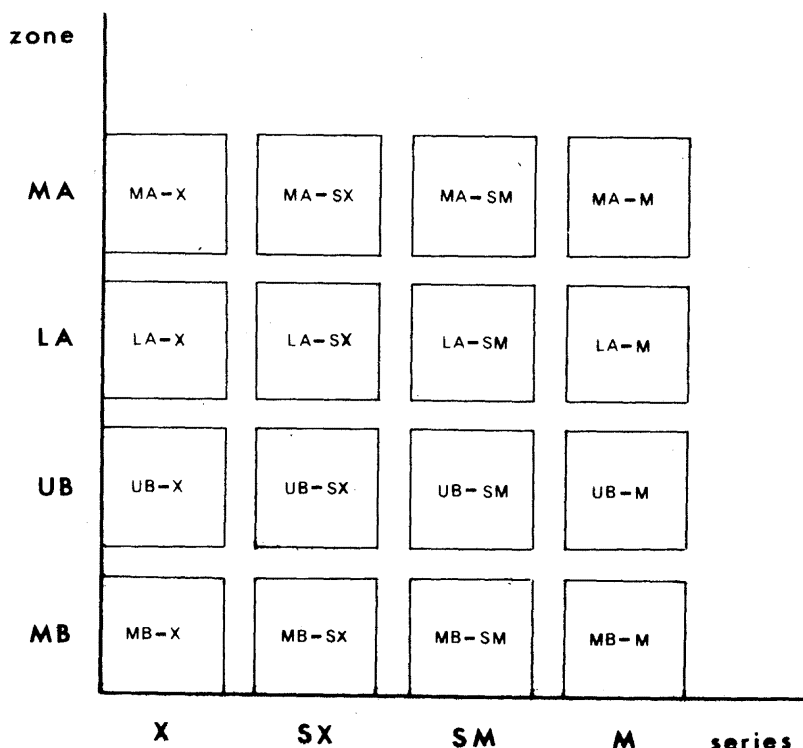


Fig. 6. The classification system used in the present work. The site-types are shown as squares in a two-gradient system. Series along the complex-gradient topographic moisture-snow cover on the horizontal axis are X - xeric, SX - subxeric, SM - submesic, M - mesic. Zones along the vertical gradient are MB - middle boreal, UB - upper boreal, LA - low alpine, MA - middle alpine.

previous works. The delimitation of types along the two gradients is considered to be a classification in a continuum, and the site-types intergrade continuously. For practical purposes intermediates between the site-types have been omitted and the site-types are to be considered as types in the sense of Whittaker (1962, 1978c) or *noda* in the meaning of Poore (1955a, 1955b, 1955c, 1956, 1962, 1964).

All site-types at a given position along the zonal gradient are defined as constituting a zone. All site-types with corresponding moisture-snow cover conditions make up a series. The classification system adopted for the Grunningsdalen area uses a division into 4 zones and 4 series. Naming of the site-types is done by a combination of zone and series designations. The gradient representation of the system is given in Fig. 6.

The criteria used to divide the gradients are discussed in the sections on the zonal gradient and the complex-gradient topographic moisture-snow cover, and only their practical adaptation to the Grunningsdalen area will be treated here.

DIVISION OF THE VERTICAL GRADIENT

As all variation along the zonal gradient in the area is due to altitude, it will be referred to as the *vertical* gradient.

The following 4 vegetation zones were recognized in the Grunningsdalen area (cf. Bendiksen & Halvorsen 1981):

Middle boreal zone (MB)
Upper boreal zone (UB)
Low alpine zone (LA)
Middle alpine zone (MA)

The MB-UB limit. The following criteria were used: (1) The upper limit of *Alnus incana* forests. (2) The lower limit of some alpine species in natural habitats, e.g., *Arctostaphylos alpina*, *Juncus trifidus*, *Loiseleuria procumbens*, and *Phyllodoce caerulea*. (3) The lower limit of dominant *Athyrium distentifolium* and occurrence of *Gentiana purpurea* in tall fern vegetation. (4) The upper limit of dominant *Athyrium filix femina*. (5) The upper limit of some warmth-demanding species, e.g., *Anemone nemorosa* and *Rhizomnium punctatum*. (6) The limit between dominance by conifers (*Picea abies* and *Pinus sylvestris*) and *Betula pubescens*. The zonal border lies approximately 200 m below the forest limit; at ca. 850 m in slopes with southerly aspect, at 750-800 m in north-facing slopes.

The UB-LA limit. The forest limit was taken as the UB-LA limit.

The altitude of the forest limit normally varies from 1000 to 1080 m, highest in sheltered, southerly exposed stations. Local suppression due to topographic causes and mires is frequently encountered.

The LA-MA limit. The upper limit of *Vaccinium myrtillus*-heaths was used as the zone divide. In the study area the LA-MA limit occurs at 1250-1280 m. Outlying low alpine vegetation stands are occasionally observed in strongly south-facing slopes up to 1330 m. The LA-MA limit is situated lower than expected from comparison with Central Norwegian studies (Nordhagen 1943, Dahl 1957, E. Dahl pers. comm.). A possible reason for the low LA-MA limit in the Grunningsdalen area may be its isolated occurrence in the periphery of the Norwegian montain range, and thus an inverse "mass heaving effect" (cf. Nordhagen 1943). The regional distribution of the upper limit of *Vaccinium myrtillus* heaths should be subjected to a detailed study.

DIVISION OF THE COMPLEX-GRADIENT TOPOGRAPHIC MOISTURE-SNOW COVER

The classification into series was in accordance with Fig. 2. The three most xeric series encountered in Fig. 2 were easily recognized in the Grunningsdalen area. Low amounts of snow in winter make the late snow bed series very rare, only occupying a few minute patches. The extreme snow-bed series is almost totally absent. The continuous intergradation of the late and moderate snow beds with the mesic series, and the poor representation of all these series in the alpine zones in the area, suggested an amalgamation of these three series. The aggregate series at the mesic end of the scale was named mesic series. The following 4 series are used to classify the vegetation of the Grunningsdalen area:

- Xeric series (X)
- Subxeric series (SX)
- Submesic series (SM)
- Mesic series (M)

The following criteria are used to differentiate between series:

The X-SX limit. In the alpine zones the important ecological limit between areas with and areas without a stable snow cover in winter is reflected in the often coinciding distributional limits downwards in the zonation for the "wind lichens" *Alectoria nigricans*, *A. ochroleuca*, *Cetraria cucullata* and *Cornicularia divergens* (cf. Nordhagen 1937, 1943, Jonasson 1981). The lower limit for the occurrence of these species and dominance of the wind lichen *Cetraria nivalis* was used as the main field criterion of the limit. The inability of *Vaccinium myrtillus*, *Deschampsia flexuosa* and many other vascular plants to grow in sites without snow cover in the winter (Nordhagen 1937, 1943, Du Rietz 1942, Dahl 1957, Jonasson 1981) provided additional field criteria of the limit.

The gradually decreased effect of snow cover towards lower altitudes and the disappearance of wind lichens in the upper boreal zone made criterion 1 useless in the middle boreal zone. However, in the middle boreal zone the more mesic species *Vaccinium myrtillus*, *Deschampsia flexuosa* and *Melampyrum pratense* as well as most mosses and liverworts showed distinct limits towards the tops of morainic crags. Absence or almost absence of these species and an almost total dominance of lichens in the bottom layer was taken as the X-SX limit in the middle boreal zone. The use of one group of vascular plant species as indicators in all zones was taken as strong evidence for correspondence between the xeric site-types of all zones.

The SX-SM limit. Field criteria for establishing the SX-SM border in zones MB, UB and LA were the disappearance of *Calluna vulgaris*, and the shift in dominance from *Calluna vulgaris* and *Empetrum hermaphroditum* to *Vaccinium myrtillus*. Occurrence of herbs like *Cornus suecica*, *Maianthemum bifolium* and *Trientalis europaea* was taken as indications of the SM series, while

Arctostaphylos alpina and *Loiseleuria procumbens* indicate the SX series.

Most SM indicators did not reach the LA-MA limit. The poverty of species in the middle alpine zone made a distinction between the SX and SM series difficult. By means of zonation complexes the following decisions were made: Dominance of *Empetrum hermaphroditum* and occurrence of *Loiseleuria procumbens* and *Cladonia stellaris* indicated SX, dominance of *Juncus trifidus* and occurrence of *Lycopodium alpinum*, *Solidago virgaurea*, *Trientalis europaea*, *Carex brunnescens* and *Stereocaulon* spp. indicated SM.

The SM-M limit. The collective use of the name "mesic series" in this work made criteria for both of the dividing lines SM-M *sensu stricto*, and SM-MS applicable. In the boreal zones, where the narrow and wide concepts of the mesic series coincide, positive differential species for the mesic series were *Athyrium distentifolium*, *A. filix-femina*, *Dryopteris assimilis*, *Gentiana purpurea*, *Gymnocarpium dryopteris*, *Melandrium rubrum*, *Oxalis acetosella*, *Potentilla erecta*, and *Rumex acetosa*. In the alpine zones, the criteria for separation of the submesic and moderate snow bed series were also used. The moderate snow bed series was positively differentiated from SM by dominance of grasses and sedges (*Anthoxanthum odoratum*, *Nardus stricta*, and *Deschampsia flexuosa* instead of *Vaccinium myrtillus* (or *Juncus trifidus* in the middle alpine zone)).

MATERIAL AND SAMPLING PROCEDURE

Four transects T1-T4, each running from the bottom of the Grunningsdalen valley to the summit of a surrounding mountain (Fig. 4), were chosen for sampling of vegetation. Selection of sample plots was done in accordance with the following criteria: (1) Each sample plot should be representative of a site-type; classification was carried out in the field. (2) The set of sample plots from each site-type should represent the variation in slope, aspect and other factors normally encountered. A sample plot was regarded as homogeneous if all of its parts belonged to one site-type.

Square sample plots, 5 x 5 m, were used. This sample size agrees well with previous studies of Scandinavian boreal forests, ranging from 4 sq. m (Nordhagen 1928, 1943) to 25 - 100 sq. m, or sometimes even larger (Kielland-Lund 1962b, 1967, 1981, Aune 1973 etc.). However, Arnborg (1949), Hämet-Ahti (1963) and Ahti et al. (1968) emphasized the need for large sample sizes, minimum 100 sq.m., to give adequate representation of the tree layer. Alpine vegetation is usually analysed by means of small plots. A sample plot size of 1 sq. m (Nordhagen 1928, 1943) is frequently encountered. However, Dahl (1957) used variable sample plot sizes ranging from 1 to 40 m.

To make possible a direct comparison of sample plots from different site-types, the plot size was kept uniform. A plot size of 25 sq.m. was considered an optimal compromise between representativity, homogeneity, and suitability for comparison with previous works. Considerations of minimal area have not been taken into account, as we consider it hard to obtain an area that is strictly homogeneous in the sense of Dahl (1957:29) due to the prevailing continuity of vegetation.

Vascular plants, mosses, liverworts, and macrolichens were recorded. Crustose lichens were not included. The vegetation was stratified into four layers in accordance with the Scandinavian tradition (Du Rietz 1921, Trass & Malmer 1978), designated A (tree layer), B (shrub layer), C (field layer) and D (bottom layer). Total cover of each layer was estimated and recorded on a 1 - 10 scale with ten per cent steps. Similarly, the proportion of the sample plot area covered by naked soil (E) and rocks (F) was noted. Cover of each species was assigned by the Hult-Sernander - Du Rietz scale (Du Rietz 1921) with two modifications:

(1) Species with high frequency in the plot but low cover were raised from cover degree 1 to 2.

(2) A + sign was used for vascular plant species with low vitality and low cover. A species with cover degree 3, 4 or 5 was considered a dominant (cf. Hafsten 1958).

Altitudes were recorded by an air pressure altimeter regularly adjusted to map values. The observed values always lay within 40 m of the correct value. Slope and aspect were recorded by a clinometer compass. Soil profiles were dug when appropriate.

DESCRIPTION OF INVESTIGATED TRANSECTS

The geographic position of transects T1-T4 is shown in Fig. 4. A simplified diagram showing the zonation of vegetation and major features of topography in each of the transects is given in Fig. 7.

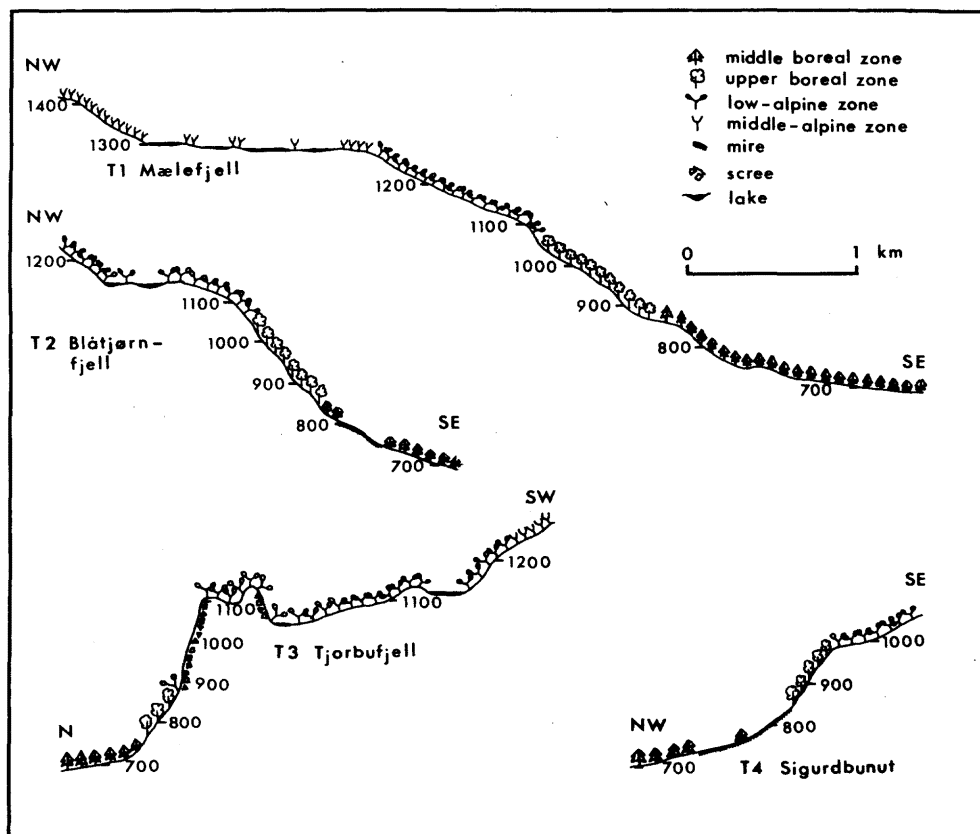


Fig. 7. Profiles of transects 1-4 showing topography and zonation of the vegetation.

T 1 - Mælefjell. This transect comprises a belt with a length of approximately 5 km and a width of approximately 500 m, running in an ESE to WNW direction from west of Lake Slåkåvatnet, 690 m, to the summit of Mælefjell, 1415 m. The lower part of the transect, up to ca. 850 m, is forested with conifers. The area close to Lake Slåkåvatnet is mostly covered

with a subxeric mixed pine and spruce forest. Along the Londøla river as well as along the numerous small creeks and in small local valleys, mesic tall herb and fern vegetation occurs. Above the flats in the bottom of the valley, submesic *Vaccinium myrtillus*-spruce forests replace the subxeric forests as the main vegetation type.

At about 850 m the MB-UB transition is characterized by shift in dominance from *Picea abies* to *Betula pubescens*. In the upper part of the upper boreal zone the forest vegetation is partly split by sloping fens. Submesic vegetation dominates in the lower parts of this zone, and gives way to subxeric vegetation on the ridges between the sloping fens. At sheltered, favourably exposed stations the forest limit reaches 1060 m.

Above the forest limit the vegetation is dominated by submesic and subxeric vegetation, the extreme series are only sparsely present. Boulder fields are progressively more common towards the upper part of the zone.

At 1280 m *Juncus trifidus* has replaced the ericaceous species as dominant in submesic vegetation; the top plateau of Mælefjell is consequently situated in the middle alpine zone. The vegetation is patchy owing to the rich occurrence of boulders and small lakes. Snow bed vegetation is very rare in this transect.

T 2 - Blåtjørnfjell. This transect includes the south slope of Blåtjørnfjell from north of Lake Slåkåvatnet to the summit, 1235 m. The middle boreal zone reaches up to ca. 850 m, but between 750 and 820 m by sloping fens are dominant. Subxeric vegetation is most important close to the lake, while submesic vegetation dominates between the fens. Mesic vegetation occurs sparsely in small valleys.

The steep and dry, southerly exposed upper boreal slope is dominated by subxeric vegetation, partly interrupted by vertical walls. In the sheltered groove in the upper part of the slope of Blåtjørnfjell the forest limit reaches 1080 m, the highest position of the forest limit observed in the Grunningsdalen area.

All vegetation above the forest limit is low alpine. The gently sloping terrain mostly contains well-developed subxeric and submesic vegetation.

Xeric vegetation is sparsely encountered on the most exposed ridges and at the summit of Blåtjørnfjell.

T 3 - Nordfjell - Tjorbufjell. This transect comprises a broad, broken belt from the bottom of the Grunningsdalen valley in south-westerly direction to the summit of Nordfjell, 1144 m, then turning SSW and running to the summit of Tjorbufjell, 1291 m. The valleys west of Nordfjell and between the two mountains are also included in the transect.

The extreme steepness and unfavourable northerly aspect cause a compression of vegetation zones at the northern slope of Nordfjell. Subxeric mixed pine and spruce forests prevail on the plains in the bottom of the Grunningsdalen valley, but give way to submesic and mesic site-types when the slope increases. The gradual displacement of spruce by birch at ca. 750 m indicates the transition to the upper boreal zone. Here the slope is steep and the vegetation becomes interrupted by vertical rock faces and screes. The narrow border above 850 m,

below the nearly 200 m high and almost vertical north face of Nordfjell is occupied by patches of tree-less, clearly alpine vegetation. In the valley west of Nordfjell, *Betula pubescens* forests occur up to ca. 1020 m.

The upper part of this valley as well as the greater part of the mountainous plateau of the Nordfjell-Tjorbufjell massif belong to the low alpine zone, dominated by subxeric and submesic vegetation. Snow bed vegetation is better developed in this transect than elsewhere in the study area.

The limit to the middle alpine zone is diffuse. From 1200 to 1250 m, *Vaccinium myrtillus* is replaced by *Juncus trifidus* as the dominant of the submesic series. Well-developed middle alpine zonation complexes with site-types ranging from xeric to moderate snow beds were observed at 1250 m.

T 4 - *Sigurdbunut*. This transect is the shortest one, comprising the north-west slope of Sigurdbunut, 1078 m. Below ca. 750 m middle boreal submesic spruce forests dominate, occasionally replaced by mixed subxeric forests at exposed crags.

A sloping fen zone with a vertical extent of 100 m is inserted between the spruce and birch forests. The upper boreal birch forests on the rather steep slope of Sigurdbunut are predominantly mesic and submesic.

The topography is even and causes no depression of the forest limit, which occurs at 980-990 m. The low alpine vegetation of Sigurdbunut is mainly submesic and subxeric in the lower parts, mainly xeric and subxeric on the wind-exposed summit.

DESCRIPTION OF THE VEGETATION OF THE SITE-TYPES AND COMPARISON WITH CORRESPONDING VEGETATION DESCRIBED BY OTHER AUTHORS

Vegetation tables for each site-type are compiled following the Scandinavian tradition, listing species in alphabetical order according to layer and growth-form (Du Rietz 1921, Trass & Malmer 1978). Sample plots are listed in order of increasing altitude within each transect.

For each species in each table, constancy percentage (C; Dahl 1957, Trass & Malmer 1978, Westhoff & Maarel 1978), and characteristic degree of cover (c; calculated by conversion of the cover values into mid-points of cover classes according to Sjörs 1954, Persson 1961) are given.

Species with $C < 20$ are considered occasional and listed at the bottom of the table.

Surveys of series and zones are given in Tabs. 6 and 7.

Comparisons with other investigations are presented in a series of tables, one for each site-type (except the low and middle alpine mesic site-types which are treated collectively). The geographic location of studies used for comparison is shown in Fig. 8, with explanations in Tab. 8. Particularly thorough comparisons are made with other works from Southern Norway. It is primarily aimed at depicting ecologically corresponding vegetation types in the same vertical zone, although the vegetation at the middle boreal site-types is also compared with the vegetation described from the lower boreal zone. In works from other areas, including a great number of early Swedish and Finnish investigations, the floristically most similar types within the corresponding site-type are depicted.

XERIC SERIES

Middle boreal zone

The floristic composition of this site-type is given in Tab. 9. The constant species are: *Pinus sylvestris*, *Calluna vulgaris*, *Vaccinium vitis-idaea*, *Dicranum scoparium*, *Pohlia drummondii+nutans*, *Cephaloziella* spp., *Cetraria islandica*, *Cladonia arbuscula*, *C. bellidiflora*, *C. coccifera*, *C. mitis*, *C. pleurota*, *C. rangiferina*, *C. squamosa*, *C. stellaris*, *C. sulphurina*, and *C. uncialis*.

The tree layer is dominated by *Pinus sylvestris*. The only dominant in the field layer is *Calluna vulgaris*. The bottom layer is dominated by *Cladonia mitis*, *C. stellaris*, *C. rangiferina*, and less often *Cladonia arbuscula*.

The mean number of species is 24, while the total number in the 5 sample plots is 35.

This site-type is characterized by having pine in the tree layer and a dense carpet of lichens, especially *Cladonia* spp., in the bottom layer. More than half of the species recorded in the analyses from this site-type belong to *Cladonia*, while bryophytes are of minor importance. The field layer is very

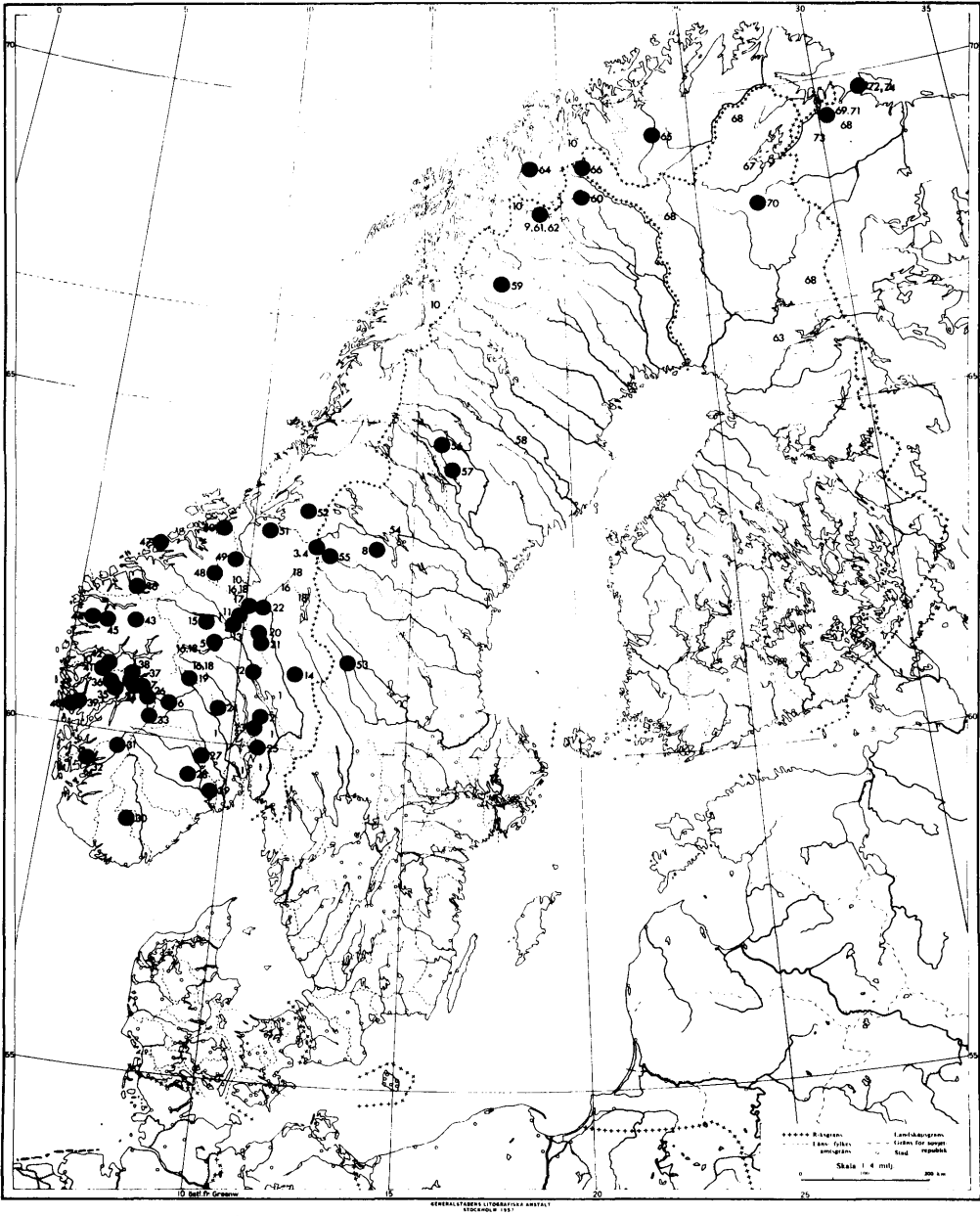


Fig. 8. Locataion of works used for comparison of vegetation types. See Table 8 for explanation.

Tab. 6. Distribution of species along complex-gradient topographic moisture-snow cover. Constancy and characteristic degree of cover for each species in each of the site-types are given.

Series	X				SX				SM				M			
Zone	MB	UB	LA	MA	MB	UB	LA	MA	MB	UB	LA	MA	MB	UB	LA	MA
<i>Dicranum spurium</i>	20-1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lophozia bicrenata</i>	20-1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sphenolobus minutus</i>	-	33-1	50-1	-	-	-	15-1	13-1	-	13-1	-	13-1	-	-	-	-
<i>Alectoria nigricans</i>	-	33-1	63-1	67-1	-	-	-	-	-	-	-	-	-	-	-	-
<i>A. ochroleuca</i>	-	100-3	100-4	100-4	-	13-1	-	-	-	-	-	-	-	-	-	-
<i>Cetraria cucullata</i>	-	67-2	88-3	100-2	-	-	15-1	-	-	-	-	-	-	-	-	-
<i>C. nivalis</i>	20-1	100-2	100-3	100-3	-	13-1	38-1	88-1	-	-	-	-	-	-	-	-
<i>Cladonia floerkeana</i>	-	33-1	50-1	33-1	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. macrophylla</i>	60-1	33-1	50-1	33-1	-	-	-	13-1	-	-	-	-	-	-	-	-
<i>C. phyllophora</i>	40-1	-	-	-	-	-	-	-	9-1	-	-	-	-	-	-	-
<i>Cornicularia aculeata</i>	-	67-1	13-1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>C. divergens</i>	-	33-1	100-2	83-1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sphaerophorus fragilis</i>	-	33-1	25-1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pinus sylvestris</i>	100-4	-	-	-	53-3	25-1	-	-	-	-	-	-	-	-	-	-
<i>Arctostaphylos alpina</i>	-	100-1	75-1	-	-	75-1	46-2	-	-	-	-	-	-	-	-	-
<i>Calluna vulgaris</i>	100-3	67-3	38-1	-	93-4	100-4	77-3	-	27-1	25-1	20-1	13-1	-	-	13-1	-
<i>Loiseleuria procumbens</i>	-	67-2	100-3	50-1	-	13-1	69-2	50-2	-	-	-	-	-	-	-	-
<i>Dicranum polysetum</i>	40-1	-	-	-	14-1	25-1	-	-	-	-	-	-	-	-	-	-
<i>Leucobryum laeue</i>	-	33-1	-	-	20-1	-	8-3	-	-	-	-	-	-	-	-	-
<i>Racomitrium lanuginosum</i>	-	67-2	50-1	-	14-2	13-1	-	-	-	-	-	-	-	-	-	-
<i>Cladonia arbuscula</i>	100-2	100-3	63-2	67-1	86-2	100-2	100-2	100-2	36-1	-	60-1	75-1	-	-	7-1	40-1
<i>C. deformis</i>	20-1	33-1	-	17-1	7-1	-	25-1	-	9-1	-	-	-	-	-	-	-
<i>C. mitis</i>	100-4	67-1	38-1	17-1	73-3	88-2	85-1	50-1	9-1	-	30-1	13-1	-	-	-	-
<i>C. squamosa</i>	100-1	67-1	100-1	100-1	80-1	88-1	62-1	100-1	18-1	-	40-1	88-1	-	-	-	90-1
<i>C. stellaris</i>	100-4	100-3	88-2	100-2	20-1	50-2	62-2	100-1	-	-	10-1	-	-	-	-	-
<i>C. uncialis</i>	100-1	100-2	100-2	83-1	66-1	25-1	77-1	100-1	9-1	-	30-1	25-1	-	-	13-1	10-1
<i>Empetrum hermaphroditum</i>	40-1	100-2	100-3	100-3	93-2	100-4	100-5	100-5	82-1	88-2	100-3	75-1	-	33-1	60-1	70-1
<i>Vaccinium vitis-idaea</i>	100-1	67-1	63-1	100-2	100-2	100-3	77-2	100-2	73-1	88-1	40-1	38-1	33-1	33-1	27-1	-
<i>Cetraria delisei</i>	-	-	13-1	17-1	-	-	8-1	63-1	-	-	-	25-3	-	-	-	-
<i>C. ericetorum</i>	40-1	100-2	100-2	100-3	-	13-1	85-1	100-3	-	-	10-1	63-2	-	-	-	-
<i>C. islandica</i>	100-1	100-2	88-1	100-2	86-2	88-3	100-4	100-4	73-1	63-1	100-2	100-4	-	17-1	67-1	100-1
<i>Cladonia crispata</i>	40-1	-	13-1	-	33-1	15-1	-	-	9-1	25-1	10-1	13-1	-	-	-	-
<i>C. gracilis</i>	20-1	33-1	63-1	83-1	60-1	50-1	69-1	88-1	36-1	-	30-1	88-1	-	8-1	7-1	30-1
<i>C. metacoralifera</i>	-	-	38-1	83-1	-	13-1	15-1	88-1	-	-	25-1	-	-	-	-	-
<i>C. rangiferina</i>	100-3	100-2	88-1	83-1	100-2	100-2	85-1	75-1	55-1	38-1	70-1	25-1	-	8-1	13-1	-
<i>Sphagnum nemoreum</i>	-	-	-	-	33-1	25-1	-	-	18-2	13-3	30-1	-	-	-	7-1	10-3
<i>Barbilophozia hatcheri</i>	-	-	-	-	14-1	50-2	8-1	50-1	-	25-2	-	38-1	-	8-1	13-1	10-1
<i>Ptilidium ciliare</i>	-	-	25-1	-	73-1	75-2	77-1	88-1	64-1	75-1	30-1	38-1	25-1	25-1	13-1	-
<i>Betula pubescens</i>	20-1	33-1	13-1	-	80-1	100-4	-	-	91-2	100-4	-	-	75-3	100-4	7-1	-
<i>Picea abies</i>	-	-	-	-	73-2	25-2	15-1	-	91-4	50-1	-	-	92-4	25-2	-	-
<i>Phyllocladus caerulea</i>	-	-	-	-	-	-	-	25-2	-	38-1	50-1	-	-	-	40-1	-
<i>Vaccinium myrtillus</i>	-	-	-	-	100-3	88-2	92-2	88-2	100-5	100-5	100-5	100-2	100-2	92-4	100-2	90-2
<i>Melampyrum pratense</i>	-	-	-	-	60-1	50-1	-	-	73-1	100-1	-	-	42-1	67-2	20-1	-
<i>Rubus chamaemorus</i>	-	-	-	-	-	13-1	15-1	13-1	18-2	25-2	50-1	13-1	8-1	33-1	20-1	30-1
<i>Deschampsia flexuosa</i>	-	100-1	-	17-1	93-2	100-2	85-1	100-2	100-3	100-4	100-3	100-3	100-3	100-5	93-4	100-4
<i>Hylocomium splendens</i>	-	-	-	-	14-2	25-1	15-2	-	82-1	63-2	20-2	-	67-2	75-2	7-1	-
<i>Plagiothecium piliferum</i>	-	-	-	-	-	50-1	8-1	13-1	-	25-1	30-1	-	8-1	25-1	20-1	-
<i>Pleurozium schreberi</i>	20-1	-	-	-	86-3	88-2	46-3	25-2	100-2	100-3	50-3	-	58-1	67-2	13-1	-
<i>Barbilophozia barbata</i>	-	-	-	-	-	50-1	8-1	-	9-1	13-1	-	-	42-1	17-1	-	-
<i>B. floerkei</i>	-	-	17-1	-	86-3	50-1	77-1	100-1	31-4	75-4	80-3	100-2	67-1	82-2	93-3	100-3
<i>B. lycopodioides</i>	-	-	-	-	73-2	63-2	38-1	25-1	100-4	100-3	70-3	25-1	92-3	100-3	87-1	40-1
<i>Lophozia obtusa</i>	-	-	-	-	-	25-1	-	-	9-1	38-1	-	-	50-1	50-1	20-1	-
<i>Cladonia carneola</i>	80-1	-	13-1	-	93-1	63-1	85-1	13-1	82-1	75-1	80-1	13-1	50-1	67-1	47-1	20-1
<i>C. cornuta</i>	-	-	-	-	27-1	13-1	-	-	9-1	13-1	-	-	17-1	8-1	-	-
<i>C. ecmocyna</i>	-	-	-	-	7-1	25-1	8-2	13-1	-	25-1	30-2	13-1	-	-	13-1	70-2
<i>C. fimbriata</i>	-	-	13-1	-	47-1	63-1	23-1	-	18-1	63-1	40-1	-	42-1	33-1	47-1	10-1
<i>C. furcata</i>	20-1	67-1	-	-	67-1	63-1	54-1	38-1	82-1	38-1	80-1	50-1	25-1	8-1	40-1	50-1
<i>Ptilium crista-castrensis</i>	-	-	-	-	7-1	-	-	-	27-1	13-2	-	-	-	-	-	-
<i>Sorbus aucuparia</i>	-	-	-	-	7-1	25-1	-	-	91-1	100-1	30-1	-	92-2	100-3	20-1	-
<i>Lycopodium alpinum</i>	-	-	-	-	-	-	-	-	-	-	10-1	50-2	-	20-1	40-2	-
<i>L. annotinum</i>	-	-	-	-	-	-	-	-	18-1	25-1	-	-	58-1	58-1	7-1	-
<i>Blechnum spicant</i>	-	-	-	-	-	-	-	-	27-1	-	-	-	92-3	8-1	7-1	-
<i>Cornus suecica</i>	-	-	-	-	-	-	8-1	-	55-2	88-3	70-3	-	17-1	83-2	47-2	-
<i>Hieracium alpinum</i>	-	-	-	-	-	-	-	-	-	-	10-1	13-1	-	13-1	10-1	-
<i>Linnaea borealis</i>	-	-	-	-	-	-	-	-	18-1	-	-	-	33-1	-	-	-
<i>Maianthemum bifolium</i>	-	-	-	-	7-1	25-1	-	-	45-1	50-1	10-2	-	92-1	67-1	40-1	-
<i>Solidago virgaurea</i>	-	-	-	-	-	13-1	-	-	18-1	50-1	50-1	25-1	92-2	100-1	80-1	70-1
<i>Trientalis europaea</i>	-	-	-	-	7-1	38-1	-	-	45-1	88-1	80-1	25-1	100-1	92-1	93-1	60-1
<i>Carex brunneocens</i>	-	-	-	17-1	-	-	-	-	-	20-1	63-1	-	-	73-1	100-2	-
<i>Brachythecium reflexum</i>	-	-	-	-	-	-	-	-	18-1	25-1	-	-	83-1	17-1	20-1	-
<i>B. starkei</i>	-	-	-	-	-	38-1	-	-	18-1	75-3	40-1	-	75-2	75-3	73-2	20-1
<i>Dicranum majus</i>	-	-	-	-	-	-	8-1	-	82-1	13-1	10-1	-	83-1	17-2	-	20-1
<i>Plagiothecium curv.+dent.+laet.</i>	-	-	-	-	20-1	38-1	23-1	-	82-1	88-1	80-1	13-1	100-1	92-1	73-1	30-1
<i>Polytrichum formosum</i>	-	-	13-1	-	-	13-1	8-1	-	27-1	38-1	40-1	-	92-1	67-1	60-1	-
<i>Rhytidadelphus loreus</i>	-	-	-	-	-	-	-	-	18-2	-	-	-	42-1	42-2	7-1	-
<i>Sphagnum girgensohnii</i>	-	-	-	-	-	-	-	-	9-5	-	-	-	50-3	33-3	13-4	-
<i>S. rusowii</i>	-	-	-	-	-	-	-	-	18-1	25-1	30-2	-	25-1	42-4	7-3	20-1
<i>Calypogeia integristipula</i>	-	-	-	-	-	13-1	-	-	45-1	25-1	40-1	-	58-1	17-1	-	10-1
<i>C. neesiana</i>	-	-	-	-	14-1	-	-	-	27-1	13-1	40-1	-	-	17-1	7-1	10-1
<i>Lophocolea heterophylla</i>	-	-	-	-	-	-	-	-	-	38-1	-	-	42-1	33-1	27-1	-
<i>Stereocaulon sp.</i>	-	-	-	-	-	-	-	-	-	-	-	25-1	-	-	-	30-1

Tab. 6 (continued)

	X				SX				SM				M			
	MB	UB	LA	MA	MB	UB	LA	MA	MB	UB	LA	MA	MB	UB	LA	MA
<i>Alnus incana</i>	-	-	-	-	-	-	-	-	-	-	-	-	17-3	-	-	-
<i>Salix glauca</i>	-	-	-	-	-	-	-	-	-	-	-	-	8-1	13-2	-	-
<i>S. lapponum</i>	-	-	-	-	-	-	-	-	-	-	-	-	8-1	27-4	-	-
<i>Alchemilla alpina</i>	-	-	-	-	-	-	-	-	-	-	-	-	8-1	-	53-2	30-4
<i>Anemone nemorosa</i>	-	-	-	-	-	-	-	-	-	-	-	-	58-1	-	-	-
<i>Athyrium distentifolium</i>	-	-	-	-	-	-	-	-	-	-	-	-	67-3	50-2	80-4	30-4
<i>A. filix-femina</i>	-	-	-	-	-	-	-	-	-	-	-	-	67-4	8-1	-	-
<i>Campanula rotundifolia</i>	-	-	-	-	-	-	-	-	-	-	-	-	8-1	-	7-1	-
<i>Chamaenerion angustifolium</i>	-	-	-	-	-	-	-	-	-	-	-	-	33-1	-	27-1	-
<i>Crepis paludosa</i>	-	-	-	-	-	-	-	-	-	-	-	-	25-1	-	-	-
<i>Cryptogramma crispata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20-1	50-1
<i>Dryopteris aemilialis</i>	-	-	-	-	-	-	-	-	18-1	-	20-1	-	75-2	75-3	13-1	-
<i>D. filix-mas</i>	-	-	-	-	-	-	-	-	-	-	-	-	8-2	8-1	-	-
<i>Epilobium hornemannii</i>	-	-	-	-	-	-	-	-	-	-	-	-	25-1	-	13-1	-
<i>Gentiana purpurea</i>	-	-	-	-	-	-	8-4	-	-	13-1	20-1	-	42-1	83-2	100-2	50-2
<i>Geranium sylvaticum</i>	-	-	-	-	-	-	-	-	-	-	-	-	42-2	-	13-1	-
<i>Gnaphalium supinum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20-1	20-1
<i>Gymnocarpium dryopteris</i>	-	-	-	-	-	-	-	-	-	13-1	-	-	100-2	92-2	47-1	-
<i>Hieracium sylvaticum</i>	-	-	-	-	-	-	-	-	-	-	-	-	17-1	8-1	20-1	-
<i>Lactuca alpina</i>	-	-	-	-	-	-	-	-	-	-	-	-	33-1	-	-	-
<i>Listera cordata</i>	-	-	-	-	-	-	-	-	-	13-1	-	-	42-1	25-1	-	-
<i>Melampyrum sylvaticum</i>	-	-	-	-	-	-	-	-	-	13-1	-	-	25-1	67-1	27-1	-
<i>Melandrium rubrum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	33-1	53-1	10-1
<i>Oxalis acetosella</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20-2	-
<i>Potentilla erecta</i>	-	-	-	-	-	-	-	-	-	-	-	-	92-1	-	-	-
<i>Pilidium aquilinum</i>	-	-	-	-	-	-	-	-	-	-	-	-	75-1	42-1	33-2	-
<i>Ranunculus acris</i>	-	-	-	-	-	-	-	-	-	-	-	-	17-2	-	-	-
<i>R. platanifolius</i>	-	-	-	-	-	-	-	-	-	-	-	-	17-1	-	7-1	-
<i>Rubus saxatilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	42-1	-	-	-
<i>Rumex acetosa</i>	-	-	-	-	-	-	-	-	-	-	-	-	42-1	50-1	93-2	30-2
<i>Thelypteris phegopteris</i>	-	-	-	-	-	-	-	-	-	-	-	-	83-2	-	20-1	-
<i>Viola palustris</i>	-	-	-	-	-	-	-	-	-	-	-	-	8-1	-	7-1	20-1
<i>Anthoxanthum odoratum</i>	-	-	-	-	-	-	-	-	-	13-1	10-1	-	25-1	25-1	80-2	60-2
<i>Calamagrostis purpurea</i>	-	-	-	-	-	-	-	-	-	-	-	-	25-1	-	-	-
<i>Equisetum pratense</i>	-	-	-	-	-	-	-	-	-	-	-	-	25-2	-	-	-
<i>E. sylvaticum</i>	-	-	-	-	-	-	-	-	-	-	-	-	50-3	-	-	-
<i>Luzula pilosa</i>	-	-	-	-	-	-	-	-	-	13-1	-	-	83-1	58-1	20-1	-
<i>Millium effusum</i>	-	-	-	-	-	-	-	-	-	-	-	-	42-1	17-2	27-1	-
<i>Nardus stricta</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	17-1	47-3	70-4
<i>Bryum pseudotriquetrum</i>	-	-	-	-	14-2	-	-	13-1	18-1	25-1	40-1	-	-	-	-	-
<i>B. weigelii</i>	-	-	-	-	-	-	-	-	-	-	-	-	25-1	-	-	-
<i>Drepanocladus uncinatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	33-1	33-1	47-1	10-1
<i>Herzogiella striatella</i>	-	-	-	-	-	-	-	-	-	-	-	-	33-1	-	-	-
<i>Kiaeria starkii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	13-1	-	-
<i>Mnium hornum</i>	-	-	-	-	-	-	-	-	-	-	-	-	25-1	-	27-4	50-1
<i>Oligotrichum hercynicum</i>	-	-	-	-	-	-	-	-	-	-	-	-	8-1	-	33-1	10-1
<i>Plagiommium affine</i>	-	-	-	-	-	-	-	-	-	-	-	-	25-2	-	-	-
<i>Plagiothecium cavifolium</i>	-	-	-	-	-	-	-	-	-	-	-	-	25-1	42-1	33-1	10-2
<i>Polytrichum sexangulare</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20-2	20-1
<i>Pseudobryum cinclidioides</i>	-	-	-	-	-	-	-	-	-	-	-	-	25-2	-	-	-
<i>Rhizomnium pseudopunctatum</i>	-	-	-	-	-	-	-	-	-	-	-	-	33-1	25-1	7-2	-
<i>R. punctatum</i>	-	-	-	-	-	-	-	-	-	-	-	-	50-2	-	-	-
<i>Rhodobryum roseum</i>	-	-	-	-	-	-	-	-	-	-	-	-	42-1	-	-	-
<i>Rhynchodermis subpinnatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	33-2	-	-	-
<i>R. triquetrum</i>	-	-	-	-	-	-	-	-	-	-	-	-	17-1	-	-	-
<i>Anethia juratzkana</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7-1	10-1
<i>Blepharotoma trichophyllum</i>	-	-	-	-	-	-	-	-	-	-	-	-	25-1	-	7-1	-
<i>Calypogeia fissae</i>	-	-	-	-	-	-	-	-	-	-	-	-	17-1	42-1	-	-
<i>C. muelleriana</i>	-	-	-	-	-	-	8-1	-	-	13-1	10-1	-	92-1	33-1	-	-
<i>Chiloscyphus pallescens</i>	-	-	-	-	-	-	-	-	-	-	-	-	25-1	-	-	-
<i>Diplophyllum taxifolium</i>	-	-	-	-	-	-	-	-	9-1	-	-	13-1	58-1	8-1	-	-
<i>Harpanthus flotovianus</i>	-	-	-	-	-	-	-	-	-	-	-	-	17-1	17-1	13-1	-
<i>Moerchia blythii</i>	-	-	-	-	-	-	-	-	-	-	-	-	8-1	-	33-1	30-1
<i>Pellia neesiana</i>	-	-	-	-	-	-	-	-	-	-	-	-	42-1	-	7-1	-
<i>Plagiochila asplenoides</i>	-	-	-	-	-	-	-	-	-	-	-	-	25-1	-	-	-
<i>Pleurocladia albescens</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7-2	10-1
<i>Forella platyphylla</i>	-	-	-	-	-	-	-	-	-	-	-	-	17-1	-	-	-
<i>Tritomaria quinqueidentata</i>	-	-	-	-	-	-	-	-	9-1	-	-	-	17-2	-	-	-
<i>Lycopodium selago</i>	-	-	25-1	33-1	-	-	15-1	50-1	-	-	-	38-1	8-1	-	13-1	10-1
<i>Salix herbacea</i>	-	-	13-1	33-1	-	-	-	13-1	-	-	-	10-2	13-1	-	-	40-4
<i>Vaccinium uliginosum</i>	-	67-2	100-1	17-1	93-3	100-3	77-3	-	55-2	100-3	90-3	-	-	75-2	60-3	10-1
<i>Carex bigelowii</i>	-	-	38-2	17-1	-	25-1	38-1	-	-	-	30-1	13-1	-	-	50-3	-
<i>Juncus trifidus</i>	-	-	100-1	100-2	100-1	-	25-1	46-1	100-1	-	-	10-1	100-5	-	-	7-1
<i>Dicranum fuscens</i>	-	-	25-1	-	53-1	13-1	38-1	38-1	9-1	13-1	60-1	25-1	25-1	17-1	27-1	-
<i>D. scoparium</i>	100-1	33-1	38-1	67-1	100-3	100-2	100-2	100-2	100-3	100-2	100-3	100-2	75-1	100-1	80-2	100-1
<i>Pohlia drummondii+nutans</i>	100-1	100-1	63-1	83-1	20-1	75-1	54-1	88-1	9-1	25-1	100-1	88-1	17-1	33-1	93-1	100-1
<i>Lophozia ventricosa</i>	-	33-1	50-1	33-1	40-1	38-1	54-1	63-1	73-1	88-1	80-1	63-1	92-1	92-1	93-1	90-1
<i>Cladonia bellidiflora</i>	100-2	67-1	38-1	67-1	86-1	63-1	69-1	88-1	82-1	25-1	60-1	100-1	33-1	33-1	33-1	90-1
<i>C. coccifera</i>	100-1	100-1	88-1	100-1	-	25-1	54-1	100-1	-	-	30-1	63-1	50-1	33-1	13-1	40-1
<i>C. pleurota</i>	100-1	100-1	50-1	67-1	33-1	63-1	62-1	88-1	45-1	25-1	70-1	88-1	33-1	33-1	20-1	20-1
<i>C. pyxidata coll.</i>	80-1	100-1	63-1	33-1	93-1	100-1	100-1	88-1	73-1	63-1	80-1	88-1	33-1	75-1	80-1	70-1
<i>C. sulphurina</i>	100-1	100-1	50-1	50-1	40-1	50-1	54-1	100-1	45-1	38-1	30-1	63-1	42-1	42-1	-	10-1

Tab. 7. Distribution of species along the vertical gradient. Constancy and characteristic degree of cover for each species in each of the site-types are given.

Zone	MB				UB				LA				MA			
	X	SX	SM	M	X	SX	SM	M	X	SX	SM	M	X	SX	SM	M
<i>Alnus incana</i>	-	-	-	17-3	-	-	-	-	-	-	-	-	-	-	-	-
<i>Picea abies</i>	-	73-2	91-4	92-4	-	25-2	50-1	25-2	-	15-+	-	-	-	-	-	-
<i>Pinus sylvestris</i>	100-4	53-3	-	-	-	25-1	-	-	-	-	-	-	-	-	-	-
<i>Anemone nemorosa</i>	-	-	-	58-1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Athyrium filix-femina</i>	-	-	-	67-4	-	-	-	8-1	-	-	-	-	-	-	-	-
<i>Blechnum spicant</i>	-	-	27-1	92-3	-	-	-	8-1	-	-	-	7-1	-	-	-	-
<i>Lactuca alpina</i>	-	-	-	33-1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Linnaea borealis</i>	-	-	18-1	33-1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Oxalis acetosella</i>	-	-	-	92-1	-	-	-	-	-	-	-	20-1	-	-	-	-
<i>Ptilidium aquilinum</i>	-	-	-	17-2	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rubus saxatilis</i>	-	-	-	42-1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Thelypteris phegopteris</i>	-	-	-	83-2	-	-	-	-	-	-	-	20-1	-	-	-	-
<i>Equisetum pratense</i>	-	-	-	25-2	-	-	-	-	-	-	-	-	-	-	-	-
<i>E. sylvaticum</i>	-	-	-	50-3	-	-	-	-	-	-	-	-	-	-	-	-
<i>Dicranum majus</i>	-	-	82-1	83-1	-	-	13-1	17-2	-	8-1	10-1	-	-	-	-	20-1
<i>D. spurium</i>	20-1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Herzogiella striatella</i>	-	-	-	33-1	-	-	-	-	-	-	10-1	-	-	-	-	-
<i>Mnium hornum</i>	-	-	-	25-1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Plagiommium affine</i>	-	-	-	25-2	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pseudobryum cinclidioides</i>	-	-	-	25-2	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rhizomnium punctatum</i>	-	-	-	50-2	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rhodopryum roseum</i>	-	-	-	42-1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rhytidiadelphus subpinnatus</i>	-	-	-	33-2	-	-	-	-	-	-	-	-	-	-	-	-
<i>R. triquetrus</i>	-	-	-	17-1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lophozia bicrenata</i>	20-1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Plagiochila asplenoides</i>	-	-	-	25-1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Porella platyphylla</i>	-	-	-	17-1	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cladonia phyllophora</i>	40-1	-	9-1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Betula pubescens</i>	20-1	80-1	91-2	75-3	33-1	100-4	100-4	100-4	13-+	-	-	7-1	-	-	-	-
<i>Sorbus aucuparia</i>	-	7-1	91-1	92-2	-	25-1	100-1	100-3	-	-	30-1	20-1	-	-	-	-
<i>Lycopodium annotinum</i>	-	-	18-1	58-1	-	-	25-1	58-1	-	-	7-1	-	-	-	-	-
<i>Dryopteris assiniensis</i>	-	-	18-1	75-2	-	-	-	75-3	-	-	20-1	13-1	-	-	-	-
<i>Listera cordata</i>	-	-	-	42-1	-	-	13-1	25-1	-	-	-	-	-	-	-	-
<i>Maianthemum bifolium</i>	-	7-1	45-1	92-1	-	25-1	50-1	67-1	-	-	10-2	40-1	-	-	-	-
<i>Melampyrum pratense</i>	-	60-1	73-1	42-1	-	50-1	100-1	67-2	-	-	-	20-1	-	-	-	-
<i>Luzula pilosa</i>	-	-	-	83-1	-	-	13-1	58-1	-	-	-	20-1	-	-	-	-
<i>Dicranum polysetum</i>	40-1	14-1	-	-	-	25-1	-	-	-	-	-	-	-	-	-	-
<i>Rhizomnium pseudopunctatum</i>	-	-	-	33-1	-	-	-	25-1	-	-	-	7-2	-	-	-	-
<i>Rhytidiadelphus loreus</i>	-	-	18-2	42-1	-	-	-	42-2	-	-	-	7-1	-	-	-	-
<i>Barbilophozia barbata</i>	-	-	9-1	42-1	-	50-1	13-1	17-1	-	8-1	-	-	-	-	-	-
<i>Calypogeia fissia</i>	-	-	-	17-1	-	-	-	42-1	-	-	-	-	-	-	-	-
<i>C. muelleriana</i>	-	-	-	92-1	-	-	13-1	33-1	-	8-1	10-1	-	-	-	-	-
<i>Lophozia obtusa</i>	-	-	9-1	50-1	-	25-1	38-1	50-1	-	-	-	20-1	-	-	-	-
<i>Cladonia cornuta</i>	-	27-1	9-1	17-1	-	13-1	13-1	8-1	-	-	-	-	-	-	-	-
<i>Betula nana</i>	-	27-3	-	-	-	13-1	-	-	-	38-1	15-2	20-3	13-1	-	-	-
<i>Calluna vulgaris</i>	100-3	93-4	27-1	-	67-3	100-4	25-1	-	-	38-1	77-3	20-1	13-1	-	13-+	-
<i>Vaccinium uliginosum</i>	-	93-3	55-2	-	67-2	100-3	100-3	75-2	-	100-1	77-3	90-3	60-3	17-1	-	10-1
<i>Cornus suecica</i>	-	-	55-2	17-1	-	-	88-3	83-2	-	-	8-1	70-3	47-2	-	-	-
<i>Gymnocarpium dryopteris</i>	-	-	-	100-2	-	-	13-1	92-2	-	-	-	47-1	-	-	-	-
<i>Hieracium sylvaticum</i>	-	-	-	17-1	-	-	-	8-1	-	-	-	20-1	-	-	-	-
<i>Melampyrum sylvaticum</i>	-	-	-	25-1	-	-	13-1	67-1	-	-	-	27-1	-	-	-	-
<i>Potentilla erecta</i>	-	-	-	75-1	-	-	-	42-1	-	-	-	33-2	-	-	-	-
<i>Milium effusum</i>	-	-	-	42-1	-	-	-	17-2	-	-	-	27-1	-	-	-	-
<i>Brachythecium reflexum</i>	-	-	18-1	83-1	-	-	25-1	17-1	-	-	-	20-1	-	-	-	-
<i>B. starkei</i>	-	-	18-1	75-2	-	38-1	75-3	75-3	-	-	40-1	73-2	-	-	-	20-1
<i>Drepanocladus uncinatus</i>	-	-	-	33-1	-	-	-	33-1	-	-	-	47-1	-	-	-	10-1
<i>Hylacomium splendens</i>	-	14-2	82-1	67-2	-	25-1	63-2	75-2	-	15-2	20-2	7-1	-	-	-	-
<i>Plagiothecium cavifolium</i>	-	-	-	25-1	-	-	-	42-1	-	-	-	33-1	-	-	-	10-2
<i>P. curvident. laet.</i>	-	20-1	82-1	100-1	-	-	38-1	88-1	92-1	-	23-1	80-1	73-1	-	13-1	30-1
<i>Pleurozium schreberi</i>	20-1	86-3	100-2	58-1	-	88-2	100-3	67-2	-	46-3	50-3	13-1	-	25-2	-	-
<i>Polytrichum formosum</i>	-	-	27-1	92-1	-	13-1	38-1	67-1	13-1	8-1	40-1	60-1	-	-	-	-
<i>Barbilophozia lycopodioides</i>	-	73-2	100-4	92-3	-	63-2	100-3	100-3	-	38-1	70-3	87-1	-	25-1	25-1	40-1
<i>Calypogeia integristipula</i>	-	-	45-1	58-1	-	13-1	25-1	17-1	-	-	40-1	-	-	-	-	10-1
<i>C. neesiana</i>	-	14-1	27-1	-	-	-	13-1	17-1	-	-	40-1	7-1	-	-	-	10-1
<i>Lophocolea heterophylla</i>	-	-	-	42-1	-	-	38-1	33-1	-	-	-	27-1	-	-	-	-
<i>Cladonia carneola</i>	80-1	93-1	82-1	50-1	-	63-1	75-1	67-1	13-1	85-1	80-1	47-1	-	13-1	13-1	20-1
<i>C. fimbriata</i>	-	47-1	18-1	42-1	-	63-1	63-1	33-1	13-1	23-1	40-1	47-1	-	-	-	10-1
<i>Arctostaphylos alpina</i>	-	-	-	-	100-1	75-1	-	-	75-1	46-2	-	-	-	-	-	-
<i>Salix glauca</i>	-	-	-	-	-	-	-	8-1	-	-	-	13-2	-	-	-	-
<i>S. lapponum</i>	-	-	-	-	-	-	-	8-1	-	-	-	27-4	-	-	-	-
<i>Melandrium rubrum</i>	-	-	-	-	-	-	-	33-1	-	-	-	53-1	-	-	-	10-1
<i>Plagiothecium piliferum</i>	-	-	-	8-1	-	50-1	25-1	25-1	-	8-1	30-1	20-1	-	13-1	-	-
<i>Cornicularia aculeata</i>	-	-	-	-	67-1	-	-	-	13-1	-	-	-	-	-	-	-
<i>Sphaerophorus fragilis</i>	-	-	-	-	33-1	-	-	-	25-1	-	-	-	-	-	-	-
<i>Loiseleuria procumbens</i>	-	-	-	-	67-2	13-1	-	-	100-3	69-2	-	-	50-1	50-2	-	-
<i>Phyllocladus caeruleus</i>	-	-	-	-	-	-	38-1	-	-	-	50-1	40-1	-	38-1	-	-
<i>Juncus trifidus</i>	-	-	-	-	100-1	25-1	-	-	100-2	46-1	10-1	7-1	100-1	100-5	90-3	-
<i>Barbilophozia hatcheri</i>	-	14-1	-	-	-	50-2	25-2	8-1	-	8-1	-	13-1	-	50-1	38-1	10-1
<i>Alectoria nigricans</i>	-	-	-	-	33-1	-	-	-	63-1	-	-	-	-	67-1	-	-
<i>A. ochroleuca</i>	-	-	-	-	100-3	13-1	-	-	100-4	-	-	-	100-4	-	-	-
<i>Cetraria cucullata</i>	-	-	-	-	67-2	-	-	-	88-2	13-1	-	-	100-2	-	-	-
<i>C. ericetorum</i>	40-1	-	-	-	100-2	13-1	-	-	100-2	85-1	10-1	-	100-3	100-3	63-2	-
<i>C. nivalis</i>	20-1	-	-	-	100-2	13-1	-	-	100-3	38-1	-	-	100-3	88-1	-	-
<i>Cladonia emecocyna</i>	-	7-1	-	-	-	25-1	25-1	-	-	8-2	30-2	13-1	-	13-1	13-1	70-2

Tab. 7 (continued)

	MB				UB				LA				MA			
	X	SX	SM	M	X	SX	SM	M	X	SX	SM	M	X	SX	SM	M
<i>Cladonia floerkeana</i>	-	-	-	-	33-1	-	-	-	50-1	-	-	-	33-1	-	-	-
<i>Cornicularia divergens</i>	-	-	-	-	33-1	-	-	-	100-2	-	-	-	83-1	-	-	-
<i>Lycopodium alpinum</i>	-	-	-	-	-	-	-	-	-	-	10-1	20-1	-	-	50-2	40-2
<i>L. selago</i>	-	-	-	8-1	-	-	-	-	25-1	15-1	-	-	33-1	50-1	38-1	10-1
<i>Salix herbacea</i>	-	-	-	-	-	-	-	-	13-1	-	10-2	40-4	33-1	13-1	13-1	10-2
<i>Alchemilla alpina</i>	-	-	-	8-1	-	-	-	-	-	-	-	53-2	-	-	-	30-4
<i>Cryptogramma crispa</i>	-	-	-	-	-	-	-	-	-	-	20-1	-	-	-	-	50-1
<i>Gnaphalium eupinum</i>	-	-	-	-	-	-	-	-	-	-	20-1	-	-	-	-	20-1
<i>Hieracium alpinum</i>	-	-	-	-	-	-	-	-	-	10-1	13-1	-	-	-	13-1	10-1
<i>Carex bigelowii</i>	-	-	-	-	25-1	-	-	-	38-2	38-1	30-1	40-1	17-1	-	13-1	50-3
<i>C. brunnescens</i>	-	-	-	-	-	-	-	-	-	20-1	73-1	17-1	-	-	63-1	100-2
<i>Nardus stricta</i>	-	14-2	18-1	-	-	-	25-1	17-1	-	-	40-2	47-3	-	13-1	-	70-4
<i>Conostomum tetragonum</i>	-	-	-	-	-	-	-	-	-	8-1	-	-	-	13-1	25-1	30-1
<i>Kiaeria starkiei</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13-1	50-1
<i>Polytrichum sexangulare</i>	-	-	-	-	-	-	-	-	-	-	-	20-2	-	-	-	20-1
<i>Antheilia juratzkana</i>	-	-	-	-	-	-	-	-	-	-	-	7-1	-	-	-	10-1
<i>Marsipella brevissima</i>	-	-	-	-	-	-	-	-	13-1	-	-	-	33-1	13-1	13-1	30-1
<i>Moerchia blyttii</i>	-	-	-	8-1	-	-	-	-	-	-	33-1	-	-	-	-	30-1
<i>Pleurocladia albescens</i>	-	-	-	-	-	-	-	-	-	-	-	7-2	-	-	-	10-1
<i>Cetraria delisei</i>	-	-	-	-	-	-	-	-	13-1	8-1	-	-	17-1	63-1	25-3	-
<i>Cladonia metacorallifera</i>	-	-	-	-	13-1	-	-	-	38-1	15-1	-	-	83-1	88-1	25-1	-
<i>Stereocaulon sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25-1	30-1
<i>Empetrum hermaphroditum</i>	40-1	93-2	82-1	-	100-2	100-4	88-2	33-1	100-3	100-5	100-3	60-1	100-3	100-5	75-1	70-1
<i>Vaccinium myrtillus</i>	-	100-3	100-5	100-2	-	88-2	100-5	92-4	-	92-2	100-5	100-2	-	88-2	100-2	90-2
<i>V. vitis-idaea</i>	100-1	100-2	73-1	33-1	67-1	100-3	40-1	33-1	63-1	77-2	40-1	33-1	100-2	100-2	38-1	-
<i>Athyrium distentifolium</i>	-	-	-	67-3	-	-	-	50-2	-	-	-	-	-	-	-	30-4
<i>Gentiana purpurea</i>	-	-	-	42-1	-	-	13-1	83-2	-	8-+	20-1	83-2	-	-	-	50-2
<i>Rubus chamaemorus</i>	-	-	19-2	8-1	-	13-1	25-2	33-1	-	15-1	50-1	20-1	-	13-1	13-1	30-1
<i>Rumex acetosa</i>	-	-	-	42-1	-	-	-	50-1	-	-	-	93-2	-	-	-	30-2
<i>Solidago virgaurea</i>	-	-	18-1	92-2	-	13-1	50-1	100-1	-	-	50-1	80-1	-	-	25-1	70-1
<i>Trientalis europaea</i>	-	7-1	45-1	100-1	-	38-1	88-1	92-1	-	-	80-1	93-1	-	-	25-1	60-1
<i>Anthoxanthum odoratum</i>	-	-	-	25-1	-	-	13-1	25-1	-	-	10-1	80-2	-	-	-	60-2
<i>Deschampsia flexuosa</i>	-	93-2	100-3	100-3	100-1	100-2	100-4	100-5	-	85-1	100-3	93-4	17-1	100-2	100-3	100-4
<i>Dicranum fuscescens</i>	-	53-1	9-1	25-1	-	13-1	13-1	17-1	25-1	38-1	60-1	27-1	-	38-1	25-1	-
<i>D. scoparium</i>	100-1	100-3	100-3	75-1	33-1	100-2	100-2	100-1	38-1	100-2	100-3	80-2	67-1	100-2	100-2	100-1
<i>Pohlia drummondii+nutans</i>	100-1	20-1	9-1	17-1	100-1	75-1	25-1	33-1	63-1	54-1	100-1	93-1	83-1	88-1	88-1	100-1
<i>Barbilophozia floerkei</i>	-	86-3	91-4	67-1	-	50-1	75-4	82-2	-	77-1	80-3	93-3	17-1	100-1	100-2	100-3
<i>Lophozia ventricosa</i>	-	40-1	73-1	92-1	33-1	38-1	88-1	92-1	50-1	54-1	80-1	93-1	33-1	63-1	63-1	90-1
<i>Ptilidium ciliare</i>	-	73-1	64-1	25-1	-	75-2	75-1	25-1	25-1	77-1	30-1	13-1	-	88-1	38-1	-
<i>Cetraria islandica</i>	100-1	86-2	73-1	-	100-2	88-3	63-1	17-1	88-1	100-4	100-2	67-1	100-2	100-4	100-4	100-1
<i>Cladonia arbuscula</i>	100-2	86-2	36-1	-	100-3	100-2	-	-	63-2	100-2	60-1	7-1	67-1	100-2	75-1	40-1
<i>C. bellidiflora</i>	100-2	86-1	82-1	33-1	67-1	63-1	25-1	33-1	38-1	69-1	60-1	33-1	67-1	88-1	100-1	30-1
<i>C. coccifera</i>	100-1	-	-	-	100-1	25-1	-	-	88-1	54-1	30-1	13-1	100-1	100-1	63-1	40-1
<i>C. deformis</i>	20-1	7-1	9-1	-	33-1	-	-	-	-	-	-	-	17-1	25-1	-	-
<i>C. furcata</i>	20-1	67-1	82-1	25-1	67-1	63-1	38-1	8-1	-	54-1	80-1	40-1	-	38-1	50-1	50-1
<i>C. gracilis</i>	20-1	60-1	36-1	-	33-1	50-1	-	8-1	63-1	69-1	30-1	40-1	83-1	88-1	88-1	30-1
<i>C. macrophylla</i>	60-1	-	-	-	33-1	-	-	-	50-1	-	-	-	33-1	13-1	-	-
<i>C. mitis</i>	100-4	73-3	9-1	-	67-1	88-2	-	-	38-1	85-1	30-1	-	17-1	50-1	13-1	-
<i>C. pleurota</i>	100-1	33-1	45-1	50-1	100-1	63-1	25-1	33-1	50-1	62-1	88-1	20-1	67-1	88-1	88-1	20-1
<i>C. pyxidata coll.</i>	80-1	93-1	73-1	33-1	100-1	100-1	63-1	75-1	63-1	100-1	90-1	60-1	33-1	88-1	88-1	70-1
<i>C. rangiferina</i>	100-3	100-2	55-1	-	100-2	100-2	38-1	8-1	88-1	85-1	70-1	13-1	83-1	75-1	25-1	-
<i>C. squamosa</i>	100-1	80-1	18-1	-	67-1	88-1	-	-	100-1	62-1	40-1	-	100-1	100-1	88-1	90-1
<i>C. stellaria</i>	100-4	20-1	-	-	100-3	50-2	-	-	88-2	62-2	10-1	-	100-2	100-1	-	-
<i>C. sulphurina</i>	100-1	40-1	45-1	50-1	100-1	50-1	38-1	8-1	50-1	54-1	30-1	-	50-1	100-1	63-1	10-1
<i>C. uncialis</i>	100-1	60-1	9-1	-	100-2	25-1	-	-	100-2	77-1	30-1	13-1	83-1	100-1	25-1	10-1

poor in species. Only the most drought-resistant dwarf shrubs are common, while *Vaccinium myrtillus* and *Deschampsia flexuosa* are absent.

