PICEA ABIES AND *ABIES ALBA* FORESTS OF THE AUSTRIAN ALPS: NUMERICAL CLASSIFICATION AND ORDINATION

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Abstract: A TWINSPAN classification of a representative set of 3026 relevés of spruce and fir forests from the Eastern Alps (Austria) is presented. Ecological features of relevé clusters and species groups are described by means of Ellenberg indicator values, site factors and stand characteristics. The most important floristic discontinuity in the data set separates acidophilous communities on mostly silicate substrates from basiphilous communities on mostly carbonate substrates. Further divisions reflect a combined gradient of temperature, nutrient regime and shading. This is supported by the correlation of average Ellenberg values of sample plots with DCA axes. A qualitative comparison between TWINSPAN clusters and a syntaxonomic system widely used in the Austrian Alps is drawn. The two orders *Piceetalia excelsae* and *Athyrio-Piceetalia* largely coincide with the clusters of the first level of divisions. Alliances are partly reproduced by TWINSPAN. Clusters on the fifth and fourth level of division mostly correspond to associations. However, a considerable portion of the lower level clusters is of a transitional type. Out of thirteen fir and spruce associations described for the Austrian Alps, five associations are not reproduced by TWINSPAN, i.e. *Bazzanio-Piceetum*, *Veronico-Piceetum*, *Adenostylo alliariae-Abietetum*, *Asplenio-Piceetum* and *Carici-Piceetum*. Three associations are split on the second level of division, i.e. *Larici-Piceetum*, *Luzulo nemorosae-Piceetum* and *Calamagrostio variae-Piceetum*.

Keywords: Detrended correspondence analysis, Fir, Spruce, Syntaxonomy, TWINSPAN, Vegetation survey

Nomenclature: ADLER et al. (1994), FREY et al. (1995)

INTRODUCTION

The investigation of *Picea abies* and *Abies alba* forests according to the Braun-Blanquet approach has a long history in Austria, dating back to AICHINGER (1933). MAYER (1963) introduced concepts of the Swiss school of forest vegetation ecology (ETTER 1943, KUOCH 1954) into Austrian forest typology. ZUKRIGL (1973) applied the conceptual framework developed by Mayer, but his classification system also reflected a considerable influence of traditional syntaxonomy in the sense of the Braun-Blanquet school (OBERDORFER 1957, BRAUN-BLANQUET 1964). Partly to underpin their large-scale typologies, partly for local purposes of site description and forest management, forest ecologists have accumulated a great number of relevés of both spruce and fir forests (e.g. JELEM et al. 1964, JELEM & KILIAN 1966, 1975).

Classification systems of neighbouring countries have had little influence on spruce and fir forest systematics in Austria for a long time since the major reference point was the comprehensive overview given by MAYER (1974). WALLNÖFER (1993) made an attempt to

connect the systems of Mayer and Zukrigl with German (OBERDORFER 1957, 1992) as well as Swiss typologies (ELLENBERG & KLÖTZLI 1972). Since her classification was mainly based on a qualitative review and compilation of literature, a critical revision including phytosociological tables was necessary (see GRABHERR & MUCINA 1993). As a result of these efforts, EXNER (2001) presented a preliminary systematic concept for all Central European spruce and fir forests. Recently, GRABHERR et al. (unpubl.) analyzed floristic similarity patterns within a data set of Austrian forest vegetation, resulting from a stratified random sampling approach, by means of numerical classification (TWINSPAN, HILL 1979) and gave an outline of syntaxonomic implications. Furthermore, numerical ordination techniques were used for analysis of forest data sets in the Alpic region of Switzerland (WOHLGEMUTH et al. 1999) and Germany (EWALD 1997, 1999), but these have not yet been applied to Austrian forest vegetation on a large scale.

The objective of this paper is to present a numerical classification and ordination of *Picea abies* and *Abies alba* forests of the Austrian Alps. In detail, we address the following questions: What plant communities can be detected? What are the main ecological gradients governing floristic composition of these communities? What is the relationship between the numerically derived communities and syntaxonomic units?

STUDY AREA

The study area covers the whole of the Austrian Alps, which are the major part of the Eastern Alps (KILIAN et al. 1994). Habitat conditions are very diverse. Both limestone and silicate substrates are common, but carbonate soils are rare in the Central Alps. *Picea* and *Abies* forests are located at about 500 to 2000 m a.s.l. A distinct gradient of continentality ranges from the comparatively oceanic Outer Alps dominated by *Fagus sylvatica* forests to the inner continental regions. Natural spruce forests are restricted to continental regions, cold timberline zones, disturbed areas and sites with wet or infertile soils (MAYER 1974, ELLENBERG 1996). Under natural conditions, fir would be a dominant tree species together with spruce in moderately continental areas of the mountainous zone, but suffers from deer browsing, clear cutting and air pollution. In the Outer Alps, spruce has often been planted for forestry purposes on former broad-leaved woodland sites.

MATERIALS AND METHODS

Data set

Phytosociological data of Austrian forests were usually sampled within the same methodological framework (BRAUN-BLANQUET 1964, DIERSCHKE 1994), although syntaxonomy was the motivation of only a part of the sampling activities. We thus collected all available data from the literature and also included unpublished relevés. Input and editing of the data were performed by using the program TURBOVEG (HENNEKENS & SCHAMINÉE 2001). All data sources are given in the Appendix.

The following selection criteria were defined: For all relevés, at least 50% of the canopy layer had to be covered by *Picea abies* or *Abies alba* – separately or in mixture. The maximal proportion of *Fagus sylvatica* allowed was 25%. This criterion corresponds to the

delimitation of natural mountain beech forests in Austrian forest ecology (ZUKRIGL 1973, MAYER 1974). Only relevés with a crown cover of at least 20% and sampling areas between 100 and 1000 m^2 were accepted. Relevés of authors who did not record cryptogams were excluded as well as cryptogam taxa which were not determined in all studies. A total of 3026 samples could be used for the analysis.

Because of frequent inconsistencies concerning the definition of vegetation layers, species occurrences in different layers were combined. Subspecies and varieties were not taken into account. In some cases species which are hardly identifiable were merged (e.g. *Hieracium bifidum* and *H. murorum*) or aggregated on the level of genera. Merged taxa or genera were used in the analysis only if they are widespread in certain habitats and if an ecological interpretation appeared useful (see Table 1; not shown: *Taraxacum* sp., *Peltigera* sp., *Sphagnum* sp. and *Cladonia* sp.).

