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Epiphytic vegetation on pollarded trunks of *Fraxinus excelsior* in four different habitats at Grinde, Leikanger, western Norway

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Abstract

The epiphytic vegetation on 24 pollarded trees of *Fraxinus excelsior* at the farm Grinde, Leikanger, western Norway was investigated. Each trunk was divided into a basal zone, a middle zone and a top zone. In each zone the four different aspects were analysed (12 sampling units from each trunk). Within a total of 276 sampling units, 162 taxa were recorded (99 lichens, 56 bryophytes, 7 vascular plants). The trunks were covered mainly by an old, thick and occasionally swollen bark, but decaying wood did not occur. Their habitats were different, and each trunk was classified into one of four categories: open meadow, wooded hay meadow, deciduous wood, and spruce plantation. A climate station was established in each habitat to measure important parameters. The floristic and environmental data were analysed by canonical correspondence analysis (CCA). The floristic data were classified into eight TWINSPAN groups that have been taken into account in the CCA diagrams. At Grinde all the pollarded trunks grew under fairly homogeneous conditions during a more extensive agricultural period until about 1962. The deciduous wood developed by tree colonization on old meadows and wooded hay meadows, whilst spruce has been planted in a small part of the area. Floristic differences in the epiphytic vegetation between the four different habitats were found, which suggests that changes in the vegetation have developed during the last two or three decades. The spruce plantation was the most shady habitat having a very sparse epiphytic vegetation, mainly remnants from vegetation established during more open area conditions.

Introduction

In western Norway pollarded trees are very common in the cultural landscape and in some types of deciduous woodland. This reflects the importance of the practice of chopping twigs and leaves for winter fodder in this district (Austad 1988). However, during recent decades this practice has almost totally ceased, and pollarded trees are now disappearing. The aging tree trunks are weakened by heavy branches, and they are not being replaced by young, pollarded trees. Their habitat, namely open or semiopen fields, is being taken over by deciduous-tree growth which establishes a shadier habitat (Austad & Skogen 1990). Spruce plantations and modern forestry are also responsible for the deterioration of the habitats and the subsequent disappearance of old pollarded trees. Changes in the habitats, especially with respect to an increasing area of woodland, may have an influence on the pollarded trunks in different ways, and an interesting question is whether their epiphytic vegetation will respond to these changes? According to Olsson (1995), denser canopies will bring about significant changes in the epiphytic vegetation. Epiphytic bryophytes and lichens are known to be sensitive to microclimatic variations (Hoffman & Kazmierski 1969).

This paper considers the epiphytic vegetation on pollarded trunks growing under different ecological conditions, with particular emphasis on floristic differences caused by the reduction of traditional managements. A specific cultural landscape with pollarded trees growing in clearly defined habitats was investigated. The epiphytic vegetation was studied at different heights on the trunks to see whether it shows differences between the lower and upper parts.

The management and preservation of the pollarded trees represent a long continuous period of perhaps several hundred years. The huge boles provide habitats for many slowly colonizing epiphytes (Rose 1992). Investigations in Great Britain and Sweden have shown that pollarded trees may have a variety of different ecological niches providing a particularly favourable habitat for lichens (Andersson & Johansson 1984; Nilsson et al. 1994; Rose 1992). Several rare lichen species were reported from pollarded ash trunks in old cultural landscapes in the oceanic region of western Norway (Moe & Botnen 1997; Tønsberg 1994). The epiphytes on pollarded trees therefore contribute greatly to the biodiversity of the old cultural landscape.

The aims of this study are (1) to contribute to a more detailed knowledge of the epiphytic flora on old deciduous trees, (2) by using multivariate data analysis, to describe the floristic variation in the epiphytic vegetation on pollarded trunks of *Fraxinus excelsior* in four different habitats on the farm Grinde, and (3) to relate the floristic variations and the ecological conditions of the tree boles to environmental variables measured within the four different habitats.

Methods

The study area

The farm Grinde (61°12′ N, 6°44′ E) is situated on the northern side of the Sognefjord in Leikanger municipality, Sogn og Fjordane county, western Norway (Figure 1). Topographically, Grinde is situated on an east-facing slope above the river Grindselva in the valley Grindsdalen, and the distance to the fjord below is about 1 km. The distance from the coastline of western Norway is 115 km, and hence Grinde belongs to the middle region of the Sognefjord. The climate is transitional between a fairly oceanic type towards the west of the fjord and a more continental type towards the east. The annual precipitation is 1000 mm (Utaaker 1979). January is the coldest month (mean temperature −0.6 °C), and July the warmest (16.0 °C). The mean monthly temperature during the year is 7.0 °C (period 1931–1960). The bedrock consists of a migmatitic gneiss (Sigmond et al. 1984).

The size of the investigated area is approximately 0.15 km^2. The fields of the farm slope fairly steeply, from 230 to 50 m a.s.l., and the farm house is situated at 140 m in the southern part of the area. The fields have been managed in a traditional way with haymaking, grazing, and manuring until about 1962. Later such use of the land has been reduced and restricted to the meadows surrounding the farm house. The lower part of the fields consisted of wooded hay meadows maintained by pollarding and grazing. The trees were chopped every fourth or fifth year, but today since pollarding ceased around 1972, the canopies of the trees have become large and heavy (cf., Austad & Losvik 1998).

The fields in the northern part of the farm have been colonized by trees, mainly *Alnus incana*, *Betula pubescens* and *Sorbus aucuparia* to form deciduous woodland. These trees are mainly younger than 40 years. Above this woodland a part of the field was planted with *Picea abies* in 1962. Pollarded trees, mainly *Fraxinus excelsior* and *Ulmus glabra*, are common all over the farm, and depending on the use of the land during the last decades, they now grow under different ecological conditions. The sites that the investigated pollarded trees belong to, can be classified into four habitats: open meadow, wooded hay meadow, deciduous wood and spruce plantation (Figures 1 and 2).

In order to eliminate floristic variations caused by different bark substrates (cf., Bates & Brown 1981), only one porophyte species, *Fraxinus excelsior*, was investigated. The ash trunks are old, some of them probably more than 300 years, while others may be much younger. Different ages are randomly distributed all over the area, and most of the trees appear to have passed the period of extensive growth. Therefore the trunks have principally an old thick bark with a rather rough texture which is important for water retention (Adams & Risser 1971; Culberson 1955; Harris 1971a; Pitkin 1975). Decaying wood does not occur, but some of the trunks include fissures and swollen bark, and on this surface the bark may collect accumulations of dust containing nutrients (Gauslaa 1985; Hoffman & Boe 1977).

Vegetation sampling

A total of 24 pollarded ash trunks were investigated, representing the four different habitats mentioned above. These habitats represent a gradient from open meadow to dense wood. The total epiphytic vegetation was analysed at different heights and from different aspects around the trunks. Each tree was divided into