Apart from some variations in the dominance relations of the *Cladonia* species, the floristic variation is small.

The type is extremely rare, only found in the most extremely wind-exposed and dry places. It has been developed at the top of some morainic crags west of lake Slåkvatnet (Fig. 9).

Comparison with other investigations is given in Tab. 10.

Upper boreal zone

The floristic composition of this site-type is given in Tab. 11. The constant species are: *Arctostaphylos alpina*, *Empetrum hermaphroditum*, *Deschampsia flexuosa*, *Juncus trifidus*, *Pohlia*

Tab. 8. Geographical situation of investigations used for comparing vegetation types in Tabs 10, 12, 14, ... , 38. Numbers in Fig. 8 are indicated as map nr. A number without dot is used for investigations comprising vast areas.

Map nr.	Reference	Geographic position
1	Kielland-Lund 1981	N/South-East Norway, with few exceptions the counties: Hedmark, Oppland, Akershus, Oslo, Buskerud, Østfold and Vestfold
2	Kielland-Lund 1962b	N/Akershus: Hurdal: Skrukkelia
3	Nordhagen 1928	N/Sør-Trøndelag: Tydal: Sylene
4	Christophersen 1925	N/Sør-Trøndelag: Tydal: Sylene
5	Nordhagen 1943	N/Oppland: Kvikne: Sikilsdalen
6	Nordhagen 1943	N/Buskerud: Hol: Ørterdalen + Haugastøl
7	Nordhagen 1943	N/Sogn og Fjordane: Flåm: Myrdal
8	Gjærevoll 1949	S/Jämtland: Oviksfjällen
9	Gjærevoll 1950	S/Lappland: Region of Torneträsk
10	Gjærevoll 1956	N,S/The Scandes between the Voss-Vik Mts. in the south and the Varanger Peninsula in the north. Most comprehensive investigations in Dovrefjell-Trollheimen (+ map nos 8, 9)
11	Dahl 1957	N/Oppland: Sel + Dovre/Hedmark: Folldal
12	Gjerlaug 1973	N/Oppland: Lillehammer + Fåberg + Mesna
13	Haug 1970	N/Oppland: Kvam: Furusjøen
14	Mork & Låg 1959	N/Hedmark: Søre Osen: Ulvsjøberget
15	Resvoll-Holmsen 1912	N/Oppland: Lom: Tesse
16	Resvoll-Holmsen 1918	N/Oppland, Hedmark, Sør-Trøndelag, mountain forest regions in central South Norway from Vang: Helin in SW to Tolga: Hummelfjell in NW.
17	Resvoll-Holmsen 1914b	N/Hedmark: Folldal: Folldalsfjellene
18	Resvoll-Holmsen 1920	N/Oppland, Hedmark, Sør-Trøndelag, alpine regions in central South Norway from Vang: Helin in SW to Røros: Vigelfjellene
19	Resvoll-Holmsen 1932	N/Oppland: Vang, Vestre Slidre + Buskerud: Hemsedal
20	Mork & Heiberg 1937	N/Oppland: Ringebu: Hirkjølen
21	Bendiksen & Schumacher 1982	N/Hedmark: Storelvdal + Oppland: Ringebu: Watercourses Imsa and Trya
22	DuRietz 1925a	N/Hedmark: Alvdal + Tydal: Tronfjell
23	Bendiksen 1980	N/Oppland: Lunner: S.Oppdalen
24	Aune 1978	N/Oppland: Sør-Aurdal + Buskerud: Nes, Flå: Vassfaret
25	Bendiksen & Salvesen 1985	N/Oslo + Akershus: Nittedal: Røverkollen
26	Samuelsson 1917b	N/Hordaland: Ulvik: Finse area
27	Hadac 1971	N/Buskerud: Flesberg: Blefjell (+Telemark?)
28	Halvorsen & Bendiksen 1985	N/Telemark: Bø + Seljord + Hjartdal + Sauland
29	Bjørndalen 1977, 1980b	N/Telemark: Skien + Porsgrunn + Bamble (Grenland)
30	Bergland 1975	N/Vest-Agder: Åseral
31	Odland 1978, 1981c	N/Hordaland: Røldal
32	Huseby & Odland 1981	N/Rogaland: Vikedal: Vikedal
33	Lye 1972	N/Hordaland: Eidfjord: Stigstuv
34	Omberg 1980	N/Hordaland: Ulvik
35	Nedkvitne & Tomter 1953	N/Hordaland: Voss: Kvitli
36	Odland 1979	N/Hordaland: Vinje + Voss: Vosso, upper part
37	Rodvelt & Sekse 1980	N/Hordland: Ullensvang + Sogn & Fjordane: Flåm

Tab. 8 (continued)

Map. nr.	Reference	Geographic position
38	Odland 1981a	N/Sogn og Fjordane: Undredal
39	Naustdal 1951	N/Hordaland: Bergen + Samnanger: Gullfjellet
40	Losvik 1978	N/Hordaland: Bergen, Birkeland: Helldal-Sandal
41	Fredriksen 1978	N/Hordaland: Eksingedal: Eksingedalen, upper part
42	Knaben 1952	N/Sogn og Fjordane: Vik + Arnafjord/Hordaland: Modalen + Eksingedal + Vinje
43	Fægri 1934	N/Sogn og Fjordane: Balestrand + Luster + Stryn: Jostedalsbreen
44	Kummen 1977	N/Sogn og Fjordane: Eikefjord: Ramsdalen
45	Kummen 1977	N/Sogn og Fjordane: Naustdal: Vonavatnet
46	Odland 1981b	N/Møre og Romsdal: Ørsta: Ørstadalen
47	Malme 1971	N/Møre og Romsdal: Hustad: Talstadhesten
48	Hagen 1976	N/Møre og Romsdal: Romfo: Grøvdalen
49	Moen 1978	N/Sør-Trøndelag: Rennebu: Nerskogen
50	Aune 1973	N/Sør-Trøndelag: Hemne: Holladalen
51	Klokk 1974	N/Sør-Trøndelag: Klæbu: Selbusjøen N
52	Kjelvik 1978	N/Nord-Trøndelag: Hegra + Markabygd: Øvre Forra
53	Samuelsson 1917a	S/Dalarna: Alpine parts, in the region of Idre, Särna, Transtrand, Lima, Älfadalen and Våmhus
54	Henning 1889	S/Jämtland
55	Smith 1920	S/Jämtland, SW part + Härjedalen NW part, Hälagsfjellet in the central part
56	Arnborg 1943	S/Västerbotten: Dorotea: Granberget
57	Arnborg 1940	S/Västerbotten: Dorotea: Vallsjö forest
58	Malmström 1949	S/Västerbotten
59	Tengwall 1920	S/Lappland: Lule Lappmark: Sarek
60	T. Fries 1913	S/Lappland: Torne Lappmark: the northernmost triangle of Sweden, incl. Torneträsk in the SW and Karesuando area in SE
61	Du Rietz 1942	S/Lappland: Torne Lappmark: Area of Torneträsk
62	Sonesson & Lundberg 1974	S/Lappland: Torne Lappmark: Area of Torneträsk
63	Lakari 1920	SF/Österbotten + Lappland
64	Resvoll-Holmsen 1914a	N/Troms: Målselv: Målselvdalen
65	Tannheiser 1975	N/Finnmark: Kautokeino: Masi area
66	Lippmaa 1929	SF/Lappland: Kilpisjärvi (main area with analyses) (several other localities in Finnish Lappland and Petsamo + Northern Norway incl. Seiland)
67	Hult 1887	SF/Lappland: Larger area in the region of Enare
68	Kalliola 1939	SF/Lappland + CCCP/Petsamo Lappland (earlier SF): Petsamo Lappland, several localities in vast area
69	Kalliola 1939	CCCP/Petsamo Lappland (earlier SF): Petsamontunturit: Kammikivi area
70	Söyrinki 1938	SF/Lappland: Raututunturit + Nattastunturit
71	Söyrinki 1938	CCCP/Petsamo Lappland (earlier SF): Petsamontunturit
72	Söyrinki 1938	CCCP/Petsamo Lappland (earlier SF): Fisher Peninsula (Prov. Rybatjij)
73	Kujala 1929	CCCP/Petsamo Lappland (earlier SF) + SF/Lappland, region of Enare
74	Kalela 1939	CCCP/Petsamo Lappland (earlier SF): Fisher Peninsula (Prov. Rybatjij)

Tab. 9. The vegetation of the middle boreal xeric site-type.

Transect No.	1					C- \bar{C}
	1	2	3	4	5	
Plot No.	1	2	3	4	5	C- \bar{C}
Altitude (m)	700	700	700	700	700	
Slope ($^{\circ}$)	15	10	15	10	10	
Aspect	S	WNW	WSW	SW	S	
TA	3	4	4	2	4	
TB	0	0	0	0	0	
TC	1	2	2	2	3	
TD	5	7	8	9	6	
TE	4	2	2	1	3	
TF	0	0	+	+	+	
A <i>Pinus sylvestris</i>	4	4	4	3	4	100-4
C <i>Pinus sylvestris</i>	1	+	1	1	1	100-1
<i>Calluna vulgaris</i>	1	3	3	3	4	100-3
<i>Empetrum hermaphroditum</i>	1	.	1	.	.	40-1
<i>Vaccinium vitis-idaea</i>	2	1	1	1	2	100-1
D <i>Dicranum polysetum</i>	.	1	.	.	1	40-1
<i>D. scoparium</i>	2	1	1	1	2	100-1
<i>Orthodicranum montanum</i>	.	.	.	1	1	40-1
<i>Pohlia drummondii+nutans</i>	1	1	1	1	1	100-1
<i>Cephaloziella</i> spp.	1	1	1	1	1	100-1
<i>Cetraria ericetorum</i>	1	.	1	.	.	40-1
<i>C. islandica</i>	2	1	2	1	1	100-1
<i>Cladonia arbuscula</i>	2	1	2	3	3	100-2
<i>C. bellidiflora</i>	1	1	1	1	3	100-2
<i>C. carneola</i>	1	1	1	1	.	80-1
<i>C. coccifera</i>	1	1	1	1	2	100-1
<i>C. crispata</i>	.	1	1	.	.	40-1
<i>C. digitata</i>	1	1	.	.	.	40-1
<i>C. macrophylla</i>	.	.	1	1	1	60-1
<i>C. mitis</i>	1	2	4	5	1	100-4
<i>C. phyllophora</i>	.	.	1	1	.	40-1
<i>C. pleurota</i>	1	1	1	1	1	100-1
<i>C. pyxidata</i> coll.	.	1	1	1	1	80-1
<i>C. rangiferina</i>	3	2	2	2	4	100-3
<i>C. squamosa</i>	1	1	1	1	2	100-1
<i>C. stellaris</i>	4	5	4	2	2	100-4
<i>C. sulphurina</i>	1	1	1	1	1	100-1
<i>C. uncialis</i>	1	1	1	1	1	100-1
Vascular plants	4	3	4	3	4	4
Bryophytes	3	5	4	4	6	4
Lichens	15	16	17	17	13	16
Total number of species	22	24	25	24	23	24

Additional species occurring in 1 sample plot (Plot No.:cover):

C: *Betula pubescens* (5:1).D: *Dicranum spurium* (2:1), *Pleurozium schreberi* (5:1); *Lophozia bicrenata* (3:1); *Cetraria nivalis* (1:1), *Cladonia deformis* (4:1), *C. furcata* (2:1), *C. gracilis* (4:1).

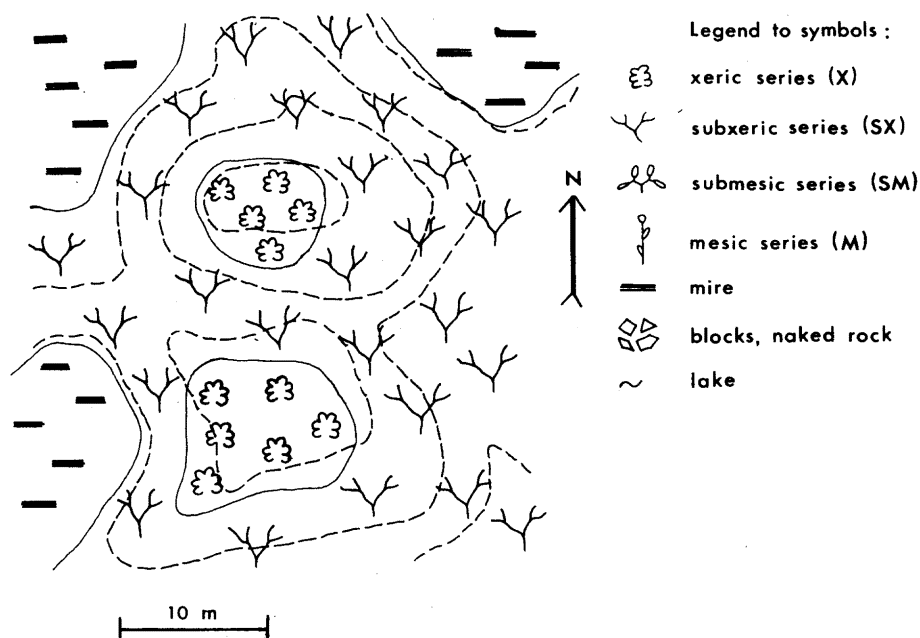


Fig. 9. Sketch map of the vegetation of two morainic crags west of Lake Slåkavatnet. The segment mapped is situated in the middle boreal zone in position UTM MM 884 011, altitude 700 m. Contour lines are hatched, contour interval ca. 2 m.

drummondii+nutans, *Alectoria ochroleuca*, *Cetraria ericetorum*, *C. islandica*, *C. nivalis*, *Cladonia arbuscula*, *C. coccifera*, *C. pleurota*, *C. pyxidata* coll., *C. rangiferina*, *C. stellaris*, *C. sulphurina*, and *C. uncialis*.

The sample plots are devoid of tree layer, but they are situated adjacent to small birch stands. *Calluna vulgaris* and *Empetrum hermaphroditum* dominate different plots. Chionophobous lichens and *Cladonia* species, particularly *Cladonia arbuscula* and *C. stellaris*, are recorded as dominants. Bryophytes are of less importance, but *Racomitrium lanuginosum* locally dominates small patches on shallow, gravelly soil.

The mean number of species is 32, while the total number in the 3 sample plots is 48.

The site-type is characterized by a dense carpet of lichens, and lichen species make up more than half the total number of species. *Cladonia* species as well as the "wind lichens" *Alectoria ochroleuca*, *Cetraria cucullata*, and *C. nivalis* are important. The field layer is characterized by dwarf shrubs, including the alpine species *Arctostaphylos*

Tab. 10. Types described by other authors corresponding to the middle boreal xeric site-type. D - important difference from Grunningsdalen.

Reference	Name of vegetation types	Comments
Kielland-Lund 1967: 135, 1971: 21, 1973: 181, 1981, (1962a: 137), Dahl et al. 1967: 512	Cladonio-Pinetum boreale p.p.	The moister part incl. <i>Vaccinium myrtillus</i> , <i>Pleurozium schreberi</i> etc. as constants corresponds to SX in Grunningsdalen
Gjerlaug 1973: 70	Lichen pine forest p.p.	<i>Vaccinium myrtillus</i> and <i>Pleurozium schreberi</i> are constants; the type includes part of SX
Resvoll-Holmsen 1918: 186	Lichen-rich pine forests, lower parts	
Bendiksen & Schumacher 1982: 36	Xeric series (lichen pine forest)	D: <i>Dicranum drummondii</i> constant
Aune 1978: 20	Cladonio-Pinetum	
Bendiksen & Salvesen 1985	Xeric series (lichen pine forest)	D: Rich in <i>Juniperus</i> and <i>Populus</i> . <i>Carex brunnescens</i> and <i>C. pilulifera</i> characteristic for the type in the Oslo area
Huseby & Odland 1981: 13	Lichen rich pine forest	
Omberg 1980: 94	Cladonia pine forest (<i>Racomitrio lanuginosi</i> -Pinetum prov. ass.) p.p.	Constants indicating that the drier part of SX is included
Odland 1979: 42	<i>Calluna</i> - <i>Cladonia stellaris</i> -dominated pine forest	
Klokk 1974: 71	<i>Cladonia</i> community, <i>Cladonia</i> var.	
Malmstrøm 1949: 50	Sociations of lichen-rich forests	Lichen forest of <i>Calluna</i> type most similar; nearly all constants in common.
Arnborg 1942: 185	Lavristyp	
Arnborg 1945	Skarp ristyp	
Eneroth 1931: 130, 1937: 835	Primär lavhed	
Ronge 1936a: 158	Lavtyp	
O. Tamm 1935: 290	Extrem tallhedtyp	
Kalela 1961	Cladina-Typ (ClT)	ClT of <i>Peräpohjola</i> closest floristically corresponding type
Nihlgård 1980: 27	Pine forest of lichen type	

alpina and *Loiseleuria procumbens*.

Plot No. 3 deviates in having greater cover of the wind lichens, particularly *Alectoria ochroleuca*, than the other plots, and by having the locally rare *Arctostaphylos uva-ursi* as an important species.

This site-type covers extremely small areas at highly convex and extremely dry and wind-exposed places (Fig. 10). The exposure to drought is illustrated by the lack of a tree layer and the large areas covered by dead *Calluna vulgaris* in 1980, the latter probably due to the dry summers of 1975 and 1976. The extreme conditions are also shown by the occurrence of

Tab. 11. The vegetation of the upper boreal xeric site-type.

Transect No.	1	2		
Plot No.	1	2	3	C-C
Altitude (m)	960	900	960	
Slope (°)	20	25	20	
Aspect	NE	SSE	S	
TA	0	0	0	
TB	0	0	0	
TC	2	1	3	
TD	6	4	7	
TE	1	2	+	
TF	2	3	1	
C <i>Betula pubescens</i>	.	1	.	33-1
<i>Arctostaphylos alpina</i>	2	1	1	100-1
<i>A. uva-ursi</i>	.	.	2	33-2
<i>Calluna vulgaris</i>	.	3	3	67-3
<i>Empetrum hermaphroditum</i>	3	1	2	100-2
<i>Juniperus communis</i>	.	1	.	33-1
<i>Loiseleuria procumbens</i>	2	.	1	67-2
<i>Vaccinium uliginosum</i>	2	.	1	67-2
<i>V. vitis-idaea</i>	1	.	1	67-1
<i>Deschampsia flexuosa</i>	1	1	1	100-1
<i>Juncus trifidus</i>	1	1	1	100-1
D <i>Dicranum scoparium</i>	1	.	.	33-1
<i>Leucobryum glaucum</i>	.	1	.	33-1
<i>Orthodicranum montanum</i>	1	1	.	67-1
<i>Pohlia drummondii-nutans</i>	1	1	1	100-1
<i>Polytrichum juniperinum</i>	1	.	1	67-1
<i>P. piliferum</i>	.	1	1	67-1
<i>Racomitrium lanuginosum</i>	2	1	.	67-2
<i>Cephalozia</i> spp.	1	.	.	33-1
<i>Lophozia ventricosa</i>	1	.	.	33-1
<i>Sphenolobus minutus</i>	1	.	.	33-1
<i>Alectoria nigricans</i>	.	.	1	33-1
<i>A. ochroleuca</i>	1	1	4	100-3
<i>Cetraria cucullata</i>	1	.	3	67-2
<i>C. ericetorum</i>	2	1	2	100-2
<i>C. islandica</i>	3	1	1	100-2
<i>C. nivalis</i>	2	2	3	100-2
<i>Cladonia arbuscula</i>	4	3	2	100-3
<i>C. bellidiflora</i>	1	1	.	67-1
<i>C. coccifera</i>	2	1	1	100-1
<i>C. deformis</i>	.	.	1	33-1
<i>C. floerkeana</i>	.	.	1	33-1
<i>C. furcata</i>	.	1	1	67-1
<i>C. gracilis</i>	1	.	.	33-1
<i>C. macrophylla</i>	.	.	1	33-1
<i>C. mitis</i>	.	1	1	67-1
<i>C. pleurota</i>	1	1	1	100-1
<i>C. pyxidata</i> coll.	1	1	1	100-1
<i>C. rangiferina</i>	3	1	1	100-2
<i>C. squamosa</i>	1	1	.	67-1
<i>C. stellaris</i>	3	1	3	100-3
<i>C. sulphurina</i>	1	1	1	100-1
<i>C. uncialis</i>	1	3	1	100-2
<i>Coriscium viride</i>	.	1	.	33-1
<i>Cornicularia aculeata</i>	.	1	1	67-1
<i>C. divergens</i>	1	.	.	33-1
<i>Pseudephebe minuscula</i>	.	.	1	33-1
<i>Sphaerophorus fragilis</i>	.	.	1	33-1
Vascular plants	7	7	9	8
Bryophytes	8	5	3	5
Lichens	17	18	22	19
Total number of species	32	30	34	32

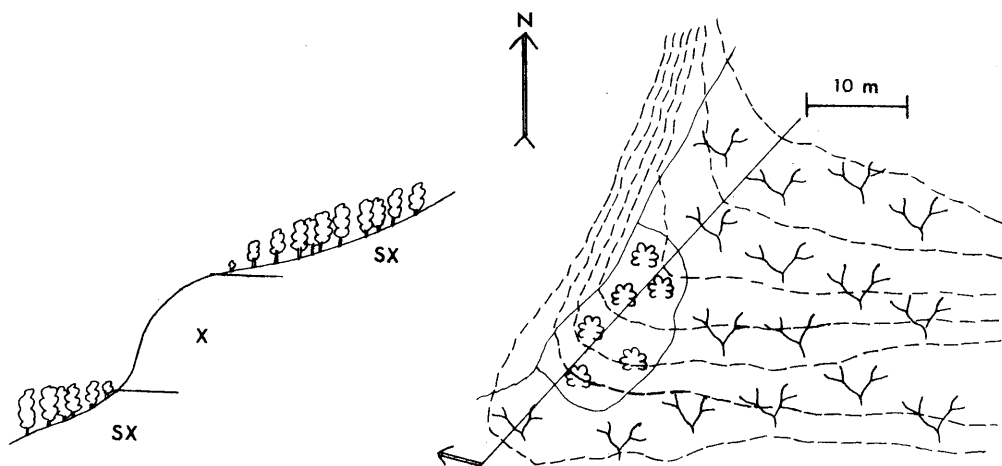


Fig. 10. Sketch map of the vegetation along the south-west edge of the southern slope of Blåtjørnfjell in the upper boreal zone, position UTM MM 888 024, altitude 900 m. Xeric vegetation has only been developed on the projecting, most severely exposed segment of the edge. Contour interval ca. 2 m. Key to symbols in Fig. 9. Side view of the site with indications of birch growth is shown to the left.

degenerate pines, birches, and small *Juniperus* shrubs. Species demanding more stable conditions generally grow in the lee of stones.

Comparison with other investigations is given in Tab. 12.

Low alpine zone

The floristic composition of this site-type is shown in Tab. 13. The constant species are: *Empetrum hermaphroditum*, *Loiseleuria procumbens*, *Vaccinium uliginosum*, *Juncus trifidus*, *Polytrichum piliferum*, *Alectoria ochroleuca*, *Cetraria cucullata*, *C. ericetorum*, *C. islandica*, *C. nivalis*, *Cladonia coccifera*, *C. rangiferina*, *C. squamosa*, *C. stellaris*, *C. uncialis*, and *Cornicularia divergens*.

The field layer is dominated by *Empetrum hermaphroditum* and *Loiseleuria procumbens*, while *Alectoria ochroleuca*, *Cetraria nivalis*, and sometimes *Cladonia stellaris* dominate in the bottom layer.

The mean number of species is 31, while the total number in 8 sample plots is 63.

The site-type is characterized by a yellow, dense mat of wind lichens, and *Cladonia* spp. are sometimes co-dominants. Bryophytes are of minor importance. The field layer is characterized by drought tolerant dwarf shrubs, sometimes

Tab. 12. Types described by other authors corresponding to the upper boreal xeric site-type. D - important difference from Grunningsdalen.

Reference	Name of vegetation types	Comments
Nordhagen 1928: 102	Empetrum-reicher Flechtenbirkenwald p.p.	D: Calluna and Alectoria ochroleuca rare. Constancy of Vaccinium myrtillus and Pleurozium indicates inclusion of drier SX.
Christophersen 1925: 509	Betula forest with bottom layer rich in lichens	
Nordhagen 1943: 114, (1937)	Lichen-dominated birch forests in Loiseleurieto-Arctostaphylica	
Haug 1970: 31	Cladonio-Pinetum boreale p.p.	Several constants indicate inclusion of drier SX. D: Stereocaulon paschale common in this as well as in several other corresponding types, absent in Grunningsdalen.
Kjelland-Lund 1981: 127	Cladonio-Pinetum boreale p.p.	
Resvoll-Holmsen 1912: 17	Pine forests	Including many eutrophic spp.
Resvoll-Holmsen 1918: 186	"Lavrik furuskogsbund", lichen rich birch forests	
Mork & Heiberg 1937: 644	Lichen pine forest, Calluna-Cladonia-Pinus soc. p.p.	Incl. part of MB.
Samuelsson 1917a: 40	Flechtenreiche Kiefernwälder	
Tengwall 1920: 376	Flechtenreiche Diapensia-Loiseleuria-Heide	Alpine type also occurring in strongly wind-exposed sites in UB.
T. Fries 1913: 54	Heideartiger Flechtenbirkenwald	
Kalela 1961: 77, 81	Cladina-Typ (CLT) (Wald-Lappland), subalpiner Empetrum-Lichenes-Typ (sELiT) (Fjeld-Lappland)	
Hämet-Ahti 1963: 37	Subalpiner Empetrum-Lichenes type (sELiT)	
Lakari 1920: 5	Flächtenwälder (CLT)	
Thannheiser 1975: 53	Empetrum-Heide-Birkenwälder: Flechtenreicher Krähenbeer-Birkenwald p.p.	D: Influenced by reindeer grazing
Kujala 1929: 72, 38	Vaccinium-Empetrum-Cladonia-Typ (VECLoT). Vaccinium-Cladonia-Typ (VCLoT)	Birch forest Pine forest

accompanied by graminids.

The variation among sample plots is mainly restricted to the composition and relative importance of lichen species. However, plot No. 4 differs somewhat by having *Juncus trifidus* and *Cetraria cucullata* as the most important species.

The site-type does not occupy large areas in the Grunningsdalen area, but is common on the driest and most wind exposed localities with an unstable snow cover in winter. Most often it is situated at the top of crags, but it has also been observed on the edges of cliffs. Somewhat larger areas with xeric vegetation occur along a few long ridges. In the most

Tab. 13. The vegetation of the low alpine xeric site-type.

Transect No.	1				2				3				4				C-E
Plot No.	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	
Altitude (m)	1160	1080	1080	1230	1110	1010	1040	1080									
Slope (°)	15	10	20	10	15	15	10	5									
Aspect	NNE	SSE	S	WNW	NW	WNW	W	NNE									
TA	0	0	0	0	0	0	0	0									
TB	0	0	0	0	0	0	0	0									
TC	2	2	3	3	3	2	2	4									
TD	7	7	8	7	5	6	5	7									
TE	1	1	+	+	0	0	+	0									
TF	2	2	1	2	4	4	4	2									
C <i>Arctostaphylos alpina</i>	2	1	2	.	1	1	.	1	75-1								
<i>Betula nana</i>	.	.	+	.	1	.	.	1	38-1								
<i>Calluna vulgaris</i>	.	.	1	.	.	1	1	.	38-1								
<i>Empetrum hermaphroditum</i>	3	2	2	2	3	2	2	3	100-3								
<i>Loiseleuria procumbens</i>	3	3	4	1	1	2	2	4	100-3								
<i>Lycopodium selago</i>	1	.	1	.	25-1								
<i>Vaccinium uliginosum</i>	1	1	1	1	2	2	2	1	100-1								
<i>V. vitis-idaea</i>	2	1	1	.	1	.	.	1	63-1								
<i>Carex bigelowii</i>	.	.	.	3	2	1	.	.	38-2								
<i>Juncus trifidus</i>	1	1	1	4	1	1	2	1	100-2								
D <i>Cynodontium tenellum</i>	1	.	1	25-1								
<i>Dicranum fuscens</i>	.	.	.	2	1	.	.	.	25-1								
<i>D. scoparium</i>	1	.	.	.	1	.	.	1	38-1								
<i>Orthodicranum montanum</i>	1	.	.	.	1	.	1	.	38-1								
<i>Pohlia drummondii-nutans</i>	1	.	.	.	1	1	1	1	63-1								
<i>Polytrichum commune</i>	.	.	1	.	1	1	.	.	38-1								
<i>P. piliferum</i>	1	1	1	2	1	1	1	1	100-1								
<i>Racomitrium lanuginosum</i>	1	1	1	1	50-1								
<i>Lophozia ventricosa</i>	1	.	.	.	1	.	1	1	50-1								
<i>Ptilidium ciliare</i>	.	.	.	1	.	1	.	.	25-1								
<i>Sphenolobus minutus</i>	1	1	1	1	50-1								
<i>Alectoria nigricans</i>	1	.	.	1	1	1	.	1	63-1								
<i>A. ochroleuca</i>	3	5	5	1	4	4	3	4	100-4								
<i>Cetraria cucullata</i>	2	1	3	5	.	2	1	2	88-3								
<i>C. ericetorum</i>	1	2	2	2	2	2	2	2	100-2								
<i>C. islandica</i>	2	1	1	1	1	2	1	.	88-1								
<i>C. nivalis</i>	4	3	3	1	3	3	4	3	100-3								
<i>Cladonia arbuscula</i>	2	.	1	.	1	2	2	.	63-2								
<i>C. bellidiflora</i>	.	.	.	1	1	.	1	.	38-1								
<i>C. coccifera</i>	1	1	1	.	1	1	2	2	88-1								
<i>C. floerkeana</i>	1	1	1	1	50-1								
<i>C. gracilis</i>	1	.	.	2	1	1	1	1	75-1								
<i>C. macrophylla</i>	1	.	.	.	1	.	1	1	50-1								
<i>C. metacorrallifera</i>	1	.	.	.	1	.	1	.	38-1								
<i>C. mitis</i>	.	1	1	.	.	1	.	.	38-1								
<i>C. pleurota</i>	.	.	.	1	1	1	1	.	50-1								
<i>C. pyxidata coll.</i>	1	1	1	1	1	.	.	.	63-1								
<i>C. rangiferina</i>	2	1	1	.	1	2	2	1	88-1								
<i>C. squamosa</i>	1	1	1	1	1	1	1	1	100-1								
<i>C. stellaris</i>	3	1	1	.	2	4	2	1	88-2								
<i>C. sulphurina</i>	1	.	.	.	1	1	1	.	50-1								
<i>C. uncialis</i>	1	1	1	3	1	2	2	2	100-2								
<i>Cornicularia divergens</i>	1	2	2	2	2	1	2	1	100-2								
<i>Sphaerophorus fragilis</i>	.	.	1	.	.	1	.	.	25-1								
Vascular plants	7	6	8	5	10	8	6	7	8								
Bryophytes	7	1	1	4	11	8	9	9	6								
Lichens	18	14	17	14	20	20	20	15	17								
Total number of species	32	21	26	23	41	36	35	31	31								

Additional species occurring in 1 sample plot (Plot No.:cover):

C: *Betula pubescens* (5:1); *Salix herbacea* (1:1); *Eriophorum vaginatum* (6:1).
D: *Dicranella heteromalla* (6:1); *Polytrichum formosum* (5:1); *P. juniperinum* (7:1); *Tetraplodon mnioides* (8:1); *Cephalozia* spp. (7:1); *Chandonanthus setiformis* (7:1); *Gymnocolea inflata* (5:1); *Gymnomitrium concinnum* (1:1); *Lophozia sudetica* (8:1); *Marsupella brevissima* (1:1); *Cetraria delisei* (7:1); *Cladonia carneola* (2:1); *C. crispata* (6:1); *C. macrophyllodes* (3:1); *Cornicularia aculeata* (4:1); *Sphaerophorus globosus* (3:1).

exposed localities there is often a mosaic of vegetation and naked rock and the vegetation is restricted to those small patches attaining sufficient shelter. The site-type most often forms small, isolated stands in the subxeric series. A zone with scattered *Calluna vulgaris*, often with low vitality, indicates a transition towards the subxeric series. The transition is mostly gradual.

Comparison with other investigations is given in Tab. 14.

Middle alpine zone

The floristic composition of this site-type is given in Tab. 15. The constant species are: *Empetrum hermaphroditum*, *Vaccinium vitis-idaea*, *Juncus trifidus*, *Pohlia drummondii* + *nutans*, *Polytrichum piliferum*, *Alectoria ochroleuca*, *Cetraria cucullata*, *C. ericetorum*, *C. islandica*, *C. nivalis*, *Cladonia coccifera*, *C. gracilis*, *C. metacorallifera*, *C. rangiferina*, *C. squamosa*, *C. stellaris*, *C. uncialis*, and *Cornicularia divergens*.

The field layer is dominated by *Empetrum hermaphroditum*, and the bottom layer by *Alectoria ochroleuca*, *Cetraria ericetorum*, and *C. nivalis*, less often by *C. islandica*.

The mean number of species is 26, while the total number in the 6 sample plots is 44.

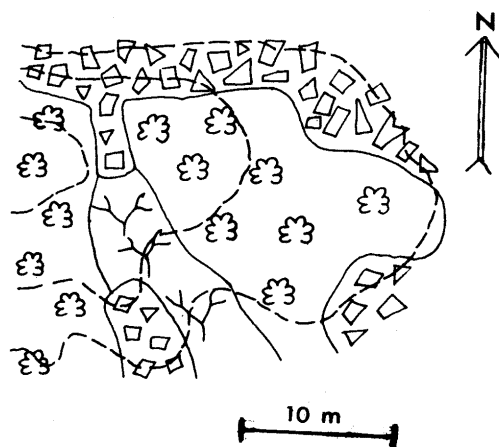


Fig. 11. Sketch map of the vegetation just below the summit of Mælefjell in the middle alpine zone, position UTM MM 840 028, altitude 1400 m. The strong exposure of the summit causes a mosaic of bare rock, xeric and subxeric vegetation. Contour interval ca. 1 m. Key to symbols in Fig. 9.

Tab. 14. Types described by other authors corresponding to the low alpine xeric site-type. D - important difference from Grunningsdalen.

Reference	Name of vegetation types	Comments
Nordhagen 1943:59	Loiseleurieto-Arctostaphylion p.p especially Loiseleuria-Empetrum-Alectoria ochroleuca-soc. (Loiseleuria-Vaccinium uliginosum-Alectoria ochroleuca-soc. (Sikilsdalen), Empetrum-Cetraria nivalis-Soc. (Tronfjell, Ørterdalen, Finnish Lapland))	Many sociations are ecological parallels, most different are continental types dominated by Arctostaphylos uva-ursi and Betula nana
Nordhagen 1928: 203, 198, 202	Cetraria nivalis-Alectoria ochroleuca-reiche Loiseleuria-Ass., Betula nana-reiche Cladonia silvatica-Cetraria nivalis-Ass., Empetrum-reiche Cladonia alpestris-Ass.	The second type is ecologically parallel, the third type transitional to SX.
Nordhagen 1937: 64	Loiseleurieto-Vaccinium p.p., incl. Loiseleuria-Alectoria ochroleuca-Cetraria nivalis-soc. and Vaccinium uliginosum-Alectoria ochroleuca-Cetraria-soc.	
Nordhagen 1954a: 84	Loiseleurieto-Diapsietum P.P.	
Dahl 1957: 88	Arctostaphyleto-Cetrarion nivalis p.p., best corresp.: Cetrarion nivalis typicum	D: Betula nana important
Resvoll-Holmsen 1912: 17, 1914b: 36, 1920:187, 1932: 32	Lichen heaths	Chionophobous lichens abundant
Bendiksen & Schumacher 1982: 49	Xeric series ("vindlavhei")	D: Festuca ovina, high cover of Betula nana
Du Rietz 1925a	Numerous associations dominated by Alectoria ochroleuca and/or Cetraria nivalis	Floristical and/or ecological parallels
Lye 1972: 104	Oligotrophic lichen heaths	
Knaben 1952: 68, 70	Loiseleurieto-Arctostaphylion: Empetrum-Cladonia rangiferina-soc.	
Odland 1979: 65	"Rabbesamfunn" (exposed heath-vegetation)	
Huseby & Odland 1981: 20	"Rabbesamfunn" (exposed heath-vegetation)	More mesic spp. indicate affinity also to SX
Malme 1971: 21	Loiseleurieto-Diapsietum loiseleuriosum	More mesic spp. indicate affinity also to SX
Poore & McVean 1957: 425, 37	Lichen heaths	
McVean & Ratcliffe 1962: 37		
Samuelsson 1917a: 161	Cetraria nivalis-Heiden (Empetrum-, Loiseleuria-, and Arctostaphylos alpina-dominated types)	

Tab. 14 (continued)

Reference	Name of vegetation types	Comments
Smith 1920: 34	Diapensia-Loiseleuria heath	
Tengwall 1920: 375	Diapensia-Loiseleuria heath	
T. Fries 1913: 66	Flechtenreiche Empetrum-Ass.,	
Du Rietz 1942	Empetrium	
Gjærevoll & Bringer 1965: 258	Empetrium	
Thannheiser 1975: 35, 40	Gemsheide-Diapensie-Gesellschaft, Cetraria nivalis-Krähenbeer-Gesellschaft	
Lippmaa 1929: 43	Die Formation der Zwergstrauchheide: Diapensia-Loiseleuria-Ass., Empetrum-Diapensia-Heide	
Hult 1887: 176, 179	Alectoria- and Cladonia-formations	Wider circumscription than xeric.
Kalliola 1939: 175, 185	Flechtenreiche Loiseleuria-Empetrum-Soz., Empetrum-Cetraria nivalis-Soz.	b) applies to plot Nos 1 and 7
Kalliola 1932: 29, 31	Cetraria nivalis-Heide	
Sjöyryinki 1938: 26, 28	Cetraria nivalis-Alectoria-Heide	
Kalela 1939: 67, 68	Halboffene Empetrum nigrum-Tundra, Cetraria nivalis-reichen Empetrum nigrum-Tundra	
Dahl et al. 1971: 10	Arctostaphyleto-Cetrarion nivalis, xerophilous parts	
Waldemarson Jensen 1980: 53	Empetrum-heath	The first of several subtypes shows closest affinity

This site-type is characterized by dominance of wind lichens. The only other lichen species having any importance, is *Cladonia stellaris*. Bryophytes are of minor importance. Dwarf shrubs and scattered individuals of *Juncus trifidus* characterize the field layer.

There is only minor floristic variation between the sample plots.

Ecologically this site-type does not deviate from the corresponding type in the low alpine zone (Figs 11, 12). Plot No. 1 was situated on a flat-topped ridge where the site-type covered some hundred square metres. This is the largest stand of alpine xeric vegetation observed in the Grunningsdalen area.

Comparison with other investigations is given in Tab. 16.

Survey of the xeric series

Physiognomically, the xeric series is homogeneous throughout the vertical zones. The field layer mainly consists of dwarf shrubs, but normally with considerably lower cover than in the other series. Graminids may be present, mostly in the higher

Tab. 15. The vegetation of the middle alpine xeric site-type.

Transect NO.	1			3			
Plot No.	1	2	3	4	5	6	C- \bar{c}
Altitude (m)	1300	1400	1400	1260	1280	1300	
Slope ($^{\circ}$)	10	10	5	15	5	10	
Aspect	ESE	ESE	E	NE	NW	NE	
TA	0	0	0	0	0	0	
TB	0	0	0	0	0	0	
TC	3	2	1	3	2	3	
TD	7	6	5	5	9	5	
TE	1	1	1	0	0	+	
TF	1	3	4	4	1	4	
C <i>Empetrum hermaphroditum</i>	3	3	2	3	3	3	100-3
<i>Loiseleuria procumbens</i>	2	.	.	1	.	1	50-1
<i>Lycopodium selago</i>	.	1	1	.	.	.	33-1
<i>Salix herbacea</i>	.	1	1	.	.	.	33-1
<i>Vaccinium vitis-idaea</i>	2	2	2	1	2	1	100-2
<i>Juncus trifidus</i>	1	1	2	1	1	2	100-1
D <i>Dicranum scoparium</i>	.	.	1	1	1	1	67-1
<i>Pohlia drummondii+nutans</i>	1	1	1	1	.	1	83-1
<i>Polytrichum commune</i>	.	1	.	.	1	.	33-1
<i>P. piliferum</i>	1	2	1	1	1	.	83-1
<i>Gymnocolea inflata</i>	.	.	1	.	.	1	33-1
<i>Lophozia ventricosa</i>	.	1	1	.	.	.	33-1
<i>Marsupella brevissima</i>	1	1	33-1
<i>Alectoria nigricans</i>	1	1	.	1	.	1	67-1
<i>A. ochroleuca</i>	4	3	4	3	5	4	100-4
<i>Cetraria cucullata</i>	1	2	2	1	3	1	100-2
<i>C. ericetorum</i>	1	4	2	2	4	3	100-3
<i>C. islandica</i>	2	1	3	3	1	1	100-2
<i>C. nivalis</i>	3	4	2	3	4	2	100-3
<i>Cladonia arbuscula</i>	.	1	.	2	1	1	67-1
<i>C. bellidiflora</i>	.	.	1	1	1	1	67-1
<i>C. coccifera</i>	1	1	1	1	1	1	100-1
<i>C. floerkeana</i>	1	1	33-1
<i>C. gracilis</i>	1	1	1	.	1	1	83-1
<i>C. macrophylla</i>	1	.	1	.	.	.	33-1
<i>C. metacorallifera</i>	1	1	1	1	.	1	83-1
<i>C. pleurota</i>	1	.	1	1	.	1	67-1
<i>C. pyxidata coll.</i>	.	.	1	.	1	.	33-1
<i>C. rangiferina</i>	2	1	1	1	1	1	100-1
<i>C. squamosa</i>	1	1	1	1	1	1	100-1
<i>C. stellaris</i>	2	2	2	1	3	1	100-2
<i>C. sulphurina</i>	.	.	1	1	1	.	50-1
<i>C. uncialis</i>	1	1	.	1	2	1	83-1
<i>Cornicularia divergens</i>	1	1	.	1	1	1	83-1
Vascular plants	4	6	5	5	4	5	5
Bryophytes	3	7	5	3	3	3	4
Lichens	17	15	18	18	18	18	17
Total number of species	24	28	28	26	25	26	26

Additional species occurring in 1 sample plot (Plot No.:cover):

C: *Vaccinium uliginosum* (5:1); *Carex bigelowii* (6:1), *C. brunnescens* (2:1), *Deschampsia flexuosa* (4:1).D: *Barbilophozia floerkei* (2:1); *Cetraria delisei* (3:1), *C. pinastri* (4:1), *Cladonia deformis* (5:1), *C. mitis* (5:1), *Solorina crocea* (3:1).

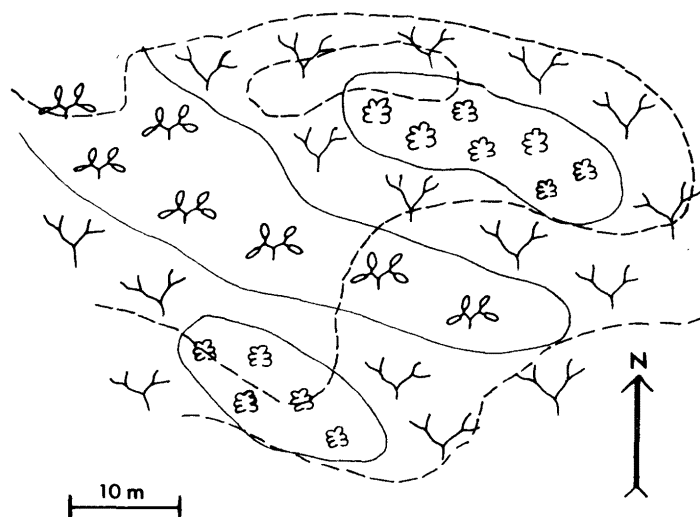


Fig. 12. Sketch map of the vegetation of a ridge in the middle alpine zone of Mælefjell, position UTM 854 020, altitude 1300 m. The xeric, subxeric, and submesic series alternate according to topographic positions. Contour interval ca. 1 m. Key to symbols in Fig. 9.

zones, but herbs do not occur. The bottom layer is characterized by lichens; all site-types have on average more lichen species per sample plot than vascular plants and bryophytes taken together. Bryophytes are of minor importance in all zones. The dominance relations in both of the two lowermost layers change considerably throughout the zones.

The following species are limited to the middle boreal zone (see Tab. 7): *Pinus sylvestris*, *Dicranum polysetum*, *D. spurium*, *Pleurozium schreberi*, *Lophozia bicrenata*, and *Cladonia phyllophora*. The greatest shift in species composition appears to be found between the middle and upper boreal zones because of the many alpine species entering the latter. The following species occur in more zones from the upper boreal and upwards: *Arctostaphylos alpina*, *Loiseleuria procumbens*, *Vaccinium uliginosum*, *Juncus trifidus*, *Racomitrium lanuginosum*, *Sphenolobus minutus*, *Alectoria nigricans*, *A. ochroleuca*, *Cetraria cucullata*, *Cornicularia aculeata*, *C. divergens*, and *Sphaerophorus fragilis*. *Empetrum hermaphroditum* increases markedly from the middle boreal to the low alpine zone. The chionophobous lichens *Alectoria ochroleuca*, *Cetraria cucullata*, and *C. nivalis* may attain a high cover already in the upper boreal zone.

Between the upper boreal and low alpine zones there is only minor variation in species composition. The most important differences are found in dominance relations; the frequency of

Tab. 16. Types described by other authors corresponding to the middle alpine xeric site-type. D - important difference from Grunningsdalen. Note: Most authors have treated wind-exposed vegetation types in the alpine zones collectively. The vegetation types corresponding to the low alpine xeric site-type are therefore, in many cases, meant to be relevant in the middle alpine zone, too.

Reference	Name of vegetation types	Comments
Nordhagen 1937, 1943	Juncion trifidi scandinavicum, Loiseleurieto-Arctostaphylion p.p.	Most of MA is included in the first type, Sociations rich in Cetraria nivalis have a slight floristic affinity. Most of the alliance is ecologically rather than floristically corresponding. When floristic correspondence is emphasized, Loiseleurieto-Arctostaphylion corresponds to this site-type.
Dahl 1957: 99	Cetrarietum nivalis trifidetosum	D: Empetrum absent, Alectoria ochroleuca sparse
Resvoll-Holmsen 1920: 213, 1932: 31	Grass-rich lichen heaths	Ecologically parallel
Samuelsson 1917b: 18	Juncus trifidus-reiche/Carex rigida reiche Flechtenheiden (p.p.)	
Tengwall 1920: 375	Flechtenreiche Diapensia-Loiseleuria-Heide	
Waldemarson Jensen 1980: 53	Empetrum heath (incl. "vindblottetyp")	

Empetrum hermaphroditum and *Loiseleuria procumbens* increases, while *Calluna vulgaris* loses its importance. The chionophobous lichens become dominants of the bottom layer, and the *Cladina* spp. gradually decrease in amount as also mentioned by Resvoll-Holmsen (1914b: 38). In the middle alpine zone the number of species in the sample plots decreases; *Arctostaphylos alpina* and *Calluna vulgaris* are among the species that disappear. In other respects there are only minor differences from the low alpine zone.

Dry soil, exposure to strong winds, and unstable snow cover in winter are ecological factors stressed by most authors who have treated vegetation corresponding to our alpine xeric site-types. The overburden may be shallow and formed autochthonously as in most of Grunningsdalen, or it may consist of thick sand and gravel with low water capacity.

SUBXERIC SERIES

Middle boreal zone

The floristic composition of this site-type is given in Tab. 17. The constant species are: *Calluna vulgaris*, *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *V. uliginosum*, *V. vitis-idaea*, *Deschampsia flexuosa*, *Dicranum scoparium*, *Pleurozium*

Tab. 17. The vegetation of the middle boreal subxeric site-type.

Transect No.	1			2			3					4					
Plot No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	C-Σ	
Altitude (m)	700	700	710	710	770	810	690	690	690	690	720	710	710	720	760		
Slope (°)	15	20	25	15	25	10	15	10	15	5	10	20	15	10	15		
Aspect	NNE	NNE	S	SSE	S	SE	ENE	NW	N	NNW	SSW	WNW	WNW	W	N		
TA	1	+	5	2	1	1	0	2	3	+	+	+	4	1	3		
TB	+	0	0	0	0	0	+	0	+	1	0	+	1	0	0		
TC	7	6	4	6	5	4	5	4	6	2	4	4	4	5	6		
TD	8	10	1	2	3	6	7	8	8	6	8	9	8	9	6		
TE	+	0	6	3	2	4	2	2	1	4	1	+	1	+	1		
TF	0	0	+	0	+	2	0	0	0	0	1	0	+	0	+		
A <i>Betula pubescens</i>	2	2	1	1	1	.	33-1	
<i>Picea abies</i>	2	1	.	.	1	1	.	3	1	1	1	.	2	3	.	67-2	
<i>Pinus sylvestris</i>	.	.	5	3	3	1	.	.	4	.	4	40-4	
B <i>Betula pubescens</i>	1	1	.	1	2	.	1	2	.	.	40-1	
C <i>Betula pubescens</i>	2	1	.	.	1	.	.	1	1	1	1	47-1	
<i>Betula nana</i>	4	2	1	1	27-3	
<i>Calluna vulgaris</i>	4	3	4	2	4	3	4	2	2	3	.	4	4	2	4	93-4	
<i>Empetrum hermaphroditum</i>	2	3	1	1	1	1	1	1	3	.	2	2	3	2	4	93-2	
<i>Vaccinium myrtillus</i>	2	2	1	3	3	3	1	3	2	1	1	2	3	4	2	100-3	
<i>V. uliginosum</i>	3	3	1	4	2	.	2	2	2	1	4	3	2	3	3	93-3	
<i>V. vitis-idaea</i>	1	2	2	1	2	2	1	1	1	1	2	2	2	2	2	100-2	
<i>Melampyrum pratense</i>	.	.	.	2	.	1	1	1	1	.	1	1	1	1	.	60-1	
<i>Deschampsia flexuosa</i>	2	2	2	3	1	2	3	4	2	1	1	3	2	2	.	93-2	
D <i>Dicranum fuscescens</i>	.	.	1	1	1	2	.	.	.	1	1	.	1	.	1	53-1	
<i>D. scoparium</i>	2	2	1	3	1	1	2	2	4	2	2	3	3	3	2	100-3	
<i>Pleurozium schreberi</i>	2	5	.	2	2	1	2	2	1	.	2	3	2	2	3	86-3	
<i>Sphagnum nemoreum</i>	2	1	1	.	.	.	1	.	2	33-1	
<i>Barbilophozia floerkei</i>	3	4	.	1	.	2	3	2	3	1	1	2	3	4	1	86-3	
<i>B. lycopodioides</i>	2	1	.	1	.	1	3	2	1	.	1	1	1	2	.	73-2	
<i>Lophozia ventricosa</i>	1	1	1	.	1	.	1	1	.	.	.	40-1	
<i>Ptilidium ciliare</i>	2	.	.	1	.	1	1	1	1	.	1	2	2	1	1	73-1	
<i>Cetraria islandica</i>	2	2	1	2	.	2	2	3	4	2	2	.	1	2	2	86-2	
<i>Cladonia arbuscula</i>	3	1	1	.	3	1	1	1	.	1	4	3	2	1	1	86-2	
<i>C. bellidiflora</i>	1	1	1	1	1	1	.	1	1	1	1	1	1	1	.	86-1	
<i>C. carneola</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	.	93-1	
<i>C. cornuta</i>	.	1	1	1	1	.	.	.	27-1	
<i>C. crispata</i>	1	1	.	.	1	.	1	.	1	1	.	33-1	
<i>C. fimbriata</i>	1	1	1	1	1	1	1	47-1	
<i>C. furcata</i>	1	1	.	1	1	1	.	.	.	1	1	1	.	1	1	67-1	
<i>C. gracilis</i>	1	1	.	.	1	.	.	1	.	.	1	1	1	1	1	60-1	
<i>C. mitis</i>	.	.	2	1	1	2	.	2	1	3	3	.	4	4	2	73-3	
<i>C. pleurota</i>	1	.	1	1	1	1	33-1	
<i>C. pyxidata coll.</i>	1	1	1	1	1	1	1	1	1	.	1	1	1	1	1	93-1	
<i>C. rangiferina</i>	2	1	1	1	2	2	2	2	1	1	2	4	3	2	2	100-2	
<i>C. squamosa</i>	1	1	1	.	.	1	1	1	1	1	1	.	1	2	1	80-1	
<i>C. sulphurina</i>	1	1	.	.	.	1	.	.	.	1	1	.	.	1	.	40-1	
<i>C. uncialis</i>	1	1	2	.	2	2	1	1	.	1	1	60-1	
Vascular plants	9	8	8	8	8	10	11	10	11	9	10	11	11	10	7	9	
Bryophytes	12	14	2	7	4	9	9	5	7	3	8	8	7	6	7	7	
Lichens	13	12	10	8	11	13	8	12	10	13	15	8	10	12	11	11	
Total number of species	34	34	20	23	24	32	28	27	28	25	33	27	28	28	25	28	

Additional species occurring in 3 sample plots or less (Plot No., cover - constancy-characteristic degree of cover):

B: *Picea abies* (13:1 - 7-1).C: *Picea abies* (3:1 - 7-1), *Pinus sylvestris* (1:1, 14:1, 15:1 - 20-1), *Sorbus aucuparia* (11:1 - 7-1), *Juniperus communis* (7:1, 12:1, 13:1 - 20-1), *Maianthemum bifolium* (11:1 - 7-1), *Trientalis europaea* (11:1 - 7-1), *Juncus squarrosus* (6:1 - 7-1), *Nardus stricta* (6:2, 7:1 - 14-2).D: *Dicranum polysetum* (7:1, 11:1 - 14-1), *Hylacomium splendens* (2:2, 12:1 - 14-2), *Leucobryum glaucum* (1:1, 4:1, 6:2 - 20-1), *Plagiothecium curv.+dent.+laetum* (1:1, 2:1, 7:1 - 20-1), *Pohlia drummondii+nutans* (1:1, 2:1, 5:1 - 20-1), *Polytrichum juniperinum* (6:1 - 7-1), *Ptilium crista-castrensis* (2:1 - 7-1), *Racomitrium lanuginosum* (6:1, 15:3 - 14-2), *Barbilophozia hatcheri* (2:1, 12:1 - 14-1), *Calypogeia neesiana* (2:1, 7:1 - 14-1), *Cephalozia* spp. (1:1, 2:1 - 14-1), *Cephalozia* spp. (1:1, 14:1 - 14-1), *Cladonia deformis* (11:1 - 7-1), *C. ecmocyna* (8:1 - 7-1), *C. stellaris* (9:1, 10:1, 15:1 - 20-1).

schreberi, *Barbilophozia floerkei*, *Cetraria islandica*, *Cladonia arbuscula*, *C. bellidiflora*, *C. carneola*, *C. pyxidata* coll., and *C. rangiferina*.

The tree layer is dominated by *Pinus sylvestris*. Dominants in the field layer are *Calluna vulgaris*, *Vaccinium myrtillus*, and *V. uliginosum*, less commonly *Betula nana* or *Deschampsia flexuosa*. *Dicranum scoparium*, *Pleurozium schreberi*, *Barbilophozia floerkei*, and *Cladonia mitis* are common as dominants in the bottom layer, but dominance of other *Cladonia* spp. or *Cetraria islandica* has also been observed.

The mean number of species is 28, while the total number in the 15 sample plots is 56.

Most often the type is a mixed pine and spruce forest, sometimes also with scattered birches. The field layer is well developed, dominated by dwarf shrubs. *Melampyrum pratense* is the only common herb in the site-type.