Data analysis

Following the principles of complementarity analysis (KENT & BALLARD 1988), we combined methods of classification and ordination. The entire data set (3026 samples; 1057 taxa) was classified using TWINSPAN (HILL 1979), a divisive classification method based on correspondence analysis (HILL 1973), as provided by MEGATAB (HENNEKENS 1996). Calculations were run with presence-absence data. Minimum group size for division was 5 samples. The maximum number of indicators per division was 7 and the maximum level of divisions was 5.

Correspondence analysis (CA) and detrended correspondence analysis (DCA) (HILL & GAUGH 1980) were performed by the software package CANOCO version 4.0 (TER BRAAK & ŠMILAUER 1998). Both methods detected similar patterns; however, only DCA results are presented here, because they are less influenced by rare species and can better be interpreted in terms of compositional turnover (gradient length). Default settings were used, including detrending by segments. Only presence-absence data were used for calculation. All samples for which Ellenberg indicator values could be calculated were analyzed by DCA (3023 samples; 1057 taxa). Three extremely species-poor samples had no values for some parameters and were thus excluded.

For all samples, unweighted average Ellenberg indicator values were calculated, using the list in ELLENBERG et al. (1992) as available in the program JUICE (TICHÝ 2002). Indicator values for cryptogams were added from ELLENBERG (1996). Indicator values of *Picea abies* were not used, because the natural occurrence of the species is strongly altered by forestry.

Ellenberg indicator values are mostly intuitive estimates of species ecological optima based on field experience (ELLENBERG et al. 1992). Ellenberg explicitly states that in many cases, especially with respect to N-values, he "also took into account the sociological behaviour, i.e. adjusting the N-values of a species to those of other species of the same phytosociological order, which were already classified" (ELLENBERG et al. 1992). Therefore Ellenberg values are not independent of the vegetation data. In contradiction to DIEKMANN & LAWESSON (1999) it has thus to be stressed, that the application of ordination and indicator values at the same time is circular, when pan-regional data sets covering broad ecological amplitudes are analyzed, since phytosociological patterns and the distribution of Ellenberg

values must then largely coincide. Generally speaking, the more similar two plant species are in terms of indicator values, the more likely it is that they grow together and vice versa (TER BRAAK & GREMMEN 1987). Ellenberg values represent external and a priori information relative to our study, but are not independent of our data matrix. In fact, it might well include phytosociological data used by Ellenberg for calibrating the values. Furthermore, we agree with EWALD (1997), that "mean Ellenberg indicator values are no parameters measured independently from floristic data. Their correlation with ordination axes solely enables an interpretation of the inner structure of the pattern of variation".

ELLENBERG et al. (1992) recommend that the indicator values of cryptogams not growing on soil should be treated separately from vascular plants, because ecological conditions greatly differ between soil and other substrates. We did not follow this recommendation, since we consider all substrates within a given site as part of the habitat complex constituting a plant community.

Species richness was calculated for vascular plants only, since cryptogam species are often not completely recorded.

RESULTS

Classification

On the first level of division, TWINSPAN separated acidophilous (group 0) from basiphilous (group 1) communities (Table 1). A close correspondence to the geological substrate was evident (Table 2). *Avenella flexuosa* and *Luzula luzuloides* were the only highly frequent species with a distinct optimum on acid sites (see also Table 3), whereas base-rich soils were characterized by several species, e.g. *Daphne mezereum* and *Fragaria vesca*. Many calciphilous species (e.g. *Calamagrostis varia*) additionally differentiated group 1. However, they were mostly missing in cluster 23 (group 110), which was dominated by sites over silicate bedrock.

On the second level, subdivisions of groups 0 and 1 followed roughly the same gradient. Floristic turnover went parallel with changes in nutrient and light values as well as temperature values and altitude (Table 2). *Vaccinium vitis-idaea* was an indicator species in both groups (00 and 10) together with other species typical of nutrient-poor soils (e.g. *Pleurozium schreberi* in group 00, *Melampyrum sylvaticum* in group 10). Their counterparts in groups 01 and 11 were *Senecio nemorensis* agg. and other mesophilous species frequent on soils with higher nutrient content (e.g. *Athyrium filix-femina* and *Mycelis muralis*). Supplementary indicator species of group 10 were elements of subalpine calcareous grasslands (i.e. *Aster bellidiastrum* and *Sesleria albicans*, class *Seslerietea albicantis*). They indicate shallow soils with low decomposition rates. Accordingly, calcicolous scree taxa (*Adenostyles glabra* and others) as well as species of montane limestone forests (e.g. *Rubus saxatilis*) had an optimum in this group (10), but lower frequency in group 11, where the relative proportion of silicate substrates was higher (Table 2). In both the acidophilous and basiphilous groups (0 and 1), the nutrient-richer subgroups (01 and 11) were on average located at lower altitudes as compared to the nutrient-poorer subgroups (00 and 10). Clusters 4 and 5 (group 001) surpassed all other groups in altitude (Table 2).

Table 1. Frequency table of TWINSPAN clusters, 3026 samples. Clusters including another cluster with less than 5 samples are marked with an asterisk; T=tree; B=bryophyte; L=lichen. All species with more than 30% frequency in a cluster are shown. Frequency values > 39% and the first species of each species group are printed in bold. The order within the species groups of the lowest level of divisions is changed. Binary codes denote the hierarchy of the species and sample clusters on the first three levels of division. TWINSPAN indicator species (see Table 3) are marked with an asterisk. *Dryopteris carth./dilat.* = *D. carthusiana* and *D. dilatata*, *Ranunculus montanus* et sp. = *R. montanus*, *R. carinthiacus*, *R. breyninus*; *Galium mollugo* et sp. = *G. mollugo*, *G. album*, *G. lucidum*; *Dicranodontium denudat.* = *D. denudatum*.