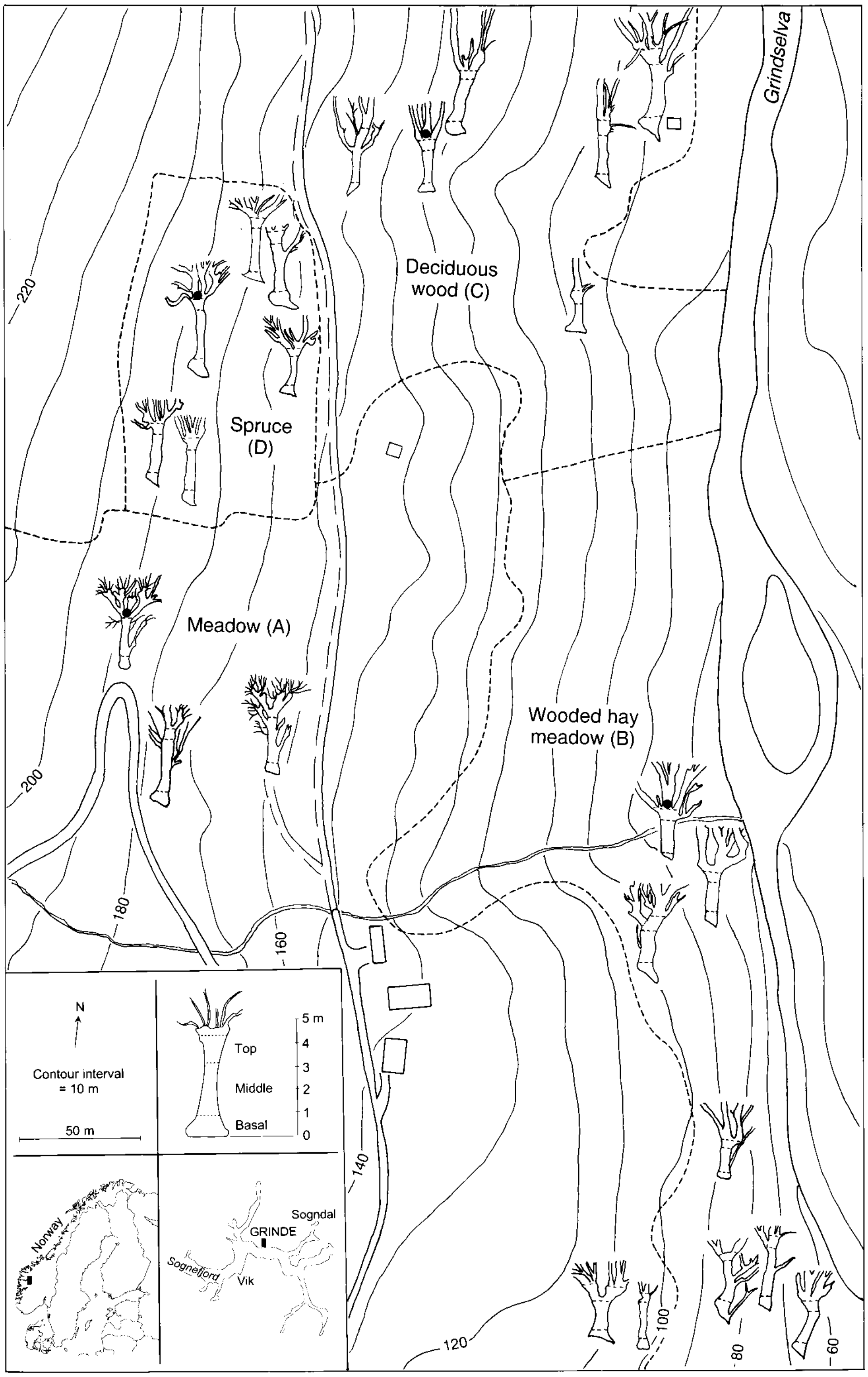

Figure 1. Map showing the study area Grinde and the positions of the investigated ash trees in the four habitats meadow (A), wooded hay meadow (B), deciduous wood (C) and spruce plantation (D). The shapes, widths and heights, and the three vertical zones (basal, middle and top) on the trunks are indicated. Dots show the positions of the climate stations.

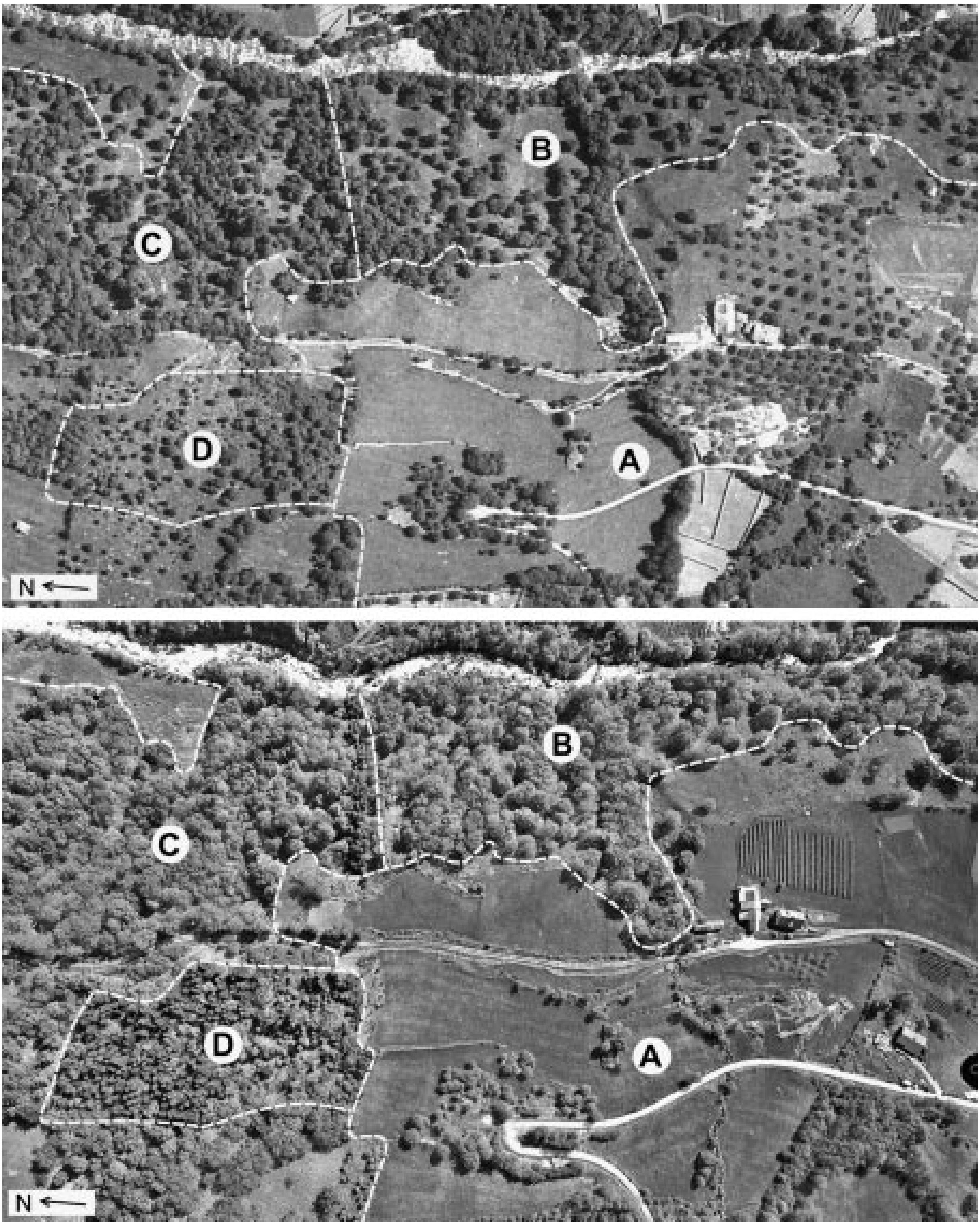

Figure 2. These two aerial photographs show the farm Grinde in the years 1963 (upper), and 1992 (lower). The four different habitats (A–D) are separated by dashed line (compare with Figure 1). Denser canopies and more woodland have developed due to reduction of traditional managements.

a basal zone (the lowest part nearest the ground), a middle zone (the central part of the trunk), and a top zone (the part just below the pollarded branches) (Figure 3). Epiphytes from the branches were not included in the study. The trees at Grinde are characterized by a high pollarding level between 2.5 and 4.5 m above the ground, and the branches were often chopped in different levels which give the tree a candelabre shape.

In each zone the four different aspects are analysed by squares, and 12 sampling units (SU) represent each trunk. From three trunks the top zone could not be separated from the middle zone, and hence squares from these top zones were not analysed. A total of 276 SU were collected to represent the epiphytic vegetation on these 24 trunks. The epiphytic species recorded are bryophytes, lichens and vascular plants, and the percentage cover of each species was estimated. The cover of bare bark was also noted. Due to the different shape and height of the trunks, the squares were irregular with a size varying from 0.02 m^2 to 0.95 m^2.

Nomenclature follows Santesson (1993) for lichens, Frisvoll et al. (1995) for bryophytes and Lid & Lid (1994) for vascular plants. Field work on the vegetation sampling was done between 1991–1994.

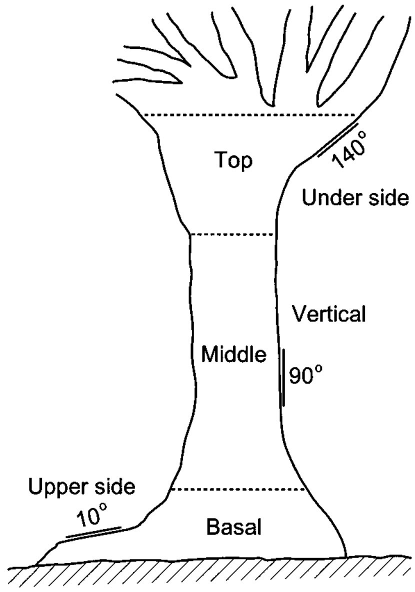

Figure 3. The 24 ash trunks were divided into a basal zone, a middle zone and a top zone. The principle for measuring the stem inclination is indicated: lowest and highest angles were 10° and 140°, respectively.

Environmental variables

For each SU several environmental variables were recorded. The altitudes (between 65 and 190 m) were measured by an altimeter. The inclination of the SU on the trunk and the four different aspects (south, east, west, north) were measured by a clinometer compass. The vertical position is 90°, lower values represent the upper side of the trunk, while higher values represent the under side. The inclination varies from 10° to 140° (Figure 3).