Bryophytes and lichens are approximately equally important regarding species number and dominance relations. The more favourable moisture conditions compared to the xeric series are illustrated by the great importance of the hepatics *Barbilophozia floerkei* and *B. lycopodioides* (cf. Kielland-Lund 1967: 133, Haug 1970: 45). The number of lichen species is almost the same as in the xeric series owing to the large number of small *Cladonia* species, but the *Cladonia* spp. are less important quantitatively than in the latter series. The most important difference from the middle boreal xeric site-type is the marked decrease of *Cladonia stellaris*.

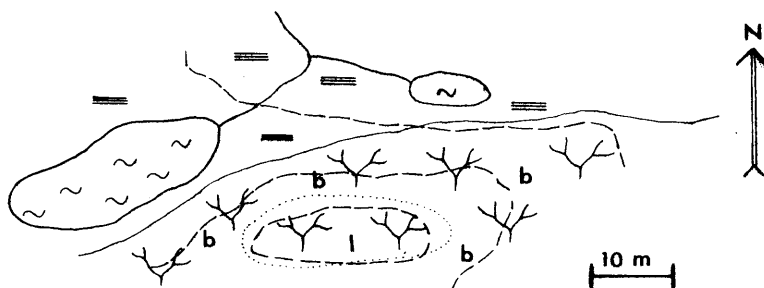


Fig. 13. Sketch map of the zonation of vegetation in a northerly-exposed slope of Nordfjell in the middle boreal zone, position UTM MM 879 007, altitude 690 m. Dominance of bryophytes and lichens in the bottom layer is indicated by b and l, respectively. Contour interval ca. 5 m. Key to symbols in Fig. 9.

Some floristic variation is observed. *Calluna vulgaris* typically dominates the field layer. More locally, *Vaccinium uliginosum* is the dominant, e.g., in plot No. 11 where *Calluna* is absent. *Betula nana* occasionally enters as a dominant (e.g., in plot No. 7). A rare form with dominance of *Racomitrium lanuginosum* was observed near the edge of a steep cliff under

Sigurd bunut (plot No. 15). It has probably originated by invasion of the moss from bare rock, and has maintained itself also after establishment of a stable bottom layer. The relative proportions of bryophytes and lichens vary. An uneven microrelief causes a mosaic of whitish green small convexities dominated by lichens (e.g., plot No. 10) against the dark level areas with bryophytes and lichens more evenly mixed (Fig. 13). The lowest cover of bryophytes is found in the southerly exposed Båtjørnfjell plots.

The site-type has a xerophilous character; it is situated on shallow overburden or sandy or gravelly morainic deposits with low water capacity. The trees are spaced, and much light passes through the lower layers. This is illustrated by the dominance of the photophilous *Calluna vulgaris*. The site-type typically occupies convexities in the terrain. The middle boreal subxeric site-type is the most important forest vegetation type in the bottom of the Grunningsdalen valley, where poor sloping fens occupy the concavities. In three of the transects this site-type terminates fairly abruptly at about 700 m where the slope of the valley sides increases strongly. Only in the southerly exposed mountain ledge of Blåtjørnfjell, where high insolation causes drying, is the site-type represented throughout the whole zone.

Comparison with other investigations is given in Tab. 18.

Upper boreal zone

The floristic composition of this site-type is given in Tab. 19. The constant species are: *Betula pubescens*, *Calluna vulgaris*, *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *V. uliginosum*, *V. vitis-idaea*, *Deschampsia flexuosa*, *Dicranum scoparium*, *Pleurozium schreberi*, *Cetraria islandica*, *Cladonia arbuscula*, *C. mitis*, *C. pyxidata* coll., *C. rangiferina*, and *C. squamosa*.

The tree and shrub layers are dominated by *Betula pubescens*. Dominants in the field layer are *Calluna vulgaris*, *Empetrum hermaphroditum*, *Vaccinium uliginosum*, and *V. vitis-idaea*. *Deschampsia flexuosa* may be dominant. *Pleurozium schreberi*, *Cetraria islandica*, and *Cladonia arbuscula* have the highest cover and are often dominants in the bottom layer.

The mean number of species is 33, while the total number in the 8 sample plots is 75.

Unlike the xeric series the subxeric series may occur as an important element in closed upper boreal birch forests. Physiognomically the site-type is characterized by the almost closed cover of *Calluna vulgaris* in the field layer, somewhat more abundant than *Empetrum hermaphroditum*. Graminids are sometimes common, herbs are scattered. Alpine species present are *Arctostaphylos alpina*, *Carex bigelowii*, and *Juncus trifidus*.

Bryophytes are quite as important as lichens, and the number of hepatic species is high. As in the xeric series, the number of lichen species is high owing to the multitude of small *Cladonia* spp. *Cetraria islandica* and *Cladonia* spp. are most important among the lichens but in contrast to the xeric series *Cladonia stellaris* is mostly unimportant in the subxeric

Tab. 18. Types described by other authors corresponding to the middle boreal subxeric site-type. D - important difference from Grunningsdalen.

Reference	Name of vegetation types	Comments
Kielland-Lund 1967: 132, 1971: 21, 1973: 182, 1981: 132 (Kielland-Lund 1962a: 138, Dahl et al. 1967: 512), Kielland-Lund 1962b: 53	Barbilophozio-Pinetum lapponicae	The deviant sample plot No. 15 shows a slight affinity to sub-ass. rhacomitrietosum (Kielland-Lund 1981: 134). Drier part of the site-type is included in Cladonio-Pinetum boreale. Vaccinio-Pinetum (Kielland-Lund 1981) is ecologically parallel and occurs in less humid areas. Kielland-Lund 1962b: 53 uses the name Empetro-Pinetum.
Kielland-Lund 1967: 133 (followed by several authors)	Bazzanio-Pinetum	Oceanic ecological parallel.
Gjerlaug 1973: 65, 56	Bærlingbarblandingsskog (= Vaccinio Pinetum) Empetrum spruce forest	Vaccinio-Pinetum-like forms pass gradually into Barbilophozio-Pinetum-like forms at higher altitudes. D: Empetrum more important. Greater floristic similarity than the former. D: Calluna absent, Nardus present.
Haug 1970: 44	Barbilophozio-Pinetum	Ecologically parallel.
Bendiksen & Schumacher 1982: 37	Subxeric series (heath pine forest)	
Aune 1978: 21	Barbilophozio-Pinetum	
Bendiksen & Salvesen 1985	Subxeric series (heath pine forest)	D: Moistest part, dominated by Picea and Vaccinium myrtillus, but with constant Pinus and Dicranum polysetum, covers great areas.
Bergland 1975: 35, Odland 1978	Barbilophozio-Pinetum	Great similarity in dominant species, several oceanic spp. added.
Huseby & Odland 1981: 14, Omberg 1980: 93, Aune 1973: 20	Bazzanio-Pinetum	Oceanic parallel.
Omberg 1980: 94	Hylocomium pine forest	
Nedkvitne & Thomter 1953: 257	Vaccinium vitis-idaea-type, Calluna-type	D: Rich in oceanic and humidity-demanding spp., poor in lichens.
Odland 1979: 40	Heath pine forest	Floristic correspondence great for the Calluna-dominated sample plots.
Klokk 1974: 73	Vaccinium-Hylocomium splendens-community	D: Cetraria islandica absent, Barbilophozia spp. with low cover, Hylocomium splendens dominant.
Kjelvik 1978	Barbilophozio-Pinetum cladonietosum	D: Racomitrium lanuginosum dominant, otherwise as Klokk 1974.
McVean & Ratcliffe 1962: 13, Samuelsson 1917a: 40	Pinetum Vaccineto-Callunetum Flechtenreiche/Moosreiche Kiefernwälder p.p.	Highly oceanic type.
Malmström 1949: 57	Calluna-forest (Empetrum-forest)	D: lack of hepatics.
Arnborg 1943: 163, 183	Empetrum hermaphroditum-Vaccinium myrtillus-union (Empetro-myrtilletum)/Cladina-Pleurozium schreberi-union (p.p.)	Field and bottom layers treated as synusia on their own.

Tab. 18 (continued)

Reference	Name of vegetation types	Comments
Arnborg 1940: 132	Trockene Zwergstrauchtyp/Cladina-Pleurozium schreberi-Union	
Arnborg 1942	Torr ristyp	
Eneroth 1931: 131, 1937: 835	Parts of lichen-dwarf shrub types and xeric dwarf-shrub types	
Ronge 1936a: 157	Vaccinium-type (mainly b:V) p.p.	
O. Tamm 1935: 291-292	Parts of normal pine heath type, pine heath type with transition to Vaccinium-type, moist pine heath	
Kalela 1961: 69, 73, 74	Empetrum-Calluna Typ (ECT) and Empetrum-Vaccinium-Typ (EVT) (zone of Pohjanmaa), Myrtillus-Calluna-Cladina-Typ (MCCLT) and Empetrum-Myrtillus-Typ (EMT) (zone of Peräpohjola)	None directly floristically corresponding
Hämet-Ahti 1963: 78	Empetrum type (ET)	
Lakari 1920: 4, 5	Heidekrautwälder (CT), Krähenbeerreichen Heidelbeer-Flechtenwälder (EMCLT)	
Kujala 1929: 83, 85, 73	Empetrum-Calluna-Cladina-Typ (ECCLT), Calluna-Uliginosa-Typ (CUT), Empetrum-Myrtillus-Cladina-Typ (EMCLT)	
Nihlgård 1980: 29	Calluna-Empetrum-type	Barbilophozia variant closest corresponding variant

series. Plot No. 4, situated adjacent to plot No. 2 of the upper boreal xeric site-type (cf. Tab. 11), represents the xeric end of the site-type. It almost lacks bryophytes and *Cladonia stellaris* dominates in the bottom layer, while *Alectoria ochroleuca* and *Cetraria nivalis* both are present. This is the only plot without *Vaccinium myrtillus*, clearly illustrating a transition to the xeric series. The other extreme is represented by types with a thick, moist raw humus and more moisture-demanding species like *Sphagnum nemoreum* and *Polytrichum commune*. (e.g., plots Nos 1 and 6). *Cetraria islandica* may attain high cover. Plot No. 1 contains mire species like *Andromeda polifolia*, *Rubus chamaemorus* and *Scirpus caespitosus*. Plot No. 7 also represents a fresher type with occurrence of *Trientalis europaea* and *Solidago virgaurea*. At the drier sites the birches mostly occur as scattered shrubs lower than 1.5 m, on the fresher soils there is vital birch forest.

The site-type occurs from level ground to wind exposed convexities. It is only substituted by the xeric series at the most extremely exposed sites. The dry summers of 1975 and 1976 also caused the death of *Calluna vulgaris* in the subxeric series, but by 1980 the heather was beginning to regenerate. The site-type is mostly confined to sites with a southerly to westerly aspect. It is totally absent from the moist north-facing mountain ledges of Nordfjell and Sigurd bunut and attains

Tab. 19. The vegetation of the upper boreal subxeric site-type.

Transect No.	1			2			3			
Plot No.	1	2	3	4	5	6	7	8	C- \bar{c}	
Altitude (m)	980	980	1010	920	930	990	1010	1010		
Slope ($^{\circ}$)	10	10	15	15	20	20	35	35		
Aspect	SSW	S	SE	SSE	SSW	SSW	W	W		
TA	0	0	0	0	+	0	4	3		
TB	3	4	2	0	1	2	1	+		
TC	8	6	8	7	7	7	7	6		
TD	6	5	5	4	2	3	7	7		
TE	+	1	+	1	2	1	+	+		
TF	0	0	0	+	+	0	1	+		
A <i>Betula pubescens</i>	2	.	4	4	38-4	
B <i>Betula pubescens</i>	4	4	3	.	2	1	2	1	88-3	
C <i>Betula pubescens</i>	3	2	2	1	1	1	1	1	100-2	
<i>Picea abies</i>	1	1	.	.	25-1	
<i>Sorbus aucuparia</i>	1	.	1	.	25-1	
<i>Arctostaphylos alpina</i>	1	1	.	2	1	1	1	.	75-1	
<i>Calluna vulgaris</i>	4	4	4	5	5	4	3	3	100-4	
<i>Empetrum hermaphroditum</i>	4	3	4	4	1	3	4	3	100-4	
<i>Vaccinium myrtillus</i>	3	2	2	.	1	2	2	3	88-2	
<i>V. uliginosum</i>	3	2	3	2	4	4	2	2	100-3	
<i>V. vitis-idaea</i>	2	2	1	2	2	1	4	3	100-3	
<i>Maianthemum bifolium</i>	.	.	1	.	1	.	.	.	25-1	
<i>Melampyrum pratense</i>	1	.	1	.	1	2	.	.	50-1	
<i>Trientalis europaea</i>	.	.	1	.	.	.	1	1	38-1	
<i>Carex bigelowii</i>	1	1	25-1	
<i>Deschampsia flexuosa</i>	2	1	3	1	1	3	3	3	100-2	
<i>Juncus trifidus</i>	1	1	25-1	
D <i>Brachythecium starkei</i>	1	.	2	1	38-1	
<i>Dicranum polysetum</i>	.	1	.	.	1	.	.	.	25-1	
<i>D. scoparium</i>	2	2	3	1	2	1	2	2	100-2	
<i>Hylacomium splendens</i>	1	1	.	25-1	
<i>Orthodicranum montanum</i>	1	1	1	.	38-1	
<i>Plagiothecium curv.+dent.+laet.</i>	.	.	1	.	.	.	1	1	38-1	
<i>P. piliferum</i>	1	1	1	1	50-1	
<i>Pleurozium schreberi</i>	1	1	2	.	3	3	2	3	88-2	
<i>Polytrichum commune</i>	1	2	.	.	25-2	
<i>Tetraphis pellucida</i>	1	1	25-1	
<i>Sphagnum nemoreum</i>	1	2	.	.	25-2	
<i>Barbilophozia barbata</i>	1	.	1	.	.	1	1	.	50-1	
<i>B. floerkei</i>	1	1	1	1	50-1	
<i>B. hatcheri</i>	.	.	1	.	1	.	2	2	50-2	
<i>B. lycopodioides</i>	.	.	2	.	1	2	1	2	63-2	
<i>Lophozia obtusa</i>	1	1	.	.	25-1	
<i>L. sudetica</i>	1	1	25-1	
<i>L. ventricosa</i>	1	1	1	38-1	
<i>Ptilidium ciliare</i>	2	.	1	.	1	1	2	2	75-2	
<i>Cetraria islandica</i>	2	2	1	2	1	4	3	.	88-3	
<i>Cladonia arbuscula</i>	2	2	1	1	1	1	3	4	100-2	
<i>C. bellidiflora</i>	1	1	1	.	.	.	1	1	63-1	
<i>C. carneola</i>	1	1	1	.	1	.	.	1	63-1	
<i>C. coccifera</i>	1	1	25-1	
<i>C. ecmocyna</i>	.	.	1	1	25-1	
<i>C. fimbriata</i>	.	.	1	.	1	1	1	1	63-1	
<i>C. furcata</i>	1	1	1	.	1	.	.	1	63-1	
<i>C. gracilis</i>	.	1	1	.	.	.	1	1	50-1	

Tab. 19 (continued)

Transect No.	1			2			3		
Plot No.	1	2	3	4	5	6	7	8	C-c
<i>Cladonia mitis</i>	1	3	2	1	1	.	1	1	88-2
<i>C. pleurota</i>	.	.	1	1	1	.	1	1	63-1
<i>C. pyxidata coll.</i>	1	1	1	1	1	1	1	1	100-1
<i>C. rangiferina</i>	2	1	1	2	2	2	2	2	100-2
<i>C. squamosa</i>	1	1	1	1	1	.	1	1	88-1
<i>C. stellaris</i>	1	1	.	4	.	.	.	1	50-2
<i>C. sulphurina</i>	.	1	1	.	.	.	1	1	50-1
<i>C. uncialis</i>	.	1	1	25-1
Vascular plants	16	11	10	8	12	11	12	8	11
Bryophytes	10	5	8	2	14	12	17	15	10
Lichens	10	13	16	11	10	5	13	15	12
Total number of species	36	29	34	21	36	28	42	38	33

Additional species occurring in 1 sample plot (Plot No.:cover):

- B: *Picea abies* (6:3), *Pinus sylvestris* (1:1).
 C: *Pinus sylvestris* (2:1), *Populus tremula* (5:1), *Andromeda polifolia* (1:1), *Betula nana* (6:1), *Juniperus communis* (7:1), *Loiseleuria procumbens* (4:1), *Rubus chamaemorus* (1:1), *Solidago virgaurea* (7:1), *Scirpus caespitosus* (1:1).
 D: *Ceratodon purpureus* (7:1), *Dicranum fuscescens* (5:1), *Paraleucobryum longifolium* (7:1), *Polytrichum formosum* (5:1), *P. strictum* (1:1), *Racomitrium lanuginosum* (2:1), *Splachnum* sp. (2:1), *Calypogeia integristipula* (8:1), *Cephalozia* spp. (8:1), *Cephaloziella* spp. (5:1), *Alectoria ochroleuca* (4:1), *Cetraria ericetorum* (4:1), *C. nivalis* (4:1), *Cladonia cornuta* (3:1), *C. metacoralifera* (7:1).

its greatest extension in the southerly exposed Blåtjørnfjell, where it occupies most of the upper boreal zone.

Comparison with other investigations is given in Tab. 20.

Low alpine zone

The floristic composition of this site-type is given in Tab. 21. The constant species are: *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *Deschampsia flexuosa*, *Dicranum scoparium*, *Cetraria ericetorum*, *C. islandica*, *Cladonia arbuscula*, *C. carneola*, *C. mitis*, *C. pyxidata coll.*, and *C. rangiferina*.

Dominants in the field layer are *Calluna vulgaris*, *Empetrum hermaphroditum*, *Vaccinium uliginosum*, and *V. myrtillus*. *Cetraria islandica* is the most important dominant in the bottom layer. *Dicranum scoparium*, *Pleurozium schreberi*, and *Cladonia arbuscula* are subordinate dominants.

The mean number of species is 28, while the total number in the 13 sample plots is 68.

There is a closed cover of dwarf shrubs; *Calluna vulgaris*, *Empetrum hermaphroditum*, and *Vaccinium uliginosum*. Graminids are sometimes common. Herbs have no importance. The main alpine species present are *Arctostaphylos alpina*, *Carex bigelowii*, and *Juncus trifidus*. The physiognomically most important species of the bottom layer is *Cetraria islandica*. *Cladonia* spp. are also important and the number of small *Cladonia* spp. high. A large number of bryophyte species have been recorded, but only a few of them have quantitative importance. In each transect continuous subxeric *Calluna*-heaths ascend to the low alpine

Tab. 20. Types described by other authors corresponding to the upper boreal subxeric site-type. D - important difference from Grunningsdalen.

Reference	Name of vegetation types	Comments
Kielland-Lund 1967: 132, 1971: 21, 1973: 182, 1981: 132, Dahl et al. 1967: 512, (Kielland-Lund 1962a: 138), Kielland-Lund 1962b: 53	Barbilophozio-Pinetum lapponicae (subalpine Birken- und Birken-Kiefernwald-Rasse/subalpine Birkenwaldform)	D: Some localities have high constancies of <i>Nephroma arcticum</i> , <i>Stereocaulon paschale</i> and <i>Peltigera</i> spp. Kielland-Lund 1962b: 53 uses the name <i>Empetro-Pinetum</i> .
Nordhagen 1928: 107, 1937, Christophersen 1925: 509	Empetrum-reicher Birkenwald, Calluna-reicher Birkenwald	
Nordhagen 1937: 64	<i>Betula nana</i> -Empetrum hermaproditum-Soz., <i>Betuletum</i> Empetro-Hylocomiosum	Only ecological correspondence.
Haug 1970: 61	Barbilophozio-Pinetum	Callunetosum has highest affinity.
Mork & Låg 1959: 54-56	Calluna-type, Calluna-Myrtillus-type, Empetrum-type	D: Mostly mountain pine forest
Resvoll-Holmsen 1912: 8	Mountain pine forest	D: Calluna rare, several mesophilous spp.
Resvoll-Holmsen 1914b: 11	Mountain pine forest	D: Lichens much more abundant
Resvoll-Holmsen 1918: 186	Lichen-rich mountain pine and birch forest p.p.	
Mork & Heiberg 1937: 643, 644	Empetrum-Vaccinium-Picea-Betula-soc., Calluna-Empetrum-Pinus-Picea-Betula-soc.	The latter has highest affinity.
Bendiksen & Schumacher 1982: 38	Subxeric series (lichen birch forest)	Calluna sparser, Empetrum more abundant towards upper part of UB
Aune 1978: 21	Barbilophozio-Pinetum, subalpine form	
Bergland 1975: 35	Barbilophozio-Pinetum	
Odland 1978: 32	Barbilophozio-Pinetum	D: Many moisture-demanding spp.
Fredriksen 1978: 31, 116, 126	Empetrum hermaphroditum-dominated heath, Calluna-heath, (<i>Vaccinio uliginosi</i> -Pinetum)	Calluna-heath most in common, although influenced by grazing
Fægri 1934: 84	Zwergstrauchreiches <i>Betula</i> -Gebüsch, haupt-typus	D: Some indicators of earlier successional stages
Kummen 1977: 31	Lichen rich <i>Racomitrium</i> -Empetrum-Calluna-heath	Highly oceanic type
Moen 1978: 35	<i>Pinus</i> -Empetrum-/ <i>Betula</i> -Empetrum-communities	
Samuelsson 1917a: 50	Calluna-reichen Flechten-Kiefernheide	
Tengwall 1920: 332	Empetrum nigrum-reicher Moosbirkenwald	
T. Fries 1913: 57	Empetrum-reicher Flechtenbirkenwald	
Sonesson & Lundberg 1974: 129	Empetrum-Type of mountain birch forest	
Kalela 1961: 78, 79	Uliginosum-Vaccinium-Empetrum-type (UVET), Uliginosum-Empetrum-Myrtillus-type (UEMT) (zone of Wald-Lappland)	

Tab. 20 (continued)

Reference	Name of vegetation types	Comments
Kalela 1961: 82, Hämet- Ahti 1963: 49, 52	Subalpine Empetrum-Lichenes- Pleurozium-Typ (sELiPlT), sub- alpine Empetrum-Myrtillus-Typ (sEMT) p.p. (continental subal- pine subzone)	
Hämet-Ahti 1963: 66, 70	Subalpine Empetrum type (sET), Cornus-Empetrum-Myrtillus type (CoEMT) (oceanic subalpine subzone)	
Thannheiser 1975: 59, (53, 73, 76)	Empetrum-Heide-Birkenwald: Rotstengelmoos-Krähenbeer- Birkenwald, (Flechtenreicher Krähenbeer-Birkenwald/Flechten- reicher Heidelbeer-Birkenwald, Rotstengelmoos-Heidelbeer-Bir- kenwald)	The types in parentheses are transitions to X and SM, respectively
Kujala 1929: 44	Vaccinium-Empetrum-Myrtillus- Cladina-type (VEMClT)	D: Calluna absent
Kalela 1939: 62	Empetrum nigrum-Heide, Empetrum nigrum-Vaccinium myrtillus Heide p.p.	
Nihlgård 1980: 47, 67	Mixed forest of lichen-dwarf shrub type, mountain birch for- est of lichen-dwarf shrub type	

zone. They suddenly disappear at 1120 m in Tjorbufjell, 1220 m in Blåtjørnfjell, and 1250 m in Målefjell, the last being only 10 m below its upper limit on Hardangervidda (Lid 1959). A few individuals of low vitality were found on Målefjell at 1310 m.

The most exposed plots have a sparse cover of bryophytes (e.g., plot No. 5). In contrast, plots Nos. 10 and 12 represent forms at the mesic end of the moisture range spanned by the site-type, the former containing hygrophilous species like *Molinia caerulea*, *Scirpus caespitosus*, *Conostomum tetragonum*, and *Cetraria delisei*, the latter having a high cover of bryophytes and some *Dicranum majus* and *Cornus suecica*. Plot No. 9 from the top plateau of Nordfjell has dominance of *Leucobryum glaucum*, covering about 100 sq. m at 1120 m. Here *Leucobryum* seems to replace *Cetraria islandica*; the species composition is otherwise typical for the site-type.

The site-type is situated on dry and moderately exposed localities. It has a stable protection by snow in winter as demonstrated by the occurrence of *Calluna vulgaris*, and *Empetrum hermaphroditum* (Nordhagen 1928: 111, Knaben 1952: 69). The subxeric series covers large areas in the low alpine zone in the investigation area, where it is mostly confined to convex terrain including the summits of smaller crags. A typical low alpine zonation is shown in Fig. 14.

Comparison with other investigations is given in Tab. 22.

Middle alpine zone

The floristic composition of this site-type is given in Tab. 23. The constant species are: *Empetrum hermaphroditum*,

Tab. 21. The vegetation of the low alpine subxeric site-type.

Transect No.	1				2				3				4				
Plot No.	1	2	3	4	5	6	7	8	9	10	11	12	13	C- \bar{c}			
Altitude (m)	1250	1250	1080	1080	1080	1210	1220	1230	1120	1130	990	990	990				
Slope (°)	10	10	10	10	10	15	15	20	25	10	15	15	10				
Aspect	SE	SE	ENE	ENE	SW	SSE	SE	ENE	SE	WSW	NNW	NNW	W				
TA	0	0	0	0	0	0	0	0	0	0	0	0	0				
TB	0	0	0	0	0	0	0	0	0	0	0	0	0				
TC	6	6	6	7	7	6	7	7	4	5	7	8	6				
TD	6	5	9	6	5	5	2	7	3	5	7	5	4				
TE	1	1	+	+	1	+	2	0	3	1	2	+	2				
TF	1	1	0	0	+	+	+	+	2	3	+	0	+				
C <i>Arctostaphylos alpina</i>	.	.	2	1	1	1	4	1	46-2			
<i>Calluna vulgaris</i>	3	.	4	3	2	3	3	.	3	1	1	.	5	77-3			
<i>Empetrum hermaphroditum</i>	4	5	4	5	4	4	4	5	4	4	5	5	4	100-5			
<i>Loiseleuria procumbens</i>	.	3	1	.	1	2	1	1	.	1	1	.	3	69-2			
<i>Vaccinium myrtillus</i>	3	1	1	2	2	1	3	3	1	1	1	2	.	92-2			
<i>V. uliginosum</i>	.	.	2	3	4	2	2	.	2	2	4	3	2	77-3			
<i>V. vitis-idaea</i>	.	2	1	1	1	.	.	3	1	1	2	2	2	77-2			
<i>Carex bigelowii</i>	2	1	1	.	2	.	.	1	38-1			
<i>Deschampsia flexuosa</i>	2	1	1	1	1	1	3	2	1	.	1	1	.	85-1			
<i>Juncus trifidus</i>	1	1	.	.	.	1	1	1	.	1	.	.	.	46-1			
D <i>Dicranum fuscescens</i>	1	1	1	1	1	38-1			
<i>D. scoparium</i>	3	2	1	1	1	1	2	2	2	3	2	2	2	100-2			
<i>Plagiothecium curv.+dent.+laet.</i>	.	1	.	.	.	1	1	.	.	23-1			
<i>Pleurozium schreberi</i>	.	1	.	2	1	1	1	1	1	.	4	3	1	46-3			
<i>Pohlia drummondii+nutans</i>	1	1	.	1	.	.	1	.	1	1	1	.	.	54-1			
<i>Barbilophozia floerkei</i>	2	1	.	1	.	1	1	1	1	2	1	2	.	77-1			
<i>B. lycopodioides</i>	1	.	.	1	.	.	.	1	1	.	.	1	.	38-1			
<i>Lophozia ventricosa</i>	1	1	1	1	1	1	.	1	.	54-1			
<i>Ptilidium ciliare</i>	.	1	2	2	.	1	1	1	1	.	1	2	1	77-1			
<i>Cetraria ericetorum</i>	.	1	1	1	1	1	1	2	2	2	1	.	2	85-1			
<i>C. islandica</i>	3	4	5	5	4	4	3	5	1	4	4	4	3	100-4			
<i>C. nivalis</i>	.	1	1	.	.	1	1	1	38-1			
<i>Cladonia arbuscula</i>	2	2	2	2	1	3	1	1	3	2	3	2	2	100-2			
<i>C. bellidiflora</i>	1	1	.	.	.	1	1	1	1	1	1	.	1	69-1			
<i>C. carneola</i>	1	1	1	1	1	1	1	1	.	.	1	1	1	85-1			
<i>C. coccifera</i>	1	1	.	1	.	1	.	.	1	1	1	.	.	54-1			
<i>C. fimbriata</i>	.	.	.	1	1	1	23-1			
<i>C. furcata</i>	.	.	1	.	1	1	1	1	.	.	1	.	1	54-1			
<i>C. gracilis</i>	1	1	.	1	.	.	.	1	1	1	1	1	1	69-1			
<i>C. mitis</i>	1	.	2	1	2	1	1	1	1	.	1	1	1	85-1			
<i>C. pleurota</i>	1	1	.	1	.	.	.	1	1	1	1	.	1	62-1			
<i>C. pyxidata coll.</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	100-1			
<i>C. rangiferina</i>	1	1	1	1	1	.	1	1	1	.	1	1	1	85-1			
<i>C. squamosa</i>	1	1	.	.	.	1	.	.	1	1	1	1	1	62-1			
<i>C. stellaris</i>	.	2	2	1	.	1	.	.	2	.	2	1	1	62-2			
<i>C. sulphurina</i>	1	1	.	1	.	.	.	1	1	1	1	.	.	54-1			
<i>C. uncialis</i>	1	1	1	.	.	1	1	1	1	1	1	.	1	77-1			
Vascular plants	5	7	9	9	9	10	8	9	6	11	8	8	7	8			
Bryophytes	8	9	3	8	1	6	7	6	11	6	8	9	5	7			
Lichens	15	17	11	13	9	13	11	15	15	12	17	9	15	13			
Total number of species	28	33	23	30	19	29	26	30	32	29	33	26	27	28			

Additional species occurring in 2 sample plots or less (Plot No.: cover - constancy-characteristic degree of cover):

C: *Picea abies* (3:+, 12:+ - 15:+), *Betula nana* (4:2, 5:1 - 15:2), *Juniperus communis* (2:1 - 8:1), *Lycopodium clavatum* (4:1 - 8:1), *L. selago* (8:1, 10:1 - 15:1), *Cornus suecica* (12:1, 8:1), *Gentiana purpurea* (7:1 - 8:1), *Rubus chamaemorus* (6:1, 8:1 - 15:1), *Molinia caerulea* (10:1 - 8:1), *Scirpus caespitosus* (6:1, 10:1 - 15:1).

D: *Ceratodon purpureus* (11:1, 13:1 - 15:1), *Conostomum tetragonum* (10:1 - 8:1), *Dicranum majus* (12:1 - 8:1), *Hylocomium splendens* (11:1, 12:2 - 15:2), *Leucobryum glaucum* (9:3 - 8:3), *Orthodicranum montanum* (7:1 - 8:1), *Plagiothecium piliferum* (1:1 - 8:1), *Polytrichum commune* (6:1 - 8:1), *P. formosum* (10:1 - 8:1), *P. juniperinum* (7:1, 8:1 - 15:1), *Tetraplodon mnioides* (4:1 - 8:1), *Barbilophozia barbata* (9:1 - 8:1), *B. hatcheri* (2:1 - 8:1), *Calypogeia muelleriana* (12:1 - 8:1), *Cephaloziella* spp. (1:1, 9:1 - 15:1), *Sphenolobus minutus* (6:1, 9:1 - 15:1), *Cetraria cucullata* (2:1, 8:1 - 15:1), *C. delisei* (10:1 - 8:1), *Cladonia crispata* (2:1, 11:1 - 15:1), *C. ecmocyna* (1:2 - 8:2), *C. metacorrallifera* (1:1, 9:1 - 15:1).

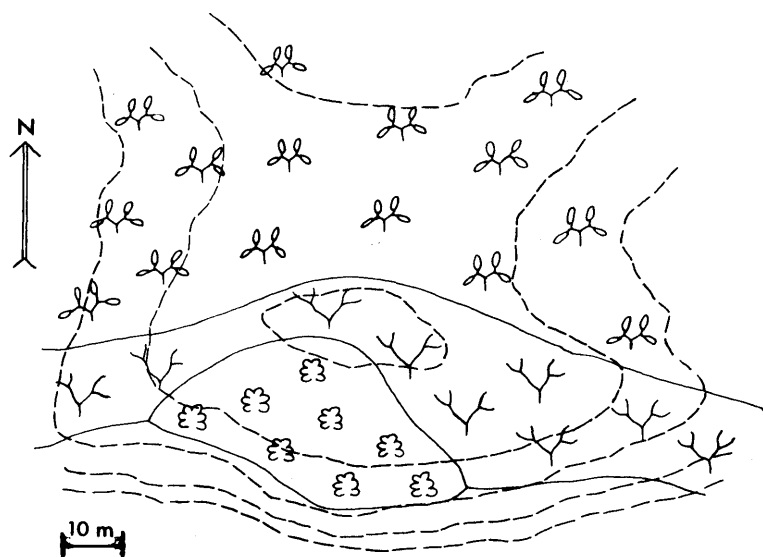


Fig. 14. Sketch map of the zonation of vegetation on an exposed, low alpine site on the southern slope of Blåtjørnfjell, position UTM MM 887 028, altitude 1080 m. Contour interval ca. 1 m. Key to symbols in Fig. 9.

Vaccinium myrtillus, *V. vitis-idaea*, *Dicranum scoparium*, *Pohlia drummondii*+*nutans*, *Barbilophozia floerkei*, *Ptilidium ciliare*, *Cetraria ericetorum*, *C. islandica*, *C. nivalis*, *Cladonia arbuscula*, *C. bellidiflora*, *C. coccifera*, *C. gracilis*, *C. metacorallifera*, *C. pleurota*, *C. pyxidata* coll., *C. squamosa*, *C. stellaris*, *C. sulphurina*, and *C. uncialis*.

Empetrum hermaphroditum is the only dominant in the field layer. Dominants in the bottom layer are *Cetraria ericetorum* and *C. islandica*, sometimes also *Dicranum scoparium*.

The mean number of species is 31, while the total number in the 8 sample plots is 55.

Physiognomically the site-type is characterized by the three dominants. Graminids are locally important, *Juncus trifidus* is somewhat more important than in the corresponding site-type in the xeric series. Herbs are not observed. The numbers of observed lichen and bryophyte species are high.

There is little variation among the sample plots. However, plot No. 6 represents a deviant type rich in *Cladonia stellaris* and with a dense but low and appressed *Juniperus communis*-thicket. *Pleurozium schreberi* and *Barbilophozia lycopodioides*, neither of them is common in the middle alpine zone in Grunningsdalen, occur in this thicket owing to favourable microclimate.

Tab. 22. Types described by other authors corresponding to the low alpine subxeric site-type. D - important difference from Grunningsdalen.

Reference	Name of vegetation types	Comments
Nordhagen 1928: 210, 218, 202	Cladonia silvatica-reiche Empetrum-Ass., Cladonia silvatica-rangiferina-reiche Calluna-Ass., Empetrum-reiche Cladonia alpestris-Ass., (Dichte Empetrum-Ass., Dichte Calluna-Ass.)	Ecologically parallel, some of them transitional to X
Christophersen 1925: 553	Empetrum-heath	
Nordhagen 1943	Empetrum-Arctostaphylos alpina-Vaccinium uliginosum-Cladonia silvatica-rangiferina-soc. (Myrdal), Betula nana-Cladonia alpestris-soc. (Sikilsdalen, Tronfjell), Betula nana-Cladonia rangiferina-silvatica-soc. (Sikilsdalen), Empetrum-Cladonia rangiferina-silvatica-soc. (Sylene, Ørterdalen), Empetrum-Cladonia alpestris-soc. (Tronfjell, Sylene), Calluna heath (Sikilsdalen), Phyllodoco-Vaccinietum myrtilli, Empetrum-var.	The first one has much in common with LA-SX floristically, the others are rather parallel ecologically, some of them transitional to X or SM
Nordhagen 1937: 64	Flechten-reiche Betula nana-Empetrum hermaphroditum-Soc.	
Dahl 1957: 114	Cladonietum alpestris	
Resvoll-Holmsen 1920: 96	Empetrum heath, Calluna heath	
Resvoll-Holmsen 1932	Vaccinium uliginosum heath	
Bendiksen & Schumacher 1982: 49	Subxeric type (Empetrum-Cladonia heath)	D: Calluna rare or absent, bottom layer normally dominated by lichens (Cladina) alone
Du Rietz 1925a: 50, 52 66, 46, 49	Empetrum nigrum-Cladonia alpestris-Ass., Calluna-Cladonia alpestris-Ass., Nackte Calluna-Ass., Betula nana-Cladonia alpestris-Ass., Betula nana-Empetrum nigrum-Cladonia alpestris-Ass.	Ecologically parallel
Samuelsson 1917b: 17	Empetrum-reiche Flechtenheiden	Probably also including X p.p.
Hadac 1971: 211, 205, 208, 210, 209	Empetro hermaphroditi-Callunetum, Cetrario islandicae-Loiseleurietum, Cetrario islandicae-Caricetum bigelowii, Empetro-Betuletum nanae, Vaccinio-Empetretum hermaphroditi scandinavicum	Only the first one has high affinity, the rest are ecologically parallel
Huseby & Odland 1981: 22	Alpine dwarf shrub heaths	
Odland 1981a: 16	Low alpine dwarf shrub heaths	
Naustdal 1951: 84	"Kreklingrabbar" (Empetrum heaths)	
Fredriksen 1978: 126	Empetrum hermaphroditum-dominated heath	

Tab. 22. (continued)

Reference	Name of vegetation types	Comments
Knaben 1952: 58, 69, 54	Calluna-heaths, Empetrum-heaths (of Empetrum-Cladonia rangiferina-soc.) p.p., Vaccinium myrtillus-Cornus suecica-Hylocomium-soc. p.p.	
Fægri 1934: 80	Empetrum-Calluna-soc. (main type)	
Odland 1981b: 15	Calluna- and Vaccinium myrtillus-dominated dwarf shrub heath	High occurrence of oceanic spp.
Malme 1971: 21, 22	Loiseleurieto-Diapsietum arctostaphylosum alpinae, Corneto-Callunetum	Ecologically parallel
Poore & McVean 1957, McVean & Ratcliffe 1962: 34, 35, McVean 1964: 482, 483	(Calluna-heaths), Arctoeto-Callunetum, Cladineto-Callunetum	Ecologically parallel
Samuelsson 1917a: 151, 154	Calluna-Heiden, Cladonia-Heiden, Zwergstrauchreiche Cladonia (silvatica)-Heiden, Zwergstrauchreiche Cladonia alpestris-Heiden	
Smith 1920: 30	Calluna-heath	
Tengwall 1920: 368, 370	Flechtenreiche Empetrum nigrum-Heide, Moosreiche Empetrum nigrum-Heide	
T. Fries 1913: 66, 68	Flechtenreiche Empetrum-Ass., Flechtenreiche Azalea-Ass.	The latter probably corresponding both to X and SX
Holmen 1965: 240	Empetrum-heath	
Thannheiser 1975	Empetrum-Heide-Gebüsche: Flechtenreiches Zwergbirken-Gebüsch	Influenced by reindeer grazing
Lippmaa 1929: 44	Lichen- and bryophyte rich Empetrum-heath	
Hult 1887: 176, 177	Cladina-formation, Empetrum-formation	
Kalliola 1939: 211, 201, 210, 193	Calluna-Cladonia alpestris-Soz., Moosreiche Empetrum-Soz., Myrtillus-Cladonia alpestris-Soz., Betula nana-Empetrum-Cladonia alpestris-Soz.	The first one floristically most similar
Kalliola 1932: 37, 119	Empetrum-Heide	
Söyrinki 1938: 26	Empetrum-Heide	
Kalela 1939: 66	Moosreiche Empetrum nigrum-Tundra	More mesic parts of SX
Dahl et al. 1971: 21	Arctostaphylo-Cetrarion nivalis p.p. (mesic part)	
Waldermarson Jensen 1980: 54	Empetrum-heath, southern Calluna-variant	

Tab. 23. The vegetation of the middle alpine subseric site-type.

Transect No.	1			3					
Plot No.	1	2	3	4	5	6	7	8	C-G
Altitude (m)	1290	1310	1400	1250	1260	1260	1260	1310	
Slope (°)	10	20	10	10	10	15	15	20	
Aspect	NNW	NNE	ESE	E	N	SSE	SSE	NNE	
TA	0	0	0	0	0	0	0	0	
TB	0	0	0	0	0	0	0	0	
TC	4	6	7	4	6	7	6	6	
TD	6	6	8	6	7	7	7	9	
TE	3	1	+	+	+	+	1	+	
TF	1	1	1	3	2	2	2	0	
C Empetrum hermaphroditum	4	5	5	4	5	4	5	5	100-5
Loiseleuria procumbens	.	1	.	.	2	.	2	3	50-2
Lycopodium selago	.	1	1	.	1	.	.	1	50-1
Phyllocladus caerulea	.	2	1	25-2
Vaccinium myrtillus	1	1	2	1	.	2	2	2	88-2
V. vitis-idaea	2	2	2	1	2	2	1	2	100-2
Deschampsia flexuosa	1	1	2	2	1	1	2	2	100-2
Juncus trifidus	2	2	1	2	1	1	1	1	100-1
D Dicranum fuscescens	.	2	1	.	1	.	.	.	38-1
D. scoparium	3	2	1	2	1	1	1	3	100-2
Pleurozium schreberi	2	.	1	25-2
Pohlia drummondii+nutans	1	1	1	1	1	1	.	1	88-1
Polytrichum commune	.	1	1	25-1
P. juniperinum	1	.	.	.	1	1	.	1	50-1
P. piliferum	.	1	1	1	.	1	.	.	50-1
Barbilophozia floerkei	2	1	1	1	1	1	1	2	100-1
B. hatcheri	.	.	1	1	1	1	.	.	50-1
B. lycopodioides	1	.	1	25-1
Cephalozia spp.	.	.	1	.	.	1	.	.	25-1
Chandonanthus setiformis	.	2	.	.	1	.	.	.	25-2
Lophozia ventricosa	.	1	1	1	1	.	.	1	63-1
Ptilidium ciliare	1	.	1	1	1	1	1	1	88-1
Cetraria delisei	1	.	1	1	1	.	1	.	63-1
C. ericetorum	1	4	2	4	3	2	3	4	100-3
C. islandica	4	3	5	3	5	5	4	3	100-4
C. nivalis	1	1	1	1	1	1	.	1	88-1
Cladonia arbuscula	2	1	1	2	2	2	2	2	100-2
C. bellidiflora	1	1	.	1	1	1	1	1	88-1
C. coccifera	1	2	1	1	1	1	1	1	100-1
C. deformis	1	1	25-1
C. furcata	.	.	.	1	1	.	1	.	38-1
C. gracilis	1	1	1	.	1	1	1	1	88-1
C. metacorrallifera	.	1	1	1	1	1	1	1	88-1
C. mitis	1	1	.	1	.	1	.	.	50-1
C. pleurota	1	.	1	1	1	1	1	1	88-1
C. pyxidata coll.	1	1	1	1	1	1	.	1	88-1
C. rangiferina	1	.	1	.	1	2	1	1	75-1
C. squamosa	1	1	1	1	1	1	1	1	100-1
C. stellaris	1	1	1	1	1	3	1	2	100-1
C. sulphurina	1	1	1	1	1	1	1	1	100-1
C. uncialis	1	2	1	1	1	1	1	1	100-1
Vascular plants	7	8	7	5	6	6	6	8	7
Bryophytes	6	10	12	7	9	11	3	8	8
Lichens	17	14	15	16	18	16	16	18	16
Total number of species	30	32	34	28	33	33	25	34	31

Additional species occurring in 1 sample plots (Plot No.:cover):

C: Juniperus communis (6:4), Salix herbacea (1:1); Rubus chamaemorus (3:1); Nardus stricta (1:1).

D: Conostomum tetragonum (3:1), Plagiothecium piliferum (6:1); Cephalozia spp. (2:1), Lophozia sudetica (1:1), Marsipella brevissima (3:1), Sphenolobus minutus (2:1); Cladonia carneola (8:1), C. cernocyna (1:1), C. macrophylla (8:1), Hypogymnia intestiniiformis (5:1).

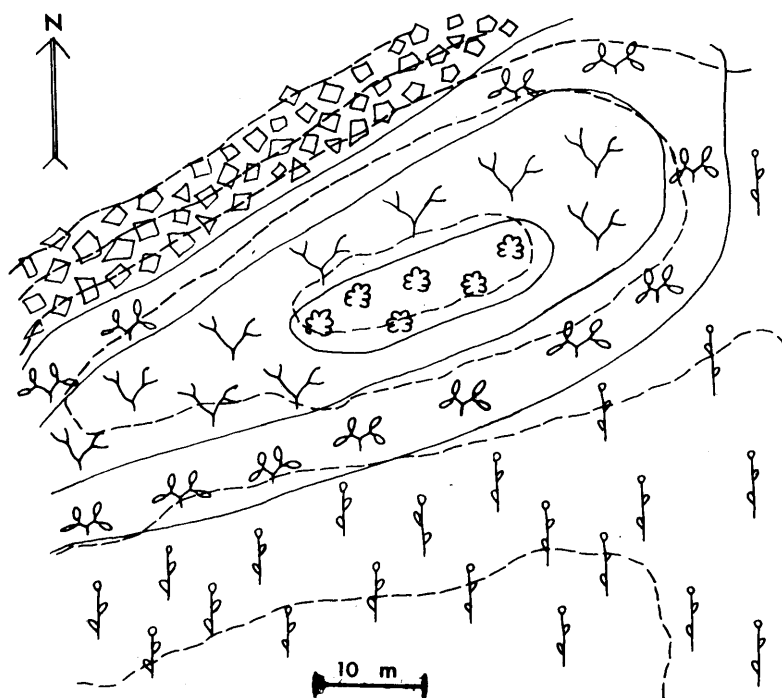


Fig. 15. Sketch map of the zonation of vegetation according to snow cover on Tjorbufjell, the middle alpine zone, position UTM ML 873 983, altitude 1280 m. Contour interval ca. 2 m. Key to symbols in Fig. 9.

The site-type is encountered on moderately dry and wind exposed sites with shallow soil and a thin, but stable snow cover in winter (Fig. 15). The occurrence of boulders and the high cover of naked ground in the sample plots are characteristic to this site-type.

Comparison with other investigations is given in Tab. 24.

Survey of the subxeric series

The subxeric series is dark owing to a dense field layer dominated by xerophytic dwarf shrubs and a bottom layer where bryophytes and dark lichens of the genus *Cetraria* are important. Graminids have some importance, but herbs are sparse.

Calluna vulgaris has the highest cover among the dwarf shrubs in the two boreal zones, while *Empetrum hermaphroditum* is the most important in the alpine zones (see Tab. 7). All *Vaccinium* spp. are important, but *Vaccinium myrtillus* far less

Tab. 24. Types described by other authors corresponding to the middle alpine subxeric site-type.

Reference	Name of vegetation types	Comments
Nordhagen 1937	Juncion trifidi scandinavicum p.p.	
Nordhagen 1943: 191, 193, 217	Festuca ovina-Cladonia alpestris-soc., Festuca ovina-Cladonia silvatica-Soc. (Sikilsdalen), Juncetum trifidi, bitype B (Hardangervidda)	Ecologically parallel
Dahl 1957	Several types dominated by Juncus trifidus	Ecologically parallel
Resvoll-Holmsen 1920: 213, Nordhagen 1928, 1937, 1943	Diverse types of Juncus trifidus and Festuca ovina-heaths	Ecologically parallel
Dahl 1957: 123	Phyllodoco-Juncetum trifidi medio-alpinum	
Resvoll-Holmsen 1932: 26	Empetrum-heaths	Increased area occupied towards altitudes corresponding to MA; reported to form a "neighbour-association" to Juncus trifidus-meadows, closely agreeing with our observations
Samuelsson 1917b: 18	Juncus trifidus-reiche Flechtenheiden, p.p. Carex rigida-reiche Flechtenheiden p.p.	
Tengwall 1920: 386	Zwergstrauchheidenaequivalente	with dominance of Juncus trifidus
T. Fries 1913: 76, 66	Flechtenreiche Juncus trifidus-Ass., Flechtenreiche Empetrum-Ass.	
Dahl et al. 1971: 10	Arctostaphylo-Cetrarion nivialis p.p., (mesic part), Phyllodoco-Vaccinon myrtilli (drier part)	

so than in the submesic series. *Cetraria islandica* is the most abundant lichen species, and increases with altitude just as the closely related *C. ericetorum* which is only common in the alpine zones. *Dicranum scoparium* is the only important bryophyte species.

Among the more common species *Melampyrum pratense*, *Sphagnum nemoreum* and the tree species are confined to the boreal zones. *Calluna vulgaris*, *Vaccinium uliginosum*, *Hylocomium splendens*, *Plagiothecium curvifolium+denticulatum+laetum* and *Cladonia fimbriata* disappear in the upper part of the low alpine zone. The same fact is true for *Arctostaphylos alpina* and *Carex bigelowii* which are restricted to the upper boreal and low alpine zones. *Loiseleuria procumbens*, *Juncus trifidus*, *Plagiothecium piliferum*, and *Cladonia coccifera* occur in the three uppermost zones.

A total of 29 species is recorded in all four zones.

Empetrum hermaphroditum, *Vaccinium vitis-idaea*, *Ptilidium ciliare*, *Cetraria islandica*, and the less abundant *Leucobryum*

glaucum have their optima in the subxeric series.

The subxeric series contains several species absent from the xeric series (cf. Tab. 6); *Picea abies*, *Melampyrum pratense*, *Rubus chamaemorus*, *Hylocomium splendens*, *Plagiothecium curvifolium+denticulatum+laetum*, *P. piliferum*, *Sphagnum nemoreum*, *Barbilophozia hatcheri*, *B. lycopodioides*, *Cladonia cornuta*, and *C. ecmocyna*. Common species in the subxeric series which are more rarely encountered in the xeric series are *Vaccinium myrtillus*, *Deschampsia flexuosa*, *Pleurozium schreberi*, *Barbilophozia floerkei*, and *Cladonia fimbriata*. Present in the subxeric series and absent from the submesic series are *Pinus sylvestris*, *Arctostaphylos alpina*, *Loiseleuria procumbens*, *Dicranum polysetum*, *Leucobryum glaucum*, and *Racomitrium lanuginosum*. *Calluna vulgaris* and the *Cladina* spp. are also much more important in the subxeric series.

The sparse occurrence of *Empetrum hermaphroditum* in the middle boreal zone is probably due to competition with *Calluna vulgaris*, a view strengthened by its increased abundance in higher zones.

Cetraria nivalis is the chionophobous lichen species with widest amplitude towards mesic habitats (cf. Nordhagen 1943: 89), and is also the only wind lichen that was found in the middle boreal zone (xeric series). This species seems therefore to be superior to the others in competitive ability.

The present study indicates that *Cetraria ericetorum* is a chionophobous species, as also pointed out by Nordhagen (1943: 178). We agree with Nordhagen (1943) that *Cetraria islandica* also increases with altitude, but in Grunningsdalen the latter cannot be classified as strictly chionophilous, as it has a wide range along the moisture-snow cover-gradient with an optimum in the subxeric series.

In Grunningsdalen *Cladonia stellaris* decreases from the xeric to the subxeric series, in contrast to the other *Cladonia* species. Some of the small *Cladonia* spp., e.g. *C. bellidiflora*, *C. coccifera*, *C. gracilis*, *C. pleurota*, *C. pyxidata* coll., *C. squamosa*, and *C. sulphurina*, seem to be ubiquitous.

The subxeric series is met with on relatively dry soil, in the bottom of the valley often on sandy or gravelly morainic deposits with low water capacity. In the mountains the soil is often sandy, and dries out rapidly. In the middle boreal zone the often scattered individuals of pine promote high insolation and a drying-out effect. The high amount of light reaching the understorey is illustrated by the great importance of photophilous species, e.g. *Calluna vulgaris* and *Cladina* spp. High summer temperatures due to high insolation may also be an important factor, giving dry conditions in the upper boreal zone. This is illustrated by the wide extension of the subxeric series in the upper boreal zone of the southerly exposed Blåtjørnfjell. On the other hand it is absent or has minor areal importance in the moist and shady northerly exposed transects (cf. Bergland 1975: 35 and Moen 1978). The birch forest in the upper boreal subxeric site-type is not as closed as in the more mesic series. The insolation is high, and so is the effect of winds (cf. Nordhagen 1943: 169).

SUBMESIC SERIES

Middle boreal zone

The floristic composition of this site-type is given in Tab. 25. The constant species are: *Betula pubescens*, *Picea abies*, *Sorbus aucuparia*, *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *Deschampsia flexuosa*, *Dicranum majus*, *D. scoparium*, *Hylocomium splendens*, *Plagiothecium curvifolium+denticulatum+laetum*, *Pleurozium schreberi*, *Barbilophozia floerkei*, *B. lycopodioides*, *Cladonia bellidiflora*, *C. carneola*, and *C. furcata*.

The site-type is spruce forest. *Vaccinium myrtillus* and *Deschampsia flexuosa* are the dominants of the field layer. The bottom layer is dominated by *Dicranum scoparium*, *Barbilophozia floerkei*, and *B. lycopodioides*.

The mean number of species is 30, while the total number in the 11 sample plots is 70.

All layers are more densely stocked than in the subxeric series. The canopy cover is greater, and in contrast to the subxeric series there is often a well-developed shrub layer with *Betula pubescens* and *Sorbus aucuparia*. The total cover in the bottom layer sometimes reaches 100 per cent.

In its typical state this site-type is physiognomically different from the middle boreal subxeric site-type. *Empetrum hermaphroditum*, *Vaccinium uliginosum* and in particular *Calluna vulgaris*, are less abundant in the submesic series. *Calluna vulgaris* only occurs accidentally. Characteristic features of this site-type are the great cover of *Deschampsia flexuosa*, and the importance of herbs, in particular *Cornus suecica*, *Maianthemum bifolium*, *Melampyrum pratense*, and *Trientalis europaea*. Bryophytes are much more important than lichens in the bottom layer. Dense stands of *Barbilophozia floerkei* and *B. lycopodioides* are commonly observed, while the *Cladonia* spp. have low cover or are absent. The small *Cladonia* spp. are, however, well-represented.

The floristic variation within the site-type is small, and the dominance relations in the field layer are stable. *Cornus suecica* may lack or have low cover near the xeric end of the site-type (e.g., plots Nos 4, 5, and 9). The variation in dominance relations in the bottom layer is considerable; for example in the relations between *Dicranum* spp., *Pleurozium schreberi*, and *Barbilophozia* spp. Plots Nos 6 and 8 illustrate more mesic forms dominated by *Sphagnum* spp.

The site-type is generally more favourable than the subxeric series regarding moisture conditions (and consequently also somewhat more favourable edaphically). The soil is often composed of fine particles, giving high water capacity. The dense canopies give shade, preventing a rapid drying-out. An effect of the closed tree layer is the poverty of photophilous species like *Calluna vulgaris* and *Cladonia* spp. The fresh character is also illustrated by the abundance of hepatics. The site-type has its widest distribution in the northerly exposed Nordfjell and Sigurdbunut transects. The site-type is normally situated on level ground or in small concavities. On the shaded northfacing slopes it also covers small convexities.

Tab. 25. The vegetation of the middle boreal submesic site-type.

Transect No.	1			2		3				4		C- \bar{C}
Plot No.	1	2	3	4	5	6	7	8	9	10	11	
Altitude (m)	770	770	780	710	730	710	720	730	710	710	750	
Slope (°)	25	25	35	25	15	20	30	30	15	25	20	
Aspect	SSE	ESE	NE	SW	ESE	N	N	NNW	NNW	WNW	W	
TA	2	3	+	2	3	3	3	0	1	6	6	
TB	+	1	1	0	+	+	1	+	+	+	1	
TC	6	7	7	7	8	6	8	6	6	8	9	
TD	8	9	10	9	6	9	10	10	9	6	6	
TE	1	+	0	+	1	+	0	0	+	1	+	
TF	+	0	0	+	0	0	0	+	1	+	0	
A <i>Betula pubescens</i>	2	1	2	.	.	2	4	45-3
<i>Picea abies</i>	3	4	1	3	4	4	3	.	2	5	4	91-4
B <i>Betula pubescens</i>	.	2	2	.	1	1	2	1	1	1	1	82-1
<i>Sorbus aucuparia</i>	1	1	1	.	.	1	2	1	.	.	1	64-1
C <i>Betula pubescens</i>	1	1	1	.	.	1	1	.	1	.	1	64-1
<i>Picea abies</i>	.	.	1	+	.	1	1	36-1
<i>Sorbus aucuparia</i>	1	1	1	+	.	1	1	1	1	1	1	91-1
<i>Calluna vulgaris</i>	.	.	1	1	.	.	1	27-1
<i>Empetrum hermaphroditum</i>	1	1	1	.	.	1	1	2	3	1	1	82-1
<i>Vaccinium myrtillus</i>	4	5	5	5	5	4	5	4	4	5	4	100-5
<i>V. uliginosum</i>	.	.	1	.	2	1	.	3	2	.	1	55-2
<i>V. vitis-idaea</i>	2	1	1	1	1	.	.	.	1	1	1	73-1
<i>Blechnum spicant</i>	.	.	1	.	1	1	27-1
<i>Cornus suecica</i>	2	.	3	.	.	2	2	2	1	.	.	55-2
<i>Maianthemum bifolium</i>	1	1	1	.	1	.	1	45-1
<i>Melampyrum pratense</i>	.	.	.	1	1	1	2	2	1	1	2	73-1
<i>Trientalis europaea</i>	1	1	.	.	1	1	1	45-1
<i>Deschampsia flexuosa</i>	3	3	2	4	2	4	3	2	2	2	5	100-3
D <i>Dicranum majus</i>	1	2	2	1	1	.	2	1	.	1	1	82-1
<i>D. scoparium</i>	4	1	1	3	3	1	4	2	1	2	2	100-3
<i>Hylocomium splendens</i>	1	1	2	1	.	1	3	1	1	1	.	82-1
<i>Plagiothecium curv.+dent.+laet..</i>	1	1	1	1	1	1	1	1	1	1	.	82-1
<i>Pleurozium schreberi</i>	1	2	2	2	2	1	2	1	3	1	1	100-2
<i>Polytrichum formosum</i>	.	.	1	.	1	.	1	27-1
<i>Ptilium crista-castrensis</i>	.	.	1	.	1	.	1	27-1
<i>Barbilophozia floerkei</i>	2	5	5	1	1	.	1	5	4	4	1	91-4
<i>B. lycopodioides</i>	3	4	2	5	4	1	5	1	2	3	5	100-4
<i>Calypogeia integristipula</i>	1	1	1	.	.	1	.	.	.	1	.	45-1
<i>C. neesiana</i>	.	.	1	1	.	1	27-1
<i>Cephalozia spp.</i>	1	1	1	.	.	1	.	.	.	1	.	45-1
<i>Lophozia ventricosa</i>	1	1	1	1	1	.	1	1	.	1	.	73-1
<i>Ptilidium ciliare</i>	1	1	1	1	.	.	1	.	.	1	1	64-1
<i>Cetraria islandica</i>	.	1	1	1	1	.	.	3	1	1	1	73-1
<i>Cladonia arbuscula</i>	1	.	.	1	.	.	.	1	1	1	.	36-1
<i>C. bellidiflora</i>	1	1	1	1	1	.	1	1	1	1	.	82-1
<i>C. carneola</i>	1	1	1	1	1	.	.	1	1	1	1	82-1
<i>C. furcata</i>	1	2	1	1	1	.	1	1	1	1	.	82-1
<i>C. gracilis</i>	1	1	1	1	.	36-1
<i>C. pleurota</i>	1	1	1	1	.	.	.	45-1
<i>C. pyxidata coll.</i>	1	1	.	1	1	.	.	1	1	1	1	73-1
<i>C. rangiferina</i>	1	1	1	1	2	1	.	55-1
<i>C. sulphurina</i>	1	1	1	1	1	.	.	45-1
Vascular plants	10	11	14	9	10	13	13	10	11	8	10	11
Bryophytes	15	12	17	11	11	16	11	11	7	12	6	12
Lichens	12	11	9	6	5	0	2	9	10	10	3	7
Total number of species	37	34	40	26	26	29	26	30	28	30	19	30

Additional species occurring in 2 sample plots or less (Plot No., cover - constancy-characteristic degree of cover):

B: *Picea abies* (11:1 - 9-1).

C: *Juniperus communis* (9:1 - 9-1), *Lycopodium annotinum* (2:1, 7:1 - 18-1), *L. clavatum* (4:1 - 9-1), *Dryopteris assiniensis* (2:1, 7:1 - 18-1), *Linnaea borealis* (3:1, 7:1 - 18-1), *Rubus chamaemorus* (6:2, 8:1 - 18-2), *Solidago virgaurea* (3:1, 6:1 - 18-1), *Nardus stricta* (4:1, 8:1 - 18-1).