	1*	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20*	21	22	23	24	25*	26	27	28*
1st level of divisions	0															1							1					
2nd level of divisions	0							1								0							1					
3rd level of divisions	0			1				0				1				0			1				0		1			
Cluster number	1*	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20*	21	22	23	24	25*	26	27	28*
Number of samples	34	35	17	122	154	694	205	56	54	49	70	91	127	165	29	67	45	82	55	123	117	59	90	203	134	49	49	51
111																												
Sphagnum magellanicum (B)	**68**	11	6	3	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Sphagnum capillifolium (B) *	**77**	**86**	**71**	18	16	13	12	4	2	.	4	.	2	1	3	.	2	1	.	.	.	.	.	.	.	+	.	.
Sphagnum palustre (B) *	12	**86**	**82**	3	.	+	+	.	.	.	1	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Betula pubescens (T)	38	**57**	6	2	.	.	1	2	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1	.	.	.	.	.
Climacium dendroides (B)	.	**77**	12	6	.	.	.	2	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.
Agrostis canina	.	**66**	18	+	1	+	.	2	2	.	1	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.
Carex nigra	3	**66**	18	12	9	2	.	.	.	.	.	.	+	.	.	.	4	.	.	+	.	.	.	.	.	.	.	.
Galium palustre agg.	.	**57**	29	+	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Persicaria bistorta	.	**46**	12	5	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.
Calypogeia muelleriana (B)	.	**54**	6	.	.	+	.	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sphagnum angustifolium (B)	3	**54**	.	+	.	+	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sphagnum warnstorfii (B)	.	**60**	6	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lysimachia vulgaris	.	**57**	24	.	.	+	.	4	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	2	.
Lythrum salicaria	.	31	12	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Nardus stricta	3	.	12	23	**68**	10	5	5	2	4	10	1	3	+	7	6	24	.	4	2	.	.	.	.	.	.	.	.
Campanula barbata	.	.	.	18	**51**	8	5	11	.	4	10	6	3	.	17	.	16	.	9	3	.	.	1	+	.	.	.	.
Arnica montana	.	.	.	7	**46**	4	4	5	2	.	1	3	.	1	7	.	2	1	4	2	+	2	.	+	.	.	.	.
Rhododendron ferrugineum	9	.	.	30	36	12	3	.	4	.	.	.	.	.	.	.	9	2	4	2	.	.	1	.	.	.	.	.
Calluna vulgaris	29	9	6	7	39	4	23	7	2	.	.	.	.	4	.	.	2	4	.	9	.	2	.	.	.	+	2	.
Pinus cembra (T)	.	.	.	31	29	18	3	5	2	.	4	.	+	.	.	2	9	4	.	+	.	.	.	.	.	.	.	.
Cetraria islandica (L)	.	.	.	11	33	16	10	.	.	2	3	.	+	.	.	2	4	.	2	+	3	.	.	.	.	.	.	.
Ptilium crista-castrensis (B)	32	.	.	8	3	14	5	5	.	.	.	.	.	+	7	5	9	5	2	7	3	3	2	+	+	.	.	.
Sphagnum girgensohnii (B)	**59**	6	29	11	5	11	5	7	6	.	1	.	2	2	.	.	.	.	.	.	.	.	.	.	+	2	.	.
Luzula luzuloides *	.	.	.	**44**	**66**	**58**	**61**	**64**	**63**	**78**	**60**	**81**	**88**	**84**	**93**	21	13	17	4	5	15	9	**53**	30	10	18	10	6
Phyteuma michelii agg.	.	.	.	3	18	2	4	4	9	.	1	1	+	4	**45**	.	1	.	2	.	3	3	3	+	.	.	.	.
Avenella flexuosa *	9	31	35	**79**	**91**	**86**	**84**	**52**	**69**	**59**	**69**	**84**	**82**	**70**	**79**	28	18	15	7	13	4	2	**31**	9	14	20	6	2
Calamagrostis villosa *	6	.	24	**57**	**52**	**57**	16	**43**	**93**	**45**	**60**	10	24	14	**45**	12	29	17	13	11	2	2	8	9	2	2	.	.
Plagiothecium undulatum (B)	**65**	.	6	9	9	20	4	21	6	10	21	1	9	9	.	2	.	6	.	2	4	.	1	6	8	2	.	.
110																												
Vaccinium myrtillus	**100**	**91**	**94**	**88**	**97**	**95**	**98**	**84**	**54**	**49**	**83**	**54**	**91**	**81**	**62**	**78**	**87**	**83**	**66**	**85**	**58**	20	18	39	**55**	**45**	10	31
Dicranum scoparium (B)	**91**	**80**	**71**	**61**	**67**	**68**	**70**	**75**	37	20	**44**	8	**49**	**55**	**69**	**45**	**71**	**65**	**67**	**53**	37	17	18	34	**49**	12	12	4
Larix decidua (T) *	9	.	18	**51**	**57**	**58**	**61**	29	20	**53**	**40**	**62**	**58**	**49**	**48**	**55**	**49**	**54**	16	**48**	**56**	**42**	31	**44**	26	**43**	39	10
Hylocomium splendens (B)	**97**	**77**	**77**	**71**	**61**	**71**	**69**	**68**	**67**	10	21	4	25	**55**	**76**	16	**69**	**57**	**76**	**72**	**47**	**49**	16	25	29	**41**	25	24
Polytrichum formosum (B)	**71**	23	**65**	**57**	**51**	**53**	33	**57**	39	**55**	**67**	22	**59**	**53**	38	27	**40**	**49**	38	17	5	7	19	26	**58**	12	8	14
Dryopteris carth./dilat.	12	37	**53**	**59**	**42**	**63**	29	**73**	**76**	**59**	**80**	**52**	**68**	**61**	**41**	37	36	**46**	24	8	5	3	31	37	**53**	10	12	6
Luzula pilosa	3	**54**	**53**	15	21	25	27	34	20	20	**46**	36	**42**	**47**	28	12	7	12	7	14	9	5	16	19	**45**	35	4	26
Pleurozium schreberi (B) *	**88**	**43**	**47**	**59**	**70**	**55**	**57**	39	24	4	10	1	13	26	**45**	5	**47**	18	20	35	15	**42**	7	5	5	18	6	33
Melampyrum pratense	12	9	35	7	16	11	36	.	.	.	4	2	7	24	3	3	4	1	2	7	10	19	1	3	4	22	6	33
Lycopodium annotinum	24	.	18	34	17	32	9	29	24	6	36	2	22	10	.	19	27	**42**	27	36	10	2	.	13	19	2	.	.
Blechnum spicant	15	.	6	34	29	22	21	**46**	6	8	30	7	24	20	.	2	11	10	15	13	+	.	2	5	32	2	.	.
Thelypteris limbosperma	.	.	.	31	25	12	3	**57**	11	18	21	2	21	14	.	6	16	6	26	17	+	2	7	5	21	4	.	.
Rhytidiadelphus loreus (B)	**41**	.	12	21	14	20	3	27	9	12	39	3	7	11	3	3	13	18	16	8	.	.	1	8	25	2	.	.
Bazzania trilobata (B)	**53**	**74**	**41**	2	5	12	35	4	2	2	6	.	11	21	.	2	.	15	7	11	6	3	.	4	31	2	2	2
Carex brizoides	.	9	35	+	+	2	2	4	.	2	3	.	2	6	.	.	.	.	.	.	.	.	.	1	5	.	.	.
Caltha palustris	.	**46**	**88**	16	2	+	.	14	4	20	3	1	2	1	.	2	.	.	6	+	+	.	11	1	13	.	.	.
Myosotis palustris	.	31	**65**	9	.	+	.	14	4	4	1	.	+	+	3	.	.	1	.	.	.	.	8	1	10	.	.	.
Cardamine amara	.	**57**	29	9	+	+	.	27	2	.	1	.	+	2	.	2	.	.	.	.	.	.	6	1	2	.	.	.
Valeriana dioica	.	**71**	**65**	2	.	+	.	2	.	2	.	.	+	+	.	.	.	.	2	.	+	.	2	+	5	.	.	4
Calliergonella cuspidata (B)	.	**66**	29	3	.	+	.	7	6	2	1	.	.	.	.	.	.	2	11	2	.	2	2	.	2	.	.	2
Equisetum sylvaticum	9	.	35	12	1	2	1	20	6	10	3	.	.	2	.	.	.	.	1	11	+	.	2	.	12	.	.	2
Vaccinium vitis-idaea *	**68**	**80**	**65**	**66**	**81**	**62**	**61**	21	11	6	11	1	13	6	38	36	**49**	**43**	20	**73**	33	27	3	3	2	10	.	4
Homogyne alpina *	.	.	12	**93**	**86**	**70**	9	**68**	**61**	**49**	**94**	28	**51**	7	14	**58**	**93**	**82**	**73**	**87**	22	14	7	15	31	12	.	2
Agrostis capillaris	.	.	12	19	23	3	3	21	6	.	3	7	4	6	7	2	33	6	2	12	3	3	7	3	3	2	.	2
Calypogeia azurea (B)	12	**63**	12	+	3	4	1	.	.	4	3	.	+	.	.	6	2	1	6	+	.	2	.	.	5	.	.	.
Potentilla aurea	.	.	.	32	33	2	+	13	4	10	1	2	+	.	.	27	**42**	.	7	6	2	.	.	2	.	.	.	.
Rhytidiadelphus triquetrus (B)	9	**46**	**59**	**55**	**45**	**45**	32	**41**	35	10	31	3	19	24	**45**	34	**58**	**51**	**60**	**63**	**40**	**42**	11	29	19	**41**	8	31
Anthoxanthum odoratum agg.	.	.	12	30	**55**	4	2	7	6	.	4	1	+	1	10	18	**47**	4	26	22	4	5	2	2	3	2	.	.
Festuca rubra agg.	.	3	.	12	**42**	2	2	9	.	2	4	2	+	+	3	15	**44**	4	11	15	2	5	6	3	2	2	.	4