According to the positions of the trunks in the field, each of the SU were assigned to one of the four previous described habitats (with abbreviations used in the diagrams): meadow (mead), wooded hay meadow (whm), deciduous wood (dwood) and spruce plantation (spruce). In an attempt to separate these habitats ecologically, a climate station was established in each of them to measure important parameters (their positions are shown in Figure 1). Since the size of the area is small, and the habitats are well-defined (Figure 2), all the SU from a given habitat share a single climate station. The measurements were done every hour (24 times a day) during 53 days in the early growing season (the period 9 May to 30 June, 1997). The values from these measurements were used to express the local climate in each SU that belongs to the respective habitats. The following four parameters were included in the data set: maximum temperature (T_{max}) is the mean value (°C) of the highest temperature measured each day, minimum temperature (T_{min}) is the mean value (°C) of the lowest temperature measured each day (mainly the night temperature), the relative humidity is the daily mean value (%) of the whole period, and light intensity is expressed as the daylight radiation ($W\ m^{-2}$), viz. the amount of eight measurements each day in the time between 0930 a.m. and 1630 p.m.

Data analysis

The species data were classified by TWINSPAN version 2.1 a (Hill 1979, modified by C. J. F. ter Braak and H. H. B. Birks). Six pseudospecies (1–6) were used with cut levels 0, 2, 6, 16, 31, and 61, respectively, for the per cent data. CANOCO 3.12 (ter Braak 1987, 1990) was used for all ordinations. The plots were drawn by CANODRAW 3.0 (Smilauer 1993). Rare species were downweighted. Direct gradient analysis, canonical correspondence analysis, CCA, was performed in order to examine the relationships of the floristic composition to the environmental variables. In order to eliminate the effect caused by the different sizes of the squares, this parameter was used as covariable in the CCA ordinations (Jongman et al. 1987).

Results

The epiphytic vegetation data consist of 162 taxa: 99 lichens (49 foliose and fruticose lichens and 50 crustose lichens), 56 bryophytes (46 mosses and 10 hepatics), and 7 vascular plants. Some of the lichens were not identified to species level because the material was too scanty, and the genus name indicated may include the same species as those which have been identified. The real number of lichen taxa may therefore be less than 99.

TWINSPAN classification

The 276 SU were classified into eight TWINSPAN groups (Figure 4). The third level of division separates group A1 characterized by *Collema furfuraceum*, *Orthotrichum obtusifolium*, and *Physconia distorta* from group A2 characterized by *Frullania dilatata* and *Physcia tenella.* Group A3 is characterized by *Porella platyphylla* and abundant *Leucodon sciuroides*, and group A4 by *Cladonia* spp., *Hypnum cupressiforme, Lecidella elaeochroma, Pterigynandrum filiforme*, and *Radula complanata.* Group B1 is characterized by *Acrocordia gemmata*, *Zygodon rupestris*, and abundant *Leucodon sciuroides* and group B2 is characterized by abundant *Hypnum cupressiforme* and abundant *Pseudoleskeella nervosa.* Group B3 has *Isothecium alopecuroides, Plagiomnium cuspidatum*, abundant *Hypnum cupressiforme* and *Radula complanata* as indicators whereas group B4 has *Frullania dilatata, Lecidella elaeochroma* and *Leucodon sciuroides.*

In the eight TWINSPAN groups the species have been assigned to five constancy classes, where species that occur in less than 20.0% of the SU are assigned to class I, 20.1–40.0% in class II, 40.1–60% in class III, 60.1–80% in class IV, and more than 80.1% in class V. The species are arranged into the eight groups with constancy classes and mean percentage cover (Table 1). Species in constancy classes IV and V are termed *constants*, and those with a mean cover of more than 7% in a group are called *dominants* if the constancy class is II or higher. Only a few species are strictly limited to a single group, but several species attain an optimum as faithful to one of the groups (cf., Phillips 1959). A *faithful* species is defined here as those epiphytes that occur in only one group with a constancy class II or higher, or those that occur in several groups but have a constancy class at least two levels higher in one group (the one it is faithful to) than in the others (Jonsgard & Birks 1993). Species in constancy class I and lowest cover are referred to as *occasional.*

Group A1. Physconia enteroxantha –
Orthotrichum obtusifolium *group*

The 11 SU in this group are present on three trunks from the meadow (9 SU) and the wooded hay meadow (2 SU). On the tree bole 1 SU is from the basal, 9 from the middle, and 1 from the top zone. The total number of species in this group is 59, of which 26 are occasional. In this group lichens are characteristic, especially the constant and dominant species *Lecanora subfusca* and *Lecidella elaeochroma.* Faithful species in the group are *Collema furfuraceum*, *Physconia distorta*, *P. enteroxantha* and *Orthotrichum obtusifolium.* The lichen species *Bacidia circumspecta*, *B. hegetschweileri*, *Ochrolechia pallescens*, *Physconia perisidiosa*, *Rinodina sophodes* and *Usnea* sp. occur only in this group. The species in group A1 are mainly obligate epiphytes and there are many photophilous species that avoid the shady habitats.

Group A2. Physcia tenella –
Orthotrichum lyellii *group*

The 30 SU are from five trunks in the meadow (15 SU) and in the wooded hay meadow (15 SU). On the bole 18 SU are from the middle, 11 from the top and 1 from the basal zone. The total number of species is 68, of which 24 are occasional. *Bacidia rubella*, *Leucodon sciuroides* and *Melanelia fuliginosa* are both dominant and constant species. The faithful species are *Arthonia radiata*, *Lecania cyrtella*, *Lecanora carpinea* and *Physcia tenella.* The lichen species *Candelaria concolor* and *Rinodina colobina* occur only in this group.

Group A3. Leucodon sciuroides –
Porella platyphylla *group*

The 48 SU are from 15 trunks in the meadow (11 SU), wooded hay meadow (27 SU), and in the deciduous wood (10 SU). On the bole 6 SU are from the basal, 14 from the middle, and 28 from the top zone. The total number of species is 80, of which 37 are occasional. *Leucodon sciuroides* is very important occurring in all of the squares with an extremely high cover (mean value 51.4%). *Porella platyphylla* is another constant and dominant species. *Catillaria* sp., *Orthotrichum*

Table 1. The recorded species from the 24 ash trunks, arranged in order of occurrence in the eight TWINSPAN groups. Five constancy classes (I–V) and the mean cover percentage are given on each group.