D: *Brachythecium reflexum* (6:1, 7:1 - 18-1), *B. starkei* (2:1, 4:1 - 18-1), *Dicranum fuscescens* (1:1 - 9-1), *Orthodicranum montanum* (1:1 - 9-1), *Pohlia drummondii+nutans* (6:1 - 9-1), *Polytrichum commune* (6:3 - 9-3), *Rhytidiadelphus loreus* (3:2, 6:1 - 18-2), *Tetraphis pellucida* (10:1 - 9-1), *Sphagnum angustifolium* (6:1 - 9-1), *S. girgensohnii* (6:5 - 9-5), *S. nemoreum* (5:1, 8:2 - 18-2), *S. russowii* (3:1, 6:4 - 18-3), *Barbilophozia attenuata* (1:1, 9:1 - 18-1), *B. barbata* (5:1 - 9-1), *Cephalozia spp.* (1:1 - 9-1), *Diplophyllum taxifolium* (1:1 - 9-1), *Lophozia obtusa* (6:1 - 9-1), *Tritomaria quinqueidentata* (3:1 - 9-1), *Cladonia cornuta* (3:1 - 9-1), *C. crispata* (9:1 - 9-1), *C. deformis* (1:1 - 9-1), *C. fimbriata* (1:1, 10:1 - 18-1), *C. mitis* (9:1 - 9-1), *C. phyllophora* (1:1 - 9-1).

Tab. 26. Types described by other authors corresponding to the middle boreal submesic site-type. D - important difference from Grunningsdalen.

Reference	Name of vegetation types	Comments
Kielland-Lund 1981: 164, 1962b: 45	Eu-Piceetum myrtilletosum, Wald- hochgebiets from (Barbilophoz- ia-Ausbildung) (= typical var. 1962) and Hochlagenform (Rhyti- diadelphus loreus-Ausbildung) (= Cornus-var. 1962)	Corresponding to types without and with oceanic/moisture-de- manding spp. respectively, ele- ments of both are present in Grunningsdalen
Kielland-Lund 1962a: 136, 1965a: 38, 1965 b: 31, 1971: 24, 1973: 186, Dahl et al. 1971: 513	Eu-Piceetum myrtilletosum	
Gjerlaug 1973: 55	Vaccinium myrtillus-dominated forest	D: Gymnocarpium dryopteris constant
Resvoll-Holmsen 1918: 203	Spruce forest rich in bryophytes	
Bendiksen & Schumacher 1982: 39	Submesic series (Vaccinium myr- tillus-spruce forest)	D: Herbs often lacking, Cor- nus absent, Hylocomium splen- dens main bottom layer domi- nant
Bendiksen 1980: 27	Eu-Piceetum myrtilletosum	D: Empetrum, Vaccinium uligi- nosum, Cornus, Barbilophozia floerkei absent
Aune 1978: 24	Eu-Piceetum myrtilletosum, montane form	D: Same tendencies as above
Bendiksen & Salvesen 1985	Submesic series (Vaccinium myr- tillus-spruce forest)	D: Same tendencies as above
Bergland 1975: 78, 96	Eu-Piceetum myrtilletosum	D: Greater importance of Pteri- dium, sparse occurrence of bryophytes
	Eu-Piceetum cornetosum	Floristically more similar
Odland 1978: 41	Corno-Betuletum myrtilletosum, typicum and Cornus suecica- variant	D: Ferns, grasses and herbs more important
Huseby & Odland 1981: 14	Vaccinium myrtillus-dominated birch and pine forest	D: As above
Odland 1979: 35	Prealpine Vaccinium myrtillus- dominated birch forest	D: As above
Losvik 1978: 39	Corno-Betuletum myrtilletosum	Earlier successional stages
Omberg 1980: 95	Eu-Piceetum	D: Lower affinity in the bot- tom layer
Rodvelt & Sekse 1980: 107	Eu-Piceetum myrtilletosum	
Nedkvitne & Thomter 1953: 256	Vaccinium myrtillus-type	D: More eutrophic spp., incl. low ferns
Odland 1981b: 9	Vaccinium myrtillus-dominated birch and pine forest	D: More ferns, less of Barbi- lophia spp.
Aune 1973: 24	Corno-Betuletum subass. myrtil- letosum	D: Low importance of Barbilo- phozia spp.
Klokk 1974: 74	Vaccinium myrtillus-community	D: Lower affinity in the bot- tom layer
Kjelvik 1978: 74	Eu-Piceetum myrtilletosum	
Moen 1979	Vaccinium myrtillus spruce forest	

Tab. 26 (continued)

Reference	Name of vegetation types	Comments
McVean & Ratcliffe 1962: 15	Betuletum Oxaletum-Vaccinietum	Highly oceanic ecological parallel
Samuelsson 1917a: 59	Heidenfichtenwälder: Cornus suecica-reichen Fichtenwald and Heidelbeerreichen Fichtenwald	
Malmström 1949: 60	Vaccinium myrtillus-forest Cornus-forest	D: Cornus absent, hepatics sparse, lichens \pm abundant
Arnborg 1943: 167, 185	Vaccinium myrtillus-union, subtypes with and without Cornus. Ptilium crista-castrensis-Hylocomium splendens-union (incl. Barbilophozia-rich types)	Field layer synusium Bottom layer synusium
Arnborg 1940: 135	Frische Zwergstrauchtyp/Ptilium christa-castrensis-Hylocomium splendens-Union	
Arnborg 1942: 187, 1945, Frisk ristyp Eneroth 1937: 835		
Eneroth 1931: 132, Ron-ge 1936a: 154	Myrtillus-Typ	
O. Tamm 1935: 292	Vaccinium-typ with and without Sphagnum	
Kalela 1961: 70, 74	Vaccinium-Myrtillus-Type (VMT) and Deschampsia-Myrtillus-Typ (DMT) (zone of Pohjanmaa), Hylocomium-Myrtillus-Typ (HMT) (Peräpohjola)	
Hämet-Ahti 1963: 81	Cornus-Myrtillus type (CoMT)	
Lakari 1920: 3	Hylocomium-Myrtillus-Typ (HMT)	
Resvoll-Holmsen 1914a: 13	(corresponding birch forests rich in Cornus suecica)	
Kujala 1929: 47	Cornus-Myrtillus-Typ (CoMT)	
Nihlgård 1980: 36	Vaccinium myrtillus-type	

Plot No. 9 illustrates the vegetation of a convexity close to the transition to the subxeric series. Plot No. 1 is from a southerly exposed convexity. The reason for the development of submesic vegetation at this station is the locally humid climate in the vicinity of the River Londøla.

Comparison with other investigations is given in Tab. 26.

Upper boreal zone

The floristic composition of this site-type is given in Tab. 27. The constant species are: *Betula pubescens*, *Sorbus aucuparia*, *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *V. uliginosum*, *V. vitis-idaea*, *Cornus suecica*, *Melampyrum pratense*, *Trientalis europaea*, *Deschampsia flexuosa*, *Dicranum scoparium*, *Plagiothecium curvifolium+denticulatum+laetum*, *Pleurozium schreberi*, *Barbilophozia lycopodioides*, and *Lophozia ventricosa*.

Betula pubescens is the dominant of the tree layer, and may also dominate the shrub layer. Dominants in the field layer are *Vaccinium myrtillus*, *V. uliginosum*, *Cornus suecica*, and *Deschampsia flexuosa*, rarely also *Empetrum hermaphroditum*. The

Tab. 27. The vegetation of the upper boreal submesic site-type.

Transect No.		1				2		3		C- \bar{c}
Plot No.		1	2	3	4	5	6	7	8	
Altitude (m)		870	880	980	1000	1000	1060	820	830	
Slope (°)		20	25	25	30	20	30	25	30	
Aspect		NE	NE	NE	NE	S	SSE	NW	NNW	
TA		3	2	4	2	7	0	2	1	
TB		+	1	+	1	+	6	+	+	
TC		8	8	9	9	8	8	8	5	
TD		9	10	6	9	+	+	9	10	
TE		0	0	+	+	+	1	1	0	
TF		+	0	0	+	+	+	+	+	
A	<i>Betula pubescens</i>	4	3	4	3	5	.	3	2	88-4
	<i>Picea abies</i>	1	2	25-2
	<i>Sorbus aucuparia</i>	1	1	25-1
B	<i>Betula pubescens</i>	1	2	1	2	.	5	1	1	88-3
	<i>Sorbus aucuparia</i>	1	1	1	1	1	1	.	1	88-1
C	<i>Betula pubescens</i>	1	1	1	1	.	1	1	1	88-1
	<i>Picea abies</i>	.	1	.	1	25-1
	<i>Populus tremula</i>	1	1	.	.	25-1
	<i>Sorbus aucuparia</i>	1	1	1	1	1	.	1	1	88-1
	<i>Calluna vulgaris</i>	1	.	1	.	25-1
	<i>Empetrum hermaphroditum</i>	1	2	2	4	.	1	1	3	88-2
	<i>Juniperus communis</i>	1	2	.	.	25-2
	<i>Lycopodium annotinum</i>	.	1	1	.	25-1
	<i>Phyllocladus caerulea</i>	.	.	1	1	.	.	.	1	38-1
	<i>Vaccinium myrtillus</i>	5	4	5	4	3	4	5	4	100-5
	<i>V. uliginosum</i>	2	1	2	3	1	3	4	2	100-3
	<i>V. vitis-idaea</i>	1	1	1	1	1	1	1	.	88-1
	<i>Cornus suecica</i>	3	3	3	3	2	.	3	2	88-3
	<i>Maianthemum bifolium</i>	.	1	1	.	1	1	.	.	50-1
	<i>Melampyrum pratense</i>	2	1	1	1	3	1	1	1	100-1
	<i>Rubus chamaemorus</i>	1	2	25-2
	<i>Solidago virgaurea</i>	1	1	.	.	1	1	.	.	50-1
	<i>Trientalis europaea</i>	1	1	1	1	2	1	1	.	88-1
	<i>Deschampsia flexuosa</i>	3	4	3	3	5	4	3	3	100-4
	<i>Nardus stricta</i>	1	1	25-1
D	<i>Brachythecium reflexum</i>	1	1	.	.	25-1
	<i>B. starkei</i>	4	2	4	3	.	.	1	1	75-3
	<i>Dicranum scoparium</i>	2	3	2	1	1	1	2	2	100-2
	<i>Hylacomium splendens</i>	2	2	.	1	.	.	3	1	63-2
	<i>Orthodicranum montanum</i>	1	1	.	.	25-1
	<i>Plagiothecium curv.+dent.+laet.</i>	1	1	1	1	1	.	1	1	88-1
	<i>P. piliferum</i>	1	1	.	.	25-1
	<i>Pleurozium schreberi</i>	2	3	2	4	1	1	3	1	100-3
	<i>Pohlia drummondii+nutans</i>	1	1	.	.	25-1
	<i>Polytrichum formosum</i>	1	2	1	.	38-1
	<i>P. strictum</i>	.	.	1	.	.	.	1	2	38-1
	<i>Tetraphis pellucida</i>	.	.	1	1	.	.	1	.	38-1
	<i>Sphagnum russowii</i>	1	1	25-1
	<i>Barbilophozia floerkei</i>	3	5	.	2	.	1	1	5	75-4
	<i>B. hatcheri</i>	.	.	1	2	25-2
	<i>B. lycopodioides</i>	3	2	4	4	1	1	2	1	100-3
	<i>Calypogeia integristipula</i>	.	.	1	1	25-1
	<i>Cephalozia spp.</i>	1	.	1	.	.	.	1	1	50-1
	<i>Lophocolea heterophylla</i>	1	.	1	.	1	.	.	.	38-1
	<i>Lophozia obtusa</i>	1	1	2	.	38-1
	<i>L. ventricosa</i>	1	1	1	1	1	.	1	1	88-1
	<i>Ptilidium ciliare</i>	1	2	1	1	1	.	1	.	75-1

Tab. 27 (continued)

Transect No.	1				2		3			
Plot No.	1	2	3	4	5	6	7	8	C-C	
<i>Cetraria islandica</i>	1	2	1	1	.	.	.	1	63-1	
<i>Cladonia bellidiflora</i>	.	1	1	25-1	
<i>C. carneola</i>	1	1	1	1	.	1	.	1	75-1	
<i>C. crispata</i>	.	1	1	25-1	
<i>C. ecmocyna</i>	.	.	1	1	25-1	
<i>C. fimbriata</i>	1	.	.	1	1	1	1	.	63-1	
<i>C. furcata</i>	.	.	1	.	.	.	1	1	38-1	
<i>C. pleurota</i>	.	.	.	1	1	.	.	.	25-1	
<i>C. pyxidata</i> coll.	1	.	1	.	1	.	1	1	63-1	
<i>C. rangiferina</i>	.	1	.	1	.	.	.	1	38-1	
<i>C. sulphurina</i>	1	1	1	38-1	
Vascular plants	12	15	12	12	15	16	15	13	14	
Bryophytes	14	11	13	12	14	9	21	16	14	
Lichens	6	6	7	6	3	2	4	6	5	
Total number of species	32	32	32	30	32	27	40	35	33	

Additional species occurring in 1 sample plot (Plot No:cover):

B: *Picea abies* (8:1).

C: *Andromeda polifolia* (8:1); *Gentiana purpurea* (6:1); *Gymnocarpium dryopteris* (6:1); *Listera cordata* (8:1); *Melampyrum sylvaticum* (7:1); *Anthoxanthum odoratum* (6:1); *Luzula pilosa* (5:1).

D: *Calliergon stramineum* (7:1); *Dicranum fuscescens* (5:1); *D. majus* (7:1); *Polytrichum commune* (5:1); *P. juniperinum* (5:1); *P. longisetum* (6:1); *Ptilium crista-castrensis* (7:2); *Sphagnum nemoreum* (8:3); *Barbilophozia barbata* (7:1); *Calypogeia muelleriana* (8:1); *C. neesiana* (7:1); *Cephaloziella* spp. (5:1); *Kurzia trichoclados* (7:1); *Mylia anomala* (8:1); *M. taylorii* (8:1); *Sphenolobus minutus* (8:1); *Cladonia cornuta* (1:1); *Nephroma arcticum* (7:1).

main dominants in the bottom layer are *Brachythecium starkei*, *Pleurozium schreberi*, *Barbilophozia floerkei*, and *B. lycopodioides*.

The mean number of species is 33, while the total number in the 8 sample plots is 78.

This site-type is a moderately closed birch forest characterized by dominance of *Vaccinium myrtillus*, *Deschampsia flexuosa*, and *Cornus suecica*. The latter reaches its optimum here. Another characteristic feature is the thick bryophyte carpet in the bottom layer. The lichens, though numerous in species, have low abundance.

A strong contrast in floristic composition is found between the humid, north-facing and the drier, south-facing slopes. The former contain a fresh form of the site-type with abundance of *Vaccinium myrtillus*, *Cornus suecica*, and with bryophytes prevailing. Plot No. 8 from Nordfjell is the moist extreme, dominated by *Barbilophozia floerkei*, with subdominance of *Sphagnum nemoreum*, and presence of *Andromeda polifolia*, *Listera cordata*, *Polytrichum strictum*, *Mylia anomala*, and *M. taylorii*. On the drier south-facing slopes of Blåtjørnfjell, *Deschampsia flexuosa* is more abundant, *Juniperus communis* and *Populus tremula* occur, and the bryophytes form a less vital and more open bottom layer (cf. plots Nos 5 and 6). Plot No. 4 is an *Empetrum*-rich type and No. 7 a type rich in *Hylocomium splendens* and *Ptilium crista-castrensis*.

Tab. 28. Types described by other authors corresponding to the upper boreal submesic site-type. D - important difference from Grunningsdalen.

Reference	Name of vegetation types	Comments
Kielland-Lund 1981: 165, (1971, 1973)	Eu-Piceetum myrtilletosum, sub-alpine Birkenwaldform	
Nordhagen 1928: 112, 1937: 71	Myrtillus-reicher Birkenwald, main type and Cornus-variety	D: Incl. more eutrophic spp.
Christophersen 1925: 505	Vaccinium myrtillus-Betula pubescens-forest	
Nordhagen 1943: 146	Betuletum Myrtillo-Hylocomiosum Betula tortuosa-Vaccinium myrtillus-soc. Betula tortuosa-Vaccinium myrtillus-Cornus suecica-soc.	(continental type), D: More eutrophic, poor in bryophytes (oceanic type), D: Gymnocarpium constant
Gjerlaug 1973: 49, 57	Mountain spruce forest, mountain birch forest	D: Gymnocarpium and Nardus common
Haug 1970: 82	Barbilophozio-Pinetum	A few analyses transitional to SX, most of them typical SM
Mork & Låg 1959: 53	Myrtillus type	Spruce forest
Resvoll-Holmsen 1918: 190, 194	(Corresponding birch and pine forests)	
Resvoll-Holmsen 1914b: 14	(birch forests p.p.)	
Resvoll-Holmsen 1932: 19	Vaccinium myrtillus-dominated birch forest	
Mork & Heiberg 1937: 641	Vaccinium-Picea-Betula-soc.	
Bendiksen & Schumacher 1982: 40	Submesic series (Vaccinium myrtillus- birch forest)	
Aune 1978: 24	Eu-Piceetum myrtilletosum, sub-alpine form	
Bergland 1975: 78	Eu-Piceetum p.p. incl. subass. cornetosum	
Huseby & Odland 1981: 14	Vaccinium myrtillus-dominated birch and pine forest	
Odland 1979: 37	Subalpine Vaccinium myrtillus-dominated birch forest	
Rodvelt & Sekse 1980: 104	Myrtillo-Betuletum subass. myrtilletosum	cf. Nordhagen 1943, Kielland-Lund 1973 D: High constancies of Gymnocarpium and Potentilla
Fredriksen 1978: 52	Corno-Betuletum myrtilletosum	D: Poor in Barbilophozia spp., Hylocomium splendens abundant
Fægri 1934: 91	Gras-Myrtillus-reiches Betula-Gebüsch	D: Earlier successional stage
Kummen 1977: 51	Eu-Piceetum myrtilletosum	D: High constancy of low ferns and oceanic spp., Barbilophozia spp. sparse
Odland 1981b: 9	Vaccinium myrtillus-dominated birch and pine forest	D: More ferns, Barbilophozia spp. sparse
Hagen 1976: 125	Betula pubescens-Vaccinium Myrtillus community	Only one stand poor
Moen 1978: 52	Myrtillus-community	
Samuelsson 1917a: 61	Heidelbeer-reichen Fichtenwald	Both spruce and birch forests
Smith 1920: 34	Vaccinium myrtillus-rich birch forest	

Tab. 28 (continued)

Reference	Name of vegetation types	Comments
Tengwall 1920: 330	Vaccinium myrtillus-rich birch forest	
Malmström 1949: 61	Cornus-forest	Partly birch-, partly conifer-dominated
T. Fries 1913: 59	Moosbirkenwald, Betula odorata-Hylocomium-ass.	
Sonesson & Lundberg 1974: 130	Empetrum-Vaccinium myrtillus-type, Vaccinium myrtillus-type	Particularly great affinity with Cornus-var. of the latter
Kalela 1961: 82	Ledum-Myrtillus-Typ (LMT)	D: Presence of Ledum
Kalela 1961: 82, Hämet-Ahti 1963: 52	Subalpine Empetrum-Myrtillus-Typ (sEMT)	
Hämet-Ahti 1963: 70, 74	Cornus-Empetrum-Myrtillus type (CoEMT) p.p., Cornus-Myrtillus type (CoMT)	
Resvoll-Holmsen 1914a: 13	(Corresponding forest types)	D: Somewhat more eutrophic
Thannheiser 1975: 78, 81	Myrtillus-Heide-Birkenwald; Etagenmoos-Heidelbeer-Birkenwald, Hartriegel-Heidelbeer-Birkenwald (Cornus-rich form)	
Lippmaa 1929: 34	Die Formation der Heidelbeerwälder	
Kujala 1929: 47	Cornus-Myrtillus-Typ (CoMT)	
Kalela 1939: 63, 62	Vaccinium myrtillus-Heide, Empetrum nigrum-Vaccinium myrtillus-Heide p.p.	
Nihlgård 1980: 48, 68	Mixed forest of dwarf shrub-grass-type, mountain birch forest of dwarf shrub-grass-type	

The submesic series covers large areas in the steep and shaded north-facing mountain slopes in the upper boreal zone where it also may cover convex terrain forms. On the southerly exposed Blåtjørnfjell it is mostly replaced by the subxeric series.

Comparison with other investigations is given in Tab. 28.

Low alpine zone

The floristic composition of this site-type is given in Tab. 29. The constant species are: *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *V. uliginosum*, *Deschampsia flexuosa*, *Dicranum scoparium*, *Pohlia drummondii+nutans*, *Cetraria islandica*, and *Cladonia pyxidata* coll.

Dominants in the field layer are *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *V. uliginosum*, *Deschampsia flexuosa*, and sometimes also *Cornus suecica*. Species that have been observed as dominants in the bottom layer are *Dicranum scoparium*, *Pleurozium schreberi*, *Barbilophozia floerkei*, *B. lycopodioides*, and *Cetraria islandica*.

Tab. 29. The vegetation of the low alpine submesic site-type.

Transect No.	1			2			3			4			
Plot No.	1	2	3	4	5	6	7	8	9	10	C-E		
Altitude (m)	1090	1100	1330	1070	1140	1140	930	960	1000	1000			
Slope (°)	15	15	35	25	10	15	35	35	30	25			
Aspect	E	E	SSE	SSW	NW	WNW	NE	NNE	NNW	NW			
TA	0	0	0	0	0	0	0	0	0	0			
TB	0	0	0	0	0	0	0	0	0	0			
TC	8	8	7	9	7	7	8	7	8	9			
TD	4	6	3	+	5	6	10	6	9	6			
TE	1	+	2	1	+	+	0	1	+	+			
TF	+	+	0	0	1	1	0	0	0	+			
C <i>Sorbus aucuparia</i>	1	1	1	.	30-1		
<i>Empetrum hermaphroditum</i>	3	2	2	1	2	3	3	2	4	2	100-3		
<i>Phyllocladus caerulea</i>	1	.	.	.	1	.	1	2	1	.	50-1		
<i>Vaccinium myrtillus</i>	5	5	5	5	4	5	4	5	5	5	100-5		
<i>V. uliginosum</i>	2	3	3	3	1	.	4	1	1	4	90-3		
<i>V. vitis-idaea</i>	1	1	.	1	1	40-1		
<i>Cornus suecica</i>	2	3	.	1	.	.	2	3	3	2	70-3		
<i>Rubus chamaemorus</i>	.	1	.	.	2	1	.	1	1	.	50-1		
<i>Solidago virgaurea</i>	1	.	.	1	.	1	.	1	.	1	50-1		
<i>Trientalis europaea</i>	1	1	1	1	.	.	1	1	1	3	80-1		
<i>Carex bigelowii</i>	.	.	.	1	2	1	30-1		
<i>Deschampsia flexuosa</i>	2	3	2	4	3	4	2	4	3	4	100-3		
<i>Nardus stricta</i>	1	.	.	2	1	2	40-2		
D <i>Brachythecium starkei</i>	1	2	1	1	40-1		
<i>Dicranum fuscescens</i>	1	1	1	1	1	.	.	.	1	1	60-1		
<i>D. scoparium</i>	3	2	2	1	2	3	1	1	4	3	100-3		
<i>Plagiothecium curv.+dent.+laet.</i>	1	1	.	1	1	1	1	1	1	1	80-1		
<i>P. piliferum</i>	1	.	.	.	1	1	30-1		
<i>Pleurozium schreberi</i>	1	1	5	.	3	2	50-3		
<i>Pohlia drummondii+nutans</i>	1	1	1	1	1	1	1	1	1	1	100-1		
<i>Polytrichum formosum</i>	.	1	.	.	2	.	.	.	1	1	40-1		
<i>P. juniperinum</i>	1	.	.	1	1	30-1		
<i>P. strictum</i>	.	.	2	.	.	.	1	2	1	1	50-1		
<i>Sphagnum nemoreum</i>	1	.	1	.	1	.	.	2	.	.	30-1		
<i>S. russowii</i>	2	2	1	.	30-2		
<i>Barbilophozia floerkei</i>	1	2	.	.	2	3	2	3	5	4	80-3		
<i>B. lycopodioides</i>	1	3	.	.	1	1	4	4	2	3	70-3		
<i>Calypogeia integristipula</i>	1	.	.	.	1	.	.	1	1	.	40-1		
<i>C. neesiana</i>	1	1	.	.	1	.	.	1	.	.	40-1		
<i>Cephalozia</i> spp.	1	1	1	.	30-1		
<i>Lophozia ventricosa</i>	1	1	1	1	1	.	.	1	2	1	80-1		
<i>Ptilidium ciliare</i>	1	.	1	1	30-1		
<i>Cetraria islandica</i>	2	2	1	1	4	4	1	1	2	1	100-2		
<i>Cladonia arbuscula</i>	1	1	1	.	1	1	.	1	.	.	60-1		
<i>C. bellidiflora</i>	1	1	1	.	1	1	.	.	.	1	60-1		
<i>C. carneola</i>	1	1	.	.	1	1	1	1	1	1	80-1		
<i>C. coccifera</i>	1	.	.	1	1	.	30-1		
<i>C. ecmocyna</i>	1	2	3	30-2		
<i>C. fimbriata</i>	1	1	1	.	1	40-1		
<i>C. furcata</i>	1	1	.	1	1	1	.	1	1	1	80-1		
<i>C. gracilis</i>	1	1	1	30-1		
<i>C. mitis</i>	1	1	.	1	.	.	30-1		
<i>C. pleurota</i>	.	1	1	1	1	.	1	1	.	1	70-1		
<i>C. pyxidata coll.</i>	1	1	1	1	1	1	.	1	1	1	90-1		
<i>C. rangiferina</i>	1	1	.	.	1	.	1	1	1	1	70-1		
<i>C. squamosa</i>	1	.	.	.	1	.	.	.	1	1	40-1		
<i>C. sulphurina</i>	1	1	1	30-1		
<i>C. uncialis</i>	1	.	1	1	.	.	30-1		
Vascular plants	11	7	5	17	12	7	9	11	12	9	10		
Bryophytes	15	13	7	5	15	6	10	16	17	15	12		
Lichens	12	9	6	4	13	7	6	13	10	12	9		
Total number of species	38	29	18	26	40	20	25	40	39	36	31		

Additional species occurring in 2 sample plots or less (Plot No., cover - constancy-characteristic degree of cover):

- C: *Betula nana* (5:2, 9:3 - 20-3), *Calluna vulgaris* (1:1, 10:1 - 20-1), *Juniperus communis* (4:1 - 10-1), *Lycopodium alpinum* (4:1 - 10-1), *Salix herbacea* (5:2 - 10-2), *Dryopteris assmilis* (8:1, 9:4 - 20-1), *Gentiana purpurea* (4:1, 5:1 - 20-1), *Hieracium alpinum* (4:1 - 10-1), *Maianthemum bifolium* (4:2 - 10-2), *Anthoxanthum odoratum* (4:1 - 10-1), *Carex brunnescens* (4:1, 5:1 - 20-1), *Juncus trifidus* (4:1 - 10-1).
- D: *Dicranum majus* (5:1 - 10-1), *Herzogiella striatella* (10:1 - 10-1), *Hylocomium splendens* (7:2, 9:1 - 20-2), *Polytrichum commune* (2:1, 5:1 - 20-1), *P. longisetum* (5:1, 6:1 - 20-1), *Tetraphis pellucida* (8:1, 10:1 - 20-1), *Barbilophozia hetcheri* (1:1 - 10-1), *Bazzania tricenata* (8:1 - 10-1), *Calypogeia muelleriana* (9:1 - 10-1), *Cephalozia* spp. (2:1, 3:1 - 20-1), *Kurzia trichoclados* (8:1 - 10-1), *Mylia taylorii* (8:1 - 10-1), *Cetraria ericetorum* (5:1 - 10-1), *Cladonia crispata* (9:1 - 10-1), *C. digitata* (10:1 - 10-1), *C. stellaris* (8:1 - 10-1), *Nephroma arcticum* (8:1 - 10-1).

The mean number of species is 31, while the total number in the 10 sample plots is 77.

Dense stands of *Vaccinium myrtillus* and most often co-dominance of *Deschampsia flexuosa* give this site-type its character. Other dwarf shrubs may also play an important role. The bottom layer is characterized by bryophytes, of which *Barbilophozia* spp. and *Dicranum* spp. are the most important. Lichens are numerous in species number, but have low abundance.

Betulanana is rare outside mires, but sometimes forms thickets in the lower part of the low alpine zone. Well-developed *Betula nana*-stands are most common in Sigurd bunut (e.g., plot No. 9). Types near the xeric end of the site-type are exemplified by plots Nos 1 and 4. The former has low cover of *Barbilophozia* spp. and *Calluna vulgaris* occurs, the latter is from a southerly exposed station in Blåtjørnfjell with strong insolation. It lacks *Barbilophozia* spp. and the bottom layer is poorly developed. The more mesic form of this site-type is represented by plots Nos 7 and 8 from the northerly exposed Nordfjell transect. *Sphagnum russowii* is common, and *Dryopteris assimilis* and *Mylia taylorii* are present.

There is also a vertical variation within the sample set. The common boreal forest mosses *Hylacomium splendens* and *Pleurozium schreberi* have high cover in plot No. 7, which is situated just above the forest limit. In contrast, the highest situated plot (No. 3) is poor in species and the forest mosses mentioned are absent.

The low alpine submesic site-type is situated on moderately moist soil with stable moisture conditions. It occupies sites protected from strong winds and has a stable snow cover of fairly long duration. Most often the site-type is found in concave localities.

Below the summit of Mælefjell, at 1330 m, a low alpine outlier dominated by submesic vegetation was observed (plot No. 3). This aberrance is explained by the location of the stand. It occupies a narrow, steeply sloping belt with southerly aspect just below a vertical wall giving high insolation, favourable temperatures, and a long growing-season. Favourable soil moisture conditions are ensured by a constant supply of trickling water from below the vertical wall. The northerly exposed slope opposite a small valley is covered with large areas dominated by middle alpine submesic *Juncus trifidus*-heaths.

Comparison with other investigations is given in Tab. 30.

Middle alpine zone

The floristic composition of this site-type is given in Tab. 31. The constant species are: *Vaccinium myrtillus*, *Deschampsia flexuosa*, *Juncus trifidus*, *Dicranum scoparium*, *Pohlia drummondii-nutans*, *Barbilophozia floerkei*, *Cetraria islandica*, *Cladonia bellidiflora*, *C. gracilis*, *C. pleurota*, *C. pyxidata* coll., and *C. squamosa*.

Dominants in the field layer are *Juncus trifidus* and *Deschampsia flexuosa*. *Cetraria islandica* is the main dominant in the bottom layer.

Tab. 30. Types described by other authors corresponding to the low alpine submesic site-type. D - important difference from Grunningsdalen.

Reference	Name of vegetation types	Comments
Nordhagen 1928: 224, 148, 150	Cladonia silvatica-reiche Vaccinium myrtillus-Ass., Vaccinium myrtillus-reiches Zwergbirken-gebüsch, Myrtillus-reiches Juniperus nana-Gebüsch	More continental; ecologically parallel
Christophersen 1925: 551.	Vaccinium myrtillus-heath	
Nordhagen 1943: 125	Phyllodoco-Vaccinietum myrtilli: Vaccinium myrtillus-Cladonia silvatica-Dicranum fuscescens-soc. (Sikilsdalen, Ørterdalen, Sylene)	Continental, lichen-rich, ecologically parallel
	Vaccinium myrtillus-Cornus suecica-Hylocomium-soc. (Myrdal)	Oceanic type, stronger affinity to Grunningsdalen
	Junipereto-Betuletum nanae myrtillosum	Ecologically parallel
Dahl 1957: 117	Phyllodoco-Vaccinietum myrtilli (Hylocomieto-Betuletum nanae)	D: More lichens and Dicranum fuscescens More eutrophic
Gjerlaug 1973: 36	Vaccinium myrtillus-rich dwarf shrub heath	D: Abundance of Betula nana, Juniperus, and Pleurozium
Resvoll-Holmsen 1914b: 30	Vaccinium myrtillus-dominated dwarf shrub heath	
Resvoll-Holmsen 1920: 76, 1932: 25	Vaccinium myrtillus-heath	
Bendiksen & Schumacher 1982: 51	Submesic series (Vaccinium myrtillus-Phyllodoca caerulea-heath)	D: Phyllodoca more common
Du Rietz 1925a: 56	Vaccinium myrtillus-Cladonia rangiferina-silvatica-Ass.	D: lichen-rich type
Hadac 1971: 209-211	Phyllodoco-Vaccinietum myrtilli, Vaccinio-Empetretum hermaphoditi scandinavicum, Empetro-Betuletum nanae	The two first types transitional to SX, the third type rich in Betula nana
Huseby & Odland 1981: 22	Alpine dwarf shrub heath p.p.	Plots Nos 10-19 oceanic SM-parallel
Odland 1979: 63	Low alpine Vaccinium myrtillus-heath	D: Some more eutrophic spp.
Rodvelt & Sekse 1980: 103	Phyllodoco-Myrtillietum	
Knaben 1952: 54, 57	Parts of Vaccinium myrtillus-Cornus suecica-Hylocomium-soc., Vaccinium myrtillus-Cladonia silvatica-Dicranum fuscescens-soc., Empetrum-var.	Including the whole range SX-SM
Malme 1971: 24	Phyllodoco-Vaccinietum myrtilli	D: More Empetrum at the expense of Vaccinium myrtillus
Poore & McVean 1957: 430	Vaccinium snowbeds	
McVean & Ratcliffe 1962: 39, 43 McVean 1964: 486, 488	Vaccinietum chionophilum, Cladinetto-Vaccinietum	
Samuelsson 1917a: 188	Vaccinium myrtillus-reiche Moosheiden	
Smith 1920: 36	Vaccinium myrtillus-heath	

Tab. 30 (continued)

Reference	Name of vegetation types	Comments
Tengwall 1920: 372, 373	Flechtenreiche-/Moosreiche <i>Vaccinium myrtillus</i> -Heide	
T. Fries 1913: 89	Moosreiche <i>Empetrum nigrum</i> -Ass. P.P.	
Gjærevoll & Bringer 1965: 258	Myrtillion	
Thannheiser 1975: 62	Myrtillion: Reine <i>Myrtillus</i> -Heide-Fluren, <i>Myrtillus</i> -Heide-Gebüsch (Heidelbeer-reiches Wacholder-Zwergbirken-Gebüsch)	
Lippmaa 1929: 45	Moosreiche <i>Vaccinium myrtillus</i> -Heide	
Hult 1887: 177	Parts of <i>Empetrum</i> - and <i>Phyllo-doce</i> -Formation	
Kalliola 1939: 218	Moosreiche <i>Empetrum</i> - <i>Myrtillus</i> -Soz.	
Kalliola 1932: 35	<i>Empetrum</i> - <i>Vaccinium myrtillus</i> -Heide	
Söyrinki 1938: 30	<i>Myrtillus</i> -Heide	
Kalela 1939: 69	Moosreiche <i>Vaccinium myrtillus</i> -Tundra	
Dahl et al. 1971: 10	<i>Phyllodoco</i> - <i>Vaccinium myrtilli</i> P.P.	
Waldemarson Jensen 1980: 59	<i>Vaccinium myrtillus</i> -type proper	

The mean number of species is 24, while the total number in the 8 sample plots is 54.

This site-type is easily recognized in the field by being a brown-coloured grass heath. *Juncus trifidus*, the main dominant, gives the site-type its character. *Deschampsia flexuosa* is the only other important species. *Vaccinium myrtillus* is almost always present, but it does not reach dominance. Except for *Cetraria islandica*, bryophytes and lichens are sparse as they do not seem to thrive well in the dense graminid vegetation.

Some variation is found in the sample set. Plot No. 5 is a type rich in bryophytes; *Dicranum scoparium* and *Barbilophozia floerkei* are both dominants. An element of snow bed species is prominent in plot No. 4. *Kiaeria starkei* and *Gymnomitrium concinnatum* occur, and *Cetraria delisei*, often recognized as snow bed species (cf. Krog et al. 1980), is a dominant. Small *Vaccinium myrtillus* stands may be found behind stones and in places otherwise providing some shelter. In contrast, *Empetrum hermaphroditum* prefers small convexities in the terrain.

This site-type is restricted to places with a stable, long-lasting snow cover with protection from strong winds. A soil profile is not developed, but a faint tendency to the development of bleached soil has been observed in some places. This site-type has high areal importance in the middle alpine zone.

Tab. 31. The vegetation of the middle alpine submesic site-type.

Transect No.	1				3				
Plot No.	1	2	3	4	5	6	7	8	C- \bar{c}
Altitude (m)	1290	1300	1310	1310	1260	1260	1260	1270	
Slope (°)	10	5	30	15	10	5	25	10	
Aspect	NW	W	E	NNW	SW	SSW	WSW	NNW	
TA	0	0	0	0	0	0	0	0	
TB	0	0	0	0	0	0	0	0	
TC	6	7	3	4	8	8	7	6	
TD	7	8	2	5	5	4	2	4	
TE	1	0	+	+	0	+	0	+	
TF	2	1	6	4	2	1	2	3	
C <i>Empetrum hermaphroditum</i>	1	.	1	2	1	1	.	2	75-1
<i>Lycopodium alpinum</i>	1	1	.	3	.	.	.	2	50-2
<i>L. selago</i>	.	.	1	1	.	.	.	1	38-1
<i>Vaccinium myrtillus</i>	1	2	1	1	2	2	1	3	100-2
<i>V. vitis-idaea</i>	1	.	.	.	1	1	.	.	38-1
<i>Solidago virgaurea</i>	1	1	.	.	25-1
<i>Trientalis europaea</i>	1	1	.	.	25-1
<i>Carex brunescens</i>	1	1	.	.	1	1	.	2	63-1
<i>Deschampsia flexuosa</i>	3	3	2	1	4	4	2	3	100-3
<i>Juncus trifidus</i>	4	5	4	4	5	5	5	4	100-5
D <i>Conostomum tetragonum</i>	.	.	1	.	.	.	1	.	25-1
<i>Dicranum fuscescens</i>	1	.	.	1	25-1
<i>D. scoparium</i>	1	1	1	1	3	2	2	1	100-2
<i>Pohlia drummondii+nutans</i>	1	1	1	2	1	.	1	1	88-1
<i>Polytrichum commune</i>	.	.	1	1	25-1
<i>Barbilophozia floerkei</i>	1	1	1	1	3	2	1	2	100-2
<i>B. hatcheri</i>	.	1	.	.	2	1	.	.	38-1
<i>B. lycopodioides</i>	1	.	1	.	25-1
<i>Lophozia ventricosa</i>	.	1	1	1	.	.	1	1	63-1
<i>Ptilidium ciliare</i>	1	.	1	1	38-1
<i>Cetraria delisei</i>	.	.	.	4	.	.	.	1	25-3
<i>C. ericetorum</i>	1	.	3	.	.	1	1	1	63-2
<i>C. islandica</i>	5	5	2	1	2	4	2	4	100-4
<i>Cladonia arbuscula</i>	1	2	.	.	1	1	1	1	75-1
<i>C. bellidiflora</i>	2	1	2	1	1	1	2	1	100-1
<i>C. coccifera</i>	1	1	1	1	.	.	.	1	63-1
<i>C. furcata</i>	2	1	1	1	50-1
<i>C. gracilis</i>	1	1	1	.	1	1	1	1	88-1
<i>C. metacorallifera</i>	.	.	.	1	.	.	.	1	25-1
<i>C. pleurota</i>	1	.	1	1	1	1	1	1	88-1
<i>C. pyxidata coll.</i>	1	1	1	.	1	1	1	1	88-1
<i>C. rangiferina</i>	1	1	25-1
<i>C. squamosa</i>	1	1	1	1	1	.	1	1	88-1
<i>C. sulphurina</i>	1	1	.	.	.	1	1	1	63-1
<i>C. uncialis</i>	1	1	25-1
<i>Stereocaulon</i> sp.	.	1	1	25-1
Vascular plants	7	5	7	6	9	9	3	8	7
Bryophytes	4	6	8	9	8	3	10	5	7
Lichens	13	10	9	7	8	10	10	16	10
Total number of species	24	21	24	22	26	22	23	29	24

Additional species occurring in 1 sample plot (Plot No.:cover):

C: *Calluna vulgaris* (3:1), *Salix herbacea* (3:1), *Hieracium alpinum* (6:1), *Rubus chamaemorus* (8:1), *Carex bigelowii* (5:1).D: *Kiaeria starkei* (4:1), *Plagiothecium curv.+dent.+laet.* (7:1), *Polytrichum piliferum* (3:1), *Cephaloziella* spp. (5:1), *Diplophyllum taxifolium* (4:1), *Gymnomitrium concinnum* (4:1), *Marsupella brevisissima* (2:1), *Nardia breidlereri* (3:1), *Sphenolobus minutus* (5:1), *Cladonia carneola* (6:1), *C. crispata* (2:1), *C. ecmocyna* (1:1), *C. mitis* (3:1).

Tab. 32. Types described by other authors corresponding to the middle alpine submesic site-type.

Reference	Name of vegetation types	Comments
Nordhagen 1928: 296	Cetraria crispa - Cladonia silvatica-reiche Juncus trifidus-Ass., Vaccinium myrtillus-var.	Ecologically corresponding
Christophersen 1925: 559	Juncus trifidus-heath	
Nordhagen 1943: 177	Juncion trifidi scandinavicum p.p.	In a figure showing zonation according to the snow-cover gradient, p. 211, Nordh. revealed the existence of a type corresponding to MA-SM, mentioned as later snow-free localities dominated by Juncus trifidus-Cetraria islandica
	Juncus trifidus - Cetraria islandica - Cladonia silvatica-soc.	Closest type described from Sikilsdalen
	Juncetum trifidi, main type A	(Hardangervidda)
Dahl 1957	Phyllodoco-Juncetum trifidi p.p.	The part without chionophobus lichens and with occurrence of Vaccinium myrtillus
Resvoll-Holmsen 1914b: 54	Juncus trifidus-formation	
Resvoll-Holmsen 1920: 120, 187, 1932: 30	Juncus trifidus grass heath	
Samuelsson 1917b: 23	Lycopodium alpinum-reiche Flechtenheiden	Some affinity
Hadac 1971: 206	Juncetum trifidi scandinavicum	
Knaben 1952: 72	Juncus trifidus-heath	
McVean & Ratcliffe 1962: 75, McVean 1964: 507	Juncus trifidus-communities	
Samuelsson 1917a: 177	Lycopodium alpinum-Heide	Some affinity
Smith 1920: 40	Juncus trifidus-heath	
Tengwall 1920: 388	Juncus trifidus-Grasheide	
Gjærevoll & Bringer 1965: 262	Middle-alpine chionophobous heaths	
Hult 1887: 177	Juncus trifidus-formation	
Dahl et al. 1971: 10	Phyllodoco-Vaccinion myrtilli p.p.	The part dominated by Juncus trifidus
Waldemarson Jensen 1980: 52	Grass-rich mountain heath of Juncus trifidus-type	

Comparison with other investigations is given in Tab. 32.

Survey of the submesic series

While the xeric and subxeric series are characterized by the same dominant species or dominant life-form throughout the zones, this is not true for the submesic series (Tab. 7). There

is only minor variation in the lower layers in the three lowermost zones. The field layer is dominated by *Vaccinium myrtillus* and to a lesser degree *Deschampsia flexuosa*. The middle alpine site-type differs completely, as *Vaccinium myrtillus* is replaced by *Juncus trifidus* as the main dominant. The bottom layer is wholly dominated by bryophytes in the boreal zones. The more moisture-demanding species of bryophytes, e.g. the *Barbilophozia* spp., are more common in the submesic than in the subxeric series. The importance of lichens increases from the upper boreal to the low alpine zone. In the middle alpine zone lichens are quantitatively more important than bryophytes, mainly because of dominance by *Cetraria islandica*. As in the middle alpine subxeric site-type, *Cetraria islandica* is the most important lichen species in the middle alpine site-type of this series. In the three lowermost zones the most pronounced difference from the drier series is the higher occurrence of *Vaccinium myrtillus* which gives rise to a denser field layer, partly at the expense of other dwarf shrubs. There are 27 species which have been recorded in all zones. *Blechnum spicant*, *Rhytidiadelphus loreus*, and *Sphagnum girgensohnii* are only represented in sample plots from the middle boreal zone, while *Lycopodium annotinum*, *Melampyrum pratense*, *Brachythecium reflexum*, and *Ptilium crista-castrensis* besides spruce and birch occur also in the upper boreal zone. A large group of species is represented in the three lowermost zones, lacking in the middle alpine zone. These are *Sorbus aucuparia*, *Vaccinium uliginosum*, *Cornus suecica*, *Maianthemum bifolium*, *Nardus stricta*, *Brachythecium starkei*, *Dicranum majus*, *Hylocomium splendens*, *Pleurozium schreberi*, *Polytrichum formosum*, *Sphagnum nemoreum*, *S. russowii*, *Calypogeia integristipula*, *C. neesiana*, and *Cladonia fimbriata*. Many of them do not occur in the upper part of the low alpine zone. *Cladonia ecmocyna* is only observed in the three uppermost zones in the submesic series. Species confined to sample plots from the alpine zones are *Lycopodium alpinum*, *Salix herbacea*, *Carex brunnescens*, *C. bigelowii*, *Juncus trifidus*, *Cetraria ericetorum*, and *Cladonia coccifera*. *Lycopodium selago*, *Cetraria delisei*, and *Cladonia metacorallifera* are only recorded from the middle alpine submesic site-type.

Species with distinct optima in the submesic series are *Vaccinium myrtillus*, *Cornus suecica*, *Ptilium crista-castrensis*, *Barbilophozia floerkei*, *B. lycopodioides*, and *Cladonia furcata*.

Species absent from the subxeric series present in the submesic series are (cf. Tab. 6): *Lycopodium alpinum*, *L. annotinum*, *Blechnum spicant*, *Brachythecium reflexum*, *Rhytidiadelphus loreus*, *Sphagnum girgensohnii*, and *S. russowii*. Species common in the submesic series but only accidentally recorded in the subxeric series are *Cornus suecica*, *Solidago virgaurea*, *Dicranum majus*, *Ptilium crista-castrensis*, *Calypogeia integristipula*, and *C. neesiana*. Most of the species present in the submesic series also occur in the mesic series, but the lichens are significantly more sparse in the latter.

The ecology of the *Dicranum* species shows interesting patterns. While *D. fuscescens* is common in the subxeric series, including the middle boreal zone, *D. majus* demands more mesic conditions and is common in the middle boreal submesic site-type. However, the frequency of this species rapidly

decreases with altitude, as also observed by Arnell & Jensen (1907-10) and Mårtensson (1952, 1956) from Northern Sweden, and Aune (1978) in Vassfaret. *D. fuscescens* is very sparse in the middle boreal submesic site-type, but increases with altitude, and is common in the corresponding low alpine site-type. When *D. fuscescens* is found in the submesic and mesic series in the boreal zones, this is almost always as secondary invasion from nearby stones, rotten logs, or dead crustose lichens. This may indicate that the species is excluded from the bottom layer of these site-types owing to competition. The same applies to *Orthodicranum montanum*, *Tetraphis pellucida*, and *Lophocolea heterophylla*.

The abundance of small "pockets" or depressions in the terrain with a size up to a few sq. dm, is a typical feature of the submesic and mesic series. These "pockets" contain a characteristic flora. They often have almost permanent shade and more favourable moisture conditions than the surroundings. Several species that are absent from the forest bottom because of unfavourable moisture conditions or competition with other species may be common in the "pockets", partly as small stands, partly as individual plants. Many hepatics reach their optima in such pockets. Typical pocket species are *Calypogeia integristipula*, *C. neesiana*, *Cephalozia* spp., *Cephaloziella* spp., and *Lophozia ventricosa*. The most common mosses growing in the "pockets" are *Plagiothecium* spp. and *Pohlia nutans*. Similar depressions in the subxeric series seem to be too dry for most of these species, and the species composition of those "pockets" will either not differ much from the surrounding vegetation, or they lack vegetation completely.

The soil in the submesic series most often consists of finer particles than in the subxeric series, giving a higher water capacity. There is a well-developed podzol profile in the lowermost zones. In the upper part of the low alpine zone and in the middle alpine zone a soil profile is rarely developed.

In the boreal zones the submesic series has its widest extension in the moist and shaded northerly exposed mountain ledges. The series is most often found on concavities in the terrain. Insolation is generally less than in the drier series because of the canopy closure. In the submesic series lichens are of least importance in the upper boreal zone. This may be due to shading as indicated by Resvoll-Holmsen (1918) and Nordhagen (1943), but can also be an effect of increased climatic humidity with altitude in the boreal zones.

The series covers wide areas in the alpine zones, where it occupies localities with stable and fairly long-lasting snow cover in winter.

MESIC SERIES

Middle boreal zone

The floristic composition of this site-type is given in Tab. 33. The constant species are: *Picea abies*, *Vaccinium myrtillus*, *Blechnum spicant*, *Gymnocarpium dryopteris*, *Maianthemum*

bifolium, *Oxalis acetosella*, *Solidago virgaurea*, *Thelypteris phegopteris*, *Trientalis europaea*, *Deschampsia flexuosa*, *Luzula pilosa*, *Brachythecium reflexum*, *Dicranum majus*, *Plagiothecium curvifolium+denticulatum+laetum*, *Polytrichum formosum*, *Barbilophozia lycopodioides*, *Calypogeia muelleriana*, *Cephalozia* spp., and *Lophozia ventricosa*.

The site-type is a spruce forest. *Athyrium distentifolium* and *A. filix-femina* are both observed as the main dominant of the field layer. Other dominants are *Blechnum spicant*, *Dryopteris assimilis*, *Vaccinium myrtillus*, *Deschampsia flexuosa*, and *Equisetum sylvaticum*. Dominance relations in the bottom layer are variable. *Dicranum majus* and *Barbilophozia lycopodioides* are the most common dominants.

The mean number of species is 50, while the total number of species in the 12 sample plots is 142.

The site-type is characterized by the high cover of tall ferns, causing a scattered occurrence of plants in lower strata. The dwarf shrubs and *Cornus suecica* are of less importance, although *Vaccinium myrtillus* may sometimes attain high cover. The high occurrence of herbs in the mesic series is characteristic. The bottom layer is dominated by bryophytes. Lichens play a minor role both quantitatively and qualitatively.

The floristic variation within the sample set is considerable, but the site-type is always characterized by high importance of tall ferns. Normally the *Athyrium* spp. are most important, but *Dryopteris assimilis* may be the only dominant fern, as in plot No. 7. Forms with *Blechnum spicant* as the most important fern are also found (e.g., plots Nos 2, 4, and 5). Tall herbs indicating more eutrophic conditions sometimes occur, e.g., *Lactuca alpina* and *Ranunculus platanifolius*.

In the northerly facing Nordfjell transect the forest is open and low-grown with few species, thus having a montane character. In Blåtjørnfjell the tree layer is more densely stocked, the number of species in the field layer is higher, and several typically lowland species occur.

The three sample plots Nos 9, 10, and 11 represent a more eutrophic stand in Blåtjørnfjell with an area of approximately 5 da. *Alnus incana* occurs and is sometimes dominant. Eutrophic species like *Alchemilla glabra*, *Filipendula ulmaria*, *Paris quadrifolia*, and *Carex vaginata* are present. Plot No. 11 is dominated by *Geranium sylvaticum*. Transitions to swamp forest and spring vegetation occur at places where the ground water level is particularly high. Species from such vegetation types in the stand include *Equisetum sylvaticum*, *Dactylorhiza maculata*, *Epilobium hornemannii*, *Stellaria alsine*, *Viola palustris*, *Bryum weigelii*, *Philonotis seriata*, *Plagiomnium affine*, *Pseudobryum cinclidioides*, *Rhizomnium punctatum*, and *Sphagnum squarrosum*.

Plot No. 12 represents another moist form of the site-type, and is dominated by *Equisetum sylvaticum*. Plots Nos 7 and 8 are dominated by *Sphagnum girgensohnii*. The largest number of species in one 25 sq. m plot, 74, is recorded in Plot No. 1. Sample plots Nos 1-6 are taken from luxuriant forests influenced by spray from the River Londøla.

The site-type is typically situated in concavities in the terrain with a high level of moving ground water. Moving

surface water has sometimes been observed in periods with much precipitation. The tall ferns cause large amounts of litter. This litter combined with almost permanent shade is thought to be responsible for a bottom layer that is less well developed than in the submesic series. The soil varies from a brown soil profile in the eutrophic types to podzol in the oligotrophic.

The site-type is frequently observed, although the humid climate favours peat formation and the development of sloping fens (cf. Bendiksen & Halvorsen 1981). This is particularly important in the north-facing slopes, e.g., in Sigurd bunut, where almost all the concavities are occupied by soligenous mires.

Comparison with other investigations is given in Tab. 34.

Upper boreal zone

The floristic composition of this site-type is given in Table 35. The following constant species are recorded: *Betula pubescens*, *Sorbus aucuparia*, *Vaccinium myrtillus*, *Cornus suecica*, *Gentiana purpurea*, *Gymnocarpium dryopteris*, *Solidago virgaurea*, *Trientalis europaea*, *Deschampsia flexuosa*, *Dicranum scoparium*, *Plagiothecium curvifolium+denticulatum+laetum*, *Barbilophozia floerkei*, *B. lycopodioides*, and *Lophozia ventricosa*.

The site-type is a birch forest with *Sorbus aucuparia* as a constant in the three upper layers. The dominance relationships of the field layer are variable, and both *Dryopteris assimilis* and *Athyrium distentifolium*-dominated types occur. *Vaccinium myrtillus* and *Deschampsia flexuosa* are also frequently recorded as dominants in the field layer. *Brachythecium starkei*, *Barbilophozia floerkei*, and *B. lycopodioides* are the main dominants in the bottom layer, where also *Sphagnum* spp. may be important.

The mean number of species is 38, while the total number in the 12 sample plots is 100.

The physiognomic similarity to the submesic series is higher in the upper boreal than in the middle boreal zone. The typical species of the *Vaccinium myrtillus* heaths are more common and tall ferns often more scattered. However, the type is well characterized by the presence of tall ferns and herbs like *Gentiana purpurea*, *Melandrium rubrum*, and *Rumex acetosa*. Bryophytes are important, while lichens are of no importance.

The xeric extreme is illustrated by plots Nos 1 and 2 from the south-facing Blåtjørnfjell. *Deschampsia flexuosa* forms dense stands, while *Gymnocarpium dryopteris*, *Gentiana purpurea* and *Solidago virgaurea* are the most important herbs. Tall ferns are of little importance. The birch forest has a dense tree layer. The combination of dry upper soil layer, huge amounts of birch debris and too little light, causes poor development of the bottom layer. The mesic extreme is represented in the steep, shady and moist north-facing ledges of Sigurd bunut. Tall ferns are often sparse: the presence of *Gymnocarpium dryopteris* and *Gentiana purpurea* is typical. In the bottom layer swelling carpets of *Sphagnum angustifolium*, *S. girgensohnii*, *S. russowii*, and *Polytrichum commune* may be found, and moisture-demanding species like *Rhizomnium pseudopunctatum*,

Tab. 33. The vegetation of the middle boreal mesic site-type.

Transect No.	1						2				3				C-E
Plot No.	1	2	3	4	5	6	7	8	9	10	11	12			
Altitude (m)	740	760	760	760	760	770	750	750	850	850	850	700			
Slope (°)	35	30	35	35	35	30	10	5	25	25	25	35			
Aspect	ESE	E	E	E	SE	E	WSW	SSE	SSE	S	SSE	N			
TA	0	6	3	4	7	1	4	6	4	6	7	4			
TB	1	1	3	1	0	+	0	0	+	+	1	2			
TC	9	6	9	8	5	8	4	6	7	8	7	8			
TD	5	8	4	3	4	9	7	5	5	5	4	4			
TE	+	1	+	+	3	0	2	2	+	+	2	1			
TF	+	+	0	0	+	+	1	+	2	1	+	+			
A <i>Betula pubescens</i>	.	.	3	4	2	5	4	42-4		
<i>Picea abies</i>	.	5	3	4	5	2	4	5	.	2	3	1	83-4		
<i>Sorbus aucuparia</i>	2	2	1	2	33-2		
B <i>Betula pubescens</i>	1	1	.	2	.	1	.	.	1	1	1	2	67-1		
<i>Picea abies</i>	1	.	2	1	25-1		
<i>Sorbus aucuparia</i>	2	1	2	1	.	2	42-2		
C <i>Betula pubescens</i>	+	.	1	1	.	1	1	42-1		
<i>Picea abies</i>	1	.	1	1	1	1	1	1	58-1		
<i>Sorbus aucuparia</i>	1	.	1	.	1	1	1	1	+	1	.	1	75-1		
<i>Lycopodium annotinum</i>	1	1	.	.	1	.	1	.	1	1	1	.	58-1		
<i>Vaccinium myrtillus</i>	1	3	1	3	3	2	2	1	1	1	1	4	100-2		
<i>V. vitis-idaea</i>	1	1	+	.	1	.	33-1		
<i>Anemone nemorosa</i>	.	.	1	1	1	.	1	1	.	1	1	.	58-1		
<i>Athyrium distentifolium</i>	.	2	4	2	.	3	1	4	1	.	.	1	67-3		
<i>A. filix-femina</i>	5	1	3	.	1	.	1	.	3	5	4	.	67-4		
<i>Blechnum spicant</i>	3	3	3	4	3	1	1	1	2	1	3	.	92-3		
<i>Chamaenerion angustifolium</i>	.	.	1	1	1	1	.	33-1		
<i>Crepis paludosa</i>	1	1	1	.	25-1		
<i>Dryopteris assiniensis</i>	2	1	1	3	2	3	3	2	.	.	.	2	75-2		
<i>Epilobium hornemannii</i>	1	1	1	.	25-1		
<i>Gentiana purpurea</i>	1	1	1	1	.	1	42-1		
<i>Geranium sylvaticum</i>	1	.	1	2	2	3	.	42-2		
<i>Gymnocarpium dryopteris</i>	1	2	1	2	2	2	2	2	2	1	2	3	100-2		
<i>Lactuca alpina</i>	1	.	1	2	1	.	33-1		
<i>Linnaea borealis</i>	.	2	.	1	1	.	.	+	33-1		
<i>Listera cordata</i>	1	2	1	.	1	1	.	42-1		
<i>Maianthemum bifolium</i>	1	1	2	1	1	1	1	1	1	1	1	.	92-1		
<i>Melampyrum pratense</i>	.	1	1	1	1	1	42-1		
<i>M. sylvaticum</i>	1	1	1	.	25-1		
<i>Oxalis acetosella</i>	1	1	1	1	1	1	2	2	1	2	2	.	92-1		
<i>Potentilla erecta</i>	1	2	1	2	.	2	1	.	2	1	1	.	75-1		
<i>Rubus saxatilis</i>	2	.	1	1	1	1	.	42-1		
<i>Rumex acetosa</i>	1	1	2	1	.	.	42-1		
<i>Solidago virgaurea</i>	1	2	3	2	1	2	.	1	1	1	2	1	92-2		
<i>Thelypteris phegopteris</i>	2	1	2	2	2	2	.	2	2	2	1	.	83-2		
<i>Trientalis europaea</i>	1	1	1	1	1	1	1	1	1	1	1	1	100-1		
<i>Agrostis stolonifera</i>	2	2	1	.	25-1		
<i>Anthoxanthum odoratum</i>	.	.	1	.	.	.	1	1	25-1		
<i>Calamagrostis purpurea</i>	2	.	1	1	25-1		
<i>Deschampsia flexuosa</i>	1	4	1	2	2	4	3	2	3	1	1	3	100-3		
<i>Equisetum pratense</i>	2	2	1	.	25-2		
<i>E. sylvaticum</i>	2	1	3	2	3	3	50-3		
<i>Luzula pilosa</i>	1	.	1	1	.	2	1	1	1	2	1	1	83-1		
<i>Milium effusum</i>	.	.	1	1	2	1	1	.	42-1		
D <i>Brachythecium reflexum</i>	1	1	1	1	.	.	1	1	1	2	1	2	83-1		
<i>B. starkei</i>	3	.	1	.	.	1	1	1	3	2	2	3	75-2		
<i>Bryum weigelii</i>	1	1	1	1	.	33-1		
<i>Dicranum fuscescens</i>	1	.	1	1	25-1		
<i>D. majus</i>	2	3	3	3	2	4	1	.	1	1	1	.	83-3		
<i>D. scoparium</i>	1	1	1	1	1	1	1	1	.	.	.	2	75-1		
<i>Drepanocladus uncinatus</i>	.	1	.	1	.	1	.	.	.	1	.	.	33-1		
<i>Herzogiella striatella</i>	1	1	1	1	.	33-1		
<i>Hylacomium splendens</i>	2	2	.	1	1	3	.	.	1	1	.	2	67-2		
<i>Mnium hornum</i>	.	1	.	1	1	25-1		
<i>Plagiommium affine</i>	2	3	2	.	25-2		
<i>Plagiothecium cavifolium</i>	.	1	1	.	.	1	25-1		
<i>P. curv.+dent.+laetum</i>	1	1	1	1	1	1	1	1	1	1	1	1	100-1		
<i>Pleurozium schreberi</i>	1	1	1	1	.	1	1	1	58-1		
<i>Polytrichum commune</i>	1	1	1	.	.	.	1	33-1		
<i>P. formosum</i>	2	3	2	1	3	3	1	1	.	1	1	1	92-2		
<i>Pseudobryum cinclidioides</i>	3	2	1	.	25-2		
<i>Rhizomnium pseudopunctatum</i>	1	.	1	1	.	1	33-1		

Tab. 33 (continued)

Transect No.	1						2					3	C-C
Plot No.	1	2	3	4	5	6	7	8	9	10	11	12	
<i>Rhizomnium punctatum</i>	2	.	.	.	1	.	.	1	2	2	2	.	50-2
<i>Rhodobryum roseum</i>	1	1	.	1	1	.	1	.	42-1
<i>Rhytidiadelphus loreus</i>	1	.	.	1	.	2	.	1	.	.	.	2	42-1
<i>R. subpinnatus</i>	.	1	1	1	.	4	33-2
<i>Tetraphis pellucida</i>	1	.	.	1	1	1	.	.	1	1	1	.	58-1
<i>Sphagnum girgensohnii</i>	2	.	.	.	1	1	4	3	.	.	.	2	50-3
<i>S. russowii</i>	1	1	1	25-1
<i>Barbilophozia barbata</i>	.	1	1	1	1	1	.	42-1
<i>B. floerkei</i>	1	1	1	1	.	2	1	1	.	.	.	1	67-1
<i>B. lycopodioides</i>	3	4	3	2	2	3	2	2	1	.	1	3	92-3
<i>Blepharostoma trichophyllum</i>	1	1	.	.	.	1	.	25-1
<i>Calypogeia integristipula</i>	.	1	.	1	1	1	.	.	1	1	.	1	58-1
<i>C. muelleriana</i>	1	1	1	1	1	1	1	1	1	.	1	1	92-1
<i>Cephalozia</i> spp.	1	1	1	1	1	.	.	1	1	1	1	1	83-1
<i>Chiloscyphus pallescens</i>	1	1	1	.	.	25-1
<i>Diplophyllum taxifolium</i>	1	1	1	2	1	1	.	1	58-1
<i>Lophocolea heterophylla</i>	1	1	1	.	.	.	1	1	42-1
<i>Lophozia obtusa</i>	1	.	1	1	.	1	.	1	.	.	.	1	50-1
<i>L. ventricosa</i>	1	1	1	1	1	1	1	1	.	1	1	1	92-1
<i>Pellia neesiana</i>	1	1	1	1	1	.	42-1
<i>Plagiochila asplenoides</i>	1	1	.	1	25-1
<i>Ptilidium ciliare</i>	.	1	.	.	.	1	1	25-1
<i>Cladonia bellidiflora</i>	.	.	1	1	1	1	33-1
<i>C. carneola</i>	1	1	1	1	1	1	50-1
<i>C. coniocraea</i>	.	1	.	1	1	25-1
<i>C. fimbriata</i>	.	1	.	.	.	1	.	.	1	1	.	1	42-1
<i>C. furcata</i>	.	1	1	1	25-1
<i>C. pleurota</i>	1	.	1	1	1	1	1	50-1
<i>C. pyxidata</i> coll.	.	.	1	1	1	1	33-1
<i>C. sulphurina</i>	1	.	1	.	1	1	.	.	1	.	.	.	42-1
<i>Peltigera canina</i>	1	1	1	1	.	33-1
Vascular plants	35	20	28	21	16	18	21	23	35	39	35	15	26
Bryophytes	35	20	19	19	14	22	17	23	21	19	18	19	21
Lichens	4	4	7	8	6	6	1	0	3	2	1	2	4
Total number of species	74	44	54	48	36	46	39	46	59	60	54	36	50

Additional species occurring in 2 sample plots or less (Plot No.: cover - constancy-characteristic degree of cover):

- A: *Alnus incana* (10:4, 11:1 - 17-3).
 B: *Alnus incana* (10:1, 11:1 - 17-1).
 C: *Alnus incana* (10:1, 11:1 - 17-1); *Lycopodium selago* (1:1 - 8-1), *Selaginella selaginoides* (1:1 - 8-1), *Alchemilla alpina* (7:1 - 8-1), *A. glabra* (10:1 - 8-1), *Campanula rotundifolia* (9:1 - 8-1), *Cirsium heterophyllum* (1:1 - 8-1), *Cornus suecica* (11:1, 12:1 - 17-1), *Cystopteris fragilis* (1:1 - 8-1), *Dactylorhiza maculata* (9:1 - 8-1), *Dryopteris filix-mas* (9:2 - 8-2), *Epilobium palustre* (1:1 - 8-1), *Filipendula ulmaria* (10:1 - 8-1), *Hieracium sylvaticum* (1:1, 3:1 - 17-1), *Orthilia secunda* (3:1, 8:1 - 17-1), *Paris quadrifolia* (10:2 - 8-2), *Ptilidium aquilinum* (9:2, 11:1 - 17-2), *Ranunculus acris* (9:1, 10:1 - 17-1), *R. platanifolius* (4:1 - 8-1), *Rubus chamaemorus* (12:1 - 8-1), *R. idaeus* (1:1 - 8-1), *Stellaria alsine* (9:1, 10:1 - 17-1), *Valeriana sambucifolia* (1:1 - 8-1), *Viola palustris* (1:1, 11:1 - 17-1), *Agrostis canina* (1:1 - 8-1), *A. tenuis* (10:1 - 8-1), *Carex vaginata* (10:1 - 8-1), *Deschampsia caespitosa* (7:1, 8:1 - 17-1).
 D: *Atrichum undulatum* (1:1 - 8-1), *Brachythecium rutabulum* (1:1 - 8-1), *Bryum pseudotriquetrum* (1:1, 8-1), *Cynodontium tenellum* (3:1 - 8-1), *Ditrichum heteromallum* (1:1 - 8-1), *Hylocomium umbratum* (4:1 - 8-1), *Oligotrichum hercynicum* (1:1 - 8-1), *Philonotis seriata* (10:1 - 8-1), *Plagiomnium cuspidatum* (9:1 - 8-1), *P. medium* (1:1 - 8-1), *Plagiothecium piliferum* (9:1 - 8-1), *Pohlia drummondii-nutans* (8:1, 9:1 - 17-1), *Rhytidiadelphus triquetrus* (1:1, 4:1 - 17-1), *Tortella tortuosa* (4:1 - 8-1), *Sphagnum squarrosum* (11:1 - 8-1), *Barbilophozia attenuata* (3:1 - 8-1), *Calypogeia fissa* (9:1, 11:1 - 17-1), *Cephalozia* spp. (5:1, 8:1 - 17-1), *Geocalyx graveolens* (10:1 - 8-1), *Harpanthus flotowianus* (1:1, 8:1 - 17-1), *Lophozia sudetica* (1:1 - 8-1), *Moerchia blyttii* (6:1 - 8-1), *Porella platyphylla* (9:1, 11:1 - 17-1), *Tritomaria quinqueidentata* (4:1, 6:2 - 17-2), *Cladonia cenotea* (4:1 - 8-1), *C. cornuta* (3:1, 4:1 - 17-1), *C. digitata* (12:1 - 8-1).