	1*	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20*	21	22	23	24	25*	26	27	28*
Cluster number	1*	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20*	21	22	23	24	25*	26	27	28*
Number of samples	34	35	17	122	154	694	205	56	54	49	70	91	127	165	29	67	45	82	55	123	117	59	90	203	134	49	49	51
101																												
Gymnocarpium dryopteris	.	3	6	**40**	20	26	2	**71**	**91**	**71**	**60**	**42**	39	37	**52**	24	29	34	22	14	9	3	**41**	35	28	14	.	6
Rubus idaeus *	.	.	29	20	17	13	10	**75**	**63**	**55**	**47**	**59**	**50**	**46**	**76**	10	16	22	15	2	6	12	**67**	31	33	33	39	16
Phegopteris connectilis	.	.	18	21	5	7	+	**68**	**67**	**57**	39	19	15	30	14	.	7	10	7	2	3	.	22	18	21	.	.	.
Stellaria nemorum *	.	.	.	16	1	3	.	**50**	**56**	**59**	26	20	2	3	.	16	4	1	2	.	.	.	34	16	2	.	.	.
Ranunculus repens	.	37	**77**	17	2	+	+	**45**	9	12	3	.	+	4	7	5	16	.	2	2	.	.	14	2	5	.	2	2
Calamagrostis arundinacea	.	.	6	3	6	8	4	5	.	29	39	29	39	21	28	5	2	1	.	.	+	2	22	8	2	4	.	.
Doronicum austriacum	.	.	6	3	.	2	.	4	28	31	23	8	6	5	.	3	.	5	.	.	.	.	6	7	2	.	.	.
Polypodium vulgare agg.	.	.	.	2	4	5	12	.	20	.	1	.	2	19	**69**	2	.	7	.	2	4	9	16	7	4	14	8	.
Veronica officinalis	.	.	6	19	32	5	10	**46**	13	18	19	36	20	30	**83**	13	38	10	13	25	15	10	16	15	13	31	16	12
Senecio nemorensis agg. *	.	9	41	25	17	8	9	**75**	**67**	**88**	**69**	**86**	**63**	**71**	66	66	20	45	36	4	20	7	**90**	**71**	**80**	**55**	**88**	12
Athyrium filix-femina *	.	14	**82**	39	29	17	8	**82**	**72**	**86**	**74**	**71**	**73**	**76**	69	36	31	46	53	17	15	3	**80**	64	**83**	27	6	8
Sambucus racemosa	.	.	.	1	1	2		11	19	6	3	11	5	12	**48**	2	2	4	2	.	3	5	23	5	4	.	.	.
Anemone nemorosa	.	57	**71**	10	9	3	2	14	6	27	**40**	11	13	5	3	12	9	2	4	2	5	7	17	12	30	4	.	20
Moehringia trinervia	.	.	.	1	+	.		20	6	8	3	34	6	12	14	2	11	.	.	+	+	.	28	8	6	.	.	.
100																												
Luzula sylvatica *	.	.	.	50	46	34	1	38	30	49	**84**	13	21	3	.	**70**	62	57	56	24	15	.	7	37	19	2	.	.
Veratrum album	.	.	18	47	35	16	.	20	24	**74**	54	24	17	3	.	**60**	40	18	**67**	13	12	.	13	29	18	.	.	6
Molinia caerulea agg. *	44	80	12	2	3	1	2	.	.	.	.	+	2	.	.	.	.	.	9	5	19		.	.	3	2	2	22
Hieracium murorum/bifidum *	.	.	12	**67**	60	35	42	**73**	**72**	**71**	**81**	**76**	**76**	**79**	**86**	76	**93**	**92**	**93**	**82**	**87**	70	61	66	66	84	80	47
Picea abies (T)	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**	99	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**	99	**100**	**100**	**100**	**100**	**100**
Sorbus aucuparia (T)	32	63	**71**	53	48	54	54	66	**80**	65	69	57	**76**	**71**	**72**	**58**	47	**77**	**73**	62	56	49	**58**	54	60	63	55	24
Oxalis acetosella *	6	29	**77**	**90**	63	**79**	23	**98**	**100**	**100**	97	92	97	83	62	85	76	**87**	84	59	43	2	**92**	**95**	**92**	**59**	**63**	47
Abies alba (T)	**88**	.	12	5	3	19	**59**	21	6	55	49	65	**77**	**68**	7	13	24	44	69	49	53	10	40	56	69	55	**80**	6
Maianthemum bifolium	9	**74**	**82**	16	23	23	27	38	26	10	27	24	**45**	**50**	28	5	**49**	**54**	38	**61**	35	22	29	32	**57**	**53**	29	53
Hypnum cupressiforme (B)	**56**	.	6	8	12	11	**40**	25	28	6	11	10	22	63	**76**	13	11	20	2	11	28	25	32	16	46	33	**69**	6
Deschampsia cespitosa	.	23	**88**	**67**	30	7	3	63	26	55	37	17	16	16	17	**42**	**58**	11	**40**	11	5	3	23	16	**41**	10	2	18
Luzula luzulina	.	.	6	36	20	17	4	**45**	11	14	37	**40**	17	7	7	**78**	**40**	10	11	7	8	2	12	30	18	6	2	2