	TWINSPAN GROUP								
	A1	A2	A3	A4	B1	B2	B3	B4	
OCHR PAL	I 2.0								*Ochrolechia pallescens*
RINO SOP	I 1.0								*Rinodina sophodes*
BACI CIR	I 1.0								*Bacidia circumspecta*
BACI HEG	I 1.0								*Bacidia hegetschweileri*
USNE SP.	I 1.0								*Usnea* sp.
PHCO PER	I 1.0								*Physconia perisidiosa*
XANT SP.	III 1.2	III 1.0	I 1.5						*Xanthoria* sp.
XANT PAR	I 1.0	I 1.3	I 1.0						*Xanthoria parietina*
COLL OCC	I 1.0	I 1.0	I 1.0						*Collema occultatum*
BUEL PUN	I 1.0	I 1.0	I 1.0						*Buellia punctata*
PHCO DIS	V 6.0	II 3.7	I 6.0	I 2.0					*Physconia distorta*
BACI NAE	I 1.0	I 1.0	I 1.0	I 1.0					*Bacidia naegelii*
ARPY SP.	I 1.0	I 1.0	I 1.0	I 1.3					*Arthopyrenia* sp.
PHYS ADS	II 1.0		I 1.0						*Physcia adscendens*
CALO CHL	II 1.0		I 3.0	I 1.0					*Caloplaca chlorina*
ARTH PUN	I 2.0			I 1.0					*Arthonia punctiformis*
ULOT CRI	I 1.0	I 1.0		I 1.0					*Ulota crispa*
PHYS AIP	IV 2.5	III 1.6		I 1.0					*Physcia aipolia*
CAND CON		I 1.0							*Candelaria concolor*
RINO COL		I 1.0							*Rinodina colobina*
LECI SPP.		I 2.0							*Lecidella* spp.
MELA SUB		II 3.1	I 1.0						*Melanelia subargentifera*
MELA EXA		I 2.0	I 1.0						*Melanelia exasperata*
EVER PRU		I 1.0		I 1.0					*Evernia prunastri*
ORTH GYM			I 1.0						*Orthotrichum obtusifolium*
PHAE CIL			I 1.0						*Phaeophyscia ciliata*
CATI NIG			I 1.0						*Catillaria nigroclavata*
LEPR RIG			I 1.0	I 1.0					*Lepraria rigidula*
PERT LEI			I 1.0	I 1.0					*Pertusaria leioplaca*
HYPO TUB				I 1.0					*Hypogymnia tubulosa*
BACI BEC				I 1.0					*Bacidia beckhausii*
LEPR ELO				I 1.0					*Lepraria elobata*
PANN CON				I 1.5					*Pannaria conoplea*
PANN IGN				I 1.5					*Pannaria ignobilis*
PANN RUB				I 1.0					*Pannaria rubiginosa*
PACH FAG	II 1.0	I 1.0			I 1.0				*Pachyphiale fagicola*
PHYS TEN	I 1.0	V 1.1	I 1.0		I 1.0				*Physcia tenella*
ORTH SPE	I 1.0	I 1.0				I 1.0			*Orthotrichum speciosum*
LEPT TER	I 1.0	I 1.0	I 1.0		I 5.5	I 1.0			*Leptogium teretiusculum*
COLL SUB	I 1.0	I 3.0	I 1.0		I 1.0	I 1.0			*Collema subflaccidum*
PHYS DUB	II 1.0		I 1.0	I 1.0		I 1.0			*Physcia dubia*
CALO FLA	V 3.3	V 4.0	I 1.6	II 1.0	I 1.0				*Caloplaca flavorubescens*
PHCO ENT	IV 3.3	I 1.0	I 1.0	I 2.0			I 1.0		*Physconia enteroxantha*
LECA CAR	II 1.3	IV 1.6	I 1.3	II 1.2	I 1.0		I 1.0		*Lecanora carpinea*
CANL XAN	V 1.0	III 1.0	II 1.0	I 1.0		I 1.0	I 1.0		*Candelariella xanthostigma*
LECA SUB	V 7.9	V 3.6	II 1.2	III 1.7		I 1.0	I 4.3		*Lecanora subfusca coll.*
COLL SPP.	I 1.0	II 1.5	I 1.3	I 1.0		I 1.0	I 2.0		*Collema* spp.
PHAE ORB	IV 2.6	IV 5.4	I 1.0	II 1.0	I 1.0	I 1.0	I 1.0		*Phaeophyscia orbicularis*
ORTH OBT	V 2.2	III 1.2	III 1.5	I 1.0	I 1.0	I 1.0	I 1.0		*Orthotrichum obtusifolium*
BRYU CAP	I 1.0	I 1.0	I 1.0	I 1.3	II 3.3	II 2.1	I 1.0		*Bryum capillare*
MELA FUL	IV 3.1	V 9.6	II 2.2	III 2.0	I 1.0	I 1.0	I 1.0		*Melanelia fuliginosa*
PHYS SP.	I 2.0	II 1.6	I 1.2	I 1.0	I 1.0		I 1.0	I 1.0	*Physcia* sp.
PERT SP.	I 1.0	I 1.0	I 1.0	II 1.2				I 1.0	*Pertusaria sp.*
ARTH SP.	I 1.0		I 1.0	I 1.3			I 1.0		*Arthonia* sp.
COLL FUR	V 1.9		I 1.5	I 2.2			I 1.0		*Collema furfuraceum*
SCHI APO	I 1.0		I 1.0	I 1.0		I 1.0	I 1.0		*Schistidium apocarpum*
PARM SAX	I 5.0	I 1.0		I 2.3			I 5.5		*Parmelia saxatilis*

Table 1. Continued.

	TWINSPAN GROUP								
	A1	A2	A3	A4	B1	B2	B3	B4	
LECI FLA	I 1.0	I 1.0		I 1.0			I 1.0		*Lecidella flavosorediata*
CALO SPP.	II 1.0	I 1.0	I 1.0		I 1.0		I 1.0		*Caloplaca* spp.
PARM SUL	IV 4.6	III 2.6	I 2.0	II 2.4		I 1.0	I 1.0	II 2.4	*Parmelia sulcata*
OCHR TUR	II 1.5	II 6.0	I 6.0	I 1.0	I 1.0	I 2.0	I 1.0	I 4.5	*Ochrolechia turneri*
LECI ELA	V 10.8	V 5.8	III 1.4	V 5.5	I 1.3	I 3.6	II 4.1	IV 4.6	*Lecidella elaeochroma*
PLAM CUS	I 1.0	I 1.0	I 1.0	I 1.0	I 7.3	III 2.6	III 4.5	I 1.0	*Plagiomnium cuspidatum*
PORE PLA	I 1.0	III 4.6	IV 7.1	I 2.0	V 11.9	V 14.6	I 1.3	I 1.0	*Porella platyphylla*
HYPN CUP	I 11.5	II 9.1	II 3.6	V 7.6	IV 3.8	V 19.0	V 14.8	V 4.8	*Hypnum cupressiforme*
PSEU NER	II 3.0	I 1.4	IV 2.7	IV 5.0	V 2.3	IV 14.2	IV 4.4	III 2.2	*Pseudoleskeella nervosa*
PELT COL	I 1.0	I 2.0	I 1.8	II 3.1	I 2.0	II 6.2	II 5.4	I 2.0	*Peltigera collina*
BACI RUB	IV 1.4	V 9.3	V 1.7	V 3.2	IV 2.0	IV 1.2	II 3.2	II 1.7	*Bacidia rubella*
FRUL DIL	II 1.3	V 5.7	V 2.7	V 8.6	V 3.9	IV 3.3	III 2.1	V 1.1	*Frullania dilatata*
LEPT SAT	IV 1.0	IV 1.4	II 1.4	III 1.5	III 1.1	II 1.5	I 1.0	I 1.0	*Leptogium saturninum*
LEUC SCI	V 9.5	V 19.1	V 51.4	V 21.2	V 40.5	V 12.9	III 12.8	V 5.3	*Leucodon sciuroides*
ORTH LYE	V 3.1	V 4.6	IV 2.5	V 3.2	II 1.0	II 1.6	I 2.8	I 1.0	*Orthotrichum lyellii*
ORTH STM	IV 5.6	V 4.3	IV 2.8	IV 1.8	I 1.0	II 1.1	I 1.0	I 1.0	*Orthotrichum stramineum*
ORTH STT	V 3.4	V 3.9	II 1.6	II 1.7	I 1.0	I 1.0	I 1.0	I 1.0	*Orthotrichum striatum*
COLL FLA	I 1.0	II 1.7	II 2.8	I 1.0	III 2.2	III 5.1	I 10.0	I 1.0	*Collema flaccidum*
PTER FIL	I 1.0		I 1.3	III 1.9	I 1.0	I 2.7	III 3.9	IV 2.5	*Pterigynandrum filiforme*
GYAL TRU		I 1.0	I 1.0	I 1.0	I 1.0				*Gyalecta truncigena*
ARTH RAD		III 1.0	I 1.0	I 1.0	I 1.0	I 1.0			*Arthonia radiata*
LENI CYR		III 1.0	I 1.0	I 1.0	I 1.0	I 1.0			*Lecania cyrtella*
SYNT RUR		I 1.5	I 2.8	I 1.8	IV 4.4	III 4.9			*Syntrichia ruralis*
LAUD ACR		I 1.0		I 1.0	II 2.0	I 1.0			*Lauderlindsaya acroglypta*
OCHR SP.		I 3.0			I 3.0	I 2.0			*Ochrolechia* sp.
EURH HIA		I 1.0			I 1.0	I 1.0			*Eurhynchium hians*
OPEG SP.		II 4.1	I 1.0	I 1.0			I 1.0		*Opegrapha* sp.
HOMT SER		I 1.3	I 1.0	I 2.0	I 1.0		I 2.0		*Homalothecium sericeum*
HOMA TRI		I 1.0	I 4.8	I 30.0	I 5.0	II 7.0	I 1.5		*Homalia trichomanoides*
OPEG RUF		II 4.9	I 10.6	II 10.7	I 6.7	I 7.4	I 2.9		*Opegrapha rufescens*
PORE COR		I 1.5		I 1.0		II 7.7	I 3.0		*Porella cordaeana*
LEPO SP.			I 1.0		I 5.0				*Leproloma* sp.
PERT COR			I 1.0		I 1.0		I 1.5		*Pertusaria coronata*
NEPH RES			I 2.0	I 5.5		I 1.0	I 6.0		*Nephroma resupinatum*
PLAM UND			I 1.0	I 1.0		II 2.0	I 1.8		*Plagiomnium undulatum*
PHLY ARG			I 4.0	I 5.0			I 2.5		*Phlyctis argena*
ORTH AFF			I 1.0	I 1.0			I 1.0		*Orthotrichum affine*
ISOT ALO			I 3.7	I 2.0	I 10.5	I 9.0	IV 27.4		*Isothecium alopecuroides*
NEPH LAE			I 6.3	I 6.7	I 10.5	I 5.3	I 2.0		*Nephroma laevigatum*
LEPT LIC			I 1.0	I 1.0	IV 2.2	II 7.2	I 1.8		*Leptogium lichenoides*
POHL CRU				I 1.0	I 1.0	I 1.0			*Pohlia cruda*
LOBA SCR				I 1.5			I 1.0		*Lobaria scrobiculata*
CLAD CON				I 2.0		I 1.0	I 1.7		*Cladonia coniocraea*
GRIM SP.				I 1.0		I 1.0	I 1.0		*Grimmia* sp.
PELT PRA				I 3.0		I 3.0	II 13.1		*Peltigera praetextata*
ISOT MYO				I 1.0	I 1.0	I 5.0	I 1.5		*Isothecium myosuroides*
OXAL ACE				I 1.0	I 1.0	I 1.0	I 1.3		*Oxalis acetosella*
ANOM ATT				I 1.0	I 1.0	I 3.0	I 1.5		*Anomodon attenuatus*
LECA SPP.		I 1.8	I 1.5	I 1.0		I 1.0	I 1.0	I 1.0	*Lecanora spp.*
COLL NIG		I 2.0	I 2.8	II 1.9		I 1.0	I 1.3	I 1.3	*Collema nigrescens*
RADU COM		I 1.5	II 1.1	IV 1.6	IV 2.1	III 1.2	V 3.7	II 1.1	*Radula complanata*
LEPR LOB		I 1.0	I 2.6	III 2.4	IV 3.7	II 3.8	III 4.7	IV 1.7	*Lepraria lobificans*
ACRO GEM		I 1.0	II 3.2	II 2.0	IV 8.5	I 2.0	II 5.0	I 1.5	*Acrocordia gemmata*
ZYGO RUP			I 1.0		III 3.0	I 4.0	I 1.0	I 1.0	*Zygodon rupestris*
CLAD SPP.			I 1.0	III 1.1	I 1.0	I 1.0	II 1.3	II 1.2	*Cladonia* spp.
NEPH PAR			I 1.7	III 2.7	II 1.9	I 2.3	II 2.8	II 1.2	*Nephroma parile*
PALA TRI			I 3.5	I 5.3		I 1.0	I 5.0	I 1.0	*Parmeliella triptophylla*