Rhytidiadelphus loreus and *Bazzania tricrenata* occur. Moisture types are also observed in Nordfjell. Eutrophic herb-rich stands have not been found in the upper boreal zone.

The main ecological factors are the same as in the middle boreal zone. The site-type is common in depressions, but in the humid north-facing slopes of Sigurd bunut it has also been observed on nearly plane, steeply sloping ground. On such sites the flush effect is probably not restricted to depressions in the terrain. The mesic series often covers overgrown talus

Tab. 34. Types described by other authors corresponding to the middle boreal mesic site-type.

Reference	Name of vegetation types	Comments
Kielland-Lund 1962b: 31	Aconito-Piceetum, Athyrium-subass.	
Kielland-Lund 1971: 21, 1973: 187, 1981: 171	Eu-Piceetum athyrietosum	Our more eutrophic plots Nos 9-11 show some similarity with Melico-Piceetum aconitetosum
Nordhagen 1937: 31	Aconition septentrionalis p.p.	
Nordhagen 1943: 325	Piceetum mulgedio-athyriosum	
Bjørndalen 1977: 126, 1980b: 58	Eu-Piceetum athyrietosum	
Aune 1978: 24	Eu-Piceetum athyrietosum	
Odland 1978: 46, Losvik 1978: 37, Aune 1973: 24	Corno-Betuletum athyrietosum	
Kummen 1977: 74, Kjellvik 1978: 77	Eu-Piceetum athyrietosum	
Odland 1979: 43, 1981b: 10	Athyrium filix-femina-dominated birch forest	
Malme 1971: 10, 16	Betula-Geranium-Deschampsia caespitosa-ass., Athyrium filix femina-facies, Dryopteris dilatata-community	
Samuelsson 1917a: 62	Farnkräuterreiche Wiesenfichtenwälder	
Arnborg 1940: 145	Frische kräuterreiche typ p.p. /Ptilium crista-castrensis-Hylocomium splendens-Union	
Eneroth 1931, O. Tamm 1935, Ronge 1936a, Arnborg 1942, 1945, Malmström 1949	(Tall herb vegetation)	
Kalela 1961: 72, 77	Filices-Typ	
Hämet-Ahti 1963: 96	"Forests with tall ferns"	
Nihlgård 1980: 37, 39	Spruce forest of fern type	

slopes and is frequently met with as a mosaic with large boulder fields. The soil is mostly shallow. If a layered soil profile has been developed, this normally contains a distinct layer of bleached soil.

Comparison with other investigations is given in Tab. 36.

Low alpine zone

The floristic composition of this site-type is given in Tab. 37. The constant species are: *Vaccinium myrtillus*, *Gentiana purpurea*, *Rumex acetosa*, *Trientalis europaea*, *Deschampsia flexuosa*, *Pohlia drummondii+nutans*, *Barbilophozia floerkei*, *B. lycopodioides*, and *Lophozia ventricosa*.

This site-type is broadly circumscribed and may be divided into more types. To enhance comparability with previously described vegetation types, brief descriptions of main types roughly corresponding to described communities within the site-type will be given. Common to all types is the occurrence of dwarf shrubs and herbs typical for the submesic series, but in lower amount than in that series. Lichens are of minor importance. *Gentiana purpurea* and *Rumex acetosa* are typical species in all types.

Athyrium distentifolium-dominated vegetation is widely distributed in the low alpine zone, but covers small areas. Such vegetation is the alpine continuation of the fern-rich vegetation of the boreal zones, and is dependent on the same soil water factors as this. Plots Nos 3 and 7-11 illustrate this type. *Athyrium distentifolium* dominates totally, while *Dryopteris assimilis* is rather unimportant. The shade from the ferns often causes a sparse field layer and a low number of species. The ground is covered with a thick layer of fern litter. *Brachythecium starkei*, which thrives well on this substrate, is often the only species of importance in the bottom layer. Plots Nos 7 and 8 from Nordfjell represent the poorest form of this site-type. In contrast, plot No. 10 from Tjorbufjell represents a more eutrophic type covered with thickets of *Salix lapponum* and *S. glauca*, and including *Thelypteris phegopteris*, *Geranium sylvaticum*, *Oxalis acetosella*, *Milium effusum*, and *Phleum commutatum*.

Another eutrophic form dominated by tall herbs is confined to the lower parts of this zone in the easterly exposed slopes of Målefjell (plots Nos 1-4) where it covers some decarees. Characteristic species are *Gentiana purpurea*, *Rumex acetosa*, and *Solidago virgaurea*. *Gymnocarpium dryopteris*, *Melandrium rubrum*, and *Potentilla erecta* are important, and *Lactuca alpina* and *Ranunculus platanifolius* also occur. The oligotrophic character of the type is well demonstrated by the importance of *Vaccinium myrtillus*, *V. uliginosum*, and *Deschampsia flexuosa*, all dominants. This type is probably ecologically close to the transition to a somewhat more eutrophic form of the submesic series.

In Nordfjell and Blåtjørnfjell fern- and herb-rich vegetation is confined to distinct depressions in the terrain; sites where the subsoil water table temporarily reaches the surface. In Målefjell and Tjorbufjell such vegetation is also found over vast areas in broad, shallow concavities and on even, sloping ground. This type often covers talus slopes, and the frequent occurrence of boulders is typical.

Small areas dominated by *Athyrium distentifolium* and *Cryptogramma crispa* are common in stony depressions with a long-lasting snow cover.

Moderate snow-bed vegetation is relatively sparse in the area. Vegetation dominated by *Nardus stricta* has nearly always an element of tall herbs, e.g., *Gentiana purpurea*, *Melandrium rubrum*, and *Rumex acetosa*. Other characteristic species in the low alpine *Nardus*-heaths are *Lycopodium alpinum*, *Alchemilla alpina*, *Carex bigelowii*, *C. brunnescens*, and *Anthoxanthum odoratum*. Plot No. 15 is a type with bottom layer rich in *Sphagnum* spp. Plots Nos 5 and 6 represent a grass-heath dominated by *Deschampsia flexuosa* in the south-facing slopes of

Tab. 35. The vegetation of the upper boreal mesic site-type:

Transect No.	2				3				4				C-C
Plot No.	1	2	3	4	5	6	7	8	9	10	11	12	
Altitude (m)	950	960	750	770	780	780	860	870	860	860	900	910	
Slope (°)	25	30	20	30	30	20	25	35	35	30	20	25	
Aspect	SSE	SSW	N	NNW	N	NNW	WNW	NNE	NNW	NNW	NNW	N	
TA	5	7	3	2	1	2	1	4	3	5	2	4	
TB	+	+	+	+	1	+	1	+	2	1	3	1	
TC	7	9	9	7	8	4	9	7	7	8	7	8	
TD	+	+	5	9	8	4	7	5	10	10	10	7	
TE	+	0	+	+	0	+	+	1	0	0	0	+	
TF	2	+	+	+	1	4	1	1	0	+	+	+	
A <i>Betula pubescens</i>	4	5	4	3	2	3	2	2	3	4	3	4	100-4
<i>Sorbus aucuparia</i>	1	.	1	1	1	2	1	4	2	3	.	1	83-2
B <i>Betula pubescens</i>	1	1	1	1	.	.	1	1	3	2	4	2	83-2
<i>Sorbus aucuparia</i>	1	1	2	1	2	1	2	.	1	1	1	1	92-1
C <i>Betula pubescens</i>	4	5	.	1	.	.	1	1	1	1	1	1	75-3
<i>Sorbus aucuparia</i>	1	1	1	1	1	.	1	1	1	1	1	1	92-1
<i>Empetrum hermaphroditum</i>	1	1	1	2	.	33-1
<i>Lycopodium annotinum</i>	.	.	1	1	.	1	1	1	.	1	1	.	58-1
<i>Vaccinium myrtillus</i>	.	1	5	5	4	4	3	4	4	5	4	5	92-4
<i>V. uliginosum</i>	1	1	1	.	.	.	3	1	2	1	2	1	75-2
<i>V. vitis-idaea</i>	1	1	.	1	.	1	33-1
<i>Athyrium distentifolium</i>	1	.	3	2	3	.	.	1	.	.	.	3	50-2
<i>Cornus suecica</i>	.	.	2	3	2	2	2	1	2	3	2	2	83-2
<i>Dryopteris assimilis</i>	.	.	1	3	4	3	2	2	1	1	.	3	75-3
<i>Gentiana purpurea</i>	2	3	1	.	1	.	4	2	1	1	2	1	83-2
<i>Gymnocarpium dryopteris</i>	1	3	1	1	1	2	2	.	3	2	3	2	92-2
<i>Listera cordata</i>	1	1	1	.	25-1
<i>Maianthemum bifolium</i>	1	1	1	.	1	.	1	.	.	1	1	1	67-1
<i>Melampyrum pratense</i>	1	2	1	.	1	.	3	.	1	2	1	.	67-2
<i>M. sylvaticum</i>	1	.	.	1	.	1	1	.	1	1	1	1	67-1
<i>Melandrium rubrum</i>	2	1	.	.	.	1	1	33-1
<i>Potentilla erecta</i>	1	2	1	1	.	1	42-1
<i>Rubus chamaemorus</i>	.	.	1	1	.	1	1	.	33-1
<i>Rumex acetosa</i>	1	1	.	.	1	1	3	1	50-1
<i>Solidago virgaurea</i>	2	2	1	1	1	1	2	1	1	1	2	1	100-1
<i>Trientalis europaea</i>	1	1	1	1	1	1	1	1	.	1	1	1	92-1
<i>Anthoxanthum odoratum</i>	2	1	1	25-1
<i>Deschampsia flexuosa</i>	5	5	5	4	3	4	5	4	4	3	5	4	100-5
<i>Luzula pilosa</i>	1	1	1	1	.	1	2	1	58-1
D <i>Brachythecium salebrosum</i>	3	.	.	2	.	2	25-2
<i>B. starkei</i>	.	.	.	4	3	3	4	2	1	2	1	3	75-3
<i>Calliergon stramineum</i>	1	1	2	1	33-1
<i>Dicranum scoparium</i>	1	1	1	2	1	1	2	1	1	2	1	2	100-1
<i>Drepanocladus uncinatus</i>	1	1	1	1	33-1
<i>Hylocomium splendens</i>	.	.	1	1	3	.	2	1	1	1	3	2	75-2
<i>Plagiothecium cavifolium</i>	1	2	1	.	1	1	42-1
<i>P. curvident.+laetum</i>	.	1	1	1	1	1	1	1	1	1	1	1	92-1
<i>P. piliferum</i>	1	.	1	.	1	.	25-1
<i>Pleurozium schreberi</i>	.	.	.	2	3	2	1	.	1	1	1	1	67-2
<i>Pohlia drummondii+nutans</i>	.	1	1	.	.	.	1	.	.	.	1	.	33-1
<i>Polytrichum commune</i>	.	.	3	.	1	.	.	.	2	2	2	1	50-2
<i>P. formosum</i>	.	.	.	1	1	1	1	1	.	1	1	2	67-1
<i>Rhizomnium pseudopunctatum</i>	1	.	1	1	25-1
<i>Rhytidadelphus loreus</i>	1	.	.	.	2	2	2	1	42-2
<i>Sphagnum angustifolium</i>	.	.	1	1	1	3	.	33-2
<i>S. girgensohnii</i>	.	.	4	2	1	2	.	33-3
<i>S. russowii</i>	.	.	2	5	4	4	2	42-4
<i>Barbilophozia floerkei</i>	.	1	1	.	3	1	3	3	1	2	2	2	82-2
<i>B. lycopodioides</i>	1	1	1	3	2	2	2	4	3	2	2	3	100-3
<i>Calypogeia fissa</i>	1	.	1	1	1	1	42-1
<i>C. muelleriana</i>	.	1	1	1	1	.	.	.	33-1
<i>Cephalozia</i> spp.	.	.	1	.	.	1	1	1	1	1	1	1	67-1
<i>Lophocolea heterophylla</i>	1	1	.	1	.	.	1	33-1
<i>Lophocolea obtusa</i>	1	1	2	1	1	2	50-1
<i>L. ventricosa</i>	1	1	1	1	.	1	1	1	1	1	1	1	92-1
<i>Ptilidium ciliare</i>	1	1	.	1	.	.	.	25-1

Tab. 35 (continued)

Transect No.	2		3				4						C-c
Plot No.	1	2	3	4	5	6	7	8	9	10	11	12	
<i>Cladonia bellidiflora</i>	1	1	.	.	1	1	33-1
<i>C. carneola</i>	.	1	.	.	1	1	1	1	.	1	1	1	67-1
<i>C. fimbriata</i>	1	1	1	.	.	1	.	.	33-1
<i>C. pleurota</i>	.	1	.	1	.	1	1	33-1
<i>C. pyxidata</i> coll.	1	.	.	.	1	1	1	1	1	1	1	1	75-1
<i>C. sulphurina</i>	.	1	.	1	1	1	1	42-1
Vascular plants	23	19	17	15	14	15	19	14	17	21	23	17	18
Bryophytes	12	11	14	10	12	10	21	14	28	22	26	22	17
Lichens	2	4	0	2	3	6	6	4	1	3	5	5	4
Total number of species	37	34	31	27	29	31	46	32	46	46	54	44	38

Additional species occurring in 2 sample plots or less (Plot No.:cover - constancy-characteristic degree of cover):

A: *Picea abies* (4:2, 9:2 - 17-2).

B: *Picea abies* (11:1 - 8-1).

C: *Picea abies* (9:1 - 8-1), *Populus tremula* (1:1 - 8-1), *Juniperus communis* (1:1 - 8-1), *Salix glauca* (11:1 - 8-1), *S. lapponum* (11:1 - 8-1), *Athyrium filix-femina* (2:1 - 8-1), *Blechnum spicant* (10:1 - 8-1), *Dryopteris filix-mas* (1:1 - 8-1), *Hieracium sylvaticum* (10:1 - 8-1), *Orthilia secunda* (11:1 - 8-1), *Polypodium vulgare* (1:1 - 8-1), *Carex nigra* (11:1 - 8-1), *Milium effusum* (1:1, 2:3 - 17-2), *Nardus stricta* (9:1, 10:1 - 17-1).

D: *Atrichum undulatum* (7:1 - 8-1), *Brachythecium reflexum* (1:1, 2:1 - 17-1), *Dicranella heteromalla* (8:1 - 8-1), *Dicranum fuscescens* (1:1, 5:1 - 17-1), *D. majus* (4:1, 7:1 - 17-1), *Hylocomium umbratum* (9:1 - 8-1), *Lescurea incurvata* (1:1 - 8-1), *Orthodicranum montanum* (1:1, 2:1 - 17-1), *Polytrichum juniperinum* (1:1 - 8-1), *P. piliferum* (1:1, 2:1 - 17-1), *P. strictum* (5:1, 8:1 - 17-1), *Splachnum* sp. (9:1 - 8-1), *Tetraphis pellucida* (2:1 - 8-1), *Barbilophozia barbata* (4:1, 7:1 - 17-1), *B. hatcheri* (1:1 - 8-1), *Bazzania tricenata* (10:1 - 8-1), *Calypogeia integristipula* (6:1, 10:1 - 17-1), *C. neesiana* (3:1, 11:1 - 17-1), *C. trichomanis* (12:1 - 8-1), *Diplophyllum taxifolium* (11:1 - 8-1), *Harpanthus flotowianus* (9:1, 11:1 - 17-1), *Kurzia trichoclados* (9:1 - 8-1), *Cetraria islandica* (8:1, 11:1 - 17-1), *Cladonia cornuta* (12:1 - 8-1), *C. furcata* (6:1 - 8-1), *C. gracilis* (7:1 - 8-1), *C. rangiferina* (6:1 - 8-1), *Nephroma arcticum* (11:1 - 8-1).

Blåttjørnfjell. Dryness is caused by high insolation. The grass-heaths are generally known to be seasonally hygrophilous.

The late and extreme snow bed series sensu stricto are poorly represented in Grunningsdalen. Elements of *Salix herbacea*-dominated snow beds are only observed in Tjorbuffjell (Plots Nos 12-15 are transitional to grass heaths). *Salix herbacea*, *Kiaeria starkei*, and *Barbilophozia floerkei* are dominants of this type, and *Gnaphalium supinum*, *Oligotrichum hercynicum*, and *Polytrichum sexangulare* are common. The most extreme snow beds, almost exclusively occupied by bryophytes, are represented at this locality as small fragments on the sheltered side of northerly exposed cliffs. A few individuals of *Carex brunnescens*, *Deschampsia flexuosa*, and *Lycopodium selago* with low vitality are found in the field layer. Bryophytes which may dominate are *Kiaeria starkei*, *Polytrichum sexangulare*, *Conostomum tetragonum*, *Marsupella brevissima*, *Pleuroclada albenscens*, and *Lophozia sudetica*. Other typical species are *Pohlia drummondii*, *Anthelia juratzkana*, and *Gymnomitrium concinnatum*.

A brown soil profile is developed in the fern- and herb-rich types in the lower part of this zone. In the upper part of the zone and in the snow bed types a layered soil profile is rarely formed.

Comparison with other investigations is given in Tab. 38.

Tab. 36. Types described by other authors corresponding to the upper boreal mesic site-type. The oligotrophic UB-M-vegetation in Grunningsdalen has few counterparts in fennoscandian literature. Most UB-M vegetation described are eutrophic types.

Reference	Name of vegetation types	Comments
Kielland-Lund 1981: 172	Eu-Piceetum athyrietosum, sub-alpine Birkenwaldform	
Nordhagen 1943: 312, 325	Lactucion (Mulgedion) alpinae p.p., Betuletum mulgedio-athyriosum	Discerning of a meso-oligotrophic group of communities within Lactucion is mentioned (cf. Kalela 1939, Kalliola 1939)
Odland 1978: 110, 1981c: 675	Lactucion alpinae, suball. Dryoptero-Calamagrostenion purpureae: Geranio-Betuletum athyrietosum and Athyrium distentifolium meadow	Meso-oligotrophic type
Odland 1979: 51, 1981b: 12	Athyrium distentifolium-dominated birch forests	
Fredriksen 1978: 58	Corno-Betuletum athyrietosum	
Knaben 1952: 49	Dryopteris-Calamagrostion purpureae	
Kummen 1977: 74	Eu-Piceetum athyrietosum	
Malme 1971: 12, 16	Betula pubescens-Blechnum spicant-community	
Moen 1978: 78	Athyrium filix-femina-community	
Samuelsson 1917a: 62	Farnkräuterreiche Wiesenfichtenwälder	
Tengwall 1920: 334	Wiesenbirkenwälder (Solidago virgaurea-reicher Wiesenbirkenwald, Farnreicher Birkenwälder)	
Holmen 1965: 242	Tall-herb meadow forest rich in tall ferns	
Nihlgård 1980: 49, 73	Mountain birch forest of tall herb type, fern variety and mixed forest of herb type	

Middle-alpine zone

The floristic composition of this site-type is given in Tab. 39. The constant species are: *Vaccinium myrtillus*, *Carex brunnescens*, *Deschampsia flexuosa*, *Juncus trifidus*, *Dicranum scoparium*, *Pohlia drummondii+nutans*, *Barbilophozia floerkei*, *Lophozia ventricosa*, *Cetraria islandica*, *Cladonia bellidiflora*, and *C. squamosa*.

As in the corresponding low alpine site-type, this site-type is an agglomerate, and is divided into types.

The type dominated by *Athyrium distentifolium* is rare in this zone. Two vigorous stands are situated at 1290 m, below the top of Mælefjell (plot No. 4).

Grass-heaths are common in the middle-alpine zone. Species which may be dominants are *Anthoxanthum odoratum*, *Carex bigelowii*, *C. brunnescens*, *Deschampsia flexuosa*, *Juncus trifidus*, and *Nardus stricta*. Dominance relations are variable,

and the three last mentioned species change in being physiognomically most important. Plots Nos 2 and 7 represent *Nardus* heaths, 3 and 6 *Juncus trifidus*-rich heaths, while several graminids are important in plots Nos 9 and 10. *Gentiana purpurea*, *Rumex acetosa*, and *Solidago virgaurea* may form an important element in the grass heaths. The dense graminid field layer causes a sparse bottom layer. *Barbilophozia floerkei* is most common and sometimes dominates. One of the *Nardus*-dominated plots has dominance of *Sphagnum nemoreum*. Lichens are more important in the grass heaths than in the tall fern stands. *Cetraria islandica* and *Cladonia ecmocyna* are the most common species.

The grass heaths are seasonally hygrophilous and free from solifluction. A soil profile is rarely developed.

Meadows dominated by *Alchemilla alpina* (e.g., plot No. 5) are locally common in the area, covering smaller patches in mosaic with the grass-heaths. This type occupies sites with more stable moisture conditions than encountered by the grass heaths.

Snow beds with *Cryptogramma crispa* are common in stony depressions. The two most extreme snow bed series sensu stricto are only fragmentarily represented, and are not included among the sample plots.

Comparison with other investigations is given in Tab. 38.

Survey of the mesic series

The oligotrophic part of the mesic series sensu stricto in the Grunningsdalen area has the same physiognomic appearance in all zones. It is almost totally dominated by tall ferns. *Athyrium distentifolium* may be a dominant in all zones, but it is mostly replaced by *A. filix-femina* in the middle boreal zone. The bottom layer is sparse with *Brachythecium starkei* as the most important species. Mesotrophic types are dominated by tall herbs. Species which are typical for the submesic series normally occur richly in both oligotrophic and more mesotrophic types.

The middle alpine mesic site-type in this work is primarily made up of moderate snow bed grass heaths, while the sample plots from the other zones should be mostly classified to the mesic series in the narrow sense.

Several species only occur in the middle boreal zone. The most important oligo- and mesotrophic species with this pattern of occurrence are *Anemone nemorosa*, *Equisetum sylvaticum*, *Linnaea borealis*, *Rubus saxatilis*, *Mnium hornum*, *Plagiochila asplenioides*, *Rhodobryum roseum*, and *Rhytidiadelphus subpinnatus*. *Athyrium filix-femina* and *Diplophyllum taxifolium* show distinctly lowered frequencies in the upper boreal zone. *Listera cordata* is confined to the boreal zones. Several species disappear somewhere in the low alpine zone: *Blechnum spicant*, *Dryopteris assimilis*, *Gymnocarpium dryopteris*, *Luzula pilosa*, *Lycopodium annotinum*, *Maianthemum bifolium*, *Melampyrum pratense*, *M. sylvaticum*, *Thelypteris phegopteris*, *Pleurozium schreberi*, and *Lophozia obtusa* can be mentioned. *Barbilophozia lycopodioides*, *Calypogeia integristipula*, and *C. neesiana* occur in all zones, but decrease with altitude. *Athyrium*

Tab. 37. The vegetation of the low alpine mesic site-type.

Transect No.	1				2		3									C-E
Plot No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	C-E
Altitude (m)	1070	1070	1080	1110	1040	1050	870	950	1020	1020	1030	1050	1080	1090	1130	
Slope (°)	30	35	35	40	25	30	30	35	20	20	35	25	30	30	15	
Aspect	ESE	E	ESE	SE	SSW	SSW	N	NNW	NE	NNE	NNE	N	ENE	N	E	
TA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
TB	+	0	0	0	0	0	0	+	0	7	1	0	0	0	0	
TC	8	9	8	9	9	8	5	8	8	8	8	6	6	5	10	
TD	3	2	1	4	+	+	6	1	6	3	3	8	7	6	8	
TE	1	+	1	+	+	1	3	1	+	+	+	+	1	+	0	
TF	+	0	+	+	1	1	1	+	+	1	2	2	1	2	0	
C <i>Empetrum hermaphroditum</i>	2	1	1	2	.	2	.	.	1	.	.	1	1	1	.	60-1
<i>Phyllodoce caerulea</i>	1	.	1	2	1	.	.	.	1	1	.	40-1
<i>Salix herbacea</i>	.	.	1	3	.	.	4	5	4	2	40-4
<i>Vaccinium myrtillus</i>	4	3	2	3	1	2	2	1	2	1	1	1	1	2	2	100-2
<i>V. uliginosum</i>	3	3	1	4	3	3	.	.	1	1	2	60-3
<i>V. vitis-idaea</i>	1	1	.	.	1	1	27-1
<i>Alchemilla alpina</i>	1	2	.	.	1	2	1	2	2	.	1	53-2
<i>Athyrium distentifolium</i>	2	.	5	.	1	.	3	5	5	4	5	2	1	2	1	80-4
<i>Campanula rotundifolia</i>	1	1	1	.	1	1	33-1
<i>Chamaenerion angustifolium</i>	1	2	.	.	1	1	27-1
<i>Cornus suecica</i>	2	3	.	1	1	1	1	1	47-2
<i>Gentiana purpurea</i>	3	2	1	2	1	2	2	2	1	1	1	2	1	2	2	100-2
<i>Gymnocarpium dryopteris</i>	2	2	1	1	1	1	.	1	47-1
<i>Maianthemum bifolium</i>	2	1	1	1	1	1	40-1
<i>Melampyrum sylvaticum</i>	1	1	.	1	1	27-1
<i>Melandrium rubrum</i>	1	2	1	2	1	2	.	.	1	1	53-1
<i>Potentilla erecta</i>	1	3	1	.	1	1	33-2
<i>Rumex acetosa</i>	3	4	2	2	1	2	.	1	2	3	3	1	1	1	1	93-2
<i>Solidago virgaurea</i>	2	2	1	1	1	1	1	1	1	.	1	.	.	1	1	80-1
<i>Trientalis europaea</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	93-1
<i>Anthoxanthum odoratum</i>	1	2	1	1	1	2	.	.	2	3	2	2	1	.	2	80-2
<i>Carex bigelowii</i>	1	.	.	.	2	.	.	1	2	2	2	40-2
<i>C. brunnescens</i>	1	1	1	1	.	1	.	.	1	1	1	2	2	3	.	73-1
<i>Deschampsia flexuosa</i>	3	4	2	4	5	5	5	2	4	4	2	3	3	4	.	93-4
<i>Milium effusum</i>	.	1	.	.	1	2	1	27-1
<i>Nardus stricta</i>	.	.	2	1	.	1	.	.	1	.	.	1	2	.	5	47-3
D <i>Brachythecium starkei</i>	3	2	1	3	.	.	1	1	2	3	3	1	.	.	.	73-2
<i>Dicranella heteromalla</i>	1	1	.	1	1	.	.	1	.	33-1
<i>Dicranum fuscenscens</i>	1	1	1	1	.	27-1
<i>D. scoparium</i>	2	1	1	2	1	1	2	1	2	1	.	1	.	3	.	80-2
<i>Drepanocladus uncinatus</i>	1	.	.	1	1	.	.	.	2	1	1	1	.	.	.	47-1
<i>Kiaeria starkei</i>	1	.	.	4	5	3	.	27-4
<i>Oligotrichum hercynicum</i>	1	.	.	1	.	.	.	1	1	1	.	33-1
<i>Plagiothecium cavifolium</i>	1	1	1	2	.	.	.	1	33-1
<i>P. curv.+dent.+laetum</i>	1	.	.	1	1	1	1	1	1	1	2	1	.	1	.	73-1
<i>Pohlia drummondii+nutans</i>	1	1	1	1	1	1	.	1	1	1	1	1	1	1	1	93-1
<i>Polytrichum commune</i>	1	1	1	.	.	1	.	.	2	2	1	2	2	.	1	67-1
<i>P. formosum</i>	1	.	1	.	1	.	2	1	2	1	.	.	1	1	.	60-1
<i>Barbilophozia floerkei</i>	1	1	1	1	1	1	5	1	4	.	1	4	3	4	2	93-3
<i>B. lycopodioides</i>	2	2	1	2	1	1	2	1	2	2	1	1	.	1	.	87-1
<i>Cephalozia spp.</i>	1	.	1	1	.	1	1	1	.	1	1	53-1
<i>Cephalozia spp.</i>	1	.	.	1	.	1	.	1	.	.	.	1	.	.	.	33-1
<i>Lophocolea heterophylla</i>	.	.	.	1	1	1	1	27-1
<i>L. ventricosa</i>	1	1	1	1	1	1	1	1	.	1	1	1	1	2	1	93-1
<i>Moerchia blyttii</i>	1	1	.	.	2	1	1	.	33-1
<i>Cetraria islandica</i>	1	1	.	1	.	1	1	.	2	1	.	1	1	1	.	67-1
<i>Cladonia bellidiflora</i>	1	.	.	.	1	.	.	.	1	.	.	.	1	1	.	33-1
<i>C. carneola</i>	1	1	.	.	1	1	1	1	.	1	.	47-1
<i>C. fimbriata</i>	1	1	1	.	1	1	1	.	.	1	47-1
<i>C. furcata</i>	.	1	1	.	.	1	.	.	1	.	.	1	1	.	.	40-1
<i>C. pyxidata coll.</i>	1	1	1	1	1	1	.	.	1	1	1	1	1	1	.	80-1
Vascular plants	28	25	26	18	22	23	10	13	26	23	20	19	17	18	13	20
Bryophytes	17	9	10	14	17	13	13	17	15	19	14	19	12	18	12	15
Lichens	6	4	3	4	3	7	3	0	5	4	2	7	4	8	0	4
Total number of species	51	38	39	36	42	43	26	30	46	46	36	45	33	44	25	39

Tab. 7 (continued)

Additional species occurring in 3 sample plots or less (Plot No., cover - constancy-characteristic degree of cover):

- B: *Betula pubescens* (1:1 - 7-1), *Salix lapponum* (10:5, 11:2 - 13-4), *Sorbus aucuparia* (8:1 - 7-1).
- C: *Sorbus aucuparia* (1:1, 2:1 - 13-1), *Betula nana* (9:1, 14:1 - 13-1), *Calluna vulgaris* (1:1, 2:1 - 13-1), *Juniperus communis* (1:1, 4:1 - 13-1), *Lycopodium alpinum* (3:1, 13:1, 15:1 - 20-1), *L. annotinum* (7:1 - 7-1), *L. selago* (9:1, 14:1 - 13-1), *Salix glauca* (9:1, 11:3 - 13-2), *S. lapponum* (3:1, 11:2, 12:1 - 20-1), *Alchemilla glabra* (10:1 - 7-1), *Blechnum spicant* (3:1 - 7-1), *Cerastium cerastoides* (10:1 - 7-1), *Coeloglossum viride* (11:1 - 7-1), *Cryptogramma crispa* (3:1, 12:1, 13:1 - 20-1), *Dryopteris assimilis* (7:2, 8:1 - 13-1), *Epilobium anagallidifolium* (12:1 - 7-1), *E. hornemannii* (10:1, 11:1 - 13-1), *Geranium sylvaticum* (10:2, 11:1 - 13-1), *Gnaphalium norvegicum* (3:1 - 7-1), *G. supinum* (9:1, 12:1, 13:1 - 20-1), *Hieracium alpinum* (1:1, 9:1 - 13-1), *H. sylvaticum* (5:1, 6:1, 9:1 - 20-1), *Melampyrum pratense* (2:1, 5:1, 6:1 - 20-1), *Oxalis acetosella* (9:1, 10:2, 11:2 - 20-2), *Polygonum viviparum* (9:1, 11:1 - 13-1), *Pyrola minor* (9:1 - 7-1), *Ranunculus acris* (10:1 - 7-1), *R. platanifolius* (1:1, 2:1, 11:1 - 20-1), *Rubus chamaemorus* (7:1, 8:1, 14:2 - 20-1), *Saxifraga stellaris* (12:1, 14:1 - 13-1), *Thelypteris phegopteris* (3:1, 10:1, 11:2 - 20-1), *Viola palustris* (10:1 - 7-1), *Carex lachenalii* (12:1 - 7-1), *Eriophorum vaginatum* (14:1 - 7-1), *Juncus trifidus* (13:1 - 7-1), *Luzula frigida* (3:1 - 7-1), *L. pilosa* (1:1, 2:1, 6:1 - 20-1), *Phleum commutatum* (10:1, 11:1 - 13-1).
- D: *Bartramia ithyphylla* (10:1, 12:1 - 13-1), *Brachythecium reflexum* (5:1, 10:1, 11:1 - 20-1), *Calliergon stramineum* (15:1 - 7-1), *Hylocomium splendens* (7:1 - 7-1), *Lescurea radicata* (1:1, 2:1, 4:1 - 20-1), *Orthodicranum montanum* (5:1, 6:1, 14:1 - 20-1), *Plagiothecium piliferum* (1:1, 4:1, 6:1 - 20-1), *Pleurozium schreberi* (1:1, 9:1 - 13-1), *Polytrichum juniperinum* (1:1, 6:1, 14:1 - 20-1), *P. longisetum* (3:1, 12:1 - 13-1), *P. piliferum* (6:1 - 7-1), *P. sexangulare* (8:1, 12:2, 13:3 - 20-2), *P. strictum* (14:2, 15:2 - 13-2), *Racomitrium canescens* (4:1 - 7-1), *Rhizomnium pseudopunctatum* (11:2 - 7-1), *Rhytidadelphus loreus* (7:1 - 7-1), *Sphagnum compactum* (15:1 - 7-1), *S. girgensohnii* (10:1, 15:5 - 13-4), *S. nemoreum* (15:1 - 7-1), *S. russowii* (15:3 - 7-3), *S. squarrosum* (10:1 - 7-1), *Anthelia juratzkana* (12:1 - 7-1), *Barbilophozia hatcheri* (5:1, 6:1 - 13-1), *Calypogeia fissa* (10:1 - 7-1), *C. neesiana* (7:1 - 7-1), *Harpanthus flotowianus* (10:1, 11:1 - 13-1), *Jungermannia sphaerocarpa* (5:1 - 7-1), *Lophozia obtusa* (8:1, 9:1, 10:1 - 20-1), *L. opacifolia* (14:1 - 7-1), *L. sudetica* (14:1 - 7-1), *Pellia neesiana* (9:1 - 7-1), *Pleurocladus albens* (12:2 - 7-2), *Ptilidium ciliare* (1:1, 5:1 - 13-1), *Scapania irrigua* (5:1 - 7-1), *S. paludicola* (11:1 - 7-1), *Cladonia arbuscula* (12:1 - 7-1), *C. coccifera* (12:1, 14:1 - 13-1), *C. cernuina* (4:1, 14:1 - 13-1), *C. gracilis* (14:1 - 7-1), *C. pleurota* (1:1, 4:1, 6:1 - 20-1), *C. rangiferina* (6:1, 14:1 - 13-1), *C. uncialis* (7:1, 12:1 - 13-1).

distentifolium increases up to the low alpine zone, and then rapidly decreases.

A large number of species are confined to the mesic series. The most common species which are typical of this series and absent or rare in the submesic series are *Athyrium distentifolium*, *A. filix-femina*, *Dryopteris assimilis*, *Gentiana purpurea*, *Gymnocarpium dryopteris*, *Luzula pilosa*, *Melampyrum sylvaticum*, *Melandrium rubrum*, *Milium effusum*, *Potentilla erecta*, *Rumex acetosa*, *Drepanocladus uncinatus*, and *Plagiothecium cavifolium*.

Luzula pilosa is almost restricted to the mesic series in Grunningsdalen. Similar observations are made by Klok (1974). Over most of Southern Norway it is equally common in submesic and mesic vegetation (cf. Kielland-Lund 1981).

Brachythecium reflexum (probably mostly used in a wide sense, including *B. starkei* of this work) is reported as the most typical bryophyte species growing in fern debris in *Athyrium distentifolium* stands by Nordhagen (1943), Gjærevoll (1956), and Dahl (1957).

The mesic series *sensu stricto* occupies localities with a permanent supply of water rich in oxygen. Such water is characterized by Dahl (1957) as wet flushes, defined as water moving sideways or upwards through the soil. Mineral salts dissolved in the water are continuously supplied to the vegetation. Leaching of minerals from the upper layers is counteracted and the vegetation receives an improved nutrient supply. These conditions are most often realized in concavities or linear depressions in the terrain, and also in places with a steep slope on plane ground. In the poorest types the soil is podzolized, while the mesotrophic types have a brown soil profile.

The mesic series *sensu stricto* has its optimal occurrence in northerly exposed sites. In the alpine zones it occupies sites with a stable and long-lasting snow cover. According to

Tab. 38. Types described by other authors corresponding to the low and middle alpine mesic site-types. D - important difference from Grunningsdalen. Note: The wide range of vegetation types referred to these site-types, the lack of consistent qualitative differences between them, and the poverty of indications of zonal affinity in the literature, made a collective comparison of alpine mesic site-types convenient. Attention is only given to corresponding oligotrophic tall fern vegetation and grass heaths with high floristic affinity to LA-M and MA-M of Grunningsdalen. Such types are ecological equivalents to the mesic (s. str.) and moderate snow-bed series, respectively.

Reference	Name of vegetation types	Comments
	Tall fern vegetation (Mesic series s-str.)	The importance of <i>Rumex acetosa</i> is mentioned by several authors
Nordhagen 1928: 339	<i>Athyrium alpestre</i> -Ass.	
Nordhagen 1937: 51, 1943: 304	Allosoreto-Athyrium alpestris: <i>Athyrium alpestris</i> chionophilum, <i>Allosoretum</i> chionophilum	
Nordhagen 1943	<i>Lactucion alpinae</i> , subgroup <i>Dryoptero-Calamagrostion purpureae</i> p.p.	The subgroup takes a position intermediate between <i>Phyllo-doco-Myrtillion</i> and typical <i>Lactucion alpinae</i> according to Nordhagen
Gjærevoll 1949: 38, 1950: 408, 1956: 149	<i>Athyrium alpestris</i>	
Dahl 1957: 190	<i>Lactucion alpinae</i> : <i>Athyrium alpestris</i> chionophilum	
Resvoll-Holmsen 1920: 104, 1932: 28	<i>Athyrium alpestre</i> -urtemark	
Bendixsen & Schumacher 1982: 53	Mesic series (tall fern meadow)	
Samuelsson 1917b: 40	<i>Vaccinium myrtillus</i> -reiche Moosheiden, var. with <i>Athyrium distentifolium</i> and some herbs	
Hadac 1971: 214	<i>Athyrium alpestris</i> chionophilum	Incl. <i>Gentiana purpurea</i>
Knaben 1952: 49	Tall fern vegetation	Incl. snow-bed/and meadow types
Malme 1971: 25	<i>Athyrium alpestris</i>	
McVean & Ratcliffe 1962: 82, McVean 1964: 515	<i>Cryptogrammo-Athyrium chionophilum</i>	Hyperoceanic type
Henning 1889: 24	<i>Athyrium distentifolium</i> -dominated vegetation	
Samuelsson 1917a: 188	<i>Athyrium alpestre</i> -Bestand	
Smith 1920: 76	Highgrown meadow characterized by <i>Athyrium alpestre</i>	
Tengwall 1920: 355	<i>Athyrium alpestre</i> -Wiese	
T. Fries 1913: 113	<i>Phegopteris alpestris</i> -Wiese	
Gjærevoll & Bringer 1965: 263	<i>Cryptogrammo-Athyrium alpestris</i>	
Kalliola 1939: 168	<i>Athyrium alpestris</i> : <i>Athyrium alpestre</i> -soc.	
Kalliola 1932: 60	<i>Athyrium alpestre</i> -Krautwiesen	
Söyrinki 1938: 39, Kalela 1939: 247	<i>Athyrium alpestre</i> -Wiese	
Dahl et al. 1971: 8	Allosoreto-Athyrium alpestris, <i>Dryoptero-Calamagrostion purpureae</i>	
Waldemarson Jensen 1980: 77, 93	Snow-bed vegetation of fern type and tall herb meadow without shrubs, oligotrophic var.	

Tab. 38 (continued)

Reference	Name of vegetation types	Comments
	Grass-heath vegetation (Moderate snow-bed series)	
Nordhagen 1928: 300, 317	<i>Deschampsia flexuosa</i> - <i>Anthoxanthum odoratum</i> -Ass., Alpine <i>Nardus</i> -Ass.	D: The latter replaced by the former above 1100 m
Christophersen 1925: 557, 558	Same as above	
Nordhagen 1937: 46	<i>Nardeto</i> - <i>Caricion rigidae</i> : <i>Deschampsia flexuosa</i> - <i>Anthoxanthum odoratum</i> -Soz., <i>Nardus stricta</i> -Soz.	
Nordhagen 1943: 236, 241	<i>Nardetum chionophilum</i> , <i>Anthoxantho</i> - <i>Deschampsietum</i> (Sikilsdalen)	D: <i>Nardus</i> and <i>Deschampsia flexuosa</i> play a minor part in MA
Gjærevoll 1956: 35, 102	<i>Anthoxantho</i> - <i>Deschampsietum flexuosae</i> , <i>Nardetum strictae</i>	
Dahl 1957, 134, 166	<i>Deschampsieto</i> - <i>Dicranetum fuscae</i> , <i>Nardetum chionophilum</i>	The <i>caricetosum brunnescentis</i> facies of the former has highest affinity to vegetation in Grunningsdalen
Resvoll-Holmsen 1914b: 55, 1920, 121	<i>Nardus</i> -græsmark (<i>Nardus</i> grass-heaths)	
Bendiksen & Schumacher 1982: 51	<i>Nardus</i> - <i>Carex bigelowii</i> heath	
Du Rietz 1925a	Nackte <i>Nardus</i> -Heide	
Hadac 1971: 211, 212	<i>Alchemillo alpinae</i> - <i>Deschampsietum flexuosae</i> , <i>Nardetum chionophilum</i>	The latter has high constancy of <i>Gentiana purpurea</i>
Samuelsson 1917b: 41, 56	<i>Nardus</i> -Heiden, <i>Anthoxanthum</i> - Wiese	
Knaben 1952: 65, 61	<i>Nardetum chionophilum</i> , (<i>Deschampsia flexuosa</i> - <i>Anthoxanthum</i> -heaths)	D: The latter differing greatly in the importance of <i>Salix herbacea</i> and bryophytes
Huseby & Odland 1981: 23	Alpine <i>Nardus</i> -heaths	
Naustdal 1951: 82	<i>Nardus</i> -heaths	
Odland 1979: 66	<i>Nardus</i> -heaths	
Fredriksen 1978: 120-135	<i>Nardus</i> -heaths	
Poore & McVean 1957: 430	<i>Nardus</i> snow-beds	
McVean & Ratcliffe 1962: 69, McVean 1964: 502	<i>Nardetum medio-alpinum</i>	
Samuelsson 1917a: 173	<i>Nardus</i> -Heide	
Smith 1920, 39, 41	<i>Nardus</i> -hed, <i>Anthoxanthum</i> -gråshedar	
Tengwall 1920: 386, 388	<i>Anthoxanthum odoratum</i> -Grasheide, <i>Nardus stricta</i> -Grasheide	
T. Fries 1913: 117	<i>Anthoxanthum odoratum</i> -Wiese	
Gjærevoll 1949: 45, 39	<i>Deschampsia flexuosa</i> - <i>Anthoxanthum</i> -soc., <i>Nardus stricta</i> -soc.	
Gjærevoll 1950: 392	<i>Deschampsietum flexuosae</i>	
Gjærevoll & Bringer 1965: 262	<i>Deschampsio</i> - <i>Anthoxanthion</i>	
Hult 1887: 195	<i>Nardus</i> -Formation	
Kalliola 1939: 145, 154	<i>Nardeto</i> - <i>Caricion rigidae</i> : <i>Deschampsia flexuosa</i> - <i>Anthoxanthum</i> -Soz., <i>Nardus stricta</i> -soz.	
Kalliola 1932: 56, 59, Sjöyinki 1938: 36, 38	<i>Deschampsia flexuosa</i> -Wiese, <i>Deschampsia flexuosa</i> - <i>Anthoxanthum odoratum</i> -Wiese, spåtausapernde <i>Nardus stricta</i> -Wiese	
Kalela 1939: 255, 259, 283	<i>Deschampsia flexuosa</i> -Wiese, <i>Deschampsia flexuosa</i> - <i>Anthoxanthum odoratum</i> -Wiese, spåtausapernde <i>Nardus stricta</i> -Wiese	
Dahl et al. 1971: 8	<i>Nardeto</i> - <i>Caricion bigelowii</i>	
Waldemarson Jensen 1980: 71	Snow-bed vegetation of <i>Anthoxanthum odoratum</i> -type ("Vårbrodd-hedtyp"), <i>Deschampsia flexuosa</i> and <i>Nardus stricta</i> -varieties	

Tab. 39. The vegetation of the middle alpine mesic site-type.

Transect No.	1										3	
Plot No.	1	2	3	4	5	6	7	8	9	10	C-5	
Altitude (m)	1280	1280	1290	1290	1290	1300	1340	1240	1250	1250		
Slope (°)	10	5	35	20	10	25	30		5	10		
Aspect	SSE	SW	SSE	SSE	NNE	ENE	SSE	SSW	S	SSE		
TA	0	0	0	0	0	0	0	0	0	0		
TB	0	0	0	0	0	0	0	0	0	0		
TC	8	9	8	7	8	6	8	8	8	9		
TD	1	2	3	2	4	4	3	1	4	4		
TE	+	0	+	+	+	+	+	0	+	0		
TF	1	1	1	2	1	3	1	2	1	1		
C Empetrum hermaphroditum	.	1	.	1	1	1	2	.	1	1	70-1	
Lycopodium alpinum	1	2	.	.	1	3	40-2	
Vaccinium myrtillus	1	1	.	2	1	1	3	2	1	1	90-2	
Alchemilla alpina	1	.	.	.	5	.	.	1	.	.	30-4	
Athyrium distentifolium	.	1	.	5	.	.	1	.	.	.	30-4	
Cryptogramma crispa	.	.	2	1	1	2	.	1	.	.	50-1	
Gentiana purpurea	.	3	3	1	1	1	50-2	
Rubus chamaemorus	.	.	.	2	.	.	1	.	.	1	30-1	
Rumex acetosa	.	.	.	2	.	1	30-2	
Solidago virgaurea	1	.	.	1	1	.	2	1	1	2	70-1	
Trientalis europaea	.	1	.	1	1	.	1	.	1	1	60-1	
Anthoxanthum odoratum	2	.	3	1	3	2	.	2	.	.	60-2	
Carex bigelowii	.	.	1	.	1	.	.	4	4	4	50-3	
C. brunnescens	2	1	1	1	1	1	1	1	3	3	100-2	
Deschampsia flexuosa	3	2	3	3	4	3	3	5	4	4	100-4	
Juncus trifidus	3	2	5	.	1	4	1	3	2	2	90-3	
Nardus stricta	4	5	.	2	3	.	5	.	4	4	70-4	
D Conostomum tetragonum	1	1	.	1	.	.	30-1	
Dicranum scoparium	1	1	1	1	1	1	1	1	2	3	100-1	
Kiaeria starkei	1	.	1	.	1	2	.	1	.	.	50-1	
Plagiothecium curv.+dent.+laet..	1	1	1	30-1	
Pohlia drummondii+nutans	1	1	2	1	1	1	1	2	1	1	100-1	
Polytrichum alpinum	1	.	.	.	3	1	30-2	
P. piliferum	1	.	2	1	.	.	30-1	
Barbilophozia floerkei	1	3	1	1	1	3	2	2	4	3	100-3	
B. lycopodioides	.	.	.	1	2	1	.	.	1	.	40-1	
Cephalozia spp.	.	.	.	1	1	.	1	.	.	.	30-1	
Lophozia ventricosa	1	1	1	1	.	1	1	1	1	1	90-1	
Marsupella brevissima	.	1	1	.	1	30-1	
Moerchia blyttii	.	.	.	1	1	1	30-1	
Cetraria islandica	2	2	1	1	1	1	1	1	2	2	100-1	
Cladonia arbuscula	1	2	.	1	.	.	1	.	.	.	40-1	
C. bellidiflora	1	1	1	1	1	1	1	1	.	1	90-1	
C. coccifera	1	1	1	.	.	1	40-1	
C. ecmocyna	1	2	3	1	1	2	1	.	.	.	70-2	
C. furcata	.	.	.	1	.	.	1	1	1	1	50-1	
C. gracilis	1	.	.	1	.	1	30-1	
C. pyxidata coll.	.	1	1	1	.	.	1	1	1	1	70-1	
C. squamosa	1	1	1	1	1	1	1	.	1	1	90-1	
Stereocaulon spp.	1	.	1	.	1	30-1	
Vascular plants	9	10	7	14	18	12	14	10	12	13	12	
Bryophytes	9	5	7	15	14	11	10	10	6	7	9	
Lichens	8	8	6	10	5	7	9	4	4	7	7	
Total number of species	26	23	20	39	37	30	33	24	22	27	28	

Additional species occurring in 2 sample plots or less (Plot No.; cover - constancy-characteristic degree of cover):

C: Lycopodium selago (6:1 - 10-1), Salix herbacea (5:2, 10-2), Vaccinium uliginosum (6:1 - 10-1), Gnaphalium supinum (3:1, 5:1 - 20-1), Hieracium alpinum (10:1 - 10-1), Mel-andrium rubrum (4:1 - 10-1), Rumex acetosella (9:1 - 10-1), Sibbaldia procumbens (5:1 - 10-1), Viola palustris (5:1, 6:1 - 20-1), Carex magellanica (4:1, 7:1 - 20-1), Eriophorum vaginatum (7:1 - 10-1), Luzula frigida (9:1, 10:1 - 20-1), Scirpus caespitosus (7:1 - 10-1).

D: Aplopon wormskioeldii (10:1 - 10-1), Brachythecium starkei (4:1, 5:1 - 20-1), Dicranum majus (7:1, 8:1 - 20-1), Drepanocladus uncinatus (5:1 - 10-1), Oligotrichum hercynicum (1:1 - 10-1), Plagiothecium cavifolium (4:2 - 10-2), Polytrichum commune (4:1, 8:1 - 20-1), P. juniperinum (4:1 - 10-1), P. sexangulare (1:1, 5:1 - 20-1), P. strictum (4:1, 7:1 - 20-1), Racomitrium fasciculare (5:1 - 10-1), Sphagnum compactum (7:1 - 10-1), S. nemoreum (7:3 - 10-3), S. russowii (4:1, 7:1 - 20-1), Anthelia juratzkana (6:1 - 10-1), Barbilophozia hetcheri (10:1 - 10-1), Calypogeia integristipula (4:1 - 10-1), C. neesiana (4:1 - 10-1), Pleuroclada albenscens (6:1 - 10-1), Cladonia carneola (4:1, 7:1 - 20-1), C. fimbriata (4:1 - 10-1), C. pleurota (1:1, 10:1 - 20-1), C. sulphurina (2:1 - 10-1), C. uncialis (6:1 - 10-1).

Gjærevoll (1956) and Dahl (1957) the snow bed type of *Athyrium distentifolium* vegetation roughly corresponds to the moderate snow beds (the grass heaths) as regards snow conditions.

The snow bed vegetation of the investigated area mostly falls within the moderate snow bed series in the narrow sense, represented by grass heaths with variable dominance relationships. The grass heaths are most common in the middle alpine zone, where they cover large areas. They are chionophilous and more or less seasonally hygrophilous. The two most extreme snow bed series are only represented by fragments in the area.

REGIONAL VARIATION IN SOUTHERN NORWEGIAN POOR FOREST AND ALPINE VEGETATION ALONG THE OCEANICITY-CONTINENTALITY GRADIENT

MATERIAL AND METHODS

As emphasized in the general part of the work, a comprehensive treatment of regional variation in poor forest and alpine vegetation of Southern Norway is not at present available. However, the vast phytosociological material resulting from intensive studies of local areas is sufficient to show major variation in forest and alpine vegetation along the oceanicity-continentality gradient as far as the xeric, subxeric, and submesic series are concerned. On the basis of the reclassification of vegetation types presented as comparisons in the previous chapter, all sets of at least five sample plots corresponding to one site-type were excerpted. For each such set the constancy and arithmetic mean of Hult-Sernander-Du Rietz cover values were calculated. For each of the three series the species were grouped as follows: (1) oceanic species in order of increasing distributional areas; (2) continental species in order of decreasing distributional areas; and (3), other species without pronounced geographical trends but with an important quantitative role in the series. Among the species with geographical preference those assumed to follow the series to the limit of their distribution were marked \$. The stations providing sample plots were numbered in order of decreasing oceanicity according to the floristic criteria above (Fig. 16). The vegetation tables and their sources are given as Tabs 40-45. It should be emphasized that different authors have varied greatly in the attention they have paid to the composition of the bottom layer. The lack of mention of a species does not necessarily indicate that it does not exist in an area.

RESULTS AND DISCUSSION

Regional variation of the xeric series

Area. Most of the studies from Western Norway do not describe xeric vegetation (e.g., Nedkvitne & Thomter 1953, Aune 1973, Bergland 1975, Kummén 1977, Fredriksen 1978, Losvik 1978, Odland 1978, 1981b). In Vikedal (station 5 in Fig. 16), xeric pine forests occur on the most exposed hills (Huseby & Odland 1981). Odland (1979) and Omberg (1980) comment on the small areas in Western Norway occupied by xeric vegetation. Knaben (1952) describes the gradual disappearance of xeric vegetation, even on the crags, along an east-west transect in Central Sogn, and ascribes it to the great increase in precipitation and thus in snow cover in winter. Xeric vegetation is described from oceanic parts of Trøndelag by Klokke (1974), but not mentioned by Kjølsvik (1978) or Moen (1978). From Northern Fennoscandia

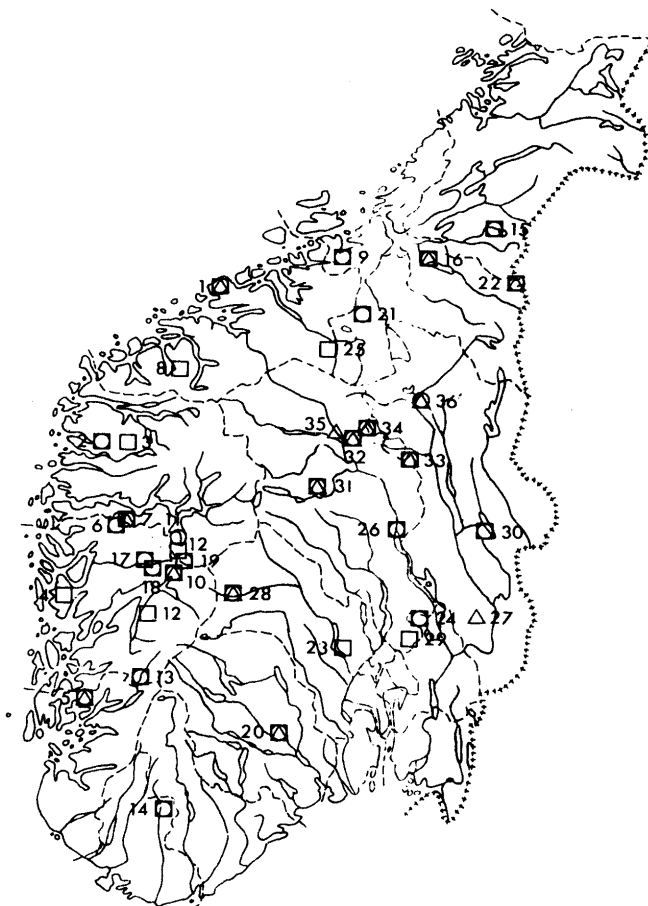


Fig. 16. Geographic position and reference number of works used in regional comparison.

Hämet-Ahti (1963) describes xeric vegetation from the continental subalpine subzone, while xeric vegetation is lacking in the oceanic subzones. In continental areas xeric vegetation covers large areas in all zones (cf. Nordhagen 1943, Kielland-Lund 1967, 1971, 1973, 1981, Bendiksen & Schumacher 1982, Bendiksen & Salvesen 1985).