Plagiomnium sp. (B)	.	37	18	8	3	4	1	32	26	4	4	2	+	15	17	2	13	7	16	16	3	14	9	3	13	12	6	22
Alnus incana *	.	**94**	53	7	3	2	3	20	15	2	.	3	2	7	17	.	2	1	4	+	2	7	23	1	6	10	.	**41**
Rhizomnium sp. (B)	6	**69**	35	20	3	3	+	**43**	17	12	6	1	2	4	14	9	16	12	29	9	5	.	7	10	19	6	.	.
Dicranodontium denudat. (B)	**68**	.	.	+	2	2	4	2	4	.	4	.	.	+	3	.	2	2	13	7	2	.	2	.	2	10	2	.	2
Solanum dulcamara	.	**43**	24	.	.	.	.	2	.	.	.	.	.	.	3	.	.	.	.	.	.	.	3	.	5	4	.	2
Solidago virgaurea	.	.	12	**45**	44	21	18	**43**	**69**	43	43	43	35	**52**	62	**58**	36	**71**	**73**	42	49	**58**	**58**	48	**58**	**69**	49	28
Melampyrum sylvaticum	3	.	.	32	**62**	21	23	20	7	6	21	22	22	13	**55**	**58**	49	**63**	**58**	**77**	**68**	**66**	12	31	20	33	10	8
Plagiochila sp. (B)	12	**51**	**53**	24	7	19	12	38	46	14	27	25	**41**	21		**40**	36	**40**	46	23	31	17	27	**45**	37	22	8	14
Huperzia selago	3	.	6	31	10	13	2	11	13	10	36	6	9	5	7	25	**44**	35	**49**	30	15	3	1	13	24	4	2	.
Moneses uniflora	.	.	.	21	6	4	+	23	7	6	4	4	6	1	7	22	38	18	11	14	6	2	.	10	2	2	.	.
Pteridium aquilinum	6	.	.	+	8	4	**32**	.	4	.	1	3	10	27	28	2	2	.	.	18	15	37	10	3	17	**55**	10	**45**
Frangula alnus	18	**80**	6	.	.	+	10	2	.	.	.	.	.	7	.	.	.	.	.	3	3	20	.	.	5	16	6	**53**
Prenanthes purpurea	.	3	.	11	8	14	11	34	24	45	49	50	**54**	43	7	13	9	**61**	**56**	37	35	17	**43**	42	**60**	**49**	37	6
Gentiana asclepiadea	.	.	.	3	10	9	7	11	9	29	37	**59**	**54**	19	.	24	11	28	**51**	21	25	22	38	**41**	34	35	18	.
011																												
Pinus sylvestris (T)	12	34	.	+	8	2	**41**	.	.	.	1	8	4	24	14	2	2	4	2	26	30	**63**	6	2	6	22	37	**47**
Leontodon hispidus	.	.	6	25	31	2	.	4	.	2	3	1	.	2	3	9	**71**	6	22	21	9	**32**	1	3	2	.	18	4
Viola biflora *	.	.	6	**75**	12	2	.	**73**	**61**	**51**	**40**	1	3	1	10	**81**	**82**	**61**	**95**	**42**	18	3	20	35	10	2	.	.
Adenostyles alliariae	.	.	.	25	4	5	.	18	20	**47**	34	11	2	1	.	**52**	27	35	22	+	+	.	6	24	6	.	.	.
Saxifraga rotundifolia	.	.	.	19	+	+	.	29	30	33	16	.	2	.	.	**46**	20	33	16	+	.	.	11	28	4	.	.	.
Crepis paludosa	.	11	29	12	+	+	+	18	6	16	7	2	2	3	.	25	2	16	31	12	3	2	16	13	8	.	.	.
Chaerophyllum hirsutum	.	3	**47**	26	7	+	.	**48**	30	**57**	7	3	2	5	3	**51**	47	28	**42**	11	7	.	32	30	33	4	.	4
Hypericum maculatum	.	3	.	16	16	1	2	23	13	31	21	9	9	4	10	**46**	**44**	15	6	4	10	5	13	24	4	8	2	2
Veronica chamaedrys	.	.	.	11	12	1	2	36	9	10	.	6	2	3	24	**42**	38	7	9	11	5	5	32	20	8	12	6	6
Poa nemoralis	.	.	.	8	5	2	+	9	13	2	4	7	2	4	35	39	11	12	7	2	5	3	24	15	7	2	12	2
Polygonatum verticillatum	.	.	.	5	10	6	3	5	7	39	39	**44**	32	4	7	**58**	36	**52**	**69**	42	42	19	20	**56**	36	20	27	4
010																												
Fagus sylvatica (T) *	27	17	12	+	1	5	28	9	2	25	19	**41**	**62**	**58**	7	10	18	**40**	15	31	**51**	42	**42**	46	**64**	**61**	**53**	**51**
Rubus fruticosus agg.	6	.	.	3	2	12	.	4	.	6	3	8	7	**46**	.	2	.	2	2	+	8	.	20	5	**49**	27	**43**	14
Epilobium montanum	.	.	6	8	6	+	+	38	20	35	4	19	3	20	**45**	12	18	9	4	2	3	2	**56**	36	17	14	12	.
Quercus robur (T)	3	.	.	.	.	+	9	.	.	.	.	.	12	3		.	.	1	.	.	+	10	4	.	5	10	2	**55**
Galium rotundifolium	.	.	6	+	+	+	3	7	.	2	3	8	2	27	3	.	9	10	11	7	9	3	8	12	**67**	31	**53**	10
Lamiastrum galeobdolon agg.*	.	.	.	2	1	+	.	11	30	**47**	9	24	4	6	.	**45**	13	39	33	4	9	3	**51**	**72**	**42**	14	10	28
Cardamine trifolia	.	.	.	3	.	.	.	7	4	**45**	11	20	4	3	.	19	.	9	.	.	5	5	24	**40**	28	4	6	8