Table 1. Continued.

	TWINSPAN GROUP								
	A1	A2	A3	A4	B1	B2	B3	B4	
DEGE PLU			I 5.0	I 1.3				I 1.0	*Degelia plumbea*
BIAL MON				I 1.0	I 1.0	I 1.0		I 3.0	*Biatorella monasteriensis*
PARA LON				I 1.0		I 1.0	I 1.0	I 1.0	*Paraleucobryum longifolium*
PANN SP.				I 1.0				I 1.0	*Pannaria* sp.
METZ FUR				I 1.0	I 1.5	I 1.0	II 3.9	I 1.0	*Metzgeria furcata*
THUI DEL				I 1.0	I 1.0	I 2.0	I 2.8	I 1.0	*Thuidium delicatulum*
POLY VUL					I 1.0				*Polypodium vulgare*
BRAC POP					I 5.0	I 1.0			*Brachythecium populeum*
STRA OCH					I 1.0		I 1.0		*Strangospora ochrophora*
FRUL TAM					I 5.0		I 7.0		*Frullania tamarisci*
PLTH NEM					I 1.0	I 1.0	I 1.0		*Plagiothecium nemorale*
PELT SP.					I 1.0	I 1.0	I 1.0	I 1.2	*Peltigera* sp.
EURH PUL					I 1.0	I 5.0	I 1.0	I 1.0	*Eurhynchium pulchellum*
LOBA PUL					I 2.0			I 1.0	*Lobaria pulmonaria*
STRA MIC						I 1.0			*Strangospora microhaema*
BRAC VEL						I 1.0			*Brachythecium velutinum*
NECK COM						I 1.0			*Neckera complanata*
POA PRA						I 1.0			*Poa pratensis*
MNIU HOR						I 1.0	I 2.2		*Mnium hornum*
DESC FLE						I 1.0	I 1.0		*Deschampsia flexuosa*
VICI SEP						I 1.0	I 1.0		*Vicia sepium*
PLAG ASP						I 1.0	II 2.4		*Plagiochila asplenioides*
RHYT SQU						I 1.0	I 1.0		*Rhytidiadelphus squarrosus*
ANTI CUR						I 1.0		I 8.8	*Antitrichia curtipendula*
HYLO SPL						I 5.0	I 3.0	I 1.3	*Hylocomium splendens*
CHIL COA							I 1.0		*Chiloscyphus coadunatus*
ANIS BIF							I 1.0		*Anisomeridium biforme*
RUME ACE							I 1.0		*Rumex acetosa*
SANI UNC							I 1.0		*Sanionia uncinata*
ANIS NYS							I 1.0		*Anisomeridium nyssaegenum*
ALCH ALP							I 1.0		*Alchemilla alpina*
CIRR PIL							I 1.3		*Cirriphyllum piliferum*
ATRI UND							I 1.4		*Atrichum undulatum*
ENTO CON							I 2.0		*Entodon concinnus*
BRAC SAL							I 4.0		*Brachythecium salebrosum*
PELT MEM							I 6.5		*Peltigera membranacea*
BARB BAR							I 7.0		*Barbilophozia barbata*
THUI TAM							I 10.0		*Thuidium tamariscinum*
CEPH SP.							I 1.0	I 1.0	*Cephalozia* sp.
AMBL SER							I 5.0	I 1.0	*Amblystegium serpens*
DICR SCO							I 3.0	I 1.0	*Dicranum scoparium*
MICA SP.								I 1.0	*Micarea* sp.
PLTH DEN								I 1.0	*Plagiothecium denticulatum*
BACI SUB								I 1.0	*Bacidia subincompta*
BIAT CHR								I 1.0	*Biatora chrysantha*
NEPH SP.								I 1.0	*Nephroma* sp.
OCHR AND								I 1.0	*Ochrolechia androgyna*
LEPT CYA								I 1.0	*Leptogium cyanescens*

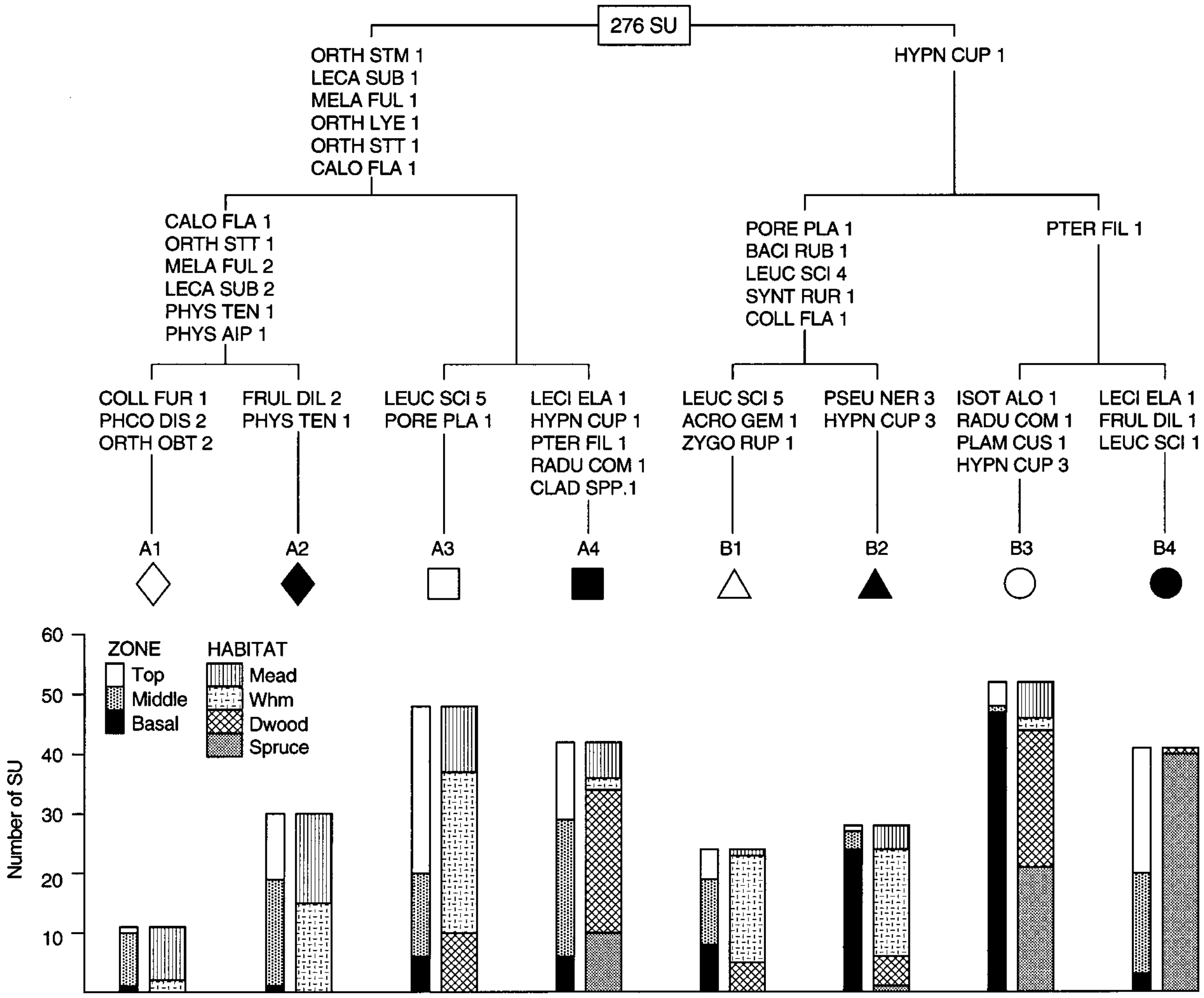

Figure 4. TWINSPAN results for the first three levels of division. Indicator species are shown. The number of SU and their arrangements into the vertical zones (narrow bars) and habitats (wide bars) are indicated. Taxon abbreviations are explained in Table 1.

gymnostomum and *Phaeophyscia ciliata* occur only in this group.