The small area occupied by the poor xeric series in the upper boreal birch forests as compared to lower coniferous forests in the same area is often commented on (cf. Resvoll-Holmsen 1918, Mork 1956, Hämet-Ahti 1963, Sonesson & Lundberg 1974). Resvoll-Holmsen (1918: 192) ascribed this to the shading by birches, while C. Tamm (1953) drew attention to the

Tab. 40. Regional variation in the composition of xeric vegetation. Constancy class and characteristic degree of cover (for material presented in this paper) or arithmetic mean of cover values according to the Hult-Sernander-Du Rietz scale (for material compiled from literature sources) are tabulated. Stations are arranged in a sequence from the most oceanic at left to the most continental at right. Station numbers correspond to numbers in Tab. 32, in which the material that forms the basis for this table is listed. Species are listed as follows: Species with a pronounced oceanic tendency in the xeric series, species with a pronounced continental tendency in the xeric series, species without pronounced distributional patterns in the xeric series. Species with a total distribution in Southern Norway more or less corresponding to its distribution in the xeric series, are marked with §.

Station No.	1	5	7	10	16	20a	20b	20c	20d	22a	22b	26	27	28a	28b	31a	31b	31c	32	33	34a	34b	35	36	
§ <i>Festuca vivipara</i>	2-1	1-1	2-1																						
<i>Racomitrium lanuginosum</i>	4-2	4-2	1-1	3-1	3-4		4-2	3-1		1-1	2-1					2-1	2-1							1-1	
<i>Arctostaphylos alpina</i>	3-2	5-2	3-2				5-1	4-1		4-1					4-3	1-1	2-1					1-1		1-1	
<i>Loiseleuria procumbens</i>	5-5	5-3	2-2				4-2	5-3	3-1	3-1	5-4				2-4		1-3					4-1	2-1	2-3	
<i>Betula nana</i>		5-2						2-1		1-1	5-2				2-1		5-2	2-3	1-1	2-2	2-2	3-1		4-2	
<i>Arctostaphylos uva-ursi</i>							2-2						1-1	2-4		4-2	3-4			1-1	2-4		5-2	2-4	
§ <i>Festuca ovina</i>										1-1				3-1	5-3	5-1	5-1	5-1			1-1	2-1	3-1	5-1	2-1
<i>Viscaria alpina</i>																1-1									
<i>Salix glauca</i>																1-1	2-2	1-1		1-2				1-1	
§ <i>Anemone vernalis</i>																	1-1	3-1				1-1			
<i>Betula pubescens</i>							1-1	2-1	1-1		5-4		4-2	1-1		5-5	1-1		4-1	5-2					
<i>Calluna vulgaris</i>		5-1	1-2	5-4	5-4	5-3	4-3	2-1		1-1	1-1	4-4	5-2			1-1			5-2	3-3	1-1		1-1	1-1	
<i>Empetrum</i> spp.	5-2	5-2	5-4		5-1	2-1	5-2	5-3	5-3	5-4	4-2	3-1	3-2		5-3		5-3	3-1						3-1	
<i>Juniperus communis</i>		3-2						2-1		2-1									4-1	3-2				2-1	
<i>Pinus sylvestris</i>				5-4	2-3	5-4										5-3	5-4							5-4	
<i>Salix herbacea</i>	4-1	1-2	1-1					1-1	2-1		1-1					1-1		1-1	5-2				1-1	1-1	
<i>Vaccinium myrtillus</i>	3-1	2-1		5-2	1-1					5-1		5-1	5-1			1-1			5-1	5-3	1-1				
<i>V. uliginosum</i>	5-1	5-3	3-1	1-2	2-1		4-2	5-1	1-1		1-1	2-1	1-1	4-2		5-2	4-2	2-2	3-1	4-2	3-1			1-1	
<i>V. vitis-idaea</i>	5-1		4-1	5-2	5-1	5-1	4-1	4-1	5-2	5-2	4-1	5-1	5-2	5-1	5-3	5-2	5-1	5-3	5-1	5-2	3-1	5-2	5-2	5-1	
<i>Diapensia lapponica</i>												1-1									1-1				
<i>Hieracium alpinum</i>	1-1															5-1	1-1	1-1	4-1	1-1		1-1	2-1	1-1	
<i>Carex bigelowii</i>	5-1	5-2	4-1					2-1	1-1		5-1				1-1	5-1			2-1	1-1		1-3	2-1	5-1	
<i>Deschampsia flexuosa</i>		2-1	2-1	3-1			5-1		1-1	3-1			3-1					4-1	1-1		5-1	5-2	1-1		
<i>Juncus trifidus</i>	5-1	4-1	4-1				5-1	5-2	5-1						1-1	5-4	2-1	2-1	5-1			4-1	5-2	1-1	
<i>Luzula spicata</i>		2-1										1-1				1-1	1-1	1-1	4-1						
<i>Hylocomium splendens</i>				5-2						3-1		3-1	1-1					2-1			1-1	2-1		1-1	
<i>Dicranum fuscescens</i>	3-1		4-2	2-1			2-1			1-1	3-1	5-2	3-1	5-2	1-1	5-1	2-1				5-3	2-1	4-1	3-1	
<i>D. scoparium</i>	5-2			3-1	5-1		2-1	2-1	4-1	5-2		3-1	3-1				2-1				5-1	3-1	2-1	3-1	
<i>D. polysetum</i>				5-1			2-1					3-1	5-1												
<i>D. spurium</i>				2-1			1-1						3-1											4-2	
<i>Pleurozium schreberi</i>	2-1	1-1	1-1	5-3	4-2	1-1				5-2		5-3	5-2			4-1	1-1		5-3	5-3				2-1	
<i>Pohlia nutans</i>						5-1	5-1	4-1	5-1		1-1	2-1	3-1	1-1	2-1	5-1	2-1	3-1		4-1	3-1	4-1	5-1	2-1	
<i>Polytrichum commune</i>								2-1	2-1	1-1			1-1							1-1	3-1	1-1		1-1	
<i>P. juniperinum</i>		5-1					4-1	1-1		5-1	1-1	3-1	2-1	3-1	5-1	5-1	4-1	4-1	5-1	3-1	3-1	4-1	3-1	2-1	
<i>P. piliferum</i>							4-1	5-1	5-1	2-1	2-1			1-1	1-2		2-1	5-1	1-1	1-2	2-1	2-1	1-1	2-1	
<i>Sphagnum nemoreum</i>												1-1	1-1								1-1				
<i>Ptilidium ciliare</i>	2-1	1-1		4-1	1-1					4-1	2-1	2-1	1-1	1-1		4-1	1-1		1-1	1-1	1-1		4-1	1-1	
<i>Gymnomitrium coralloides</i>											2-1			1-1			1-1	4-1				1-1			
<i>Alectoria nigricans</i>		1-1					2-1	4-1	4-1	1-1	4-1			2-1			2-1	3-1			3-1	5-1		3-1	
<i>A. ochroleuca</i>		5-2					5-3	5-4	5-4	1-1	5-2			4-4			3-1	5-3	5-2			5-3	3-1	5-3	
<i>Cetraria cucullata</i>							4-2	5-3	5-2	3-1	4-2			5-1	3-1	5-1	5-1	5-1				5-1	5-1	5-1	
<i>C. ericetorum</i>				2-1	5-2	5-2	5-3					1-1													
<i>C. islandica</i>	5-1	4-1	5-2				5-1	5-2	5-1	5-2		3-2		3-2		5-1	5-2	5-1	5-1	5-2	5-1	5-1	5-1	5-1	
<i>C. nivalis</i>		5-3					1-1	5-2	5-3	5-3	5-1	5-3	1-1	1-1	5-2	5-3	5-2	5-3	5-5	4-1	4-1	5-3	5-5	5-1	
<i>Cladonia arbuscula</i>	5-2			5-2			5-2	5-3	4-2	4-1		5-5	5-3	5-2	5-2		5-1	5-2	5-2	5-1	5-1	5-1	5-1	5-1	
<i>C. mitis</i>		1-3	5-4			5-4	4-1	2-1	1-1																
<i>C. rangiferina</i>	1-1	1-2		5-4	5-2	5-3	5-2	5-1	5-1	5-3	4-2	5-2	5-2		4-1	3-1	5-2	4-1	4-1	5-1	5-2	3-1	5-1	5-2	
<i>C. bellidiflora</i>							5-2	4-1	2-1	4-1	5-1	3-1	2-1		1-1	3-1			3-1	3-1	2-1	3-1		1-1	
<i>C. coccifera+pleurota</i>				4-1			5-1	5-1	5-1	5-1	5-1	5-1	2-1	2-1	2-1	5-1	5-1	3-1	2-1	5-1	2-1	5-1	5-1	1-1	
<i>C. cornuta</i>																									
<i>C. crispata</i>							2-1		1-1		4-1	1-1	1-1	2-1											
<i>C. deformis+sulphurina</i>							5-1	5-1	3-1	3-1	3-1	1-1	3-1	4-1			3-1			5-1		3-1	4-1	1-1	
<i>C. ecmocyna+gracilis</i>	1-1		2-1				1-1	2-1	4-1	5-1	5-3	5-2	4-1	2-1		4-1	5-1	5-1	5-1	5-1	5-1	3-1	5-1	4-1	
<i>C. macrophylla</i>							3-1	2-1	3-1	2-1	5-1	3-1				2-1	3-1	2-1	2-1		1-1	3-1		1-1	
<i>C. pyxidata coll.</i>	1-1						4-1	5-1	4-1	2-1	5-1	4-1	3-1		4-1	3-1	3-1	3-1	5-1	3-1	3-1	3-1	4-1	3-1	
<i>C. stellaris</i>			5-4	3-1	5-5	5-4	5-3	5-2	5-2	4-1		5-2	5-1	1-1	2-1	5-4	2-1	3-1	5-4	5-4	3-1	4-2	5-2	4-2	
<i>C. uncialis coll.</i>		1-2		2-1	1-1	5-1	5-2	5-2	5-1	5-2	5-2	1-1	3-1	5-1	5-1	4-1	5-1	5-1	5-1	4-1	3-1	3-1	5-1	4-1	
<i>Cornicularia aculeata</i>	3-1																								
<i>C. divergens</i>							2-1	5-2	5-1	1-1	3-1			2-1		1-1	4-1								
<i>Nephroma</i> spp.																									
<i>Sphaerophorus fragilis</i>							2-1	2-1			1-1								2-1			2-1			
<i>S. globosus</i>									1-1			1-1	4-1						1-1				3-1	3-1	
<i>Stereocaulon</i> spp.	4-1											5-3	5-2	2-1	2-1	1-1			2-1	5-1		1-1		1-1	
<i>Thamnia vermicularis</i>	2-1											2-1	4-1			1-1	3-1					3-1	4-1	2-1	

Tab. 41. Material forming the basis for evaluation of regional variation in the xeric series.

St. Author No.	County:Parish:Locality	Zone	Communities included	Plot size	Plot No.
1 Malm 1971	Møre og Romsdal:Hustad:Taistad-hesten	LA	Loiseleurieto-Diapsensietum loiseleurisum	1	15
5 HusebysØdland 1981	Rogaland:Vikedal:Vikedal	LA	Rabbesamfunn	1-25	11
7 Knaben 1952	Sogn og Fjordane:Vik+Arnafjord/Hordaland:Modalen+Eksingedal+Vinje	LA	Empetrum-Cladonia rangiferina-sosiasjon, stands II, III	1	10
10 Omberg 1980	Hordaland:Ulvik	LB-MB	Cladonia-type	?	?
16 Klock 1974	Sør-Trøndelag:Klebu:Selbusjøen N.	LB-MB	Lav/lyngrik furuskog Cladonia-samfunn	4	10
20 Halvorsen&Bendiksen, the present paper	Telemark:Bø+Seljord+Hjartdal+Sauland	MB	Xeric series, middle boreal zone (a)	25	5
		UB	Xeric series, upper boreal zone (b)	25	3
		LA	Xeric series, low-alpine zone (c)	25	8
		MA	Xeric series, middle-alpine zone (d)	25	6
22 Nordhagen 1928	Sør-Trøndelag:Tydal:Sylene	UB	Empetrum-reicher Flechtenbirkenwald (a)	4	10
		LA	Betula nana-reiche Cladonia silvatica-Cetraria nivalis-Ass.	1	10
		LA	Cetraria nivalis-Alectoria ochroleuca-reiche Loiseleuria-Ass. (b)	1	20
26 Gjerlaug 1973	Oppland:Lillehammer+Fåberg+Mesna	LB-MB	Lavfuruskog	25	9
27 Kielland-Lund 1981b	Akershus:Aurskog-Høland Kommune Hedmark:Stange Kommune+Elverum	LB	Cladonio-Pinetum Cladonia-Ausbildung	?	11
28 Nordhagen 1943	Buskerud:Hol:Østerdalen+Haugastøl	LA	Loiseleurieto-Diapsensietum (a)	1	20
		LA	Arctostaphyletum uva-ursi alpicolum (a)	1	20
		LA	Empetrum-Cetraria nivalis-sosiasjon (a)	1	10
		MA	Juncetum trifidi, bitype C (b)	1	15
31 Nordhagen 1943	Oppland:Kvikne:Sikilsdalen	UB	Betuletum empetro-cladonum (a)	4	13
		LA	Kryptogamfattig Arctostaphylos uva-ursi-Vaccinium uliginosum-sosiasjon (b)	1	25
		LA	Arctostaphylos uva-ursi-Alectoria ochroleuca-sosiasjon (b)	1	26
		LA	Vaccinium uliginosum-Alectoria ochroleuca-sosiasjon (b)	1	10
		LA	Betula nana-Cetraria nivalis-sosiasjon (b)	1	20
		LA	Betula nana-Alectoria ochroleuca-sosiasjon (b)	1	15
		LA	Salix glauca-Cetraria nivalis-sosiasjon (b)	1	11
		LA	Loiseleuria procumbens-Vaccinium uliginosum-Alectoria ochroleuca-sosiasjon (b)	1	12
		MA	Vaccinium vitis-idaea-Salix herbacea-Cetraria nivalis-sosiasjon (c)	1	11
32 Haug 1970	Oppland:Kvam:Furusjøen	UB	Cladonio-Pinetum	55-100	15
33 Mork&Heiberg 1937	Oppland:Ringebu:Hirkjølén	UB	Calluna-Cladonia-Pinus-sisiasjon	100	24
34 Dahl 1957	Oppland:Sel+Dovre/Hedmark:Folldal	LA	Loiseleurieto-Diapsensietum (a)	5-40	5
		LA	Cetrarietum nivalis typicum (a)	4-35	12
		MA	Alectoriecto-Arctostaphyletum uva-ursi (a)	2-8	8
		MA	Cetrarietum nivalis trifidetosum (b)	7-15	5
35 Kielland-Lund 1981b	Oppland:Sel	MB	Cladonio-Pinetum Festuca ovina-Ausbildung	?	5
36 Du Rietz 1925a	Hedmark:Alvdal+Tydal:Tronfjell	LA	Arctostaphylos uva-ursi-Alectoria ochroleuca-Ass.	1	11
		LA	Loiseleuria procumbens-Cetraria nivalis-Ass.	1	11
		LA	Empetrum nigrum-Cetraria nivalis-Ass.	1	11
		LA	Betula nana-Alectoria ochroleuca-Ass.	1	11
		LA	Betula nana-Cetraria nivalis-Ass.	1	11

shade of the litter and Hämet-Ahti (1963) pointed at the interference of base-rich litter. In contrast, Sonesson & Lundberg (1974: 129) emphasized climatic reasons. In our opinion the increasing humidity with altitude due to increasing precipitation and decreasing temperature (cf. Sjörs 1948, Laaksonen 1976a, 1976b, Førland 1979) is the main reason. In continental areas, where coniferous trees dominate up to the forest limit, xeric vegetation may cover large areas (cf. Kielland-Lund 1967, 1981).

In the alpine zones the areas occupied by the xeric series increase owing to wind action. In continental areas with low winter precipitation xeric vegetation occupies large areas (Du Rietz 1925a, Nordhagen 1943, Dahl 1957), and may even be the most important series (Resvoll-Holmsen 1914b).

Physiognomy. In the boreal zones the xeric series is a *Pinus sylvestris* (rarely *Betula pubescens*) forest with a sparse field layer and a dense, lichen-dominated bottom layer.

In the alpine zones there is considerable variation.

In the opinion of Poore & McVean (1957: 427), the Scandinavian lichen heaths are replaced by *Racomitrium lanuginosum*- and *Juncus trifidus*-dominated vegetation in the oceanic climate of Scotland. *Racomitrium*-dominated, probably xeric vegetation is described by Poore & McVean (1957), McVean & Ratcliffe (1962), and McVean (1964), from oceanic parts of Norway by Du Rietz (1925b), Malme (1971), Klokke (1974), and Omberg (1980). Except for the most oceanic areas, lichens dominate the bottom layer of the xeric series. The very dense lichen carpets of continental areas have a negative influence on dwarf shrubs (Nordhagen 1928, 1937, Knaben 1952). Thus the field layer is best developed in suboceanic areas (Nordhagen 1928).

Floristic variation of the xeric series is shown in Tab. 40. The material used is listed in Tab. 41. The series is poor in species, and only a few species have phytogeographical significance. Particularly striking is the virtually non-overlapping distributional patterns of the oceanic *Festuca vivipara* and the continental *F. ovina* (cf. Salvesen 1982, Halvorsen & Salvesen 1983), both having their main importance in the alpine zones.

Corresponding but overlapping distribution patterns are found among the dwarf shrubs. *Arctostaphylos alpina* and *Loiseleuria procumbens*, oceanic alpine plants (Dahl 1951, Böcher 1954, 1963), are most frequent in the oceanic part of the gradient, while *Arctostaphylos uva-ursi* and *Betula nana* increase towards the east. Climatic factors, e.g., maximum summer temperatures (Dahl 1951), and morphological features, e.g., the slender stems of *Loiseleuria procumbens*, making it less suited than *Arctostaphylos uva-ursi* and *Betula nana* to cope with extensive lichen carpets (Nordhagen 1943, 1954a), have been used to explain the distribution of oceanic alpine plants.

The decrease and often local disappearance of *Betula nana* in Western Norway reported by Samuelsson (1938), Ve (1940), Nordhagen (1943, 1954b), Knaben (1952), Skogen (1976), Kummen (1977), and Fredriksen (1978), have been given various explanations. The possible effect of cloud cover (shading) as suggested by Knaben (1952) is less likely because the species is locally abundant (Kummen 1977, Huseby & Odland 1981), and loses some of its continental character farther north along the coast (Dahl 1951, Skogen 1965). Dahl (1951) draws attention to the theory of A. Blytt (1876a) that in oceanic areas the continental mountain plants might suffer from the alternate freezing and thawing during winter and the long spring with variable temperature conditions, perhaps due to a physiological mechanism initiating germination at the onset of spring or when a cold period is followed by higher temperatures. The tolerance of *Betula nana* to very low temperatures in winter (cf. Nordhagen 1943, Jonasson 1981) also draws attention to the temperature change, not to the cold periods, as a possible explanation.

In oceanic Scotland and Western Norway some species elsewhere considered hygrophilous, appear in xeric vegetation (Naustdal 1951, Poore & McVean 1957, McVean & Ratcliffe 1962, McVean 1964, Malme 1971).

Species entering the xeric series in continental areas are *Salix glauca*, *Viscaria alpina*, and the relatively rare *Anemone vernalis*.

The chionophobous lichen species *Alectoria ochroleuca*, *A. nigricans*, *Cetraria cucullata*, *C. nivalis* etc. decrease in constancy and cover towards the oceanic West, where they are replaced by the more chionophilous *Cetraria islandica*, (cf. Nordhagen 1943, Knaben 1952). The xerophilous mosses *Polytrichum juniperinum* and *P. piliferum* also appear to decrease towards the west, as observed by Hämet-Ahti (1963) in Northern Fennoscandia. Variation in the composition of the bottom layer is otherwise not well documented, but it is probable that *Dicranum drummondii* and *D. spurium* increase eastwards.

The position of Grunningsdalen relative to regional variation. The area occupied by xeric vegetation in the Grunningsdalen area is small, particularly in the boreal zones. This is in accordance with the observations of Mork (1956), and an oceanic-humid feature.

Neither *Festuca vivipara* nor *F. ovina* occur. The more oceanic alpine species *Arctostaphylos alpina* and *Loiseleuria procumbens* are important as dominants in the upper boreal and alpine zones. The bottom layer is mainly occupied by lichens, but a characteristic humid feature is the occurrence of *Racomitrium lanuginosum* in the upper boreal and low alpine zones. The well-developed lichen carpet in the bottom layer shows further oceanic features in the rich occurrence of *Cetraria islandica*. Among the continental species only sparsely occurring *Arctostaphylos uva-ursi* and *Betula nana* are present. The similarity of some alpine xeric plots to the continental facies of *Loiseleurieto-Diapensietum* described by Dahl (1957) from extreme sites in Rondane should also be mentioned as a weakly continental attribute of the vegetation.

The small area occupied by the xeric series in Grunningsdalen, and the high importance of oceanic species in the three uppermost zones, justifies its classification as weakly oceanic. However, the middle boreal xeric site-type is devoid of oceanic traits. This is an example of the increasing oceanicity towards higher altitudes within the boreal zones due to increasing precipitation and lowered temperatures. The northern continental species *Cladonia mitis* and *C. stellaris* dominate in the middle boreal zone, while the more humidity-tolerating *C. arbuscula* (cf. Ahti 1961) is the most important of these three lichen species in the three uppermost zones.

Regional variation of the subxeric series

Area. The subxeric series covers large areas in all parts of Southern Norway.

Physiognomy. The physiognomy varies. In the boreal zones, *Pinus sylvestris* and *Betula pubescens* dominate the western areas, while *Picea abies* partially replaces the latter east of the mountain range.

In the bottom layer the variation along the climatic gradient is considerable. In alpine zones lichens mostly have low importance in the oceanic areas (cf. Nordhagen 1943, Knaben

Tab. 42. Regional variation in the composition of subxeric vegetation. Constancy class and characteristic degree of cover (for material presented in this paper) or arithmetic mean of cover values according to the Hult-Sernander-Du Rietz scale (for material compiled from literature sources) are tabulated. Stations are arranged in a sequence from the most oceanic at left to the most continental at right. Station numbers correspond to numbers in Tab. 34, in which the material that forms the basis for this table is listed. Species are listed as follows: Species with a pronounced oceanic tendency in the subxeric series, species with a pronounced continental tendency in the subxeric series, species without pronounced distributional patterns in the subxeric series. Species with a total distribution in Southern Norway more or less corresponding to its distribution in the subxeric series, are marked with §.

Station No.	1	2	5a	5b	6	7	9	10	11	13	14a	14b	15	16	18	19	20a	20b	20c	20d	21	22a	22b	22c	23	24a	24b	26a	26b	28a	28b	30	31a	31b	31c	32	33	34a	34b	36							
§ Polygala serpyllifolia		1-1																																													
§ Carex binervis		1-1																																													
§ Anastrepta orcadensis		1-1	1-1		1-1		1-1	1-1																																							
Mylia taylorii		1-1		1-1																																											
§ Bazzania trilobata							1-1	1-1																																							
Narthecium ossifragum		2-1	1-1	1-1																																											
Sphagnum quinquefarium					2-2		4-3	2-2																																							
§ Barbilophozia atlantica		3-1								1-1																																					
Eriophorum vaginatum		2-1		3-1			1-1		1-1																																						
Pteridium aquilinum			1-1				1-1			3-1																																					
Plagiothecium undulatum		1-1	1-1	2-1	1-1		2-1							1-1																																	
Erica tetralix		2-1		2-1							1-1	1-1																																			
Blechnum spicant		3-1	2-1		1-1		2-2						1-1			1-1	1-2																														
Rhytidiadelphus loreus	4-1	5-1		2-1	1-1		2-1	2-1		1-1						1-1	3-2																														
R. squarrosus+subpinnatus		2-1					1-1		1-1		1-1																																				
R. triquetrus								1-1																																							
Potentilla erecta	1-1	4-1	2-1	2-1	1-1		1-1		1-1	3-1						1-1																															
§ Juncus squarrosus		1-1																1-1																													
Scirpus caespitosus		5-2		3-1	3-2		1-1	1-3		2-1																																					
Molinia caerulea		5-1		4-1	2-1		1-1	1-1		3-1	2-1	1-1				1-1																															
§ Leucobryum glaucum		2-1	1-1								1-1	2-1						1-1																													
Cornus suecica	4-2	4-1	3-1	3-1	4-2		5-2	1-1	2-1	4-2	1-1	2-1	1-1	5-1	1-2																																
Andromeda polifolia		3-1	2-1	2-1	4-2		3-1	2-1		1-1		2-1	3-1																																		
§ Festuca vivipara		1-1				2-1																																									
Arctostaphylos alpina	4-2	3-1		3-1		3-3				3-1	2-1		1-1	3-1		5-3		4-1	3-2			1-1	1-1	1-1								1-1	2-1														
Racomitrium lanuginosum	3-1	5-3	1-1	2-1	2-4	1-1	1-4	1-2	1-2	1-2			4-3				1-2	1-1			1-3		1-1																								
Calluna vulgaris	4-5	5-5	5-3	5-3	5-3	1-1	5-3	5-3	4-3	5-2	5-4	5-4	5-3	5-2	3-3			5-4	5-4	4-3		5-3	5-4	3-5		5-1		2-2	1-1	1-1																	
Betula nana						4-3				1-1				2-1					1-1	1-2		3-2	1-1	3-2		3-1																					
§ Picea abies														2-1		+		4-2	2-2	1-1																											
Arctostaphylos uva-ursi									1-1																																						
§ Festuca ovina																																															
Viscaria alpina																																															
§ Pyrola chlorantha																																															
§ Lycopodium complanatum																																															
§ Anemone vernalis																																															
§ Goodyera repens																																															
Betula pubescens			5-1	4-1	1-1	4-3		2-1																																							
Empetrum spp.	5-3	5-2	3-1	3-1	5-3	5-4	5-3		5-4	5-2	3-1	5-1	5-3	5-3	3-2	5-5		5-2	5-4	5-5	5-5	5-3	5-3	5-4		5-2																					
Juniperus communis	1-2	5-2	4-2	4-2	1-1		4-2			4-1	1-2	4-2	3-1					1-1	1-1	1-1	1-4	2-1	4-1	1-1																							
Loiseleuria procumbens	3-1							3-1	1-1		1-1								4-2	5-3	3-1	1-2		3-1																							
Lycopodium alpinum						1-1				1-1																																					
L. annotinum					2-1			1-1	1-1		1-1				1-2																																
L. clavatum		2-1		2-1				1-1	1-1		2-1		1-1		1-1																																
L. selago					1-1																																										
Phyllocladus caerulea																																															
Pinus sylvestris		1-1	5-3	2-1			5-4	5-5			5-4	5-3	5-2	4-3	+		3-3	2-1																													
Salix glauca									5-2																																						
S. herbacea	1-1					3-2											4-1																														
Sorbus aucuparia			3-1	2-1			4-1			4-1	2-1	2-1		1-1				1-1	2-1			1-1	1-1																								
Vaccinium myrtillus	5-1	5-2	5-3	4-2	5-2	4-2	5-3	5-4	5-1	5-3	5-4	5-3	5-1	5-2	4-3	2-1	5																														

Tab. 42 continued.

Station No.	1	2	5a	5b	6	7	9	10	11	13	14a	14b	15	16	18	19	20a	20b	20c	20d	21	22a	22b	22c	23	24a	24b	26a	26b	28a	28b	30	31a	31b	31c	32	33	34a	34c	36	
<i>Hieracium alpinum</i>	1-1				1-1				1-1													2-1							1-1	5-1			1-1	4-1	1-1			1-1			
<i>Linnaea borealis</i>	2-1	1-1				4-1	2-1				1-1	1-1		2-1	4-2						1-1	1-1				4-1		5-2	2-1			1-1			2-1	1-1					
<i>Maianthemum bifolium</i>	2-1		2-2			1-1				4-1				5-1			1-1	2-1			1-1	1-1						1-1	1-1			1-1			1-1						
<i>Melepyrum pratense</i>	5-1	4-1	2-1	1-2		5-1	5-2			3-1	5-1	4-1	1-1	5-1	1-1		3-1	2-1			2-1	5-1			5-1	3-1	4-1	1-3	1-1		2-1	3-1			5-1	3-1					
<i>Rubus chamaemorus</i>	1-1		1-1	4-2		1-1				1-1	1-1	1-1					1-1	1-1	1-1		1-1							1-1						2-1			1-1				
<i>Solidago virgaurea</i>	1-1									1-1											2-1	4-1	1-1							2-2		5-2	2-1	4-1	3-1	3-1	1-1				
<i>Trientalis europaea</i>	2-1	3-1	2-1	4-1	2-1	1-1	3-1	1-1		4-1	2-1	3-1			2-1		1-1	2-1			3-1	4-1	1-1	3-1				3-1	1-1	2-1		5-1		5-1	1-1			4-1	3-1		
<i>Carex bigelowii</i>	3-1	2-1			5-2				3-1	4-1			1-1		2-1		2-1	2-1	1-1			5-1	5-2	1-1					5-2		2-1	3-1	2-1	1-1	5-2	4-1	3-1				
<i>Deschampsia flexuosa</i>	5-1	5-1		3-1	4-2	2-1	5-1	5-1	5-1	5-1	3-1	5-1	5-2	5-1	5-2	1-1	5-2	5-2	5-1	5-2	5-1	5-1	4-1	3-1		5-1	5-1	4-1	5-1		2-1	3-1	5-2	3-1	1-1	5-1	5-2	5-1	2-1		
<i>Juncus trifidus</i>	2-1			1-2	2-1												2-1	3-1	5-1	1-1		2-1	5-5	1-1				1-1	5-5		1-1		4-2			1-1	5-3	1-1			
<i>Luzula pilosa</i>						1-1				2-1					2-1						1-1													5-1	1-1		2-1	2-1			
<i>L. spicata</i>						1-1																		1-1	2-1									5-1			1-1		1-1		
<i>Nardus stricta</i>	3-1		2-1	2-1	2-1	1-1			1-1	3-1			1-1		1-1		1-2			1-1		1-1							2-1							2-1	1-1				
<i>Dicranum fuscescens</i>	1-1	5-1				1-2	2-1			4-1	1-1	1-1	5-1	1-1			3-1	1-1	2-1	2-1	4-1	3-1		1-1		2-1	5-1	2-1	4-1						3-1	4-1	4-1	2-2	5-1	4-1	
<i>D. scoparium</i>	5-2		3-1	3-1	5-3	4-1			2-3	4-1	2-1	4-1	5-1	5-1	3-2	5-2	5-3	5-2	5-2	5-2	5-1	5-2	5-2		5-1	5-1	5-1	5-2	3-2	5-1		5-1	5-1	2-4	3-1	1-1		5-1	5-2	1-1	
<i>D. majus</i>				1-1		3-1	3-1								2-1	3-2				1-1							4-1	3-1		1-2						1-1	1-1				
<i>D. polysetum</i>	3-1					1-1	2-1						5-2	2-1		1-1		1-1	2-1							1-1	2-1		4-2					1-1							
<i>Hylocomium splendens</i>	4-3	5-1		3-1	5-2	1-1	5-4	5-3	3-2	5-1	4-1	3-1	4-2	5-5	5-4	4-1	1-2	2-1	1-2		4-2	4-1	1-2		3-1	5-4	5-2	5-3	4-1				1-1	5-2	3-1	1-1	5-3	4-2	1-1		
<i>Pleurozium schreberi</i>	5-3	5-2		5-1	5-3	3-3	5-4	5-3	5-3	5-2	5-4	5-2	5-4	5-2	5-3	5-2	5-3	5-2	3-3	3-2	5-2	5-2	2-1		5-2		5-4	5-4	5-4	5-4				4-3	5-2	4-1	1-1	5-2	5-2	1-1	
<i>Pohlia nutans</i>				1-1		1-1							2-1				1-1	4-1	3-1	5-1											2-1			1-1	3-1	1-1	2-1	4-1	4-1	1-1	
<i>Polytrichum commune</i>	2-1				3-3					4-1	4-2	1-1		1-1	3-1			2-2	1-1	2-1	3-1								3-1	2-1					2-2	3-1	3-1			3-1	
<i>P. formosum</i>			3-1			3-1								1-1			1-1	1-1											1-1												
<i>P. juniperinum</i>				2-1			1-1			2-1		1-1	2-1			2-1		1-1	1-1	3-1	4-1	1-1	3-1		5-1			2-1	1-1	2-1	5-1	4-1		2-1	3-1	3-1	2-1	3-1	3-1	1-1	1-1
<i>P. piliferum</i>																				3-1	1-1				5-1						1-1				2-1			1-1	2-1		
<i>Ptilium crista-castrensis</i>	2-1	3-1	1-1	2-1	1-2		5-2	4-2		1-1	2-2	2-1	1-1	5-1	5-3	5-1	1-1										5-1	3-1	5-2		2-1				1-1		1-1	1-1		1-1	
<i>Sphagnum nemoreum</i>	2-1		4-1	3-2		2-2	2-3			2-2	5-3	5-1	2-2	3-2	1-1		2-1	2-2										3-2		2-1				1-1				2-2	1-1		
<i>Barbilophozia attenuata</i>						1-1					1-1	1-1	1-1																								1-1	1-1			
<i>B. barbata</i>				2-1			3-1	2-1			1-1				1-1	1-1					3-1	1-1		1-1													1-1	2-1			
<i>B. floerkei</i>	1-1	2-1	1-1	2-1	3-1		1-1	2-1		4-1	1-1	3-1	3-1	2-1	1-1					5-3	3-1	4-1	5-1	1-1	1-1	2-1	4-1			5-1				3-1			1-1	2-1	1-1		
<i>B. hatcheri</i>																					1-1	3-1	1-1	3-1		1-1	1-1	2-1		3-1	4-1						2-1	1-1			
<i>B. lycopodioides</i>			3-1		2-1	2-2							2-1							4-2	4-2	2-1	2-1	4-1	5-2	1-1								1-1	2-1	1-1		5-1	2-1	1-1	
<i>Lophozia ventricosa</i>							1-1						1-1							2-1	2-1	3-1	4-1	1-1										1-1	1-1	2-1	2-1	1-1	3-1		
<i>Ptilidium ciliare</i>	1-1	5-1		1-1	5-1		3-2	3-1		4-1	5-1	4-1	3-1	5-1	2-1		4-1	4-2	4-1	5-1	4-1	2-1	3-1	3-1	3-1	2-1	2-1			1-1		1-1	1-1	4-1	2-1	1-1	1-1		3-1	2-1	
<i>Alectoris ochroleuca</i>																				1-1		1-1		1-1																	
<i>Cetraria cucullata</i>																					1-1				3-1																
<i>C. ericetorum</i>																									1-1																
<i>C. islandica</i>	1-1	2-1		1-1	2-1	5-2				4-2	2-1		2-1				1-1	5-1	5-2	5-3	5-4	5-4	2-1	2-1	4-2		3-1	5-1													
<i>C. nivalis</i>						5-2														1-2		1-1	2-1	5-1	1-1		4-1		2-1												
<i>Cladonia arbuscula</i>	5-1						2-2	1-1		4-1										5-2	5-2	5-2	5-2		4-1	5-1															
<i>C. mitis</i>						5-3				5-1	1-2									4-3	5-2	5-1	3-1		4-1	5-2	5-3	5-2	5-1												
<i>C. rangiferina</i>	1-1	5-1		2-1			3-1	2-1	4-1	5-2	5-1	5-1	4-2	3-1		1-1	5-1	5-1	5-2	5-1	4-1	5-1	2-1	5-2		4-1	5-1	1-1													
<i>C. bellidiflora</i>							1-1				1-1	1-1	2-1							5-1	4-1	4-1	5-1	2-1	5-1	4-1	4-1														
<i>C. carneola</i>													1-1							5-1	4-1	5-1	1-1																		
<i>C. coccifera+pleurota</i>													2-1	3-1						2-1	2-1	4-1	4-1	5-1		3-1	2-1	5-1	4-1		2-1	2-1									
<i>C. cornuta</i>																				2-1	1-1																				
<i>C. crispata</i>						1-1							2-1							2-1		1-1																			
<i>C. deformis+sulphurina</i>						1-1					1-1		2-1							2-1	3-1	3-1	5-1				1-1	1-1	1-1	3-1		2-1	3-1								
<i>C. fimbriata</i>						2-1														3-1	4-1	2-1		3-1																	
<i>C. furcata</i>						1-1				1-1		1-1	1-1	1-1						4-1	4-1	3-1	2-1	1-1																	
<i>C. somocyne+gracilis</i>	1-1	2-1					1-1			1-1										5-1	3-1	3-1	4-1	5-1	2-1	5-1	5-2	5-1	3-1												
<i>C. pyxidata coll.</i>	1-1																																								

Tab. 43. Material forming the basis for evaluation of regional variation in the subxeric series.

St. Author No.	County:Parish:Locality	Zone	Communities included	Plot size	Plot No.
1 Malme 1971	Møre og Romsdal:Hustad:Talstadhesten	LA	Loiseleurieto-Diapensietum arctostaphyletosum alpinae	1	15
		LA	Corneto-Callunetum	1	20
2 Kummen 1977	Sogn og Fjordane:Eikefjord:Ramsdalen	UB	Lavrik Rhacomitrium-Empetrum-Calluna-hei	15-30	11
5 Husebys Odland 1981	Rogaland:Vikedal:Vikedal	LB-MB	Røsslyngdominert furuskog (a)	24-25	10
		LA	Alpin lynghei, plots 1-9 (b)	4-25	9
6 Fredriksen 1978	Hordaland:Eksingedal:Eksingedalen, upper part	UB	Vaccinio uliginosi-Pinetum	9-25	11
		UB	Røsslynghei	4	7
		UB	Fjellkreking-dominert hei	1	5
7 Knaben 1952	Sogn og Fjordane:Vik+Arnafjord/Hordaland:Modalen+Eksingedal+Vinje	LA	Empetrum-Cladonia rangiferina-sosiasjon, stands I, IV	1	10
9 Aune 1973	Sør-Trøndelag:Hemne:Holladalen	LB	Bazzanio-Pinetum	12-100	25
10 Omberg 1980	Hordaland:Ulvik	LB-MB	Bazzanio-Pinetum	?	?
		LB-MB	Hylocomium-typer	?	?
11 Odland 1981a	Sogn og Fjordane:Undredal	LA	Lynghei	4	5
		LA	Rabbesamfunn, plot 6	1	1
13 Odland 1978	Hordaland:Rødal	UB	Barbilophozio-Pinetum	25	8
14 Bergland 1975	Vest-Agder:Åseral	LB-MB	Barbilophozio-Pinetum, 190-300 m.a.s.l. (a)	30	6
		UB	Barbilophozio-Pinetum, 480-690 m.a.s.l. (b)	25-42	16
15 Kjelvik 1978	Nord-Trøndelag:Hegra+Markabygd, Øvre Forra	SX	Barbilophozio-Pinetum cladonietosum	16	14
16 Klock 1974	Sør-Trøndelag:Klæbu:Selbusjøen N.	LB	Lav/lyngrik furuskog Vaccinium-Hylocomium splendens-samfunn	4	10
18 Nedkvitne+Thomter 1953	Hordaland:Voss:Kvitli	LB	Tyttebærtypen	1	20
		LB	Røsslyngtypen	1	10
19 Nordhagen 1943	Sogn og Fjordane:Flåm:Myrdal	LA	Empetrum-Cladonia rangiferina-silvatica-sosiasjon	1	15
20 Halvorsen+Bendiksen, the present paper	Telemark:Bø+Seljord+Hjartdal+Sauland	MB	Subxeric series, middle boreal zone (a)	25	15
		UB	Subxeric series, upper boreal zone (b)	25	8
		LA	Subxeric series, low-alpine zone (c)	25	13
		MA	Subxeric series, middle alpine zone (d)	25	8
21 Moen 1978	Sør-Trøndelag:Rennebu:Nerskogen	UB	Pinus-Empetrum-samfunn	16	11
		UB	Betula-Empetrum-samfunn	16	11
22 Nordhagen 1928	Sør-Trøndelag:Tydal:Sylene	UB	Calluna-reicher Birkenwald (a)	4	20
		UB	Empetrum-reicher Birkenwald (a)	4	14
		LA	Empetrum-reiche Cladonia alpestris-Ass. (b)	1	10
		LA	Cladonia silvatica-reiche Empetrum-Ass. (b)	1	29
		LA	Cladonia silvatica-rangiferina-reiche Calluna-Ass. (b)	1	15
		LA	Dichte Empetrum-Ass. (b)	1	8
		LA	Dichte Calluna-Ass. (b)	1	6
		MA	Cetraria "crispa-Cladonia silvatica-reiche Juncus trifidus-Ass., stands I-III (c)	1	20
23 Kielland-Lund 1981b	Buskerud:Krødsherad	MB-UB	Barbilophozio-Pinetum callunetosum	?	5
24 Kielland-Lund 1962b	Akershus:Hurdal:Skrukkelia	LB	Vaccinio-Pinetum (a)	?	7
		MB	Empetro-Pinetum (b)	?	19
26 Gjerlaug 1973	Oppland:Lillehammer+Fåberg+Mesna	LB	Berlyngbarblandingskog, 160-370 m.a.s.l. (a)	25	7
		MB	Berlyngbarblandingskog, 510-640 m.a.s.l. (b)	25	7
		MB	Kreklinggranskog (b)	25	7
28 Nordhagen 1943	Buskerud:Hol:Ørterdalen+Haugestøl	LA	Empetrum-Cladonia rangiferina-silvatica-sosiasjon (a)	1	15
		MA	Juncetum trifidi, biotype B (b)	1	20
30 Mork&Låg 1959	Hedmark:Søre Osen:Ulvsjøberget	UB	Calluna-type	1	20
		UB	Calluna-Myrtillus-type	1	20
		UB	Empetrum-type	1	20
31 Nordhagen 1943	Oppland:Kvikne:Sikilødalen	UB	Betuletum empetro-hylocomiosum (a)	4	15
		LA	Betula nana-Cladonia alpestris-sosiasjon (b)	1	25
		LA	Betula nana-Cladonia rangiferina-silvatica-sosiasjon (b)	1	20
		LA	Salix glauca-Cladonia alpestris-sosiasjon (b)	1	10
		LA	Salix glauca-Cladonia rangiferina-silvatica-sosiasjon (b)	1	10
		LA	Røsslynghei (b)	4	5
		MA	Festuca ovina-Cladonia alpestris-sosiasjon (c)	1	10
		MA	Festuca ovina-Cladonia silvatica-sosiasjon (c)	1	40
32 Haug 1970	Oppland:Kvam:Furusjøen	UB	Barbilophozio-Pinetum sphagnetosum	30-50	15
		MB-UB	Barbilophozio-Pinetum ptilidietosum	50-80	14
		UB	Barbilophozio-Pinetum callunetosum	50-60	19
33 Mork&Heiberg 1937	Oppland:Ringebu:Hirkjølén	UB	Empetrum-Vaccinium-Picea-Betula-sosiasjon	1	80
		UB	Calluna-Empetrum-Pinus-Picea-Betula-sosiasjon	1	20
34 Dahl 1957	Oppland:Sel+Dovre/Hedmark:Follidal	LA	Cladonietum alpestris (a)	4-27	22
		MA	Phyllocladon-Juncetum trifidi medioalpinum (b)	2-16	5
36 Du Rietz 1925a	Hedmark:Alvdal:Tyldal:Tronfjell	LA	Betula nana-Cladonia alpestris-Ass.	1	11
		LA	Betula nana-Empetrum nigrum-Cladonia alpestris-Ass.	1	11
		LA	Empetrum nigrum-Cladonia alpestris-Ass.	1	11

1952, Malme 1971, Huseby & Odland 1981, Odland 1981b), while becoming dominant in continental areas (Du Rietz 1925b, Nordhagen 1943, Dahl 1957). The relatively more humid microclimate of the bottom layer in boreal than in alpine zones, makes the displacement of bryophytes by lichens occur farther east in the boreal zones.

Floristic variation of the subxeric series is shown in Tab. 42. The material used is listed in Tab. 43. In the most oceanic areas *Carex binervis* and *Polygala serpyllifolia* enter the subxeric series.

Oceanic bryophytes are well represented. *Anastrepta orcadensis*, *Bazzania trilobata*, and *Leucobryum glaucum* are all important in this series (Lye 1966, Kielland-Lund 1967). *Mylia taylorii*, *Plagiothecium undulatum*, *Rhytidiadelphus loreus*, and *Sphagnum quinquefarium* are restricted to humid areas in their total distribution, lacking in the lowlands of inner Eastern Norway. They enter the subxeric series in the extreme west or at high altitudes in the fjord districts, areas with superhumid climate. Farther east they only occur in the more mesic series and on other substrate. *Blechnum spicant* shows a similar pattern, while *Cornus suecica* has a wider total distribution than *Blechnum* and also occurs in the subxeric series in a larger area. *Rhytidiadelphus subpinnatus* and *R. triquetrus*, both confined to rich submesic sites in Eastern Norway (cf. Kielland-Lund 1962b, 1971, 1973, 1981, Dahl et al. 1967), appear in poor subxeric vegetation in Western Norway (cf. Nedkvitne & Thomter 1953, Omberg 1980).

The strong tendency towards paludification of convex, formerly dry ground typical of superhumid areas (cf. Sjörs 1947, 1948, 1967) makes the limit between the subxeric series and sloping mires indistinct in such areas. The frequent occurrence of mire plants in slightly paludified subxeric sample plots from Western Norway is typical (cf. Tab. 42).

In the alpine zones the oceanic elements are weaker. Some of the above mentioned oceanic species, as well as some of the mire plants, may be included farthest west. Some species with oceanic tendencies, e.g., *Arctostaphylos alpina* and *Racomitrium lanuginosum*, show western distribution in this series.

Barbilophozia floerkei and *B. lycopodioides*, widespread humid species (cf. E. Jørgensen 1934, Kielland-Lund 1967, 1981, have optimal occurrence in the humid forests at high altitudes, and are almost absent from the lower boreal zone in Eastern Norway (cf. Kielland-Lund 1981).

Calluna vulgaris is perhaps the physiognomically most important species in the subxeric series. In the oceanic part of the gradient this species is the main element up to the middle alpine zone (Malme 1971, Kummén 1977, Fredriksen 1978, Huseby & Odland 1981, Halvorsen & Salvesen 1983 etc.). In the Grunningsdalen area the species is common and locally dominant up to its thermal limit, 1250 m (one specimen was observed at 1310 m). In Eastern Norway *Calluna vulgaris* has low cover or only scattered occurrences in alpine vegetation (Resvoll-Holmsen 1932, Nordhagen 1943, Dahl 1957), and *Empetrum hermaphroditum* dominates the subxeric series alone. Farther north and east the amplitude of *Calluna vulgaris* is restricted further, and in continental Finland it only reaches the coniferous forest zone of Forest Lappland, a part of the upper

boreal zone (Kujala 1929, Kalela 1961). In moderately continental lowland areas it is mostly abundant (Cajander 1921a, 1926, Kujala 1929, 1961, Kalela 1961, Kielland-Lund 1967, 1971, 1973, 1981). However, from the continental Northern Gudbrandsdalen Kielland-Lund (1981) describes subxeric vegetation almost lacking *Calluna vulgaris* and *Vaccinium myrtillus*.

The distribution and autecology of *Calluna vulgaris* reveals a pattern typical of an oceanic (Samuelsson 1917a, Beijerinck 1940) and slightly southern (Kalela 1961) species. Its distribution in the mountains is due to the too dry microclimate near the ground in continental areas. The species needs snow protection in winter (Nordhagen 1943, Aichinger 1956), but does not tolerate excessive snow cover (Poore & McVean 1957).

Continental elements are few in the subxeric series. Most of the species encountered seem to follow the series to their distributional limits. Most distinctive physiognomically is the occurrence of *Picea abies* east of the mountain range, with scattered occurrences in inner Vestlandet. In the alpine zones the xero- and photophilous *Arctostaphylos uva-ursi* (cf. Nordhagen 1943) increases towards the continental areas, and *Betula nana*, *Festuca ovina*, and *Viscaria alpina* appear. In middle alpine subxeric vegetation *Juncus trifidus* increases towards the west, *Festuca ovina* towards the east.

In the moderately continental lowlands of South-eastern Norway the south-eastern or eastern species (cf. Hultén 1971, Bendiksen & Halvorsen 1981) *Anemone vernalis*, *Goodyera repens*, *Lycopodium complanatum*, and *Pyrola chlorantha* enter the subxeric series (Kielland-Lund 1981). However, all these species are rare. In the northern, strongly continental parts of the Gudbrandsdalen valley *Calluna vulgaris* partly gives way to *Festuca ovina* (cf. Kielland-Lund 1981).

In continental areas the continental *Cladonia stellaris* (Lynge 1921, Du Rietz 1925a, Ahti 1961) dominates in the bottom layer. In more humid areas it is replaced by *Cladonia arbuscula* and mosses (cf. Nordhagen 1928). Other lichen species decreasing towards humid areas are *Cladonia bellidiflora*, *C. uncialis*, *Nephroma* spp., *Peltigera* spp., and *Stereocaulon* spp.

The position of Grunningsdalen relative to regional variation. *Calluna vulgaris* is important also in the low alpine zone. The continental *Betula nana* is only rarely encountered. The oceanic species *Juncus squarrosus* and *Leucobryum glaucum* occur, and the latter reaches its upper limit in Norway, 1220 m, at Blåtjørnfjell. Humid species like *Cornus suecica* and *Racomitrium lanuginosum* are present as minor elements in subxeric vegetation, being at the edge of the area in which they occur in the subxeric series. *Blechnum spicant*, *Plagiothecium undulatum*, and *Rhytidiadelphus loreus* do not occur in the subxeric series. These features, as well as the strong dominance of *Barbilophozia floerkei* and *B. lycopodioides* in the three lowermost zones, indicate a humid and slightly oceanic affinity.

Continental and eastern elements are few. High importance of natural *Picea abies* indicates affinity to Eastern Norway, the relatively high cover of lichens in all zones (cf. Fig. 51) and the inclusion of continental species like *Cladonia*

stellaris in the vegetation also show affinity eastwards.

The middle alpine subxeric site-type is poor in species with phytogeographical indicator value. The occurrence of *Loiseleuria procumbens* and *Juncus trifidus* and total lack of *Festuca ovina*, as well as the dominance of *Cetraria islandica*, are oceanic features.

Thus all subxeric site-types show humid and slightly oceanic features.

Regional variation of the submesic series

Area. Submesic vegetation occupies large areas over the whole of Southern Norway (cf. Kielland-Lund 1973), but is in higher zones most important in oceanic and suboceanic areas (Nordhagen 1943, Dahl 1957). In the most continental mountain areas the submesic series may occupy only a small area (Du Rietz 1925a, Bendiksen & Schumacher 1982).

Physiognomy. West of the water divide *Betula pubescens* dominates in all vegetation zones (Kummen 1977, Losvik 1978, Huseby & Odland 1981), or may partly be replaced by *Pinus sylvestris* in the inner fjord districts (cf. Aune 1973, Omberg 1980, Rodvelt & Sekse 1980, Huseby & Odland 1981, Odland 1981). In the east *Picea abies* dominates in the lower and middle boreal zones, partially replaced by *Betula pubescens* in the upper boreal zone.

The physiognomy of the field layer is remarkably uniform; *Vaccinium myrtillus* is the dominant species up to the limit between the low and middle alpine zones. It is chionophilous and cold sensitive (Aichinger 1957, Havas 1965, 1971), and is squeezed out towards higher altitudes because of a too short growing season in habitats where the snow cover is appropriate (Dahl 1957, Fægri 1967). The middle alpine submesic site-type is a dry grass heath (Vestergren 1902, Samuelsson 1917a, 1917b, Nordhagen 1937, 1943).

In the boreal zones the bottom layer of the submesic series is dominated by bryophytes. Lichens occur intermixed with the bryophytes and reach highest importance in continental areas (cf. Mork & Heiberg 1937, Mork & Låg 1959, Haug 1970, Gjerlaug 1973, see also Malmström 1949, Kalela 1961 and Hämet-Ahti 1963). In the alpine zones the abundance of lichens is higher, and lichens play an important part in continental low alpine submesic vegetation (Du Rietz 1925a, Nordhagen 1928, 1943, Dahl 1957). In the middle alpine zone, *Cetraria islandica* is the most important species regardless of climate (Nordhagen 1943).

Floristic variation of the submesic series is shown in Tab. 44. The material used is listed in Tab. 45. Many oceanic species are at their optimum in the submesic series. Examples of such species are, in approximate order of decreasing restriction to oceanic and humid areas (cf. Tab. 44), *Luzula sylvatica*, *Anastrepta orcadensis*, *Galium saxatile*, *Barbilophozia atlantica*, *Lophocolea bidentata*, *Blechnum spicant*, *Plagiothecium undulatum*, *Rhytidiadelphus loreus*, and *Cornus suecica*.

There is only a slight element of mire species in Tab. 44.

Some widely distributed species only enter poor submesic vegetation in oceanic parts of Norway. *Pteridium aquilinum* is

Tab. 45. Material forming the basis for evaluation of regional variation in the submesic series.

St. Author No.	County:Parish:Locality	Zone	Communities included	Plot size	Plot No.
1 Malm 1971	Møre og Romsdal:Hustad:Talstad- hesten	LA	Phylloclad-Vaccinietum myrtilli	1	25
2 Kummen 1977	Sogn og Fjordane:Eikefjord:Rams- dalen	UB	Eu-Piceetum myrtilletosum	20-36	7
3 Kummen 1977	Sogn og Fjordane:Naustdal:Vona- vatnet	UB	Eu-Piceetum myrtilletosum	25-100	5
4 Losvik 1978	Hordaland:Bergen,Birkeland:Hell- dal-Sandal	LB	Corno-Betuletum myrtilletosum	4-25	25
5 HusebysOdland 1981	Rogaland:Vikedal:Vikedal	LB-UB	Blåberdominert bjørk- og furuskog (a) Alpin lynghei, plots 10-19 (b)	24-100 4-25	30 10
6 Fredriksen 1978	Hordaland:Eksingedal:Eksingedalen, upper part	UB	Corno-Betuletum myrtilletosum	16	10
7 Knaben 1952	Sogn og Fjordane:Vik+Arnafjord/ Hordaland:Modalen:Eksingedal+Winje	LA	Vaccinium myrtillus-Cornus suecica-Mylocomium-sos- iasjon	1	35
		LA	Vaccinium myrtillus-Cladonia silvatica-Dicranum fuscescens-sosiasjon	1	10
8 Odland 1981b	Møre og Romsdal:Ørsta:Ørstadalen	LB-UB	Blåberdominert bjørk- og furuskog	9-25	11
9 Aune 1973	Sør-Trøndelag:Henne:Holladalen	LB	Corno-Betuletum myrtilletosum	16-40	5
10 Omberg 1980	Hordaland:Ulvik	LB-MB	Eu-Piceetum	7	7
12 Rodvelts&Sekte 1980	Hordaland:Ullensvang/ Sogn og Fjordane:Flåm	LB-MB	Eu-Piceetum Myrtilletosum (a)	7	8
		UB	Myrtillo-Betuletum Myrtilletosum (b)	7	16
13 Odland 1978	Hordaland:Roldal	MB	Corno-Betuletum myrtilletosum	16	10
14 Bergland 1975	Vest-Agder:Åseral	MB-UB	Eu-Piceetum myrtilletosum	30-50	28
		MB-UB	Eu-Piceetum cornetosum	28-36	21
15 Kjelvik 1978	Nord-Trøndelag:Hegra+Markabygd, Øvre Forra	MB	Eu-Piceetum myrtilletosum	16	8
16 Klock 1974	Sør-Trøndelag:Klebu:Selbusjøen N.	LB	Blåber/ småbregnegranskog Myrtillus-samfunn	4	10
		LB	Blåber/ småbregnegranskog Blechnum spicant-samfunn	4	10
17 Odland 1979	Hordaland:Vinje+Voss:Vosso, upper part	MB	Prealpin blåberdominert bjørkeskog (a)	25-200	9
		UB	Subalpin blåberdominert bjørkeskog (b)	25	5
		LA	Levalpine blåberlyngheier, plots 1-3, 5-6 (c)	100-300	8
18 Nedkvitne&Thomter 1953	Hordaland:Voss:Kvitli	LB-MB	Blåbertypen	1	20
19 Nordhagen 1943	Sogn og Fjordane:Flåm:Myrdal	UB	Betuletum myrtillo-hylocomiosum (a)	4	28
		LA	Phylloclad-Vaccinietum myrtilli (b)	1	30
20 Halvorsen&Bendiksen, the present paper	Telemark:Bø+Seljord+Hjartdal+Sau- land	MB	Submesic series, middle boreal zone (a)	25	11
		UB	Submesic series, upper boreal zone (b)	25	8
		LA	Submesic series, low-alpine zone (c)	25	10
		MA	Submesic series, middle-alpine zone (d)	25	8
21 Moen 1978	Sør-Trøndelag:Rennebu:Nærskogen	UB	Myrtillus-samfunn	16	12
22 Nordhagen 1928	Sør-Trøndelag:Tydal:Sylene	UB	Myrtillus-reicher Birkenwald (a)	4	30
		LA	Vaccinium myrtillus-reiches Zwergbirkengebüsch, not in- cluding the "Worbodenvariante" (b)	1	18
		LA	Cladonia silvatica-reiche Vaccinium myrtillus-Ass. (b)	1	40
		MA	Cetraria *crispa-Cladonia silvatica-reiche Juncus trifidus-Ass., stand IV (c)	1	5
24 Kielland-Lund 1962b	Akershus:Hurdal:Skrukkelia	LB-MB	Eu-Piceetum Myrtillus-subassosiasjon	7	22
25 Hagen 1976	Møre og Romsdal:Romfo:Grøvdalen	UB	Betula pubescens-Vaccinium myrtillus-samfunn	16	5
26 Gjerlaug 1973	Oppland:Lillehammer+Påberg+Mesna	LB-MB	Blåberggranskog (a)	25	22
		UB	Fjellgranskog (b)	25	10
		UB	Fjellbjørkeskog (b)	25	7
		LA	Blåberrik rishei (c)	25	20
28 Nordhagen 1943	Buskerud:Hol:Ørterdalen+Haugastøl	UB	Betuletum myrtillo-hylocomiosum (a)	4	25
		LA	Phylloclad-Vaccinietum myrtilli, not including the "Dryopteris-variant" (b)	1	110
		LA	Juniperus-Betuletum nanae myrtillosum (b)	1	135
		MA	Juncetum trifidi, hovedtype A (c)	1	30
29 Bendiksen 1980	Oppland:Lunner:S.Oppdalen	MB	Eu-Piceetum myrtilletosum "gammel skog"	25	5
30 Mork&Låg 1959	Hedmark:S.Øsen:Ulvsjøberget	UB	Myrtillus-type	1	20
31 Nordhagen 1943	Oppland:Kvikne:Sikilsdalen	UB	Betula tortuosa-Vaccinium myrtillus-sosiasjon (a)	4	33
		UB	Betula tortuosa-Deschampsia flexuosa-sosiasjon (a)	4	17
		LA	Vaccinium myrtillus-Cladonia silvatica-Dicranum fus- cescens-sosiasjon, not including the "Empetrum-var."		
			(b)	1	25
		LA	Juniperus-Betula nana-Vaccinium myrtillus-sosiasjon (b)	1	25
		LA	Betula nana-Vaccinium myrtillus-sosiasjon (b)	1	10
		MA	Juncus trifidus-Cetraria islandica-Cladonia silvatica- sosiasjon (c)	1	15
32 Haug 1970	Oppland:Kvam:Furusjøen	UB	Barbilophozio-Pinetum typicum	40-90	19
33 Mork&Heiberg 1937	Oppland:Ringebu:Hirkjelen	UB	Vaccinium-Picea-Betula-sosiasjon	100	82
34 Dahl 1957	Oppland:Sel+Dovre/Hedmark:Follidal	LA	Phylloclad-Vaccinietum myrtilli	3-20	16
		LA	Hylocomieto-Betuletum nanae typicum	2-15	15

important only in forest clearings in Eastern Norway, but widely distributed in the submesic series in oceanic areas (Bergland 1975, Losvik 1978). *Hypnum cupressiforme* appears in the submesic series at most Western Norwegian stations; in the rest of Southern Norway it is a very common epixyle, epiphyte, or epilith (cf. Nyholm 1954-69). *Herzogiella striatella*, occurring in a few sample plots in Tab. 44, is widespread in Scandinavia (Nyholm 1954-69), but probably prefers microclimatically more humid habitats than the submesic series in continental areas. *Rhytidiadelphus triquetrus* has a wider distribution on poor submesic than on subxeric sites, but in most of Østlandet it is restricted to rich submesic sites. *Potentilla erecta* occurs in the submesic series in Western Norway. The species is normally also present in earlier successional stages of submesic sites in Eastern Norway (Bendiksen 1980).

The submesic series is poor in eastern elements; the most important species is *Picea abies*. The other eastern species are *Anemone vernalis*, *Betula nana*, *Festuca ovina*, *Viscaria alpina*, and *Pedicularis lapponica*. *Festuca ovina* and *Juncus trifidus* are co-dominants in continental middle alpine submesic grass heaths; in oceanic areas *Juncus trifidus* dominates alone owing to lack of competition from *Festuca ovina* or dwarf shrubs (cf. Nordhagen 1928, 1937, 1943).

The change of the bottom layer is slight. In the alpine zones *Hylocomium splendens* and *Pleurozium schreberi* have their optima in humid regions; so do *Barbilophozia* spp., rare in the eastern lowlands. Regional variation of the bottom layer mainly follows the subxeric series, but the corresponding shifts are displaced towards the continental end of the gradient.