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Cluster number	1*	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20*	21	22	23	24	25*	26	27	28*
Number of samples	34	35	17	122	154	694	205	56	54	49	70	91	127	165	29	67	45	82	55	123	117	59	90	203	134	49	49	51
Symphytum tuberosum	.	.	.	.	+	+	.	4	4	39	11	17	2	2	10	22	2	6	.	+	9	2	37	24	10	22	18	8
Ranunculus lanuginosus	.	.	.	.	.	.	.	5	13	33	1	6	+	.	.	9	2	5	6	+	4	2	13	27	11	8	.	2
Mycelis muralis *	.	.	.	+	2	2	5	18	22	**41**	7	**63**	11	**50**	**55**	24	16	18	2	2	28	9	**74**	62	63	59	78	28
Petasites albus	.	.	.	14	1	3	2	**59**	**57**	29	11	14	15	28	31	3	2	16	**62**	2	4	5	**53**	41	46	35	8	6
Dryopteris filix-mas	.	.	6	8	6	5	8	23	37	31	16	30	16	**51**	31	18	13	38	18	7	18	2	**77**	54	65	43	33	12
Paris quadrifolia	.	**66**	**59**	3	+	2	.	29	26	**59**	14	29	2	9	3	36	16	34	16	12	17	2	38	**53**	44	25	14	20
Corylus avellana	.	.	.	.	2	+	14	2	2	.	.	3	6	39	28	.	2	.	.	2	10	34	**54**	5	29	**74**	49	53
Urtica dioica	.	.	6	12	5	2	.	27	24	16	3	10	.	12	31	10	18	4	.	.	+	5	**57**	15	8	2	4	6
Plagiomnium undulatum (B)	9	.	35	8	3	2	4	21	4	12	1	2	2	10	3	3	.	5	20	7	3	7	27	16	**37**	2	4	29
Myosotis sylvatica/decumbens	.	.	12	8	1	+	1	13	17	**37**	1	6	.	5	21	28	9	6	.	2	4	.	29	21	2	6	4	.
Impatiens noli-tangere	.	.	.	.	.	+	.	13	15	6	3	6	.	9	3	.	.	1	.	.	.	.	**39**	4	12	4	.	.
Thuidium tamariscinum (B)	.	.	6	+	.	+	4	7	.	2	3	.	3	10	.	2	.	1	9	8	3	2	1	4	**37**	4	2	8
Chrysosplenium alternifolium	.	.	.	5	.	.	.	**34**	11	8	.	1	+	1	.	6	4	4	.	.	+	.	22	7	2	.	.	.
Equisetum arvense	.	6	**47**	2	+	+	.	11	4	2	1	.	.	1	7	.	.	.	2	2	.	.	9	1	10	2	.	6
Knautia drymeia	.	6	**59**	.	3	+	.	.	4	4	.	.	+	3	14	8	7	2	.	2	9	3	11	8	+	12	14	8
001																												
Fraxinus excelsior (T)	.	3	6	.	.	+	2	4	4	.	.	4	+	23	7	.	.	1	2	+	7	20	**49**	9	43	55	**84**	45
Actaea spicata	.	.	.	.	.	+	+	2	7	8	.	4	2	7	7	5	4	7	6	2	3	.	**47**	28	21	18	14	8
Geranium robertianum	.	.	.	+	.	+	.	4	2	.	.	1	+	5	21	3	2	1	.	.	2	2	**43**	21	15	6	31	2
Cruciata glabra	.	.	.	.	3	.	.	.	.	.	3	.	+	7	3	2	.	.	.	2	6	10	7	5	.	20	.	**43**
Cirsium oleraceum	.	20	**59**	2	+	.	.	5	.	2	.	.	.	+	3	2	.	2	11	2	3	5	16	.	12	2	6	28
Fragaria vesca *	.	.	12	27	20	3	3	**55**	43	8	3	13	6	23	**83**	66	69	52	51	76	67	70	70	54	59	80	76	71
Acer pseudoplatanus (T) *	.	9	.	6	3	3	8	13	15	12	24	32	24	36	10	18	4	**52**	**62**	50	46	54	71	51	71	59	76	39
Ajuga reptans	.	11	29	3	1	+	+	13	.	8	6	13	4	12	.	21	**40**	16	20	13	13	7	30	34	**57**	29	35	39
Phyteuma spicatum	.	.	.	6	.	1	1	14	19	20	10	7	2	2	.	25	11	**44**	**62**	19	18	12	23	37	34	12	10	2
Veronica urticifolia	.	.	.	7	2	4	3	16	**54**	20	11	6	4	6	28	6	18	**67**	**86**	37	21	14	21	**44**	26	27	2	2
Dactylorhiza maculata	.	3	6	9	4	+	+	23	7	12	1	2	2	2	7	5	13	6	**56**	24	15	14	18	17	19	14	.	6
Lysimachia nemorum	.	.	12	8	4	+	.	32	2	8	13	8	2	4	.	9	29	17	26	14	5	.	13	12	**55**	6	.	.
Viola reichenbachiana	.	.	6	2	5	1	.	7	2	8	1	9	2	16	7	8	24	4	22	29	24	15	29	31	**76**	57	74	49
Tussilago farfara	.	.	6	9	2	+	1	25	6	6	1	.	.	4	14	6	31	5	33	7	14	15	13	7	10	14	29	12
Sanicula europaea	.	.	.	+	.	.	1	5	2	2	1	2	4	6	.	.	9	15	42	4	18	7	4	31	**80**	49	43	24
Salvia glutinosa	.	.	.	.	+	.	.	2	.	.	1	1	+	10	14	.	.	2	6	2	21	41	37	19	66	**82**	65	71
Lonicera xylosteum *	.	.	.	1	.	.	.	4	.	.	.	1	.	1	17	.	.	7	.	3	13	39	24	10	18	**78**	61	61