Group A4. Lecidella elaeochroma – Frullania dilatata *group*

The 42 SU in this group are from 15 trunks in the meadow (6 SU), the wooded hay meadow (2 SU), the deciduous wood (24 SU) and the spruce plantation (10 SU). On the bole 6 SU are from the basal, 23 from the middle, and 13 from the top zone. The total number of species is 90, of which 42 are occasional. The bryophytes *Frullania dilatata*, *Hypnum cupressiforme* and *Leucodon sciuroides* are both constant and dominant species. Species that occur only in this group are the lichens *Bacidia beckhausii*, *Hypogymnia tubulosa*, *Lepraria elobata*, *Pannaria conoplea*, *P. ignobilis* and *P. rubiginosa*. This large group is widespread, occurring in all of the habitats, but on the trunk it is most common on the upper part.

Group B1. Acrocordia gemmata – Leptogium lichenoides *group*

The 24 SU are from six trunks mainly in the wooded hay meadow (18 SU) and the deciduous wood (5 SU) and only one from the meadow. On the bole 8 SU are from the basal, 11 from the middle, and 5 from the top zone. The total number of species is 64, of which 32 are occasional. *Leucodon sciuroides* is important occurring in all of the squares with a very high cover (mean value 40.5%). Another dominant species is *Porella platyphylla*, whereas *Acrocordia gemmata*

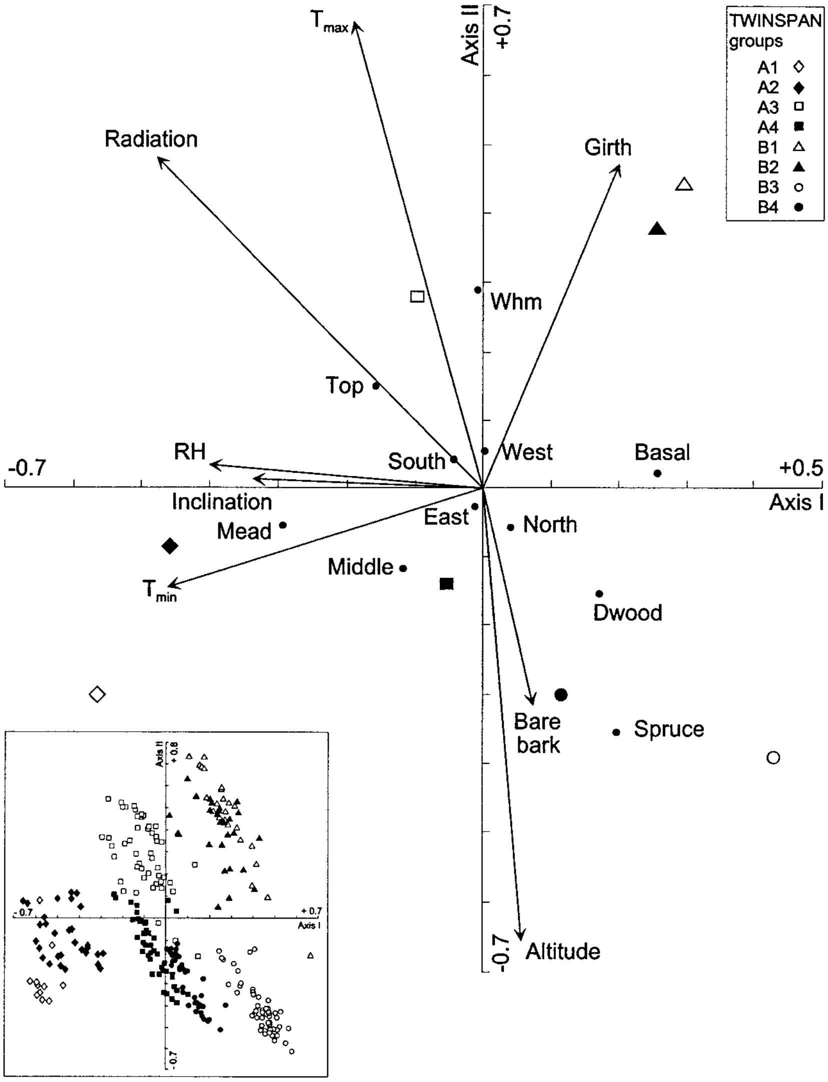

Figure 5. Ordination of environmental variables and TWINSPAN group centroids by canonical correspondence analysis (CCA) axes I and II. Small diagram: ordination of all SU on the same axes.

is both dominant and faithful. *Leptogium lichenoides* and *Zygodon rupestris* are also faithful.

Group B2. Hypnum cupressiforme – Pseudoleskeella nervosa *group*

The 28 SU in this group are from 11 trunks, most common in the wooded hay meadow (18 SU), scattered in the meadow (4 SU) and the deciduous wood (5 SU), while only one is from the spruce plantation. The basal zone dominates with 24 SU, three are from the middle, and only one is from the top zone. The total number of species is 78, of which 42 are occasional. Among the constant and dominant species *Hypnum cupressiforme* is most important followed by *Porella platyphylla*, *Pseudoleskeella nervosa* and *Leucodon sciuroides.*

Group B3. Isothecium alopecuroides – Radula complanata *group*

This is the largest group, with 52 SU on 15 trunks occurring in all the habitats. The deciduous wood (23 SU) and the spruce plantations (21 SU) are most common, while the meadow (6 SU) and the wooded hay meadow (2 SU) are more scattered. The basal zone dominates totally with 47 SU, only one is from the middle and four from the top zone. The total number

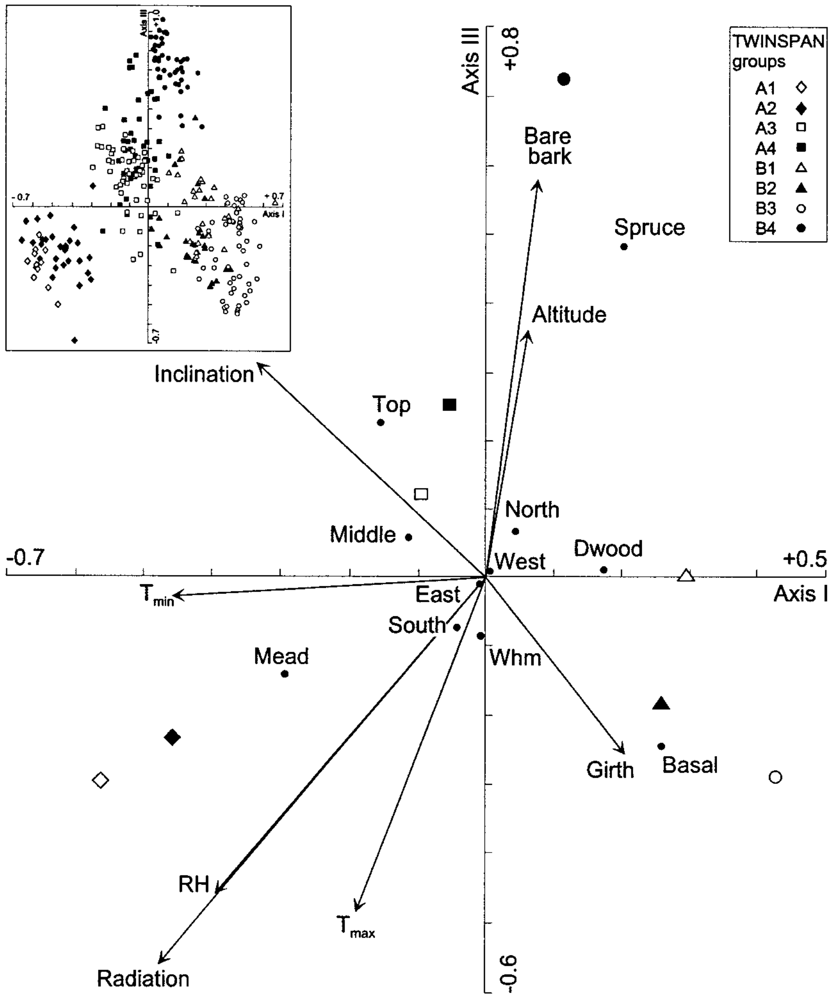

Figure 6. Ordination of environmental variables and TWINSPAN group centroids by canonical correspondence analysis (CCA) axes I and III. Small diagram: ordination of all SU on the same axes.

of species is 92, of which 39 are occasional. *Isothecium alopecuroides* is a dominant and very faithful species. The other dominants are *Hypnum cupressiforme* and *Peltigera praetextata.* Several species are limited to this group, mainly epigeous bryophytes from the ground below.