The position of Grunningsdalen relative to regional variation. *Blechnum spicant* and *Rhytidiadelphus loreus* occur in the middle boreal zone. *Cornus suecica* is a characteristic species in the three lowermost zones, particularly important in the upper boreal zone. One occurrence of *Herzogiella striatella* may also be a westerly feature. A strongly oceanic feature is the occurrence of *Kurzia trichoclados* in the upper boreal and low alpine zones. The species is otherwise restricted to the west coast of Norway and the south-west coast of Sweden (cf. E. Jørgensen 1934, S. Arnell 1956). This occurrence, as well as the sporadic occurrence of *Mylia taylorii* in the upper boreal zone, strongly underlines the humid climate of this zone. The rich occurrence of *Barbilophozia floerkei* and *B. lycopodioides* in the boreal and low alpine zones, as well as the dominance of *Juncus trifidus* in the middle alpine zone, also indicate affinity to humid, suboceanic areas.

Among the sparsely encountered easterly elements *Picea abies* is the most important. *Betula nana* is present in the low alpine zone. The importance of lichens is considerable in all zones except the upper boreal.

In summary, oceanic traits prevail in the submesic series. In particular, the upper boreal site-type shows distinct signs of high humidity.

Regional variation of the mesic series

Material for a regional survey of mesic vegetation is more

scanty, and important complications arise from the wide circumscription of the mesic series. Attention will here be restricted to comments on mesic vegetation in Grunningsdalen and its phytogeographical relationships.

Among the species with a humid-oceanic distribution pattern *Blechnum spicant* and *Rhytidiadelphus loreus* have their optima in this series, and *Plagiothecium undulatum* was observed on one occasion in the upper boreal mesic site-type (cf. Bendiksen & Halvorsen 1981). The rich occurrence of *Cornus suecica*, *Barbilophozia* spp. and the presence of *Herzogiella striatella* and *Kurzia trichoclados* are further indications of the oceanic character of the series. In the alpine zones the oceanic and humid mountain plant *Cryptogramma crispa* (cf. Fægri 1958) and the great importance of *Nardus stricta* indicate an oceanic affinity (cf. Du Rietz 1925a, 1925b, Nordhagen 1943). Apart from the presence of *Picea abies*, easterly features are hardly present in this series.

Consequently, the presence of humid and oceanic elements reaches its maximum in the mesic series. In comparison with corresponding vegetation types in other parts of Southern Norway, its position appears to be intermediate. In this connection the lack of *Thelypteris limbosperma*, an important and often dominant species in mesic vegetation farther west (Knaben 1952, Bergland 1975, Odland 1978, 1981a), should be mentioned.

Concluding remarks on the vegetation of Grunningsdalen in relation to regional variation

The importance of oceanic and humid species increases along the complex-gradient topographic moisture-snow cover, with a distinct optimum for most of these species in the mesic series. There is also a tendency for such species, e.g., *Blechnum spicant* and *Rhytidiadelphus loreus*, to reach higher altitudes in the microclimatically more favourable mesic series.

All series show distinct oceanic features. The low area importance of the xeric series, the dominant position of *Calluna vulgaris*, and the occurrence of the suboceanic species *Juncus squarrosus* and *Leucobryum glaucum* in the subxeric series are evidence of the humidity of the area. In these respects the Grunningsdalen area shows greater affinity to the western parts of Norway than to Central Østlandet. The affinity is particularly great to the vegetation described from higher altitudes in the inner fjord areas of Western Norway, for example by Odland (1979) from Voss. On the other hand, there are some continental features of the Grunningsdalen area which disturb this picture. Several humidity-dependent plant species do not occur in the subxeric series in Grunningsdalen, e.g., *Blechnum spicant*, *Rhytidiadelphus loreus*, *Potentilla erecta*.

The low number of species with phytogeographical affinity occurring in the Grunningsdalen area is striking. The continental species are mostly absent, and the less demanding oceanic species consequently give the area a distinct oceanic impression.

MATERIAL AND METHODS FOR NUMERICAL ANALYSIS

NUMERICAL ANALYSIS OF VEGETATION

Material and data preparation

The material for numerical analysis of vegetation consisted of 272 species occurring in 152 sample plots representing the 16 site-types.

Assessment of the quantity of species i in site-type j was done by conversion of constancy percentage values (c_{ij}) into constancy classes 1 - 5 (Dahl 1957: 53). The constancy class of species i in site-type j is referred to as D_{ij} . The characteristic degree of cover of species i in site-type j is denoted \bar{c}_{ij} . For species occurring in more than one layer, a synthetic \bar{c}_{ij} cover value was estimated from single-layer cover values by considering the layers as independent.

The importance of species in site-type j , I_{ij} , was calculated as

$$I_{ij} = \frac{D_{ij} \cdot \bar{c}_{ij}}{5}, \quad 0 \leq I_{ij} \leq 5$$

This importance value function parallels the Hult-Sernander-Du Rietz scale of cover and gives balanced weight to qualitative and quantitative aspects of the data set as recommended by Jensén (1978) and Maarel (1979) for multivariate analysis.

Similarity between site-types

Because the properties of similarity indices strongly affect the results of subsequent numerical analysis (cf. Campbell 1978, Maarel 1979, Green 1980, Gauch 1982a), two indices were used.

COS X. If we consider each species as an axis of an orthogonal species space (Gauch & Whittaker 1981) in which site-types are represented as points, the cosine of the angle between site-types x_j and x_k in this space is an index of similarity (cf. Orłóci 1978, Hajdu 1981). The formula reads

$$\text{COS}(x_j, x_k) = \frac{\sum_{i=1}^m I_{ij} \cdot I_{ik}}{[\left(\sum_{i=1}^m I_{ij}^2\right) \left(\sum_{i=1}^m I_{ik}^2\right)]^{0.5}}$$

where m is the total number of species in the material. As COS X squares importance values, the index is most strongly influenced by high species scores and thus emphasizes dominant species (Whittaker & Gauch 1978, Halvorsen 1980, Hajdu 1981). COS X is a non-linear function of variation in floristic composition (Hajdu 1981), and thus distorts the original importance scale.

PS. Percentage similarity (Goodall 1978a, Gauch 1982a), also known as the index of Czekanowski (1909), was introduced to phytosociology by Dahl & Hadac (1941). PS between site-types X_j and X_k was calculated as

$$PS(X_j, X_k) = \frac{2 \sum_{i=1}^m \min(I_{ij}, I_{ik})}{\sum_{i=1}^n I_{ij} + \sum_{i=1}^n I_{ik}}$$

As PS does not involve squaring of importance values, quantitative and qualitative variation is balanced in accordance with the original importance scale (cf. Gauch 1982a). It is thus an almost linear function of variation in floristic composition (Hajdu 1981). Owing to its mathematical simplicity and linear properties, PS is deemed to be among the better floristic similarity indices (Hajdu 1981, Gauch 1982a).

Cluster analysis of site-types

In order to facilitate comparison with previous Scandinavian classifications, site-types were subjected to hierarchic classification. The group-average method (Lance & Williams 1967, Pritchard & Anderson 1971), also referred to as UPGMA (Sokal & Michener 1958, Sneath & Sokal 1973) was used. It is agglomerative, and thus vulnerable to noise in the input material (Gauch & Whittaker 1981, Gauch 1982a). However, as the input material in this study is weighted averages, the noise level is low, and an agglomerative strategy less objectionable. The group-average method is generally considered superior among agglomerative techniques (Lance & W. Williams 1967, Sneath & Sokal 1973, Orłóci 1978, Gauch & Whittaker 1981).

Independent classifications were produced for the COS X and PS similarity matrices.

Ordination of site-types

Ordination was used to extract major vegetational gradients in the material. Principal coordinate analysis, PCO (Gower 1966, 1967, Pielou 1977), was used. PCO is a generalization of principal component analysis (PCA). It extracts principal components from any distance matrix with the aim of preserving the distances of the distance matrix in a space with fewer dimensions. If the distance measure does not seriously distort the original importance scale, PCO alleviates much of the criticism of PCA. Among others, Prentice (1977) and Clymo (1980) have tested PCO with satisfactory results.

Detrended correspondence analysis, DCA (Hill & Gauch 1980), a generally more suitable method for the ordination of vegetation data (Hill & Gauch 1980, Gauch et al. 1981, Gauch 1982a, 1982b), became available after this study was completed.

Distance matrices were computed from the COS X and PS similarity matrices according to Orłóci (1978).

Product moment correlation coefficients (Sokal & Rohlf 1969) were computed between each of the ordination components and the two main gradients in the investigation area in order to facilitate interpretation of the axes.

NUMERICAL ANALYSIS OF AUTECOLOGY

Material and data preparation

The material used was the same as for analysis of vegetation. However, only the 118 species satisfying one of the following criteria were included:

(1) Occurrence in 10 or more sample plots.

(2) Occurrence in 5 or more sample plots and having a constancy percentage of 50 or more in at least one site-type.

For each species i , the importance values I_{ij} , were relativized to unit sum by defining J_{ij} , the fraction of total importance of species i in site-type j as

$$J_{ij} = \frac{I_{ij}}{\sum_{j=1} I_{ij}}$$

Similarity between species distributions

Owing to the mathematical simplicity and favourable linear properties of PS, this measure was also used for calculation of similarity between species distributions. With relativized species data the index corresponds to the percentage similarity of distribution (PSD; Whittaker & Fairbanks 1958). The formula for PSD between species Y_i and Y_k is

$$PSD(Y_i, Y_k) = \frac{1}{n} \sum_{j=1}^n \min(J_{ij}, J_{kj}).$$

Cluster analysis of species

The matrix of PSD index values was subjected to hierarchic, agglomerative classification by the group average method. Reasons for choosing this method and considerations of robustness to noise are as for clustering of site-types. A plexus diagram (McIntosh 1978) was constructed on the basis of the matrix of PSD index values to give a graphical representation of distributional relationships between species.

Ordination of species

To relate the occurrence of species to positions along gradients a method was constructed to estimate centres of gravity along the recognized complex-gradients. Positions

along the two principal complex-gradients were quantified by defining indices of moisture and altitude.

Along the topographic moisture-snow cover gradient each of the four series was spaced equally along the axis and given a moisture index, Z_{mk} :

xeric series	$Z_{mk} = 0$
subxeric series	$Z_{mk} = 1$
submesic series	$Z_{mk} = 2$
mesic series	$Z_{mk} = 3.$

The centre of gravity S_i for species i along the moisture axis was then calculated according to the formula

$$S_i = \frac{1}{4} \sum_{k=1}^4 (Z_{mk} \sum_{jk} J_{ij}),$$

where the inner sum was taken over all jk being site-types of the k -th series.

Similarly, each of the four zones along the vertical gradient were spaced equally along the second axis and given an elevation index, Z_{ek} :

middle boreal zone	$Z_{ek} = 0$
upper boreal zone	$Z_{ek} = 1$
low alpine zone	$Z_{ek} = 2$
middle alpine zone	$Z_{ek} = 3.$

The centre of gravity, T_i , for species i along the vertical axis was calculated as S_i above.

To relate the GA-groups of hierarchical species classification to gradient positions, the scores S_i and T_i of the individual species were used to compute some statistics:

- \bar{S}_k - the mean of the positions of the species in GA-group k along the moisture axis.
- q_{sk} - the standard deviation of the positions of species in GA-group k along the moisture axis.
- \bar{T}_k - the mean of the positions of species in GA-group k along the vertical axis.
- q_{Tk} - the standard deviation of the positions of species in GA-group k along the vertical axis.

HOMOTONEITY AND DIVERSITY

Homotoneity

The site-types were defined by positions along complex-gradients; the traditional phytosociological criterion concerning homotoneity of vegetation was not taken into account when types were delimited (cf. Nordhagen 1943, Dahl 1957, Westhoff & Maarel 1978). Homotoneity may therefore be used as an independent measure of intra site-type variation, and as an indication of environmental (and hence floristic) heterogeneity

within the site-types.

(1) *Dahl's index of uniformity*, S_1/α (Dahl 1957, 1960). This index is based on the Fisher model (Fisher et al. 1943), and should preferably be used on plot sizes larger than the minimal area (in the sense of Dahl 1957) for the analysed vegetation type. The plot size used in this study, 25 sq.m., is large enough to fulfil these requirements. The number of plots analysed from the different site-types is not so high that the linear relation of species number to logarithm of sample plot number may be seriously questioned (cf. Preston 1948, Whittaker 1965). The "index of uniformity" may be expressed \bar{N}_j/α_j , where \bar{N}_j is the mean number of species in site-type j and α_j is the value of the parameter α in the Fisher expression for site-type j .

(2) *The ratio N_{5j}/N_{4j}* , where N_{5j} and N_{4j} are the number of species in constancy classes 5 and 4, respectively. This criterion is one of the main criteria of homotoneity based on Raunkiær's "law of frequency" (Raunkiær 1918). If the sample plot size exceeds the minimal area of a community, a vegetation table is considered homotoneous if the N_{5j}/N_{4j} ratio is higher than 1.0 (Nordhagen 1943, Dahl 1957).

The index is used by a number of Norwegian phytosociologists, e.g. Nordhagen (1943), Dahl (1957), Marker (1969), Bjørnstad (1971), Aune (1973), Fremstad (1979), and Bjørndalen (1980c), sometimes in connection with index (1).

According to Dahl (1957), there is a simple relationship between the two indices (1) and (2); $\bar{N}_j/\alpha_j > 1.2$ should imply $N_{5j}/N_{4j} > 1.0$.

Within site-type diversity

The diversity within a site-type is the alpha (α) diversity of Whittaker (1960, 1972a, 1977) and MacArthur (1965). Two different indices of alpha diversity are used:

(1) *Fisher's α* . The parameter α in the Fisher model is one of the most widely used diversity measures (cf. Whittaker 1972a, 1977). Its justification is shown by Greig-Smith (1964).

The index was calculated from nomograms in Dahl (1960). The value of α for site-type j is designated α_j .

(2) *Mean number of species per sample plot (\bar{N}_j)* is also widely used as an index of within-habitat diversity (cf. Whittaker 1960, 1972a, 1977). It is conceptually simple, and as sample size is constant, the figures for different site-types are comparable (cf. criticism in Whittaker (1972a)). It is divided into vascular plant diversity (\bar{V}_j), bryophyte diversity (\bar{B}_j) and lichen diversity (\bar{L}_j).

Within gradient diversity

The diversity within a gradient is the gamma (γ) diversity of Whittaker (1960, 1972a, 1977). Each of the eight gamma units of this study consists of four site-types forming a coenocline (Whittaker 1960, 1967, 1978b). They are named according to their position along the invariant complex-gradient. Thus gamma unit "xeric" is the four xeric site-types from different

zones.

The measures of gamma diversity are similar to measures of alpha diversity. The gamma units are designed 1, and the two indices are named

(1) Fisher's α (α_1).

(2) Mean number of species per gamma unit (\bar{N}_1), the latter divided into \bar{V}_1 (vascular plant diversity), \bar{B}_1 (bryophyte diversity), and \bar{L}_1 (lichen diversity).

Between site-type diversity along gradients

The change along a gradient is beta (β) diversity in the sense of Whittaker (1960, 1972a, 1977), MacArthur (1965), and Pielou (1975). Three different measures of beta diversity are used:

(1) The quotient $\alpha_1/\bar{\alpha}_j$. Whittaker (1960, 1972a, 1977) and Pielou (1975) interpreted beta diversity as the quotient of gamma and alpha diversities. An index of beta diversity along a complex-gradient is the quotient of α_1 , calculated as gamma diversity along the gradient, and the mean of α_j over all site-types along the gradient, $\bar{\alpha}_j$.

(2) The quotient N_1/\bar{N}_j , where N_1 is total number of species occurring along a gradient and \bar{N}_j is mean number of species in the plots representing that gradient. The index is mentioned by Whittaker (1972a, 1977).

(3) Rate of change per step along the gradient. Bratton (1975) used the rate of floristic turnover along a gradient as a measure of diversity. Her index, R_1 , was calculated as

$$R_1 = \sum_{j=1}^3 (1 - PS(X_j, X_{j+1}))$$

and is used in this study with X_j , X_{j+1} , being adjacent site-types along the gradient in question.

For all eight gamma units R_1 was calculated for total species content (R_{N1}), vascular plants (R_{V1}), bryophytes (R_{B1}) and lichens (R_{L1}).

RESULTS OF NUMERICAL ANALYSIS

VEGETATION

Similarity between site-types

Floristic similarity between site-types expressed as COS X is shown in Fig. 17, as PS in Fig. 18. COS X utilized a larger part of the 0-1-scale than PS. PS applied to layers A to C is shown in Fig. 19, and PS of the bottom layer (D) in Fig. 20.

Tab. 46. Correspondence between site-types and numbers used in Figs 17-26.

Number	Site-type	
	Series	Zone
1	Xeric	Middle boreal
2	Xeric	Upper boreal
3	Xeric	Low-alpine
4	Xeric	Middle-alpine
5	Subxeric	Middle boreal
6	Subxeric	Upper boreal
7	Subxeric	Low-alpine
8	Subxeric	Middle-alpine
9	Submesic	Middle boreal
10	Submesic	Upper boreal
11	Submesic	Low-alpine
12	Submesic	Middle-alpine
13	Mesic	Middle boreal
14	Mesic	Upper boreal
15	Mesic	Low-alpine
16	Mesic	Middle-alpine

Cluster analysis of site-types

The dendrogram produced by the group-average method based on COS X similarities is presented in Fig. 21. Site-types belonging to the same series are joined at a high level of similarity. The xeric site-types of the three uppermost zones are joined above the 0.80 similarity level, and all subxeric site-types are joined at a level above 0.70. The site-types of the three lowermost zones in the submesic series are joined at about the same similarity level. For the remaining site-types, the relationships were somewhat more complex. The submesic

Fig. 19. Floristic similarity between the site-types expressed as percentage similarity (PS) of vascular plant composition (layers A to C). Site-type numbers are in accordance with Tab. 46.

Fig. 20. Floristic similarity between the site-types expressed as percentage similarity (PS) of bottom layer composition. Site-type numbers are in accordance with Tab. 46.

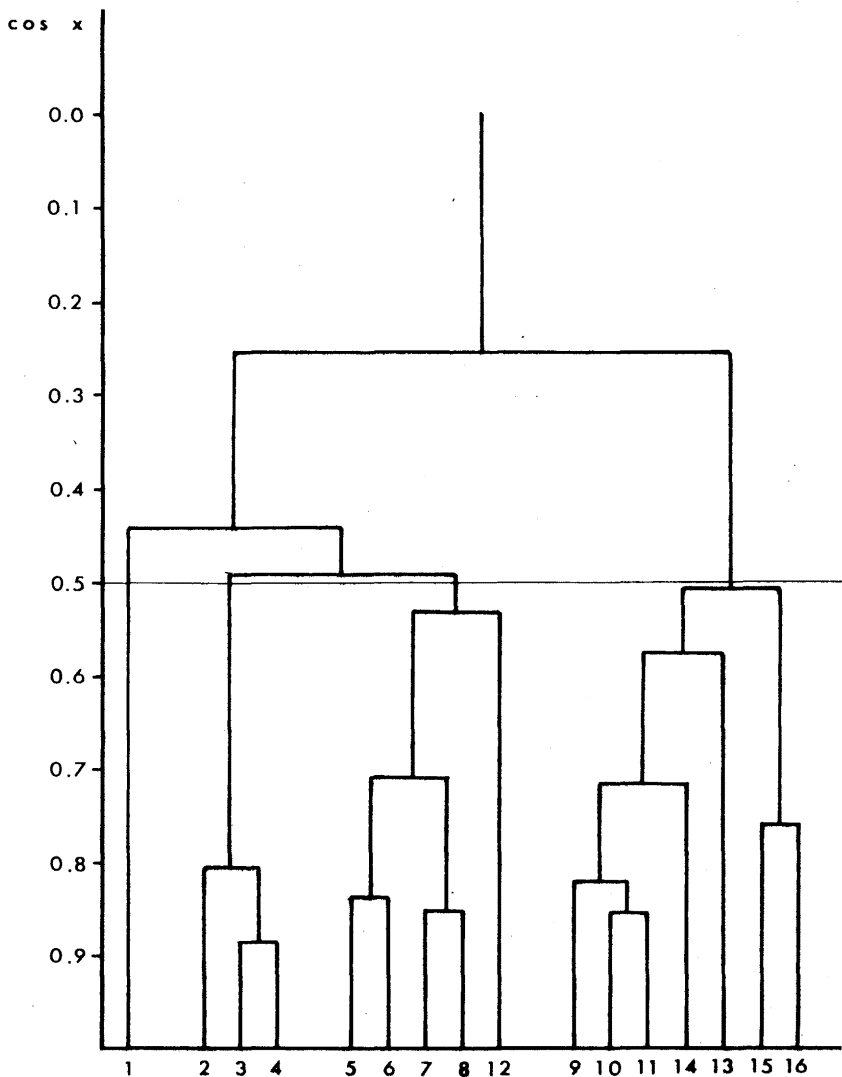


Fig. 21. Cluster analysis of site-types by the group average method, based on the secondary matrix of COS X similarities (Fig. 17). Site-type numbers are in accordance with Tab 46.

middle alpine site-type was more similar to the subxeric series than to the rest of the site-types belonging to the submesic series, and joined the site-types of the subxeric series at a moderately high similarity level. The middle boreal xeric site-type deviated strongly from the rest of the xeric series, and joined the dendrogram after the rest of the xeric site-types had fused with the subxeric series. The two alpine mesic site-types joined at the 0.75 similarity level. The boreal mesic site-types showed affinity to the submesic series, and the mesic upper boreal site-type joined the submesic series at the 0.70 similarity level. At lower levels of similarity, the middle boreal mesic, and subsequently also the alpine mesic site-types joined the submesic cluster.

The corresponding dendrogram based on PS similarities (Fig. 22) closely resembles the COS X dendrogram (Fig. 21). The only difference in the order the site-types joined to form clusters, was the joining of the middle and upper boreal mesic site-types prior to their joining the submesic series.

Ordination of site-types

The variability accounted for by the first four axes of the PCO ordinations is given in Tab. 47. A fifth axis was extracted in both cases, but was not possible to interpret ecologically.

Tab. 47. Percentage variability accounted for by the axes of the PCO ordinations.

Similarity value forming basis for ordination	Component No.	Variability accounted for (%)	Cumulative (%)
cos	1	35,83	35,83
	2	16,36	52,19
	3	13,25	65,44
	4	9,95	75,39
PS	1	26,00	26,00
	2	12,37	38,37
	3	10,66	49,03
	4	8,02	57,05

The distortion in PCO, calculated as the ratio of the sum of negative eigenvalues and the sum of all eigenvalues (Williamson 1978), was 3.64% in the COS X- and 11.37% in the PS-based ordination.

Representations of the site-types relative to axes one and two and one and three for each of the ordinations, are given in Figs 23-26. Iso-score lines for variation of component scores in the two-dimensional co-ordinate system of series and zones, were compiled for the first four axes of the two ordinations (Figs 27-34). Correlation coefficients between components and environmental gradients and the significance probabilities of the same are given in Tab. 48.

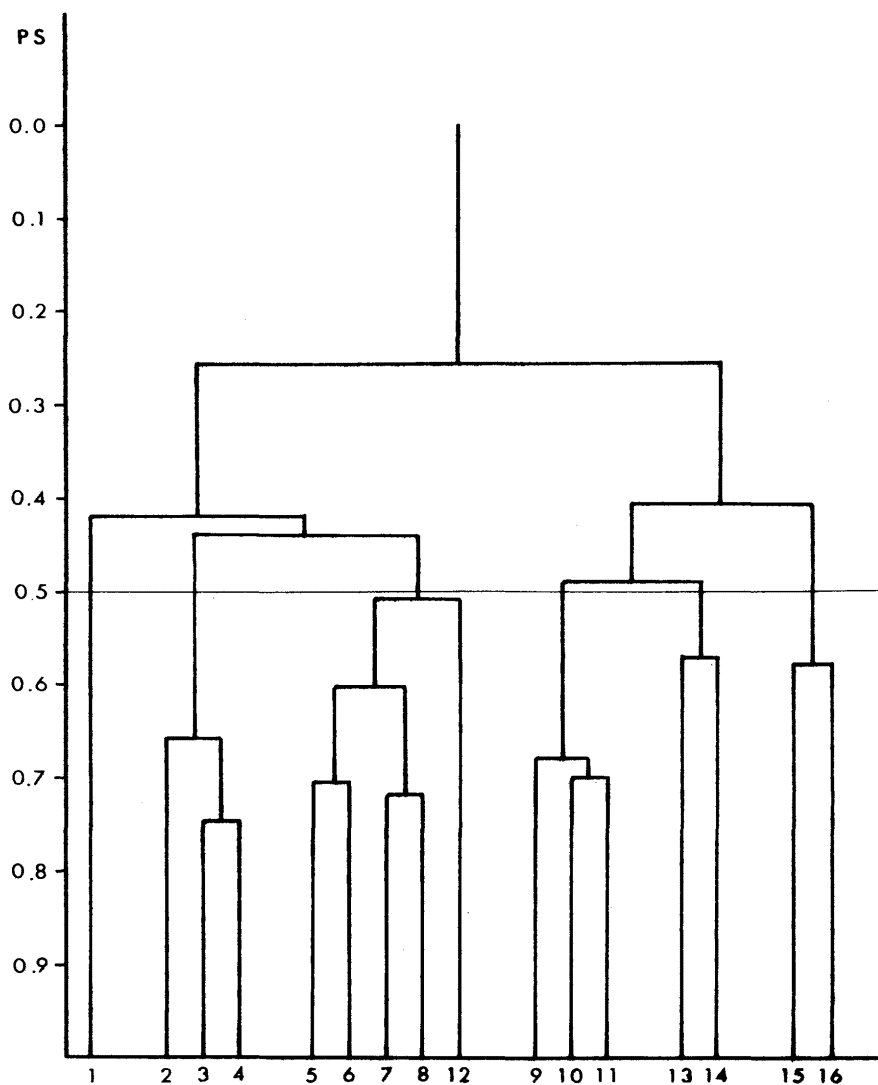


Fig. 22. Cluster analysis of site-types by the group average method, based on the secondary matrix of PS similarities (Fig. 18). Site-type numbers are in accordance with Tab. 46.

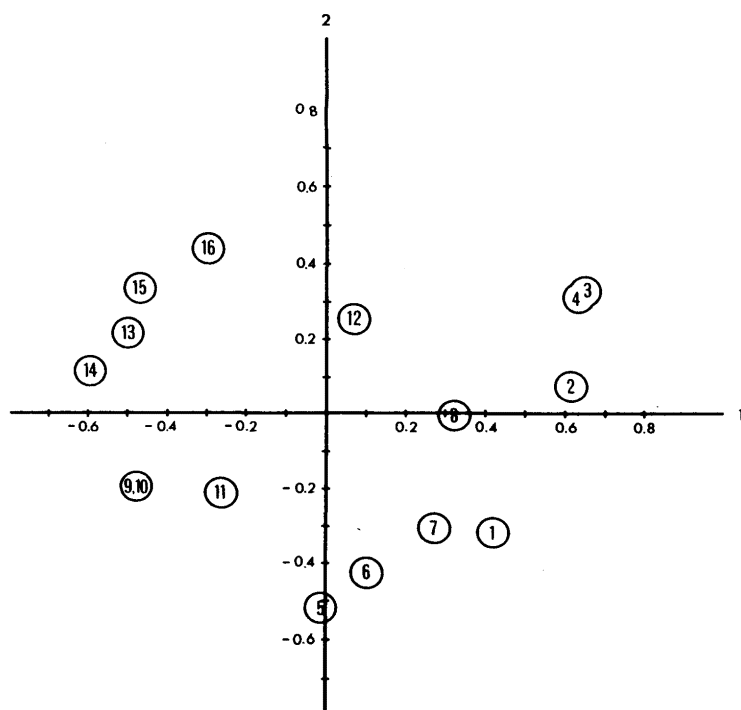


Fig. 23. Position of the site-types relative to the first two axes of the PCO ordination based on the secondary matrix of COS X similarities (Fig. 17). Site-type numbers are in accordance with Tab. 46.

The largely similar patterns shown by the two ordinations are an indication that ordination results reflect important properties of the data set. In both ordinations there was a pronounced drop in variability accounted for between the first and the second axes, while the second and the third axes accounted for roughly equal variability.

The first axes showed a distinct major vegetational gradient from high-and-dry to low-and-mesic sites although most closely approaching the topographic moisture gradient. The highest loadings were obtained for the alpine xeric site-types, the lowest for the boreal mesic site-types. With few exceptions the component scores preserved order of site-types along both gradients, viewed separately. High correlation coefficients were obtained between component scores and each gradient, particularly with the topographic moisture-snow cover gradient.

The second axes gave high loadings to alpine site-types at both ends of the moisture scale, while the lowest scores were obtained by the middle boreal subxeric site-type. For the COS X ordination, the order of site-types within each series

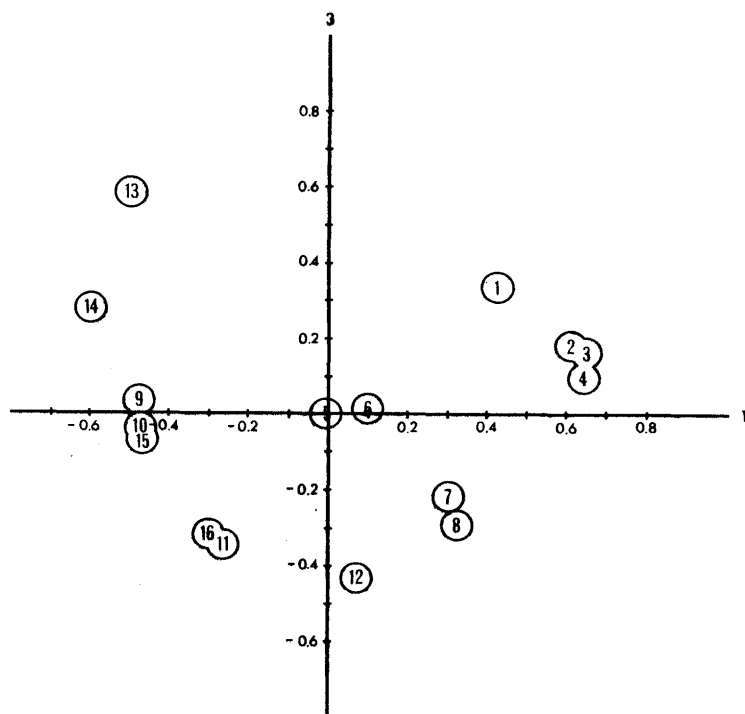


Fig. 24. Position of the site-types relative to the first and third axis of the PCO ordination based on the secondary matrix of COS X similarities (Fig. 17). Site-type numbers are in accordance with Tab. 46.

according to elevation was preserved apart from minor irregularities in the submesic and mesic series. A strongly positive correlation with the vertical gradient was also shown by the correlation coefficient. With the PS ordination vertical variation was less well explained. In both ordinations plots of axes 1 and 2 (Figs 23 and 25) show evidence that axes 2 are polynomial distortions of the topographic moisture gradient.

The third axes showed trends similar to axes 2, but with ranks according to elevation preserved in almost all cases, and more strongly positive correlations with the vertical gradient.

The fourth axes showed low loadings for the upper boreal submesic site-type, while scores increased towards the lower left and upper right corners of the two gradient-diagram. This picture is probably only an expression of residual variance after extraction of components 1 to 3.

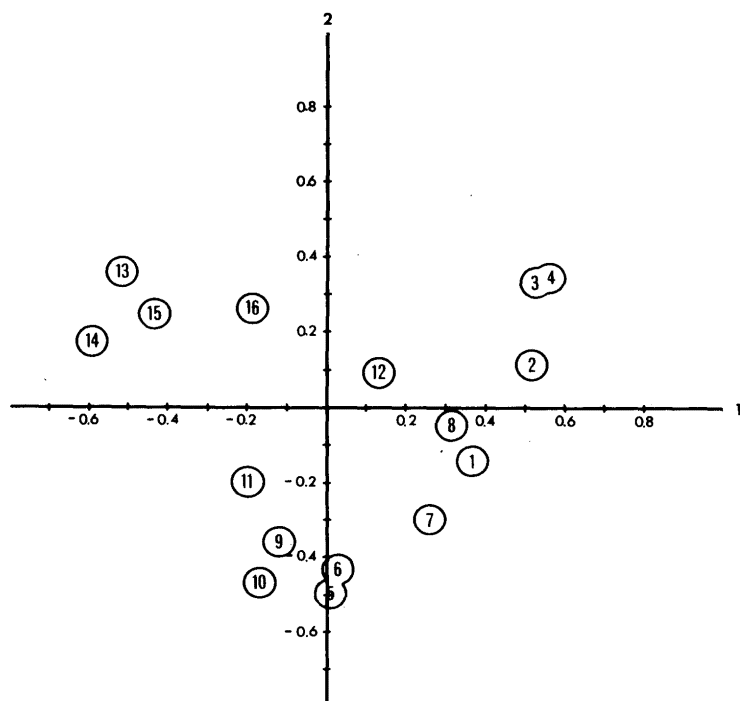


Fig. 25. Position of the site-types relative to the first two axes of the PCO ordination, based on the secondary matrix of PS similarities (Fig. 18). Site-type numbers are in accordance with Tab. 46.

AUTECOLOGY

Cluster analysis of species

The association structure of the species is shown in Fig. 35.

Two distinct species groups can be recognized. One contained the lichen species *Alectoria nigricans*, *A. ochroleuca*, *Cetraria cucullata*, *C. nivalis*, *Cladonia floerkeana*, and *Cornicularia divergens*, mainly restricted to the upper boreal and alpine xeric site-types. The other consisted of species mainly restricted to the mesic middle boreal site-type; *Anemone nemorosa*, *Athyrium filix-femina*, *Blechnum spicant*, *Equisetum sylvaticum*, *Oxalis acetosella*, *Rhizomnium punctatum*, and *Thelypteris phegopteris*. Apart from a minor group consisting of *Cladonia macrophylla* and *C. stellaris*, the other 68 species having associations at the 0.75 level formed a continuous chain, with some minor nodes. The

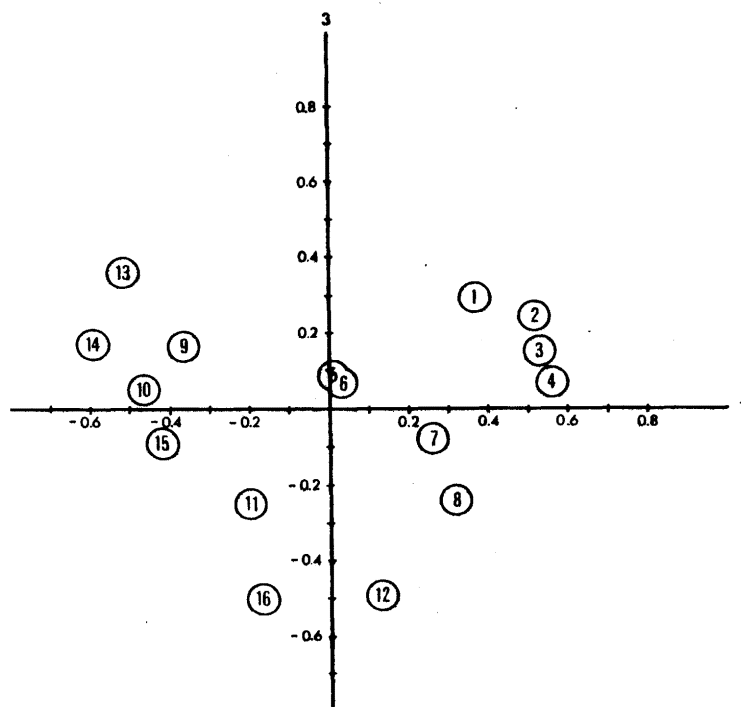


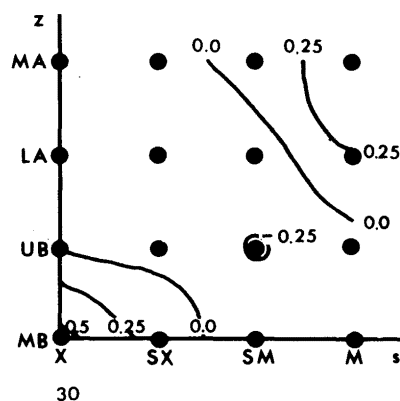
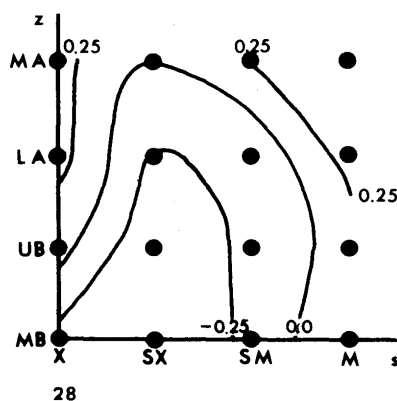
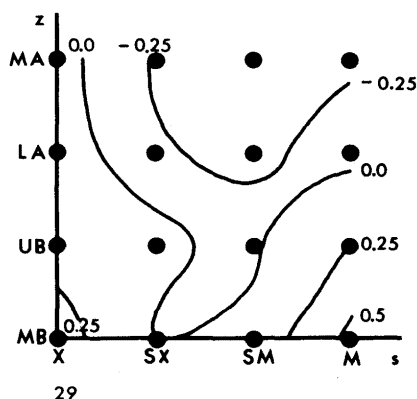
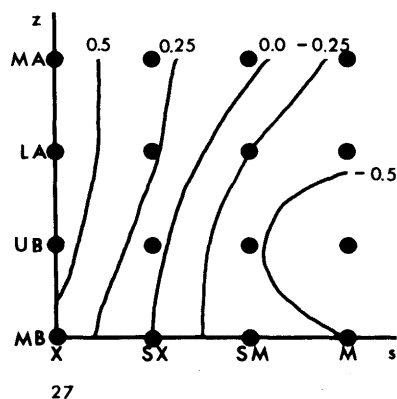
Fig. 26. Position of the site-types relative to the first and third axis of the PCO ordination, based on the secondary matrix of PS similarities (Fig. 18). Site-type numbers are in accordance with Tab. 46.

chain of relations was ordered from the more xeric species at the left end to the more mesic species at the right end. The majority of species with a wide ecological amplitude were linked in the centre of the chain, and formed a continuous pathway from *Vaccinium myrtillus* via *Plagiothecium* spp. to *Maianthemum bifolium*, indicating a shift towards a point of gravity nearer the mesic end of the moisture gradient.

Fig. 36 shows the dendrogram resulting from classification of species by the group-average method. An arbitrary level of similarity, PSD = 0.50, was chosen, and the resulting fourteen groups termed GA-groups.

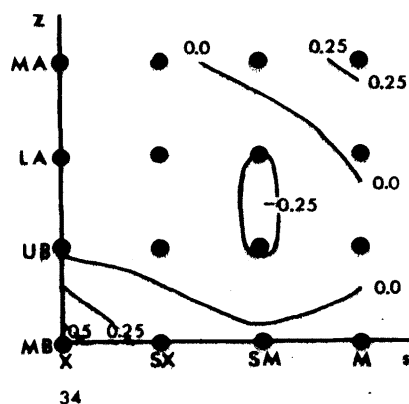
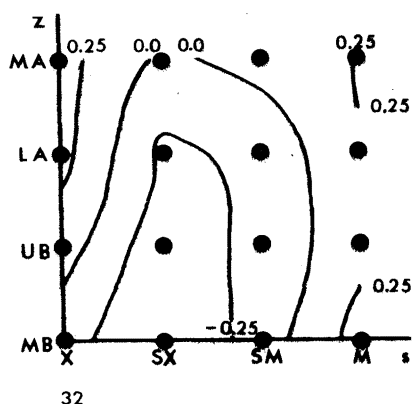
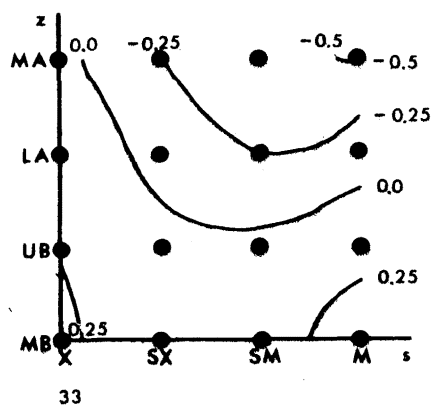
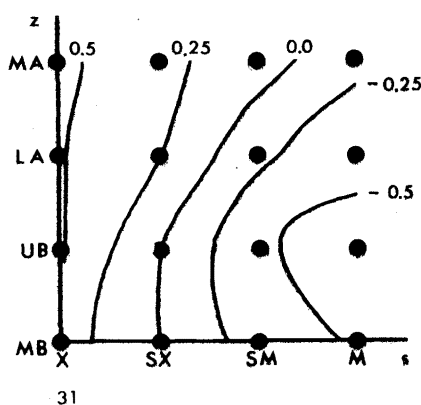
Ordination of species

Direct gradient ordination of the 118 species is shown in Fig. 37. The centres of gravity are estimates of ecological optima. There is a distinct concentration of points in Fig. 37 along an oblique axis from upper left towards the lower right of the



Figs 27-30. Diagrams showing trends in the site-type scores relative to the axes of the PCO ordination based on the secondary matrix of COS X similarities. Drawing of iso-score lines is carried out assuming equal spacing of site-types in the idealized two-gradient system, and a linear variation in component scores between neighbouring site-types. Fig. 27. The first axis. Fig. 28. The second axis. Fig. 29. The third axis. Fig. 30. The fourth axis.

figure. However, some exceptions existed. *Pinus sylvestris* occupied an isolated position at lower left in Fig. 37, and some species were scattered in the upper right half. The two distinct groups in the plexus diagram (Fig. 35) partly reappeared in the ordination, but otherwise the centres of gravity showed a strong tendency to spread in the diagram, thus indicating a continuum of species distributions.



Figs 31-34. Diagrams showing trends in the site-type scores relative to the axes of the PCO ordination based on the secondary matrix of PS similarities. Drawing of iso-score lines is carried out assuming equal spacing of site-types in the idealized two-gradient system, and a linear variation in component scores between neighbouring site-types. Fig. 31. The first axis. Fig. 32. The second axis. Fig. 33. The third axis. Fig. 34. The fourth axis.

Interpretation of GA-groups

Means of centres of gravity for each of the species belonging to a GA-group (\bar{S}_k , \bar{T}_k) and the corresponding standard deviations (q_{sk} , q_{tk}) are given in Fig. 38. The GA-groups were subjectively united into blocks (Galten 1977, Halvorsen 1980) to facilitate interpretation. Each of the

Tab. 49. Abbreviated species names used in Figs 35-36.

Abb.	Name	Abb.	Name
Al al	Alchemilla alpina	Em he	Empetrum hermaphroditum
Al ni	Alectoria nigricans	Eq sy	Equisetum sylvaticum
Al oc	Alectoria ochroleuca	Ge pu	Gentiana purpurea
An ne	Anemone nemorosa	Gy dr	Gymnocarpium dryopteris
An od	Anthoxanthum odoratum	Hy sp	Hylocomium splendens
Ar al	Arctostaphylos alpina	Ju co	Juniperus communis
At di	Athyrium distentifolium	Ju tr	Juncus trifidus
At ff	Athyrium filix-femina	Ki st	Kiaeria starkei
Ba ba	Barbilophozia barbata	Lo he	Lophocolea heterophylla
Ba fl	Barbilophozia floerkei	Lo ob	Lophozia obtusa
Ba ha	Barbilophozia hatcheri	Lo pr	Loiseleuria procumbens
Ba ly	Barbilophozia lycopodioides	Lo ve	Lophozia ventricosa
Be na	Betula nana	Lu pi	Luzula pilosa
Be pu	Betula pubescens	Ly al	Lycopodium alpinum
Bl sp	Blechnum spicant	Ly an	Lycopodium annotinum
Br re	Brachythecium reflexum	Ly se	Lycopodium selago
Br st	Brachythecium starkei	Ma bi	Maianthemum bifolium
Ca bi	Carex bigelowii	Me pr	Melampyrum pratense
Ca br	Carex brunnescens	Me ru	Melandrium rubrum
Ca in	Calypogeia integristipula	Me sy	Melampyrum sylvaticum
Ca mu	Calypogeia muelleriana	Mi ef	Milium effusum
Ca ne	Calypogeia neesiana	Na st	Nardus stricta
Ca vu	Calluna vulgaris	Or mo	Orthodicranum montanum
Ce-ia	Cephalozia spp.	Ox ac	Oxalis acetosella
Ce-la	Cephaloziella spp.	Ph ca	Phyllocladus caerulea
Ce cu	Cetraria cucullata	Pi ab	Picea abies
Ce de	Cetraria delisei	Pi sy	Pinus sylvestris
Ce er	Cetraria ericetorum	Pl ca	Plagiothecium cavifolium
Ce is	Cetraria islandica	Pl cd	Plagiothecium curv.+dent.+laetum
Ce ni	Cetraria nivalis	Pl pi	Plagiothecium piliferum
Cl ar	Cladonia arbuscula	Pl sc	Pleurozium schreberi
Cl be	Cladonia bellidiflora	Po co	Polytrichum commune
Cl ca	Cladonia carneola	Po dn	Pohlia drummondii+nutans
Cl cc	Cladonia coccifera	Po er	Potentilla erecta
Cl co	Cladonia cornuta	Po fo	Polytrichum formosum
Cl cr	Cladonia crispata	Po ju	Polytrichum juniperinum
Cl ec	Cladonia ecmocyna	Po pi	Polytrichum piliferum
Cl fi	Cladonia fimbriata	Po st	Polytrichum strictum
Cl fl	Cladonia floerkeana	Pt ci	Ptilidium ciliare
Cl fu	Cladonia furcata	Ra la	Racomitrium lanuginosum
Cl gr	Cladonia gracilis	Rh lo	Rhytidiadelphus loreus
Cl ma	Cladonia macrophylla	Rh pu	Rhizomnium punctatum
Cl me	Cladonia metacorallifera	Ru ac	Rumex acetosa
Cl mi	Cladonia mitis	Ru ch	Rubus chamaemorus
Cl pl	Cladonia pleurota	Sa he	Salix herbacea
Cl py	Cladonia pyxidata coll.	So au	Sorbus aucuparia
Cl ra	Cladonia rangiferina	So vi	Solidago virgaurea
Cl sq	Cladonia squamosa	Sp gi	Sphagnum girgensohnii
Cl st	Cladonia stellaris	Sp mi	Sphenobolus minutus
Cl su	Cladonia sulphurina	Sp ne	Sphagnum nemoreum
Cl un	Cladonia uncialis	Sp ru	Sphagnum russowii
Co di	Cornicularia divergens	Te pe	Tetraphis pellucida
Co su	Cornus suecica	Th ph	Thelypteris phegopteris
Cr cr	Cryptogramma crispa	Tr eu	Trientalis europaea
De fl	Deschampsia flexuosa	Va my	Vaccinium myrtillus
Di fu	Dicranum fuscescens	Va ul	Vaccinium uliginosum
Di ma	Dicranum majus	Va vi	Vaccinium vitis-idaea
Di sc	Dicranum scoparium		
Di ta	Diplophyllum taxifolium		
Dr as	Dryopteris assimilis		
Dr un	Drepanocladus uncinatus		

four blocks contain GA-groups with centre means within the same series.

Block I includes GA-groups Nos 12 and 14 with centres of gravity within the xeric series. Group No. 12 consists of one species, *Pinus sylvestris*, the only species in the Grunningsdalen area with a distinct lowland and xeric preference (cf. Fig. 31).

Group No. 14 contains 11 species. The core of the group consist of the six strongly chionophobous species *Alectoria nigricans*, *A. ochroleuca*, *Cetraria cucullata*, *C. nivalis*, *Cladonia floerkeana*, and *Cornicularia divergens*, all largely restricted to the xeric series and none found below the upper boreal zone (cf. Tab. 6). The rest of the species occupy somewhat isolated positions, but all show preference for the alpine zones and the xeric and subxeric series. Tolerance to snow increases from the "core" of group No. 14 via *Cetraria nivalis*, *Cladonia stellaris*, and *Loiseleuria procumbens* to *Polytrichum piliferum*.

Block II includes GA-groups Nos 1, 2, 3, 4, and 13 with centres of gravity within the subxeric series. GA-group No. 1 only included *Betula nana*, a species with local occurrence in all zones and in the three driest series.

Among the three species of GA-group No. 13, *Racomitrium lanuginosum* and *Arctostaphylos alpina* prefer the upper boreal and low alpine xeric site-type, while *Orthodicranum montanum* has a wider amplitude.

GA-group No. 2 includes 20 species. The upper left part of the continuous chain in Fig. 35, including *Dicranum scoparium* and *Cladonia furcata*, but excluding *Ptilidium ciliare*, *Cladonia metacorallifera*, and *Cetraria ericetorum*, belongs to GA-group No. 2. Most of the group 2 species have their optima in the subxeric series, but are able to withstand lack of snow cover in winter; they also occur in the xeric site-type. Three weakly characterized subgroups can be discerned (cf. Fig. 35), the most xeric including species having optimum in the xeric and subxeric series only (e.g., *Calluna vulgaris*, *Cladonia arbuscula*, *C. mitis*, *C. rangiferina*, *C. squamosa*, and *C. uncialis*), the most mesic including generally ubiquitous species and species with slight preference for the submesic series (e.g., *Cladonia pyxidata* coll., *Pohlia drummondii+nutans*, and *Dicranum scoparium*).

GA-group No. 3 consists of three rare species with low internal similarity.

Group No. 4 includes four species, all having optima in the middle alpine zone, but with occurrences also further downwards. *Cetraria ericetorum* and *Cladonia metacorallifera* prefer the xeric and subxeric series, *Lycopodium selago* is indifferent to series, while *Cetraria delisei* appears weakly chionophilous.

Block III includes GA-groups Nos 5, 6, 7, and 9 with centres of gravity within the submesic series. Three of the GA-groups (Nos 5, 6, and 9) are small and with a preference for high altitudes, while No. 7 contains 27 species. The species in GA-group No. 7 occupy positions in the middle of the chain in the species plexus (Fig. 35). Apart from *Vaccinium uliginosum*, which has a unique distribution within the sample set with high importance in most site-types below the middle alpine zone (cf.

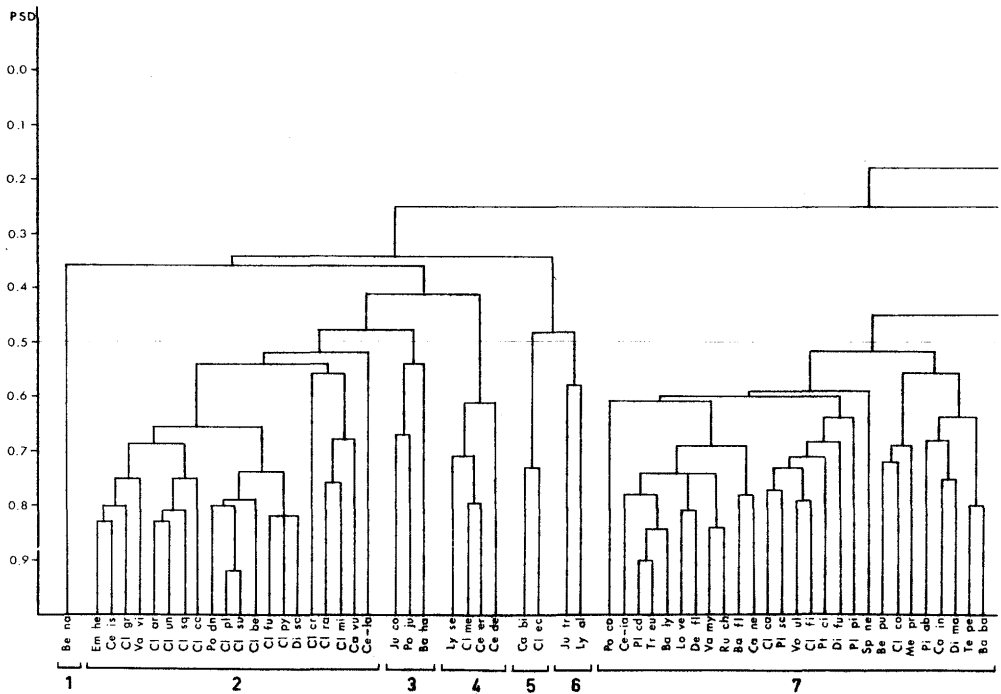


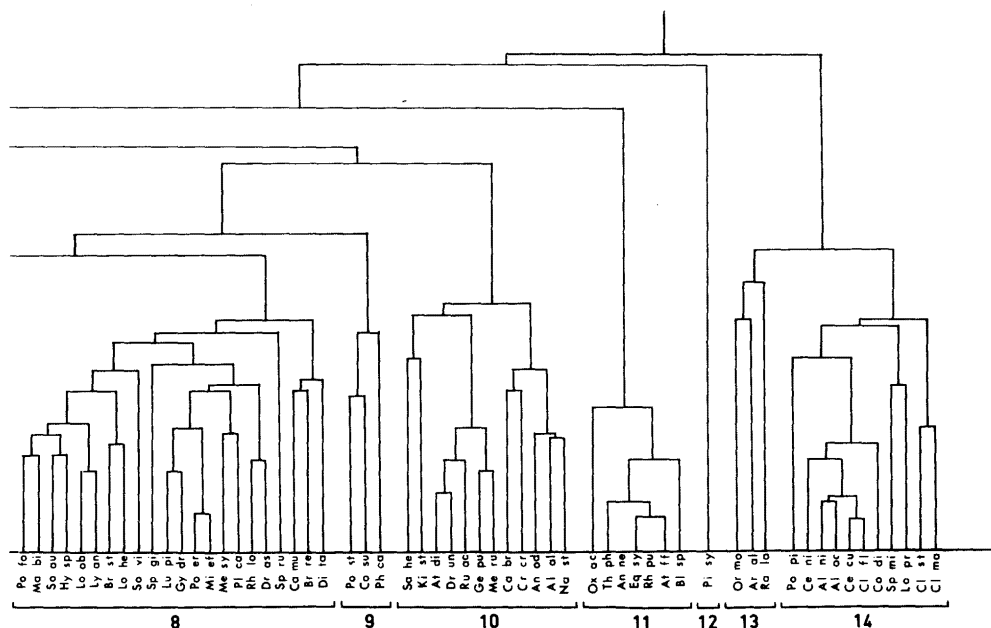
Fig. 36. Cluster analysis of the 118 most important species by the group average method, based on a secondary matrix of PSD similarities. Species names are abbreviated according to Tab. 49. GA-groups are shown at the bottom of the figure.

Tab. 6), all species avoid the xeric series. GA-group No. 7 is composed of two subgroups joining at $PSD = 0.52$. The smaller of these contains 8 species; *Barbilophozia barbata*, *Betula pubescens*, *Calypogeia integristipula*, *Cladonia cornuta*, *Dicranum majus*, *Melampyrum pratense*, *Picea abies*, and *Tetraphis pellucida*. Except for *Tetraphis pellucida*, all these species are common in the three most mesic series and are largely confined to the boreal zones. The rest of group No. 7 spans an interval along the moisture gradient defined by *Pleurozium schreberi* and *Ptilidium ciliare* at the xeric end, *Calypogeia neesiana*, *Cephalozia* spp., *Plagiothecium* spp., and *Trientalis europaea* at the mesic end.

Block IV includes GA-groups Nos 8, 10, and 11 with centres of gravity within the mesic series.

The seven species in Group No. 11 have distinct optima in the middle boreal mesic site-type.

GA-group No. 8 contains the bulk of mesic (and some submesic) forest species. All species between *Polytrichum formosum*, *Maianthemum bifolium*, and *Lophozia obtusa* on the one hand, and *Potentilla erecta*, *Plagiothecium cavifolium*, and



Milium effusum on the other hand in the plexus diagram (Fig. 35) belong to this group, with the exception of *Betula pubescens*.

GA-group No. 10 contains the upper right section of the species plexus. Among the 12 species making up the group, minor differences in detail can be traced, but all species are distinctly chionophilous and largely restricted to the mesic series. Many have an alpine distribution, both locally and generally.

HOMOTONEITY AND DIVERSITY

Homotoneity

The results of homotoneity analyses are summarized in Tab. 50. The site-types of the xeric and mostly also the subxeric and submesic series had generally high homotoneity. However, in

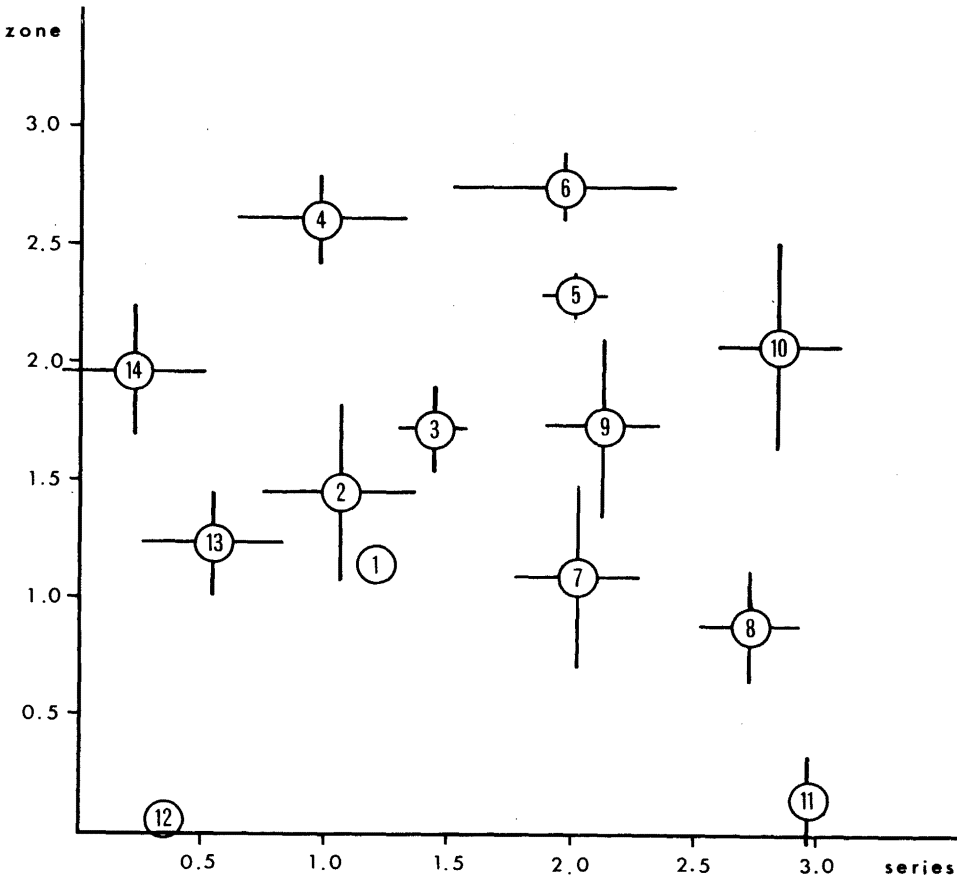


Fig. 38. Mean GA-group loading along the moisture gradient (\bar{T}_k) and along the vertical gradient (\bar{S}_k).

Within site-type diversity

(1) *Fisher's* α (α_j). Alpha diversity increased from the xeric to the mesic series (Tab. 50). In all except the mesic series, α_j increased from the middle boreal to the upper boreal zone, and decreased from the low alpine to the middle alpine zone. The highest α_j reached by any site-type, $\alpha_j = 42$, was obtained by the middle boreal mesic site-type. In the mesic series a markedly higher value was obtained by the low alpine than by the upper boreal site-type.

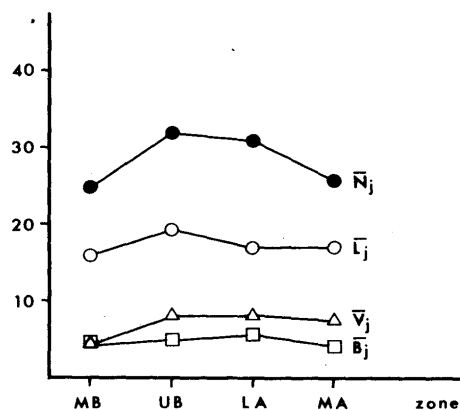
(2) *Mean number of species per sample plot*. The variation in the alpha diversity indices \bar{N}_j , \bar{V}_j , \bar{B}_j , and \bar{L}_j is shown in Figs 39-46. The xeric series (Fig. 39) had an almost uniform number of species in each of the three taxocenes (taxonomic fractions of the vegetation, cf. Whittaker 1972a) at the

Tab. 50. Some homotoneity (H) and alpha diversity (α) indices of the site-types. Indices: n - number of sample plots, N_j - total number of species in site-type j, \bar{N}_j - mean number of species per sample plot in site-type j, α_j - the Fisher diversity index of site-type j, N_{1j} - number of species reaching constancy class i in site-type j.