Brachypodium sylvaticum	.	.	.	+	+	+	+	.	2	.	1	.	.	8	7	.	.	1	6	2	13	17	11	9	**74**	45	61	47
Euphorbia amygdaloides	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	8	.	1	.	2	21	14	8	19	27	25	**71**	33
Cyclamen purpurascens *	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	2	.	1	.	+	21	15	9	13	8	31	**84**	61
Carex sylvatica	.	.	18	2	.	.	2	13	.	4	1	1	.	6	.	3	18	9	35	7	6	.	19	19	**74**	12	20	10
Asarum europaeum	.	.	12	.	.	.	.	.	.	.	1	.	2	3	.	.	.	2	.	.	5	12	22	5	**39**	8	18	29
Campanula persicifolia	.	.	.	.	.	.	+	.	.	.	.	.	+	2	7	.	.	.	.	.	3	9	17	1	2	22	**39**	4
Crataegus monogyna	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	7	1	+	2	12	37	**43**
Clematis vitalba	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	1	.	4	3	1	+	10	22	**43**	39
Ligustrum vulgare	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	9	.	.	2	2	10	**47**
Viburnum opulus	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	+	7	.	.	4	6	6	35
Galium odoratum	.	.	.	+	.	.	.	.	.	4	.	3	.	2	.	5	.	2	15	.	3	2	9	22	21	4	**45**	.
Rosa arvensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	5	2	.	+	+	**49**	4
Bromus ramosus agg.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	2	3	5	2	31	2
Acer campestre (T)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	35	4
Daphne mezereum *	.	23	**53**	5	2	+	+	2	4	6	.	2	.	4	.	**73**	56	46	42	45	61	54	31	55	53	71	67	35
Mercurialis perennis *	.	.	.	.	.	+	.	4	.	.	1	1	.	2	.	31	7	**40**	44	33	**50**	49	26	**50**	57	57	76	31
Carex alba *	.	.	.	2	2	+	+	.	.	.	1	.	.	.	7	.	4	13	24	60	55	66	2	11	35	61	80	78
Carex digitata	.	.	.	6	1	+	1	2	.	4	.	1	6	11	7	22	36	37	31	36	45	39	18	39	41	67	**86**	51
Primula elatior	.	.	6	3	.	+	.	11	.	25	3	11	.	2	10	**66**	22	11	26	4	20	7	24	41	45	8	14	12
Helleborus niger	.	.	.	3	.	+	.	.	.	4	3	2	.	.	7	**39**	13	2	.	4	26	29	1	28	16	25	8	35
Moehringia muscosa	.	.	.	3	+	+	.	.	7	2	3	1	+	7	.	37	29	**51**	2	5	26	2	1	32	13	10	27	.
Dentaria enneaphyllos	.	.	.	3	.	+	.	5	13	14	4	2	+	.	.	**64**	33	32	.	5	15	.	7	39	8	4	2	.
Neottia nidus-avis	.	.	.	.	.	.	1	.	2	.	.	.	+	2	.	3	9	1	6	11	19	24	2	12	16	20	33	4
Cirsium erisithales	.	.	6	+	7	+	.	2	.	.	.	1	.	9	.	31	.	12	2	5	36	29	9	15	4	**43**	31	12
Clinopodium vulgare	.	.	.	+	+	.	.	2	.	.	.	.	.	1	7	2	.	2	11	4	14	20	7	4	10	16	18	33
Berberis vulgaris *	.	.	.	+	.	.	+	2	.	.	1	.	.	1	3	.	.	2	.	11	10	**41**	7	+	6	41	37	69
Viburnum lantana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	3	34	.	+	2	8	14	**47**
Anemone trifolia	.	.	.	+	+	.	.	.	2	2	3	4	5	2	.	12	4	11	.	2	21	14	1	14	5	29	.	**49**
Campanula rapunculoides	.	.	.	1	+	.	.	.	.	.	.	.	+	10	.	2	.	.	.	2	19	22	8	5	+	25	**47**	.
Euphorbia cyparissias	.	.	.	+	4	.	.	.	.	.	.	.	1	10	.	13	.	.	4	2	14	34	10	4	4	27	16	28
000																												
Calamagrostis varia *	.	.	.	3	4	2	5	5	.	2	1	2	4	5	.	39	13	44	51	62	88	**93**	9	38	37	69	86	35
Melica nutans *	.	14	12	3	5	+	+	.	6	.	.	1	2	4	3	15	7	39	51	64	46	63	9	30	27	51	76	**86**
Adenostyles glabra	.	.	.	5	+	1	.	5	.	8	6	.	+	2	.	**58**	22	55	73	33	54	34	1	44	38	10	39	6
Hepatica nobilis	.	.	.	2	1	+	.	2	.	.	.	1	+	.	.	9	13	26	22	37	48	48	4	22	28	51	12	**69**
Ranunculus tuberosus	.	.	.	14	20	+	.	13	15	.	4	2	+	1	7	46	53	42	35	38	36	51	10	24	29	29	27	37
Valeriana tripteris	.	.	.	7	2	2	.	2	17	6	3	3	.	.	3	**75**	24	60	20	33	56	42	3	**41**	11	31	29	8