Group B4. Lecidella elaeochroma – Pterigynandrum filiforme *group*

This group has 41 SU occurring on 7 trunks, and all of them except one (in the deciduous wood) are from the spruce plantation. The top zone is most common, having 21 SU, followed by 17 in the middle and 3 in the basal zone. The total number of species is 49, of which 29 are occasional. The group has no dominants, but some constant bryophytes and lichens occur, viz. *Frullania dilatata, Hypnum cupressiforme, Lecidella elaeochroma, Lepraria lobificans, Leucodon sciuroides* and *Pterigynandrum filiforme.* The lichen species *Bacidia subincompta, Biatora chrysantha, Leptogium cyanescens, Ochrolechia androgyna* and the moss *Plagiothecium denticulatum* occur only in this group.

Canonical correspondence analysis (CCA)

CCA links species and their environment by calculating axes that are products of the species composition and linear combinations of the environmental variables. In an attempt to explain the relationship between the floristic composition of the epiphytic vegetation and the environmental variables, three CCA axes are considered in the interpretation (Figures 5 and 6). The main reason for this is that the eigenvalue of axis three (0.132) is not much less than the eigenvalue of axis two (0.189). The eigenvalue of axis one is 0.362. The percentages of variance accounted for by the species-environment relations are 31.5% on axis one, 16.3% on axis two, and 11.5% on axis three.

CCA axis I. The light-shade gradient

The availability of light, the radiation (W m^{-2}) seems to be an important factor reflected by all the three axes. The values measured were 2199 W m^{-2} in the meadow, 1873 W m^{-2} in the wooded hay meadow, 1207 W m^{-2} in the deciduous wood, and 144 W m^{-2} in the spruce plantation. The arrow for radiation has high negative scores both on CCA axis one and three. This parameter on axis one is correlated to the top zone and the south side of the trunk. The basal zone and the north side belong to the positive side of axis one, and hence they are negatively correlated to the radiation parameter. This indicates better light conditions at the top zone and the south side of the trunk than at the basal zone and the north side.

The SU from the meadow and the wooded hay meadow are positively correlated to the radiation parameter, while the SU from the deciduous wood and the spruce plantation are negatively correlated. The diagram shows clearly that the spruce plantation is the most shady habitat. With respect to the radiation parameter the TWINSPAN groups A1, A2 and A3 are positively correlated, groups A4, B1 and B2 are more or less uncorrelated, while groups B3 and B4 are negatively correlated.

CCA axis II. Temperature gradients

The temperature gradients show that the maximum values (T_{max}) are related to the CCA axis two. The mean maximum temperatures during the day were in the wooded hay meadow (16.6 °C), and this habitat is therefore best correlated to the T_{max} parameter. The meadow (15.9 °C) is slightly correlated, while the deciduous wood (15.7 °C) and the spruce plantation (14.6 °C) are negatively correlated.

An altitudinal gradient is reflected at the negative end of the CCA axis two, and hence this parameter is negatively correlated to the T_{max} gradient. Height above sea level seems to be an important factor even though the altitudinal range between 65 and 190 m is not very wide. The SU from the wooded hay meadow are from the most sheltered and lowest level of the farm (65–95 m), and this can explain a favourable local climate with the highest maximum temperatures. At the highest level we find the meadow and the spruce plantation between 160 and 190 m. The vertical climate gradient can not alone explain the differences in the maximum temperatures since the altitudinal gradient also accounts for the low maximum temperatures due to the very small amount of radiation in the spruce plantation.

The mean minimum temperatures (T_{min}), mainly during the night, are best reflected on CCA axis one. This parameter has the greatest values at the highest altitudes: the meadow (9.0 °C) and the spruce plantation (8.6 °C), while the deciduous wood (8.1 °C) and the wooded hay meadow (8.3 °C) are the coldest habitats during the night.

CCA axis III. Gradients related to the tree trunk

The cover of bare bark patches in the SU has a high positive score on axis three, and this parameter is highly correlated to the TWINSPAN group B4 where all except one of the 41 SU are from the spruce plantation. The radiation parameter is very negatively correlated to the bare bark patches, and this suggests that the epiphyte cover on the trunk increases towards the meadow and the wooded hay meadow where the amount of light is higher than in the deciduous wood and the spruce plantation.

The SU from the top and middle zones have positive scores on CCA axis three, while the basal zone has a negative score. This suggests that epiphyte cover increases towards the base of the tree trunk. There is an increase in the inclination towards the upper part of the trunk since the top zone is best correlated to the inclination parameter, while the basal zone is negatively correlated. The middle zone is in between, normally with a vertical trunk. The TWINSPAN groups B2 and B3 are assemblages found mainly around the basal zone where the inclination is generally less than 90° (Figure 3). Usually the tree girth is largest at the basal zone of the trunk, while the middle zone is the narrowest. The four different aspects around the trunks are separated by CCA axis three. North (positive score) and south (negative score) are best separated, while the east and west aspects are positioned close to the origin.

Discussion

It is suggested that the pollarded trunks of *Fraxinus excelsior* grew under fairly homogeneous conditions during the more extensive management period at Grinde until about 1962. The predominating habitats were meadow and wooded hay meadow, and consequently the trees' epiphytic vegetation experienced more open area conditions than today. Changes in the environment of the trunks during 30 years have probably caused alterations in the epiphytic vegetation, especially since bryophytes and lichens are sensitive indicators of small-scale environmental variation (Culberson 1955; Kenkel & Bradfield 1981). The availability of light seems to be a very important factor since the radiation parameter is reflected by strong correlation on all the three CCA axes. It is recognized that the collected data can be influenced by a bias effect caused by using only one climate station for each habitat. As one could expect, the highest daylight radiation was measured in the meadow, while the second highest was the wooded hay meadow, and these two also represent the habitats which have suffered least environmental change. The daylight radiation was lower in the deciduous wood and very faint in the spruce plantation. In these two habitats the pollarded trunks have gone through a considerable environmental change by the gradual increasing woodland around (Figure 2).

The species characteristic to the TWINSPAN groups A1 and A2 are photophilous, and all the SU from these groups are from the meadow and the wooded hay meadow where many lichens are characteristic, e.g., *Caloplaca flavorubescens*, *Melanelia fuliginosa* and some species of *Physcia*, *Physconia* and *Xanthoria*. It is suggested that these species are sensitive to shade, and they will probably not survive in a dense wood (cf., Kuusinen 1994). During the winter, the trunks in the meadow are periodically exposed to cold winds that can have a desiccatory and abrasive effect on the epiphytes (cf., Sjøgren 1961). These rather harsh conditions may be favourable to the photophilous lichen species, and in general bryophytes occur scattered. Desiccation winds tend to dry out the bark higher up on the trunk before drying out the more protected bases (Eversman 1982). Proximity to moist soil also reduce evaporation rates at the bases of the trunk (Bates 1992; Harris 1971b). This explains why SU in the top and the middle zones are most abundant in the TWINSPAN groups A1 and A2, whereas the SU in the basal zone are almost lacking. In the wooded hay meadow the epiphytes are favoured by a combination of well-lighted and sheltered, especially from cold northerly and northeasterly winds (cf., Rose 1992). Some of the photophilous lichen species are nitrophilous too, mainly occurring in the meadow, more scattered in the wooded hay meadow. Eutrophication caused by manuring may result in reduced cover of bryophytes and increased cover of nitrophilous and crustose lichens (Fuertes et al. 1996). In general, the intensity of farming can be reflected by the epiphytic lichen flora (Benfield 1994).

Outside the farmed fields, in the deciduous wood, most of the SU are dispersed on the TWINSPAN groups A4 and B3. The lowest night temperatures ($T_{\min}$) measured in this habitat were probably caused by the drainage of cold air down the valley from the mountains above. Some photophilous mosses, found mainly on the middle and the top zones of the trunks, are fairly common, e.g., *Orthotrichum lyellii*, *O. stramineum* and *Pseudoleskeella nervosa.* Woodland species like *Mnium hornum*, *Plagiochila asplenioides* and *Thuidium tamariscinum* are also found, especially on shady sites at the basal zone. In the deciduous wood there may be openings in the canopies which would be a prerequisite for the photophilous epiphytic species. These species may occur as relicts of more open conditions as the surrounding trees of *Alnus incana* are too young. They are also found in the deciduous wood because they are able to grow when the trees are leafless (Bates 1992; Schofield 1985). The trunks become moistened more quickly in winter since rain falls directly through the leafless canopy (Harris 1972). Annual growth during the season between autumn and spring may be considerable if the weather is mild and rainy (Pitkin 1975). In the suboceanic climate at Grinde, this may happen during the rainy periods, but not during the cold and dry periods that occur frequently.