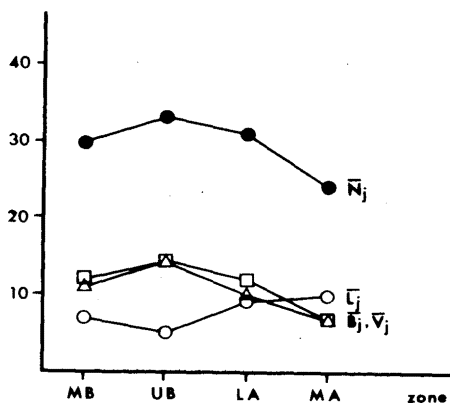
Index type			α	α	H	H
Site-type	n	N_j	\bar{N}_j	α_j	\bar{N}_j/α_j	N_{5j}/N_{4j}
Xeric middle boreal	5	35	24	7	3.5	8.5
Xeric upper boreal	3	48	32	15	2.2	-
Xeric low alpine	8	63	31	15	2.1	2.4
Xeric middle alpine	6	44	26	10	2.6	3.6
Subxeric middle boreal	15	55	28	10	2.7	2.1
Subxeric upper boreal	8	64	33	14	2.3	1.7
Subxeric low alpine	13	68	28	17	1.7	0.9
Subxeric middle alpine	8	55	31	12	2.7	7.7
Submesic middle boreal	11	70	30	18	1.7	2.7
Submesic upper boreal	9	78	33	22	1.5	1.2
Submesic low alpine	10	77	31	22	1.4	0.8
Submesic middle alpine	8	54	24	15	1.6	2.2
Mesic middle boreal	12	142	50	42	1.2	2.2
Mesic upper boreal	12	102	38	29	1.3	1.2
Mesic low alpine	15	132	39	39	1.0	0.9
Mesic middle alpine	10	77	28	25	1.1	2.0

Tab. 51. Some homotoneity (H), gamma (γ) and beta diversity (β) indices of the gradient steps (gamma units). Indices: n - number of sample plots, N_1 - total number of species in gamma unit 1, \bar{N}_1 - mean number of species per sample plot in gamma unit 1, α_1 - the Fisher diversity index of gamma unit 1.

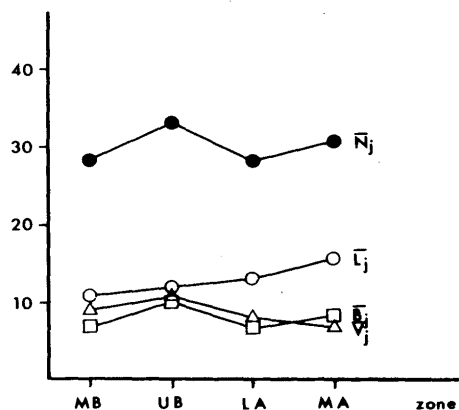
Index type			γ	γ	H	β	β
Gamma unit	n	N_1	\bar{N}_1	α_1	\bar{N}_1/α_1	$\alpha_1/\bar{\alpha}_j$	N_1/\bar{N}_1
Xeric	22	84	28	19	1.5	1.6	3.0
Subxeric	44	103	30	21	1.4	1.6	3.4
Submesic	37	119	30	27	1.1	1.4	4.0
Mesic	49	221	39	58	0.7	1.7	5.7
Middle boreal	43	176	33	47	0.7	2.5	5.3
Upper boreal	31	145	34	43	0.8	2.2	4.3
Low alpine	46	175	32	46	0.7	2.0	5.5
Middle alpine	32	111	27	29	0.9	1.8	4.1



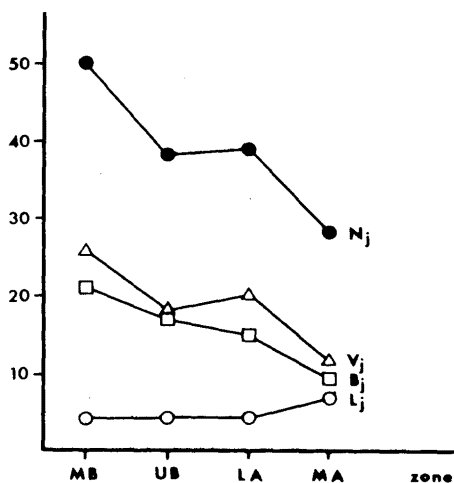
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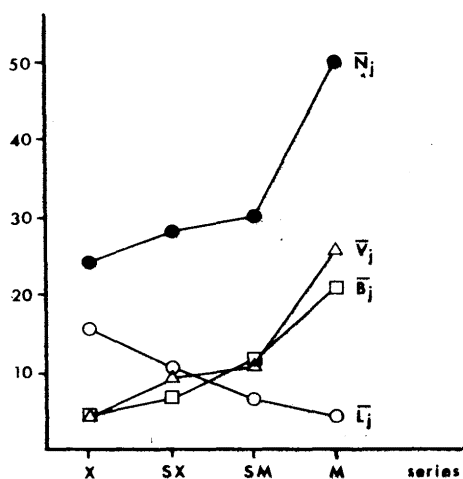
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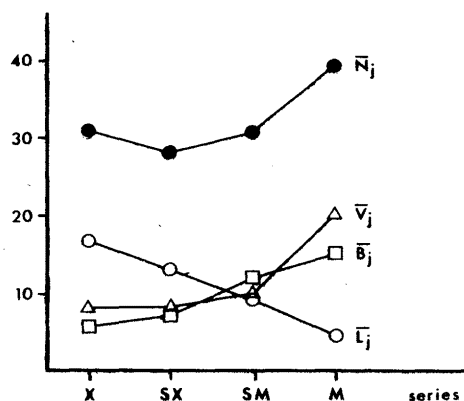
42

Figs 39-42. Mean number of species per sample plot as a function of altitude. \bar{N}_j - all species, \bar{V}_j - vascular plants, \bar{B}_j - bryophytes, \bar{L}_j - lichens. Fig. 39. The xeric series. Fig. 40. The subxeric series. Fig. 41. The submesic series. Fig. 42. The mesic series.

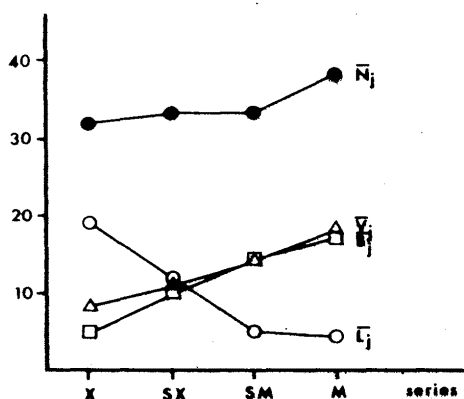
various altitudes. The subxeric series (Fig. 40) showed a slight increase in the number of lichen species, while bryophytes and vascular plants both decreased slightly from the upper boreal zone upwards. The submesic series (Fig. 41) deviated only minutely from the subxeric series. Apart from a minor increase in total number of species and number of



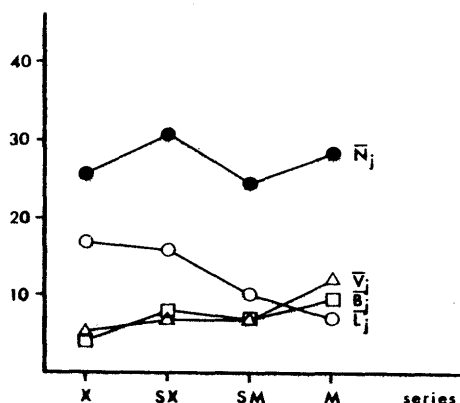
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Figs 43-46. Mean number of species per sample plot as a function of topographic moisture and snow cover. \bar{N}_j - all species, \bar{V}_j - vascular plants, \bar{B}_j - bryophytes, \bar{L}_j - lichens. Fig. 43. The middle boreal zone. Fig. 44. The upper boreal zone. Fig. 45. The low alpine zone. Fig. 46. The middle alpine zone.

vascular plants from the upper boreal to the low alpine zone, there was a decreasing number of species along the vertical gradient in the mesic series (Fig. 41). Bryophytes did not show any local maximum in the low alpine zone. The number of lichen species was generally low, but increased from the low to the

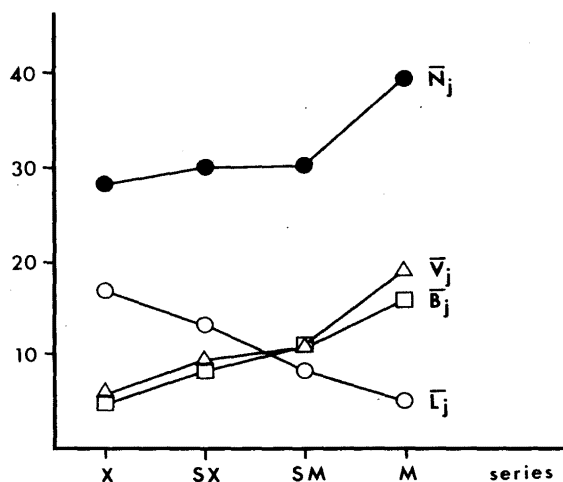


Fig. 48. Mean number of species per sample plot as a function of topographic moisture and snow cover. \bar{N}_j - all species, \bar{V}_j - vascular plants, \bar{B}_j - bryophytes, \bar{L}_j - lichens.

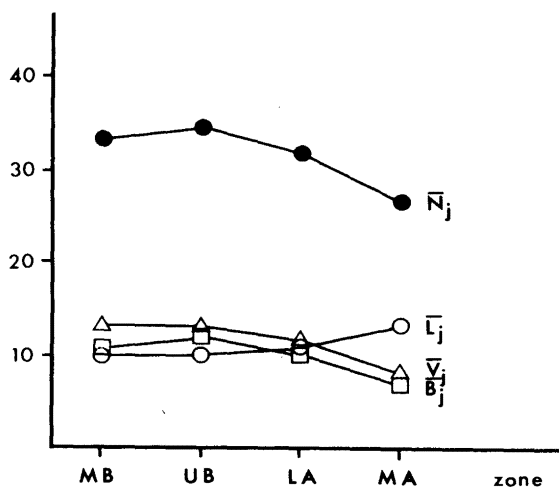


Fig. 48. Mean number of species per sample plot as a function of altitude. \bar{N}_j - all species, \bar{V}_j - vascular plants, \bar{B}_j - bryophytes, \bar{L}_j - lichens.

middle alpine zone.

The trends of all zones were similar (Figs 43-46). Increased total number of species with increasing moisture was clearly evident in the middle boreal zone (Fig. 43), while in the middle alpine zone this was not observed. Vascular plants and bryophytes both increased in species number along the moisture gradient in all zones. The opposite pattern was expressed by lichens.

Within gradient diversity

(1) *Fisher's* α (α_1). The values of the diversity index α_1 for each of the eight gamma units are shown in Tab. 51. The pattern observed for *Fisher's* α in separate site-types reappeared. Gamma diversity increased slightly between the xeric and the subxeric, and between the subxeric and the submesic series, strongly between the submesic and the mesic series.

There was virtually no difference in gamma diversities between the three lower zones, but a local minimum was observed

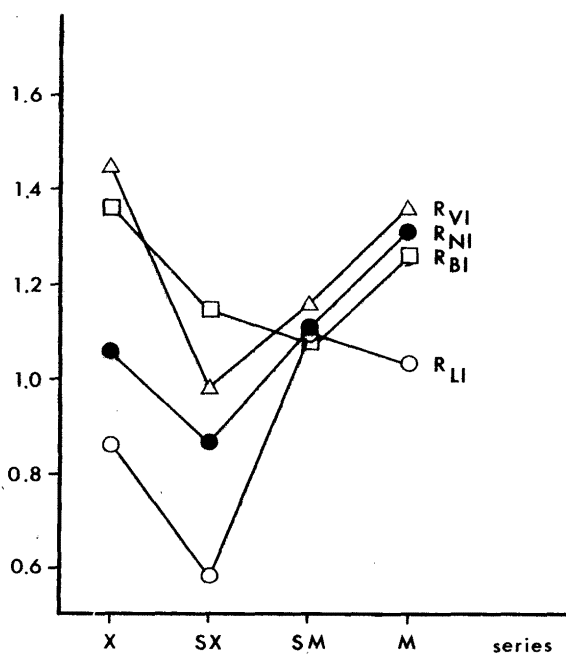


Fig. 49. Turnover rates for total floristic composition (R_{N1}), vascular plants (R_{V1}), bryophytes (R_{B1}), and lichens (R_{L1}) along the topographic moisture and snow cover gradient.

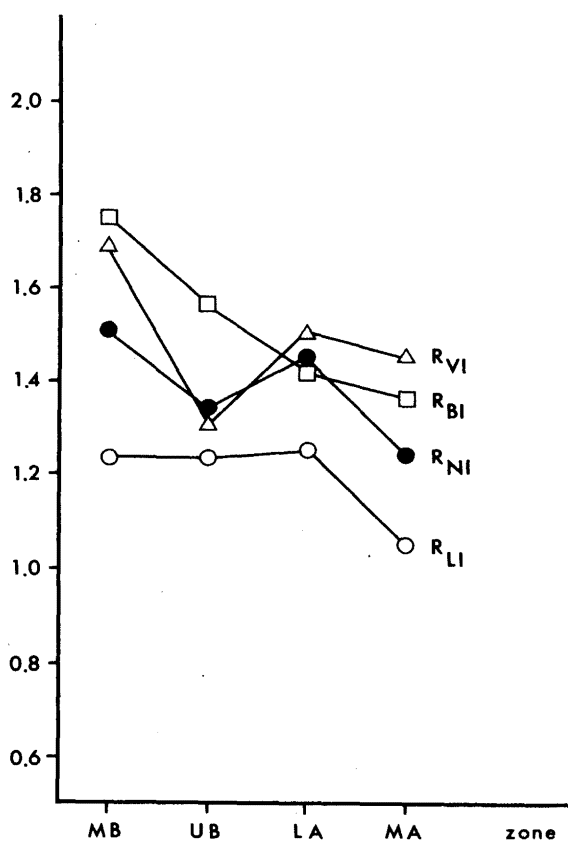


Fig. 50. Turnover rates for total floristic composition (R_{NI}), vascular plants (R_{VI}), bryophytes (R_{BI}), and lichens (R_{LI}), along the vertical gradient.

in the upper boreal zone. The middle alpine zone had the lowest value for α .

(2) *Mean number of species per gamma unit.* Number of species (\bar{N}_1), vascular plants (\bar{V}_1) and bryophytes (\bar{B}_1) increased from the xeric to the mesic series, while the number of lichen species (\bar{L}_1) declined almost linearly (Fig. 47).

The change in gamma diversity along the vertical gradient was generally slight (Fig. 48), most pronounced from the low to the middle alpine zone.

Between site-type diversity along gradients

(1) *The quotients $\alpha_1/\bar{\alpha}_1$ and N_1/\bar{N}_1 .* One trend was clearly shown by both indices; the higher beta diversity of the individual zones than of the series (Tab. 51), indicating that the change

in floristic composition was greater along the complex-gradient moisture-snow cover than along the vertical gradient. As judged from the $\alpha_1/\bar{\alpha}_j$ index, there was no significant difference in beta diversity between the series. However, the N_1/\bar{N}_1 index showed increasing change along the moisture gradient from the xeric to the mesic series.

Tab. 52. Mean turnover rate of total floristic composition (\bar{R}_{N1}), vascular plants (\bar{R}_{V1}), bryophytes (\bar{R}_{B1}), and lichens (\bar{R}_{L1}), along the two major gradients.

	\bar{R}_{N1}	\bar{R}_{V1}	\bar{R}_{B1}	\bar{R}_{L1}
Four elevation gradients from xeric to mesic	1.09	1.24	1.22	0.90
Four moisture-snow cover gradients from middle boreal to middle-alpine	1.39	1.49	1.53	1.19
Means	1.24	1.37	1.38	1.05

The $\alpha_1/\bar{\alpha}_j$ index decreased slightly towards higher altitudes, while the N_1/\bar{N}_1 index showed somewhat irregular relationship to altitude.

(2) *Rate of change per step along the gradient.* The curves for total species content (R_{N1}), vascular plants (R_{V1}), and bryophytes (R_{B1}) along the moisture-snow cover gradient were similar (Fig. 49). The lowest turnover rates were found in the subxeric series. R_{V1} and R_{B1} reached a maximum in the xeric series, while R_{N1} was highest in the mesic series. The turnover rate of lichens (R_{L1}) was irregular.

Apart from the low alpine zone where the turnover rates of total species content and vascular plants had local maxima, turnover rate decreased towards higher altitudes (Fig. 50). From Tab. 52, the higher mean turnover rate for zones than for series is evident. If turnover rates of zones and series are averaged, lichens show a far lower turnover rate than vascular plants and bryophytes (Tab. 52).

DISCUSSION

MAIN VEGETATIONAL GRADIENT IN GRUNNINGSDALEN AREA

The existence of one main vegetational gradient in the investigated area was clearly demonstrated by the PCO ordinations: (1) Both PCO ordinations showed a significant drop in variability accounted from the first to the second axes. (2) Trends showed by PCO ordinations based on similarity measures with contrasting properties were largely coincident (cf. Figs 27 and 31).

In the two-dimensional gradient representation of the investigated vegetation (cf. Figs 6, 27, and 31), the main vegetational change in the middle boreal zone runs parallel with the topographic moisture gradient. From the upper boreal zone and upwards the lines of equal component scores (Figs 27 and 31) are displaced towards the right (mesic) in the diagrams, most strongly towards the mesic series. The main vegetational gradient in the area thus runs from the upper left (middle alpine xeric) towards the lower right (upper boreal mesic), gradually approaching parallelism with the complex-gradient topographic moisture-snow cover in the middle boreal zone. The upper boreal submesic site-type deviates slightly by being more similar to the mesic series than to the middle boreal submesic site-type.

The main vegetational gradient is reflected in numerous properties of vegetation:

(1) α and γ diversity of lichens expressed as mean number of species per sample plot decreases from the xeric to the mesic series, to a lesser extent also from middle alpine to middle boreal zones within each of the three most mesic series. An aberrance is seen in the submesic series, where a minimum in lichen α diversity is observed in the upper boreal zone.

(2) In contrast, bryophyte and vascular plant α and γ diversities increase along the moisture gradient. Except for the upper boreal submesic site-type, which shows the highest vascular plant diversity of its series, almost no difference is observed in γ diversity between the middle and upper boreal zones, while at higher altitudes the diversities decrease.

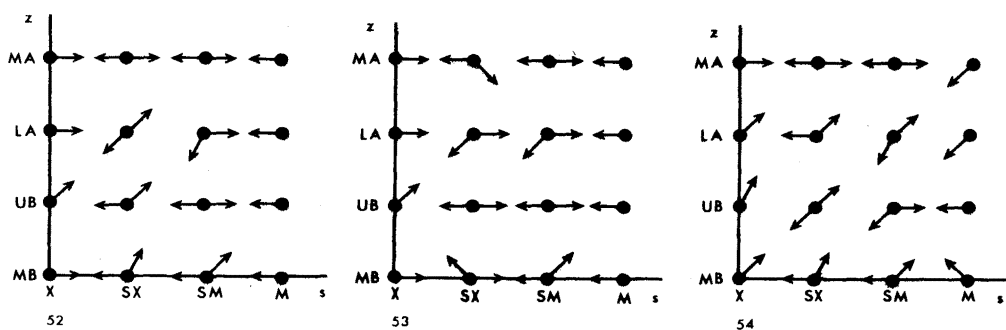
Total diversity, expressed as Fisher's α or mean number of species per sample plot, is a resultant of the opposing patterns of lichen against bryophyte and vascular plant diversities. These indices consequently show relatively poor correspondence with the main vegetational gradient, although they come most close to the trends in bryophyte and vascular plant diversities.

(3) Cluster analysis of site-types gives an indication of the gradient by showing a higher degree of similarity between the middle alpine submesic site-type and the entire subxeric series than with submesic site-types at lower altitudes. based on Fig. 19).

Fig. 54. The bottom layer (based on Fig. 20).

zone					
		X	SX	SM	M
MA	86	67	66	37	
LA	81	64	40	16	
UB	82	52	19	12	
MB	85	52	26	11	
					series

Fig. 51. Total importance of lichen species as percentage of total importance in the bottom layer.



Figs 52-54. The most similar site-type in adjacent series calculated as PS and indicated by arrows. Fig. 52. Total floristic composition (based on Fig. 18). Fig. 53. Vascular plants (layers A to C). Fig. 54. Vascular plants (layers D to F).

(4) There is a nearly direct correspondence between percentage cumulative importance of lichens in the bottom layer (Fig. 51) and scores along the first component of the PCO ordinations (Figs 23-34). The product-moment correlation coefficient (Sokal & Rohlf 1969) between these variables, when figures from the ordination based on PS are used, reaches 0.98.

(5) Figs 52-54 show for each of the site-types the most similar site-type in the neighbouring series. Overall floristic composition seems to agree best with the main vegetational gradient. Vascular plants show the highest degree of similarity between the series at corresponding altitudinal levels, while the bottom layer shows a strong tendency to having the closest connections along the diagonal from lower left to upper right in the diagram. Thus the main vegetational gradient in the investigated area can be conceived as a resultant of partly independent gradients in each of the field and bottom layers. Fig. 54 shows that the main vegetational gradient in the bottom layer has been rotated approximately 45 degrees as compared with the corresponding gradient in the upper strata (Fig. 53).

The lack of parallelism observed between vegetational gradients of different layers may be explained by taking into consideration the physiological adaptations of bryophytes and lichens. Except for a few moss genera, e.g., *Polytrichum* (Héban 1977), bryophytes and lichens are both ectohydric and poikilohydric (Buch 1947, Hosokawa et al. 1964, Blum 1973, Kappen 1973). Thus they have poor ability to take up water from dry soil (L. Anderson & Bourdeau 1955), are predominantly supplied with water and nutrients directly from the air, and change their water contents with the humidity of the surrounding air. Microclimate is the major factor affecting the occurrence of such organisms (Størmer 1969, Lee & LaRoi 1979). Especially important are those aspects of microclimate bearing directly on water relations (Buch 1947, E. Watson 1971, During 1979). The microclimate of the bottom layer depends on soil moisture and the direct action of desiccating winds.

Wind keeps air humidity low by immediately removing the water vapour and not allowing an equilibrium between water vapour pressure within and outside plants (cf. Ray 1972). The effect of wind on the microclimate near the ground strongly increases in the upper part of the upper boreal zone owing to lower tree heights and increased spacing of trees (Kärenlampi 1972). This is reflected in the uneven distribution of snow often observed in upper boreal birch forests (Lie 1919, Smith 1920, Nordhagen 1928, Mork & Heiberg 1937, Kullman 1979). Above the forest limit the winds can act directly on the vegetation (e.g., Nordhagen 1943, Dahl 1957, Baadsvik 1974). Thus the microclimate of the bottom layer becomes significantly drier in the low alpine than in the upper boreal zone given comparable soil moisture conditions (Kärenlampi 1972). The increased action of wind, and the consequent microclimatic change in the bottom layer within each of the series, are assumed to be the major cause of the rotation of the gradient in composition of cryptogams relative to the gradient in vascular plant composition. The rotation continues from the low to the middle alpine zone. This may be due to the increasing action of winds with increasing altitude, making the microclimate of one middle

alpine site-type (at least regarding moisture conditions) more similar to the low alpine than the middle alpine site-type in the adjacent, drier series.

The main vegetational gradient of the bottom layer is also paralleled by a shift in dominance from lichens to bryophytes. Generally, lichens are adapted to microclimatically more xeric, and more hostile (cold) environments than bryophytes. This involves several aspects. Lichens of the genera *Alectoria*, *Cetraria* and *Cladonia* are the quantitatively most important of the investigated vegetation. Their ability to survive severe drought is generally higher than that of bryophytes (Kappen 1973, Ahti 1977). The ability of lichens to change rapidly between activity and inactivity (Büttner 1971), coupled with their tolerance of long periods without net production of organic material (Billings & Mooney 1968), is assumed to be the most important reason for the success of lichens in xeric environments (Lambert & Maycock 1968, Blum 1973, Kappen 1973). On the other hand, bryophytes are adapted to more mesic environments by having a higher ability to accumulate water than most lichens (Blum 1973), and they also need a higher water content in the tissues to maintain turgor (Flock 1978).

The adaptation of many lichens to maximal photosynthetic activity when the thallus moisture content is low makes them less well suited to more mesic sites (Blum 1973). Many lichens are adapted to very cold environments. Kallio & Heinonen (1971) have observed a net photosynthesis in *Cetraria nivalis* even at -20°C , while Bliss & Hadley (1964) have found a corresponding adaptation to cold environments in *Cetraria islandica* and *Cladonia rangiferina*.

The most important disadvantage of lichens when compared with bryophytes is their low competitive ability (Topham 1977). This must be attributed to the low growth rates observed in lichens. The annual growth of dominating lichen species in boreal and alpine areas, e.g., *Cladonia arbuscula*, *C. mitis*, *C. rangiferina*, *C. stellaris*, *C. uncialis*, and *Stereocaulon paschale* varies from 0 to 6 mm (Tengwall 1928, Scotter 1963, Brodo 1973, Yarranton 1975). Important bryophytes of the investigated vegetation, e.g., *Dicranum majus*, *Hylocomium splendens*, *Pleurozium schreberi*, *Polytrichum commune*, and *Sphagnum girgensohnii* are reported to have annual length increments in the range 20-60 mm (Pakarinen & Rinne 1979).

Supporting evidence on increasing winds as the main reason for the rotation of the main vegetational gradient of the bottom layer in the alpine zones can also be found in literature. Nordhagen (1928, 1943) and Dahl (1957) noted that in localities with comparable duration of snow cover and similar soil moisture conditions, *Vaccinium myrtillus*-heaths with an overstory of *Betula nana* or *Juniperus communis* differs from the shrub-deficient heaths in having a higher dominance of mosses. Nordhagen (1943) attributes this to the effective shielding against evaporation provided by the shrubs. The continued displacement of mosses by lichens also from the low to the middle alpine zone can, as previously mentioned, partly be explained by increasing wind action. Many of the important shielding dwarf-shrubs also reach their thermal limits at the low alpine-middle alpine-transition, causing the microclimatically more favourable microsites to disappear.

However, other factors contribute as well. The generally better adaptation of lichens to cold environments allows them occupy the niches left vacant when the dominant boreal zone bryophytes, e.g., *Hylocomium splendens*, *Pleurozium schreberi*, and *Barbilophozia lycopodioides*, reach their thermal limit.

RELATIVE PERFORMANCE OF HOMOTONEITY INDICES

Results of this study contradict a close relationship between the two homotoneity indices \bar{N}_j/α_j and N_{5j}/N_{4j} , as stated by Dahl (1957, 1960). This is particularly well pronounced in the low alpine site-types. In the low alpine mesic site-type ecological variation is high, leading to a high number of species in the site-type compared to mean number of species per sample plot, and thus to a low \bar{N}_j/α_j ratio. Just a few species with wide ecological amplitude reach constancy class 5, and N_{5j}/N_{4j} also becomes small. This is well in accordance with Dahl's assumption. In the low alpine subxeric and submesic site-types many species constant at lower altitudes are lacking in the upper part of the zone. Thus only a few species reach constancy class 5, and N_{5j}/N_{4j} becomes low. However, as the thinning out towards higher altitudes does not imply a higher total number of species in the site-type, N_j remains low compared to \bar{N}_j , α_j is low, and \bar{N}_j/α_j is high.

The N_{5j}/N_{4j} index rests on only a few out of the total number of species in a vegetation table. On the other hand the \bar{N}_j/α_j index takes advantage of using the full species composition. Owing to its oligothetic nature, the N_{5j}/N_{4j} index is more vulnerable to noise, and thus has higher statistical variance (cf. E. Dahl, pers. comm.). Among the two indices \bar{N}_j/α_j is thus recommended.

DIVERSITY CHANGE ALONG MAJOR ENVIRONMENTAL GRADIENTS

Alpha and gamma diversity

The complex-gradient topographic moisture-snow cover. Vascular plant diversity measured as mean number of species per sample plot increases from drier to more mesic habitats, most strongly at the transitions between xeric and subxeric, and submesic and mesic series. This is an expression of the increasingly favourable habitats for vascular plants towards the mesic series. The apparently stepwise increase in vascular plant diversity may be correlated with the occurrence of two intervals along the moisture gradient where the favourability for vascular plants is particularly enhanced. Firstly, some species appear when passing from areas without stable snow cover in winter (the xeric series) to areas with a permanent snow cover. Du Rietz (1942) emphasizes *Vaccinium myrtillus* and *Deschampsia flexuosa*, but more species could be mentioned. Next, when passing into areas supplied with oxygen-rich ground

water (and also a better nutrient supply), a number of species that have demands on edaphic or moisture conditions appear. The way the mesic series is defined in the present study, as well as the inclusion of moderate and late snowbeds in the alpine zones, leads to increased species diversity due to increased habitat diversity. This is reflected in the generally low uniformity values reached in the mesic series.

Figures of vascular plant diversity in Finnish studies of boreal coniferous forests (e.g., Linkola 1917, Ilvessalo 1920, 1921, Lakari 1920, Cajander 1921b, Kalliola 1973) confirm the general trend of increasing diversity towards more mesic habitats. Norwegian studies also show a tendency for no or only slight increase in vascular plant diversity from subxeric to submesic sites (Kielland-Lund 1962b, 1981, Haug 1970, Aune 1973, Bergland 1975, Kjølvik 1978, Moen 1978, Odland 1978). Few investigations of diversity have been carried out in Scandinavian mountain areas, but the results of Dahl (1957) indicate maximal vascular plant diversity in the middle portion of the snow cover gradient in poor sites.

Numerous studies of vascular plant alpha diversity change along the moisture gradient have been performed outside Scandinavia. An overwhelming diversity of diversity patterns may be traced (cf. Whittaker 1972a, 1977, 1978b, Peet 1978a). Their comparability and therefore also their relevance to the present study is generally low.

The whole range of vegetation types shows a high total cover in the bottom layer. The mean number of cryptogams per sample plot shows only small variation among the series. Alpha diversity patterns of lichens and bryophytes are discussed in connection with the major vegetational gradient.

The vertical gradient. Vascular plant diversity decreases with increasing altitude owing to the shortening of the growing-season and generally lowered temperature (cf. Dahl 1975). In the Grunningsdalen area this decrease is particularly pronounced between the low and middle alpine zones, while there is a small increase from the middle to the upper boreal zone. The latter is a resultant of a distinct increase in the three most xeric series and a strong decrease in the mesic series. Similar trends are noted by Elven & Vorren (1980), and by Kalela (1961), who points out that when passing towards the north of Finland nearly all thermophilous, southern species are entirely absent before the alpine species appear in significant numbers. The deviating pattern of the mesic series in Grunningsdalen is due to the occurrence of many stations with favourable aspect and high number of thermophilous species in the middle boreal mesic site-type, while such stations are absent from the upper boreal zone.

Bryophytes also decrease in numbers with altitude, while lichens increase, for reasons discussed previously.

Literature sources give evidence of variable diversity patterns along altitudinal gradients in different areas. Lowered vascular plant diversities with increasing altitude are reported by Whittaker (1956, 1965), Whittaker & Niering (1965), Moral (1972), and Lee & LaRoi (1979), while Zobel et al. (1976) and Peet (1978a) find a non-linear relationship between altitude and diversity. From studies of a wide range of habitats within each altitudinal belt Slack (1977) found

bryophyte diversity to decrease with altitude. However, Lee & LaRoi (1979) have reached the opposite conclusions.

The alpha and gamma diversity approaches. In the present study there is no general correlation between gamma and alpha diversities of different layers. Similar results have been reached by Slack (1977), Lee & LaRoi (1979), and McCune & Antos (1981) for comparisons of bryophyte and vascular plant diversities, and for tree, shrub and herb strata by Whittaker (1960), Auclair & Goff (1971), Zobel et al. (1976), Glenn-Lewin (1977), and Peet (1978a). The different water relations of vascular plants and cryptogams indicate the value of treating layers separately when diversity relationships are studied. However, the observations by Auclair & Goff (1971), Moral (1972), and Peet (1978a) that the reduced irradiation caused by a dense canopy may cause a low understory vascular plant diversity, also show the possible value of combined approaches.

The apparently conflicting results of diversity studies from different vegetation types and different geographical areas make it important to stress that present results and conclusions are not transferable to different ecosystems (cf. Whittaker 1972a, Zobel et al. 1976, Peet 1978a). Comparison of present results with other studies supports the conclusion of Whittaker (1972a, 1977) that the science of species diversity consists of a small nucleus of principles and applications diverging in all directions.

Even though diversity patterns of gradients considered separately may sometimes be possible to interpret, the complex relationships of microclimate, physiological adaptations and diversity change in explaining the major vegetational gradient of the Grunningsdalen area give unequivocal support to two conclusions of Peet (1978a): (1) A full understanding of the complex relations between environment and vegetation diversity can best be reached through an integrated approach (cf. Peet 1978a). (2) Diversity values are exceptionally difficult to interpret when taken out of context, and little justification exists for their publication if such a perspective is not provided.

In this study the interpretability of α diversity measures was clearly improved by their conceptual simplicity. In spite of the lack of theoretical elegance of measures like mean species number per sample plot (cf. Peet 1974), practical use has clearly shown their merits (cf. Whittaker 1972a, Zobel et al. 1976, Peet 1978a, McCune & Antos 1981). This is in striking contrast to the problems that have arisen from the continued use of the complex concepts of evenness and heterogeneity (cf. Hurlbert 1971, Hill 1973, Peet 1974, 1975, 1978a, Alatalo 1981). In this connection Alatalo (1981: 204) stated that "in spite of their popularity, the diversity and evenness concepts have not produced much useful information in ecological studies". Our opinion is that the use of conceptually simple diversity measures used in combination with an integrated ecological approach to vegetation is well justified, but that care should be taken to avoid invalid generalizations.

Beta diversity

A comparison between β diversities measured as turnover rates along the 4 vertical gradients from xeric to mesic (Fig. 49) shows an irregular pattern with highest values for β diversities in the extreme series for most taxocenes. This apparently contradicts the theory of covariance between alpha and beta diversities (cf. Whittaker 1972a, 1977), stating that increased favourability of a habitat to a particular group of organisms implies increased number of species, increased competition, and consequently a denser packing of species along the resource gradients. However, the small number of bryophyte and vascular plant species in the xeric site-types and their predominantly occasional occurrences contribute to increase the difference between adjacent site-types and thus increase beta diversity. This is probably the main reason for the high vascular plant and bryophyte beta diversities of the xeric series, and the high beta diversity of lichens in the submesic and mesic series. From the subxeric to the mesic series, the bryophyte and vascular plant diversities increase, and trends in the statistically most reliable material thus support the general theory of a closer spacing of species optima (and narrower niches) in favourable habitats.

Patterns of turnover rates along the 4 moisture gradients from middle boreal to middle alpine zones are more regular (Fig. 50). The material is more reliable for each taxocene and zone. The general tendency for turnover rates to decrease with increasing altitude is probably due to the lowered effect of competition at higher altitudes. Particularly strong is the fall in turnover rate from low to middle alpine zone. Most dwarf shrubs and typical "boreal species" like *Cornus suecica*, *Melampyrum* spp., *Hylocomium splendens*, *Plagiothecium* spp., *Pleurozium schreberi*, *Polytrichum formosum*, and *Barbilophozia lycopodioides* reach their thermal limits in the low alpine zone. The niches occupied by these species are left empty, and to a major extent taken over by tolerant species that widen their niches in the middle alpine zone in response to reduced competition. Typical examples include *Juncus trifidus* and *Cetraria islandica*. The first is restricted to the xeric series in the upper boreal and low alpine zones (cf. Tab. 6), while the latter is a xeric and subxeric species at lower altitudes (cf. Tab. 6). Both are able to grow in all series in the middle alpine zone, where they seem to prefer the submesic series (cf. Nordhagen 1928, 1943). Other species which are mainly considered to be chionophilous show a strong tendency to spread over the full range of the snow cover gradient in the middle alpine zone (e.g., *Carex bigelowii*, *Salix herbacea*, and *Conostomum tetragonum*).

A similar tendency for β diversities to decrease with altitude is reported by Lee & LaRoi (1979) for bryophytes and vascular plants; Moral (1972), however, gives evidence for the opposite view.

For all taxocenes mean turnover rates were higher along the moisture gradient than along the vertical gradient (Tab. 52). This also agrees with the direction of the main vegetational gradient, and is an indication of greater ecotope widths along the vertical gradient. Lee & LaRoi (1979) have reached similar

results.

Bryophytes and vascular plants show largely similar beta diversities along both of the gradients, while the corresponding figures for lichens are significantly lower (Figs 49 and 50, Tab. 52).

Lee & LaRoi (1979) found similar beta diversity figures for bryophytes and vascular plants along a moisture gradient, but along a vertical gradient vascular plant β diversity was higher than that of bryophytes. They interpreted this as indicating a wider tolerance to temperature conditions among mosses than among vascular plants. This investigation does not confirm the general validity of this statement.

The low figures of lichen β diversity are probably due to low competition. Lichens are known to be slow growing organisms with a generally poor competitive ability (Topham 1977). In the vegetation studied here, lichens often dominate areas above the forest limit that are relatively dry and/or subjected to wind abrasion in winter (Nordhagen 1928, 1943, Du Rietz 1931, Kalliola 1939, Dahl 1957). Wind acts in the dispersal of lichen propagules (Du Rietz 1931), in the creation of empty niches, and in rendering the environment unstable (cf. Churchill & Hanson 1958). At lower altitudes and in the more mesic series, where lichens are less important parts of the vegetation, they predominantly occupy unstable niches, e.g., along stone margins, on decaying pieces of bark, twigs, logs etc. The low growth rate of lichens relative to the duration of many lichen-occupied habitats reduces direct competition (Slack 1977, M. Watson 1980) and makes possible the establishment of a particular species in unstable microhabitats over a wider range of site-types than is possible for species subjected to direct competition with other species. Usually only a small part of the potential amplitude of a species is realized under natural conditions in environments where competition is present (cf. Kärenlampi & Kauhanen 1972). The opportunistic nature of lichens is mentioned by Billings & Mooney (1968), Ahti (1977), and Topham (1977), and is assumed to be an important cause of the observed low β diversities of lichens.

Some authors have claimed that bryophytes, like lichens, are opportunists, and that low direct competition occurs among bryophytes (e.g., Schuster 1966, Schofield 1972, Slack 1977, M. Watson 1980). The high values for bryophyte β diversity observed in the present study seems at first glance to be in conflict with such a view. The heterogeneity of habitats available to bryophytes varies greatly within the area. The restricted occurrence of many species in the two-gradient frame owing to the rarity of suitable habitats can be demonstrated. For instance, this applies to the small species occurring in minor cavities (pocket species, cf. survey of the submesic series), e.g., *Plagiothecium cavifolium*, *P. denticulatum*, *P. piliferum*, *Tetraphis pellucida*, *Calypogeia integristipula*, and *Lophozia ventricosa*. Such a niche predominantly exists in submesic and mesic series at low altitudes. A limited range of bryophyte microniches is also provided by debris from ferns, tree leaves, bark and decaying pieces of logs. The large microniche heterogeneity available for bryophytes at lower altitudes should therefore be considered in detail before

conclusions are drawn from the present material about niche relationships and the occurrence of direct competition among bryophytes.

PHYTOSOCIOLOGICAL CLASSIFICATIONS IN THE FOREST-ALPINE TRANSITION

Even though the direct gradient approach to vegetation adopted in this work is fundamentally different from the phytosociological classificatory approach of previous authors, phytocoena corresponding to the site-types were easily depicted. The gradient reference frame thus constitutes a means for ecological evaluation of phytosociological classifications of corresponding vegetation. Numerical analysis of vegetation has particular relevance in this respect, as it rests on floristic composition alone, just as phytosociological systems are intended to do.

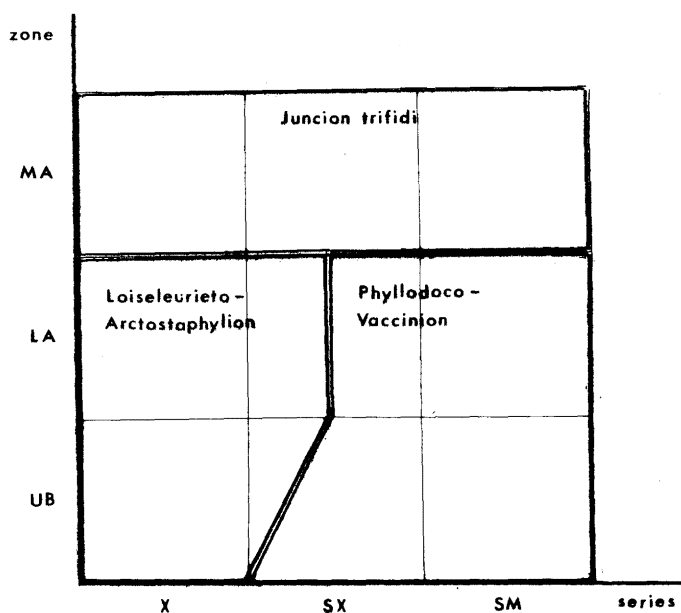


Fig. 55. Alliances in the system of Nordhagen (1937, 1943, 1954a) relative to the two-gradient representation of the studied vegetation. Names according to Nordhagen (1943).

Our attention is mainly restricted to systems proposed as valid over an area including Grunningsdalen. Our purpose is to point to weaknesses in the existing systems, not to amend these

zone			
MA		Juncion trifidi	
LA	Empetrium	Myrtillion alpinum	
UB		Myrtillion subalpinum	
	X	SX	SM series

Fig. 56. Alliances in the system of Du Rietz (1942) in relation to the two-gradient representation of the studied vegetation.

systems or outline new ones.

First a short characterization of major systems will be given.

The system of Nordhagen (1937, 1943, 1954a). Some alliances in Nordhagen's system and their approximate position in the gradient reference frame are shown in Fig. 55. The mesic series is omitted owing to its heterogeneity in the alpine zones. Nordhagen separated a grass-heath alliance, *Juncion trifidi*, proposed to be separated from *Loiseleurieto-Arctostaphylion* and *Phyllodoco-Vaccinion* along the divide between the low and middle alpine zones. However, the middle alpine xeric and subxeric site-types are intermediate between *Loiseleurieto-Arctostaphylion* and *Juncion trifidi* judging from Nordhagen's floristic criteria. *Phyllodoco-Vaccinion* is separated from *Loiseleurieto-Arctostaphylion* by having a constant occurrence of *Vaccinium myrtillus* and *Deschampsia flexuosa* on plots of 1 to 4 sq.m (Nordhagen 1943: 63). Lower units corresponding to the subxeric series are found within both alliances (cf. Tabs 43 and 45).

The system of Du Rietz (1942). Du Rietz maintained the middle alpine *Juncion trifidi* (Fig. 56). He contrasted the vaguely defined border between the alliances *Phyllodoco-Vaccinion* and *Loiseleurieto-Arctostaphylion* in the systems of Nordhagen (1937) and Kalliola (1939) with the distinctness of

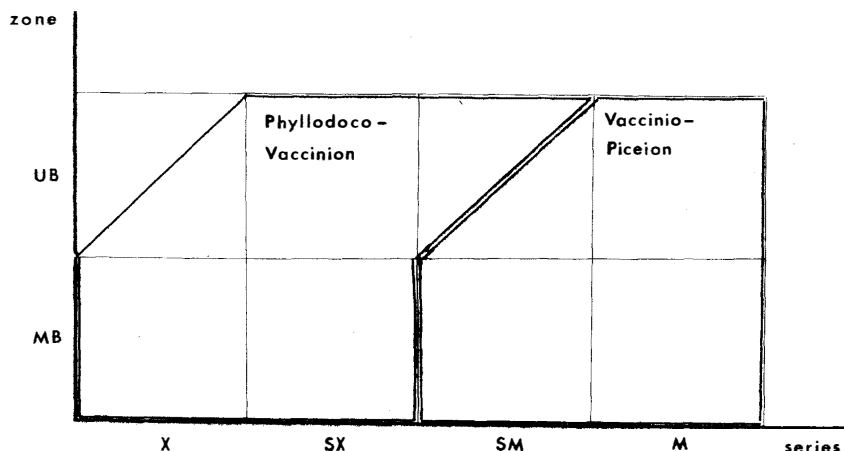


Fig. 57. Alliances in the system of Kielland-Lund (1967, 1971, 1973, 1981b), see also Dahl et al. (1967), relative to the two-gradient representation of the boreal vegetation. The alliance Dicrano-Pinion is omitted from the figure due to its sparse representation in the middle and upper boreal zones.

the ecological divide between areas with and areas without stable snow cover in winter. He correlated this limit with the nearly coincident upper borders of *Vaccinium myrtillus*, *Deschampsia flexuosa*, *Solidago virgaurea*, and *Trientalis europaea* towards the snowless crags and used these species to separate *Empetrium myrtillosum* from *Myrtillion*. The latter was divided according to zonal affinity.

The system of Kielland-Lund (1967, 1971, 1973, 1981) (see also Dahl et al. 1967) is shown in Fig. 57. Kielland-Lund (1967) following Braun-Blanquet et al. (1939) included high altitude birch and pine forests in the alliance Phyllodoco-Vaccinion of Nordhagen (1937). The associations Cladonio-Pinetum boreale and Barbilophozio-Pinetum lapponicae correspond to the middle and mostly also the upper boreal xeric and subxeric site-types (Fig. 57). Kielland-Lund (1962b, 1971, 1973, 1981) points out the close floristic connection between the spruce and birch forests corresponding to the poor submesic and mesic series and removed such birch forests from Phyllodoco-Vaccinion and included them in Vaccinio-Piceion. Vegetation referable to the alliance Dicrano-Pinion, represented by the association Vaccinio-Pinetum boreale (corresponding to the subxeric series) in South-Eastern Norway (cf. Kielland-Lund 1967, 1981) is only rarely met with in the middle and upper boreal zones and thus omitted from comparisons. Kielland-Lund (1967) recognizes *Juncion trifidi* as an alliance on its own.

The floristic basis of *Juncion trifidi*. Evidence from Grunningsdalen points in two directions. Both indices of

similarity show a higher degree of similarity for all taxocenes between the low and middle alpine xeric site-types and the low and middle alpine subxeric site-types than between site-types of the same zone (Figs 17-20). However, judging from these indices, the middle alpine submesic site-type is more similar to the middle alpine subxeric site-type than to its low alpine equivalent. Judged from the bottom layer alone, there is also a greater similarity between the middle alpine site-types of the subxeric and submesic series than between the two uppermost subxeric site-types. The hierarchical classifications of site-types (Figs 21, 22) confirm that the xeric and subxeric series are well-defined units in floristic terms, but that the submesic middle alpine site-type shows affinity to the subxeric series. This is due to the disappearance of many typical submesic species in the upper part of the low alpine zone, the strong decrease in importance of *Vaccinium myrtillus*, and the fact that the dominants of the drier series enter the middle alpine zone. The low similarity between the middle alpine xeric and submesic site-types, however, does not support the maintenance of a middle alpine Juncion trifidi. This is in accordance with Dahl (1957), who emphasized the gradual transition between the zones with species falling out one by one, and united the middle alpine communities with their low alpine equivalents as facies belonging to the same association.

The differentiation of *Loiseleurieto-Arctostaphylien* and *Phyllodoco-Vaccinion*. Subxeric vegetation is squeezed between the two alliances in the systems of Nordhagen (1937, 1943). Most of the differential species of *Loiseleurieto-Arctostaphylien* according to Nordhagen (1943) are distinctly chionophobous in Grunningsdalen. They are mainly restricted to the xeric series, and join GA-group 14 in the group-average classification of species (Fig. 36). *Juncus trifidus* enters the subxeric series sparsely in the upper boreal and low alpine zones, while *Arctostaphylos alpina* and *Loiseleuria procumbens* occur in the subxeric, but are lacking in the submesic series (Tab. 6). *Vaccinium myrtillus* and *Deschampsia flexuosa*, differential species for *Phyllodoco-Vaccinion*, were used to define the limit between the subxeric and the xeric series in Grunningsdalen. In our area there is a nearly complete negative association between chionophobous lichens on one hand and *Vaccinium myrtillus* and *Deschampsia flexuosa* on the other. In strongly continental areas *Cetraria nivalis* occurs sparsely in *Vaccinium myrtillus*-heaths (Du Rietz 1925a, 1931), and *Deschampsia flexuosa* very sparsely enters chionophobous vegetation (cf. three sample plots in Dahl 1957), causing some overlap. Among the other differential species, *Hieracium alpinum*, *Lycopodium alpinum*, *Solidago virgaurea*, and *Trientalis europaea* are mostly restricted to the submesic and mesic series in Grunningsdalen, *Phyllodoce caerulea* has only been observed in the subxeric series in the middle alpine zone, while *Alchemilla alpina*, *Gymnocarpium dryopteris*, *Luzula pilosa*, *Melampyrum sylvaticum*, and *Rumex acetosa* are all mesic species.

The results of numerical analysis (similarity indices, ordination and hierarchical classification) indicate that the subxeric series is floristically equally distinct as the xeric or submesic series. The inconsistencies resulting from using the differential species group for *Phyllodoco-Vaccinion*

proposed by Nordhagen (1943) to differentiate between phytocoena and the relative vegetational and ecological discontinuity at the xeric-subxeric limit give prevalence to Du Rietz's (1942) view.

The floristic basis of a boreal-alpine *Phyllodoco-Vaccinion*. In Kielland-Lund's system *Phyllodoco-Vaccinion* comprises site-types ranging from the middle boreal xeric to the low alpine submesic. Eight out of 11 possible character species for *Phyllodoco-Vaccinion* listed by Kielland-Lund (1967) are present in our material. None of these species show pronounced fidelity to the alliance in the Grunningsdalen area. Dahl et al. (1967) amend the list of character and differential species of the alliance. The differential species of the alliance, *Pohlia nutans*, *Cladonia squamosa*, and *C. uncialis*, are not restricted to the site-types included in *Phyllodoco-Vaccinion*, but have their optima in other site-types in the Grunningsdalen area. Kielland-Lund (1981) gives a list of ten species characteristic of the order *Cladonio-Vaccinietalia* (comprising *Phyllodoco-Vaccinion* as the major part). He further lists five character species for the alliance *Phyllodoco-Vaccinion* and two character species for the association *Barbilophozio-Pinetum*, the major representative of the alliance in the Grunningsdalen area. Of these 17 species 16 are present in our area. Their distributions on the site-types are shown in Figs 58-73. These figures show that in Grunningsdalen only *Pinus sylvestris*, *Dicranum polysetum*, and *Cladonia rangiferina*, and to some extent also *Cladonia arbuscula*, *Cladonia crispata*, *Leucobryum glaucum*, and *Vaccinium uliginosum* show some restriction to the syntaxa they are assumed to be characteristic of. Apart from the slightly higher occurrence of *Empetrum hermaphroditum* and *Dicranum fuscens* in the low alpine submesic site-type than in the other site-types of the submesic series, the occurrence of the character species of Kielland-Lund (1981) does not support the maintenance of a boreal-alpine *Phyllodoco-Vaccinion* in the way he proposes.

Neither ordination (Figs 24 and 26), similarity indices (Figs 17-20), nor hierarchical classification of site-types (Figs 21 and 22) show signs that the low alpine submesic site-type is floristically more related to the corresponding subxeric site-type than to the boreal submesic site-types. The only support for maintenance of a boreal-alpine *Phyllodoco-Vaccinion* as proposed by Kielland-Lund is the higher similarities in the bottom layer along the diagonal from lower left to upper right in the gradient reference frame (cf. Fig. 54).

Floristic evidence from Grunningsdalen supports the view that the low alpine submesic *Vaccinium myrtillus*-heaths are more closely related to *Vaccinium myrtillus*-dominated birch and spruce forests than to xerophilous pine forests. This is in favour of the system of Nordhagen (1937, 1943), and in accordance with a proposal by Rodvelt & Sekse (1980).

Justification of a *Eu-Piceetum* with wide circumscription. With the possible exception of sample plots 9-11 in Tab. 33 assigned to the middle boreal mesic site-type, all the boreal mesic sample plots belong to the subassociation *athyrietosum* of *Eu-Piceetum*. The boreal submesic site-types belong to the subassociation *myrtilletosum* in the same association in

Kielland-Lund's system. Recently Bjørndalen (1978, 1980a, 1980d) has questioned the wide circumscription of the association and criticized the maintenance of the tall fern types within the association (Bjørndalen 1980d).

The present material does not show higher similarity between the submesic and mesic than between other adjacent site-types in the boreal zones, with the exception of the upper boreal mesic and submesic site-types, showing a relatively high degree of COS X similarity (Figs 17 and 21). This points in favour of regarding the series as phytocoena of higher rank than subassociations. The large number of species with preference for one of the series (cf. Tab. 6) also supports this view.

Should the sub-alpine birch forests be classified with the vegetation of the alpine or the boreal zones? The important element of alpine plants in sub-alpine birch forests has often been used as an argument in favour of classifying birch forests with alpine vegetation (Du Rietz 1942, Nordhagen 1943, Bjørndalen 1977, 1978, 1980a, 1980d, Odland 1978, 1981c, Rodvelt & Sekse 1980). The opposite view is held by Kielland-Lund (1962b, 1967, 1973, 1981).

The Grunningsdalen material provides strong evidence for a floristic continuum in the forest-alpine transition within the xeric series. The most pronounced change in floristic composition occurs between the middle and upper boreal site-types where the alpine chionophobous species appear.

Similarity indices (Figs 17-20) and hierarchical classification of site-types (Figs 21, 22) provide evidence of a fully continuous intergradation between the middle boreal, upper boreal, and low alpine site-types within the three more mesic series. Thus in the Grunningsdalen area there is no reason, on a floristic basis, to prefer one of the two solutions. The high similarity between the upper boreal site-types and the site-types of adjacent zones within each series do not support a classification of the upper boreal site-types into a syntaxon of its own as in the system of Du Rietz (1942).

GENERAL CONCLUSION

Many, often strongly divergent systems for the phytosociological classification of the forest-alpine transition have been proposed. None of these systems are consistent with the classifications obtained by numerical analysis of the vegetation in the Grunningsdalen area.

In the general part of the present work it is shown that major variations in Southern Norwegian forest and alpine vegetation can be structured as responses to four environmental gradients. The variation in the quantitatively most important vegetation of the Grunningsdalen area is explained by two of the four gradients. We have given arguments in favour of considering the variation along each of the gradients as predominantly continuous with some relative discontinuities occurring.

MA	-	-	-	-
LA	-	-	-	-
UB	-	25-1	-	-
MB	100-4	53-3	-	-
	X	SX	SM	M

58 *Pinus sylvestris*

MA	83-1	75-1	25-1	-
LA	88-1	85-1	70-1	13-1
UB	100-2	100-2	38-1	8-1
MB	100-3	100-2	55-1	-
	X	SX	SM	M

59 *Cladonia rangiferina*

MA	67-1	100-2	75-1	40-1
LA	63-2	100-2	60-1	7-1
UB	100-3	100-2	-	-
MB	100-2	86-2	36-1	-
	X	SX	SM	M

60 *Cladonia arbuscula*

MA	-	-	-	-
LA	-	-	-	-
UB	-	25-1	-	-
MB	40-1	14-1	-	-
	X	SX	SM	M

61 *Dicranum polysetum*

MA	100-2	100-4	100-4	100-1
LA	88-1	100-4	100-2	67-1
UB	100-2	88-3	63-1	17-1
MB	100-1	86-2	73-1	-
	X	SX	SM	M

62 *Cetraria islandica*

MA	-	-	-	-
LA	-	-	-	-
UB	-	13-1	13-1	8-1
MB	-	27-1	9-1	17-1
	X	SX	SM	M

63 *Cladonia cornuta*

MA	-	-	13-1	-
LA	13-1	15-1	10-1	-
UB	-	-	25-1	-
MB	40-1	33-1	9-1	-
	X	SX	SM	M

64 *Cladonia crispata*

MA	83-1	88-1	88-1	30-1
LA	63-1	69-1	30-1	7-1
UB	33-1	50-1	-	8-1
MB	20-1	60-1	36-1	-
	X	SX	SM	M

65 *Cladonia gracilis*

MA	-	-	-	-
LA	-	8-1	-	-
UB	23-1	-	-	-
MB	-	20-1	-	-
	X	SX	SM	M

66 *Leucobryum glaucum*

MA	100-3	100-5	75-1	70-1
LA	100-3	100-5	100-3	60-1
UB	100-2	100-4	88-2	33-1
MB	40-1	93-2	82-1	-
	X	SX	SM	M

67 *Empetrum hermaphroditum*

MA	17-1	-	-	10-1
LA	100-1	77-3	90-3	60-3
UB	67-2	100-3	100-3	75-2
MB	-	93-3	55-2	-
	X	SX	SM	M

68 *Vaccinium uliginosum*

MA	100-2	100-1	-	-
LA	88-2	62-2	10-1	-
UB	100-3	50-2	-	-
MB	100-4	20-1	-	-
	X	SX	SM	M

69 *Cladonia stellaris*

MA	-	-	-	10-3
LA	-	-	30-1	7-1
UB	-	25-2	13-3	-
MB	-	33-1	18-2	-
	X	SX	SM	M

70 *Sphagnum nemoreum*

MA	-	38-1	25-1	-
LA	25-1	38-1	60-1	27-1
UB	-	13-1	13-1	17-1
MB	-	53-1	9-1	25-1
	X	SX	SM	M

71 *Dicranum fuscescens*

MA	-	-	-	-
LA	-	-	-	-
UB	-	-	-	-
MB	-	-	18-1	18-1
	X	SX	SM	M

72 *Barbilophozia attenuata*

MA	17-1	100-1	100-2	100-3
LA	-	77-1	80-3	93-3
UB	-	50-1	75-4	82-2
MB	-	86-3	51-4	67-1
	X	SX	SM	M

73 *Barbilophozia floerkei*

A hierarchic classification in a continuum cannot do justice to the natural conditions (Gams 1918, Nordhagen 1928, Kalela 1939, 1960, Tuomikoski 1942, Sjörs 1947, 1948, Cain 1947, Whittaker 1962), because by turning a network of multidimensional relationships into a hierarchy one loses information (Goodall 1978b) owing to the unidimensionality of hierarchy (Kalliola 1939). If one erects a phytosociological hierarchy for the investigated area, it seems most appropriate to follow the recommendations of Tuomikoski (1942: 74). If one wants to turn a system of multidimensional relationships into a hierarchy, this can be done by ranking the directions of variation instead of considering them as being of equal value. Furthermore, the directions of variation are divided into classes. The direction of variation giving the most sharply delimited classes is proposed to be taken as the first one. - Application of these principles to the vegetation of the Grunningsdalen area suggests taking the complex-gradient topographic moisture-snow cover as the first criterion, considering each of the series as syntaxa of equal rank. In the alpine zones it is normally necessary to consider mesic and snow-bed series in the narrow sense separately. The floristic turnover in response to the vertical gradient is less strong than along the moisture-snow cover gradient, suggesting that the vertical gradient may be used to divide the series into syntaxa in a way that makes each site-type an independent syntaxon of lower rank. Thus one obtains the gradient reference frame for the most important vegetation of the Grunningsdalen area (cf. Fig. 6). In our opinion the direct gradient approach is shown to be a most useful method for describing major variation in vegetation on a local scale.

If the hierarchical approach is not restricted to a small area, new problems are added. The second regional gradient, degree of oceanicity, represents a new source of continuous variation. Tabs 40, 42, and 44 show a pattern of species distributions along this gradient that is somewhat intermediate between a continuous series of overlapping areas and an assembly of individualistic, partly irregular, distributions. In addition, the autecology of a species varies from one part of the distributional area to another owing to ecotypic differentiation. A lot of species have different amplitudes along the moisture gradient at different points along the oceanicity gradient (cf. also Böcher 1938, 1954). Consequently, "communities" defined as relatively homogeneous units may have merely local validity (Cain 1947). The different responses of different species to the environmental gradients necessarily

Figs 58-73. Constancy percentage and characteristic degree of cover for some character species of Kielland-Lund (1981b) in each of the site-types in the Grunningsdalen area. The approximate extension of the syntaxa in the two-gradient representation of the studied vegetation is shown. Figs 58-66. Character species of the order Cladonio-Vaccinietalia. Figs 67-71. Character species of the alliance Phyllodoco-Vaccinion. Figs 72-73. Character species of the association Barbilophozio-Pinetum.

imply that, when the area is increased, a hierarchic system "becomes more and more divorced from reality and will be in still greater danger of becoming a useless end in itself" (Kalela 1960: 42, cf. also Gleason 1926, Nordhagen 1928, Kalela 1939, Cain 1947).

In our opinion the multidimensional structure of vegetation makes all approaches involving classification artificial, because they involve drawing boundaries in a basically continuous environment with its correspondingly more or less continuous vegetation. The numerous classificational approaches that have been, and are still in use, for the understanding of the structure of vegetation are per se a proof that no single correct classification exists. It thus does not seem profitable for vegetation ecology, as a branch of science, that so much effort is spent on discussions concerning details of classifications. Such discussions actually lead away from the real task of vegetation ecology - to understand the relationships between vegetation and environment. At this point we must emphasize the urgent need for integrated studies treating variation in vegetation and ecological factors simultaneously, without attaching too much importance to either component of the ecosystem.

Strong demands for the standardization of phytosociological approaches have been put forward at various times by supporters of the Braun-Blanquet approach (e.g. Barkman 1953, Barkman et al. 1976, Kielland-Lund 1980). The Braun-Blanquet approach involves hierarchic classification and the setting-up of systems proposed valid over vast areas as two of its fundamental tenets. This is not consistent with the view that vegetation is a complex, multidimensional network of variation (cf. Whittaker 1962, 1978b, McIntosh 1967). Therefore we cannot agree with those proposing one of the approaches to vegetation as having prevalence (cf. also Cain 1947, Fægri 1953, Webb 1954). The recommendation of Nordhagen (1920, 1924, 1928, 1937, 1943) that phytosociological classification must always be considered a tool, not a goal in itself, should be remembered. Furthermore, each investigator must be free to choose a method according to his own preference and the aims of the study - the suitability of different approaches is dependent on the purpose of the study (Webb 1954, Whittaker 1962). Finally, it should be emphasized that classification is an important and necessary means of structuring variation. However, we will repeat the words of Webb (1954: 370), that to choose one approach and "declare that this is the one and only system of classification and to seek to have it imposed by international authority - this surely is not science but scholasticism out of place".

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