The photophilous moss *Orthotrichum lyellii* (Størmer 1969) is an oceanic species that thrives well even when the trunk is exposed to cold and desiccatory winds. Other oceanic species occur scattered, and they seem to prefer trunks in more sheltered habitats. Examples are *Antitrichia curtipendula*, *Frullania tamarisci*, *Isothecium myosuroides*, *Metzgeria furcata*, *Mnium hornum*, *Nephroma laevigatum*, *Pannaria conoplea*, and *Plagiomnium undulatum.* At Grinde some of these facultative epiphytes grow frequently on rock or soil where the access to moisture is much better than on the trunks (cf., Barkman 1958; Piippo 1982). These species are very common epiphytes on ash trunks at Havrå, a more humid cultural landscape area nearer the coast of western Norway (Moe & Botnen 1997). The oceanic climate favours bryophytes, and hence the number of bryophyte species is higher at Havrå than at Grinde. The situation is reversed with regard to lichens where these species are more prevalent at Grinde than at Havrå. At Grinde some eastern lichen species like *Melanelia subargentifera* and *Rinodina colobina* thrive and survive, probably due to the dry and sunny climate. The investigated trunks are mainly dominated by mosses even though the number of recorded taxa is higher for the lichens than for the bryophytes. The cover of lichens tends to be greater than the cover of bryophytes in the most xeric habitats, i.e., the TWINSPAN groups A1 and A2.

The floristic relationship between the four habitats follows a sequence from the meadow to the wooded hay meadow, and further to the deciduous wood and to the spruce plantation. The same sequence can be read also from the CCA diagram axes one and three, and this suggests that the epiphytic vegetation has been shaped by the environment of the trunk. The TWINSPAN group B4 contains 56% of the 72 SU that were collected from the spruce plantation, and it is shown that this group differs considerably from the others. The impact of the planted spruce on the pollarded ash trunks has increased gradually as the plantation became denser. It is assumed that the spruce trees started to affect the pollarded trunks about ten years after planting in 1962. In the spruce plantation the cover of epiphytes on the ash trunks is often very low, and CCA axis three shows that the TWINSPAN group B4 is a 'bare bark assemblage', containing fairly few species. Also the field-layer vegetation is very sparse in the spruce plantation, and this may indicate a correlation between the properties of the soil and the bark (Gustafsson & Eriksson 1995). Many epiphytes that are common in the other habitats are rare or lacking in the spruce plantation. Mats of pleurocarpous mosses (especially *Leucodon*) are partly loosened with bare bark appearing underneath. Sometimes portions of the bryophytes are miscoloured (brown or whitish), indicating reduced vitality. The common hepatic *Frullania dilatata* occurs frequently in the spruce plantation, but the pale colour shows that this species will become sparser. In the spruce plantation the lichens also were in a poor state as some of the crustose species, e.g., *Lecanora subfusca* and *Lecidella elaeochroma* have apothecia without hymenium. The foliose lichens were small, discoloured and apparently dying. This suggests a change in the epiphytic vegetation through the development of a more shady habitat. Therefore, the epiphytes on ash in the spruce plantation are mainly remnants from a vegetation established during more open area conditions. New immigrants are lacking or occur very sporadically, but a few species that prefer shady habitats were found in the spruce plantation, viz., *Plagiothecium denticulatum*, *Bacidia subincompta* and *Leptogium cyanescens* (cf., Santesson 1993).

The evergreen conifers turn the spruce plantation into a shady habitat throughout the year, and this may be a decisive factor in preventing epiphytic growth, differing greatly from that of the deciduous wood. It was found that the spruce plantation is a fairly chilly habitat with the greatest differences to the other habitats on sunny days. Since the night temperatures were the second highest, the temperature fluctuations during the day were lower in the spruce plantation than in the other habitats. The lower maximum temperatures are probably a contributory factor in explaining the absence of termophilous species from the more shady habitats.

In the spruce plantation the relative humidity is lower than that of the other habitats, and this indicates dry conditions for the epiphytes (cf., Kuusinen 1996). The precipitation scarcely reaches the ground due to the very dense spruce canopies. Rainfall of sufficient intensity to moisten the trunks occurs much more rarely in the spruce plantation than in the other habitats (cf., Hyvärinen et al. 1992). In the TWINSPAN group B3 the habitats are mainly shady, viz., the spruce plantation and the deciduous wood, and almost all of the SU were from the basal zone on the trunk (Figure 4). Since it is suggested that the basal zone has better moisture conditions than those higher up, a low position on the trunk is a prerequisite for the epiphytic vegetation in the dry spruce plantation. This can explain why the cover of bare bark is much higher in the TWINSPAN group B4 than in group B3. The epiphytic vegetation on the ash trunks is very sparse due to several unfavourable conditions in the spruce plantation. This is caused by a vegetation change during the last two or three decades, and the process is still proceeding.

At Grinde *Leucodon* is often a very predominant moss that gives many trunks a shaggy appearance. The dense carpets of *Leucodon* will easily overgrow the pioneer species and other weak competitors. Therefore several photophilous lichens (*Physcia* spp., *Physconia distorta*, *Xanthoria* spp. and others) and small acrocarpous mosses like *Orthotrichum* spp. and *Ulota crispa* are favoured by the exposed and harsh conditions where *Leucodon* is less predominating. On the other hand, the carpets of *Leucodon* may give shelter to some epiphytes, and several acrocarpous mosses (*Bryum capillare*, *Syntrichia ruralis* and others) thrive and survive. A widely ramified carpet of *Leucodon* will sometimes loosen from the bark, and bare patches may reappear on the trunk. Then photophilous and tiny species can recolonize even on older trunks with a rough bark. The vertical trunk is a disturbed habitat where cyclical successions occurs. The epiphytic vegetation is governed by a complex of interrelating factors continually changing in time and space (Gough 1975). Obviously the species compositions in the TWINSPAN groups can not altogether be explained by the measured environmental factors. As the investigation concentrated on the effect of reduced managements, relevant ecological factors may be lacking. Hence, the floristic variation that is not related to the measured environmental factors, can not be explained by the CCA analysis.

The investigated trunks are fairly different in shape and very different in size, and it is assumed that the tree morphology affects the epiphytic vegetation. Most of the TWINSPAN groups tend to be dominated either by the basal zone only or both the top and the middle zones, and this reflects the floristic and ecologic relationship between the vertical zones. The inclination is increasing from the basal to the top zone of the trunk, and this factor will account for the floristic differences found at different heights on the trunk. An important influence of the inclination on the epiphytes is the drainage pattern caused by water trickling down the trunk (cf., Olsen 1917). Some of the predominant pleurocarpous mosses (*Hypnum cupressiforme*, *Isothecium alopecuroides* and *Leucodon sciuroides*) have a sufficient supply of moisture on the slanting upper side of the trunk while the under side sometimes becomes too dry. At the under side some specialists on very dry surfaces occur, e.g. the lichens *Opegrapha rufescens* and *Lepraria* spp., mainly *L. lobificans.* The lowest part near the ground is more slanting and moister than the upper part. Some humus and mineral soil occur (cf., Stringer & Stringer 1974), and this may be a prerequisite for the epigeous species (*Atrichum undulatum*, *Hylocomium splendens*, *Rhytidiadelphus squarrosus* and others) to survive on the trunk.

The differentiation of epiphytic vegetation growths between the vertical zones is greater than that of the different aspects around the trunk (cf., John & Dale 1995). Aspect shows no marked correlation in any direction through the ordination (cf., Kantvilas & Minchin 1989; Moe & Botnen 1997). CCA shows that the north aspect correlates slightly to the shady habitats deciduous wood and spruce plantation, while the south aspect correlates slightly to the meadow and the wooded hay meadow. It is suggested that the aspects are better separated on trunks in the open habitats where differential exposure to wind and light is more pronounced than in the habitats with closed canopies (Barkman 1958; Jonescu 1970; Kenkel & Bradfield 1981; Kuusinen 1994).

In conclusion, this investigation supports the statement that epiphytes are sensitive indicators of changes in the habitat of the porophyte. The habitats investigated have been gradually shaped during the last three decades, mainly due to alterations in the management regime of the farm. The local climate has more or less been changed with respect to the light intensity, temperature and water availability. It is a major trend in the data that these changes are reflected by the epiphytic vegetation on the pollarded ash trees.

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