Cluster number	1*	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20*	21	22	23	24	25*	26	27	28*
Number of samples	34	35	17	122	154	694	205	56	54	49	70	91	127	165	29	67	45	82	55	123	117	59	90	203	134	49	49	51
Knautia maxima	.	.	6	8	10	1	+	4	13	.	.	1	+	2	7	24	22	27	**58**	50	32	25	16	11	10	20	4	31
Tortella tortuosa (B)	.	.	.	7	2	1	+	.	.	2	1	.	2	+	.	30	**47**	34	**49**	42	44	**39**	.	21	15	4	39	2
Sorbus aria agg. (T)	.	.	.	.	.	+	.	.	2	.	.	.	+	3	.	.	2	5	6	23	33	**49**	.	5	10	37	**63**	18
Lonicera alpigena	.	.	.	.	.	+	.	4	4	2	.	.	.	.	.	25	2	23	24	8	25	10	1	17	9	16	6	8
Aconitum lycoctonum	.	.	.	6	+	+	.	2	17	4	.	.	.	.	.	25	13	33	**51**	9	13	7	7	17	2	16	2	6
Aposeris foetida	.	.	.	2	3	+	+	11	.	4	20	3	2	.	.	19	27	39	4	23	15	22	1	18	25	10	2	22
Asplenium viride	.	.	.	4	.	+	.	.	6	.	1	.	.	.	.	**49**	29	**44**	18	11	26	3	1	29	9	8	4	2
Brachypodium pinnatum agg.	.	.	.	.	2	.	+	2	.	.	.	.	.	.	+	.	.	1	4	18	13	34	2	2	3	20	4	**57**
Galium mollugo et sp.	.	.	.	4	1	+	2	2	4	.	.	.	.	4	21	19	36	7	9	30	23	46	19	9	2	16	35	33
Gymnocarpium robertianum	.	.	6	3	2	2	1	7	.	.	6	.	2	2	.	13	38	**42**	15	33	39	24	2	19	12	12	10	2
Pimpinella major	.	.	.	2	1	.	+	.	.	.	.	.	+	1	7	8	4	2	7	14	13	**42**	4	2	8	18	14	16
Ctenidium molluscum (B)	.	.	.	3	+	+	.	.	4	.	4	.	.	.	1	**51**	36	**44**	**66**	27	33	15	.	36	31	16	37	2
Carex flacca	.	.	6	5	10	+	+	2	.	.	.	.	.	.	.	3	20	5	26	37	26	**51**	.	6	14	16	22	35
Carex montana	.	.	6	+	7	.	.	2	.	.	.	.	.	.	3	.	2	.	33	15	9	7	4	.	3	12	4	14
Sesleria albicans *	.	.	.	6	3	+	+	.	2	.	.	.	.	.	.	36	**60**	35	**58**	**72**	56	**66**	1	11	7	14	**53**	10
Galium pusillum agg.	.	.	.	4	12	+	.	4	.	.	.	.	.	.	3	**54**	**71**	15	27	**39**	28	32	2	6	.	2	18	2
Carduus defloratus agg.	.	.	.	+	6	+	.	.	2	.	.	.	.	.	.	**48**	31	11	36	**52**	44	**66**	.	5	+	2	20	.
Rubus saxatilis	.	.	.	3	4	+	.	2	.	.	.	2	.	+	.	28	20	24	26	**42**	32	**42**	2	7	2	31	4	26
Thymus sp.	.	.	.	6	8	.	.	2	.	.	.	.	.	.	3	10	**58**	2	6	**45**	23	**49**	1	1	.	.	2	.
Lotus corniculatus	.	.	.	3	15	+	1	7	.	.	.	.	.	.	7	6	**51**	2	11	**39**	17	**61**	3	1	.	6	4	.
Rosa pendulina	.	.	.	+	2	2	.	2	4	2	1	.	+	+	.	**30**	18	33	38	26	24	12	3	11	2	6	6	6
Campanula cochleariifolia	.	.	.	3	+	+	.	5	.	2	.	.	.	.	3	13	38	32	35	33	21	25	.	10	8	8	2	2
Aquilegia vulgaris agg.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	3	7	12	20	33	15	**42**	.	3	4	18	6	28
Polygala chamaebuxus *	.	.	.	3	9	+	4	.	.	.	.	.	.	+	.	6	**44**	13	16	**78**	**64**	**66**	2	2	10	37	**51**	47
Erica carnea *	.	.	.	4	10	1	2	.	.	.	.	.	.	+	3	9	27	18	6	**81**	48	**75**	2	2	+	10	6	26
Buphthalmum salicifolium *	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15	.	1	2	32	33	**78**	.	2	+	14	31	4
Epipactis atrorubens	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	9	4	24	21	**51**	.	2	3	.	8	8	16
Laserpitium latifolium	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	3	.	4	2	15	15	**42**	.	.	.	4	2	10
Betonica alopecuros	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	24	.	2	.	5	32	20	.	3	+	8	.	10
Scabiosa columbaria agg.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	9	9	2	4	18	5	32	.	.	.	.	.	.
Carlina acaulis	.	.	.	.	11	+	+	2	.	.	.	.	.	+	3	8	22	.	6	18	14	36	.	3	.	2	4	4
Amelanchier ovalis	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	9	5	31	.	.	.	2	8	.
Aster bellidiastrum *	.	.	.	21	5	.	1	7	4	.	1	.	.	.	.	**55**	**73**	55	**95**	65	27	22	2	6	8	.	2	.
Valeriana montana	.	.	.	8	3	+	.	2	4	.	1	.	.	.	.	13	38	16	**67**	42	27	15	.	6	.	2	.	.
Polystichum lonchitis	.	.	.	8	.	+	+	4	4	4	.	.	.	+	.	**55**	33	34	26	8	13	.	1	13	2	.	2	.
Carex ferruginea	.	.	.	11	3	+	+	.	.	.	2	.	.	.	.	28	38	21	**80**	35	9	9	.	4	2	.	.	.
Ranunculus montanus et sp.	.	.	.	19	9	+	.	.	13	2	.	.	.	.	.	**61**	56	26	56	59	18	9	.	7	5	.	.	.
Centaurea montana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15	7	5	33	13	8	19	1	4	3	12	2	8
Trollius europaeus	.	.	.	6	.	.	.	.	.	.	.	.	.	.	.	15	33	4	35	12	2	2	.	2	+	.	.	.
Prunella vulgaris	.	.	18	12	3	.	.	7	4	.	.	.	.	1	7	.	**51**	5	7	24	6	7	3	2	8	2	.	2
Ranunculus serpens	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	7	.	33	9	+	.	.	.	+	.	.	.
Soldanella alpina	.	.	.	23	7	+	.	4	4	4	3	.	.	.	.	46	**62**	10	31	19	3	2	.	5	.	.	.	.
Geranium sylvaticum	.	.	.	12	12	+	.	2	9	.	.	.	.	.	1	39	36	33	29	17	6	7	3	4	.	.	.	.
Trifolium pratense	.	.	6	7	10	.	1	5	.	.	.	.	+	.	7	3	**53**	1	9	15	4	19	.	2	.	.	.	4
Aconitum napellus agg.	.	.	.	17	1	.	+	2	.	4	.	.	.	.	.	37	16	2	20	3	7	2	1	7	.	4	2	.
Campanula rotundifolia agg.	.	.	.	**46**	38	4	4	32	13	2	7	9	2	6	35	**85**	**67**	35	26	**63**	**52**	31	13	25	13	22	33	14
Potentilla erecta	3	9	29	35	**56**	5	2	14	4	2	6	.	2	3	17	18	**69**	18	40	**85**	27	**56**	2	5	8	2	.	10
Alchemilla sp.	.	.	.	39	9	+	.	29	9	2	.	.	.	.	.	19	**76**	20	**46**	40	3	3	2	5	+	.	.	.
Clematis alpina	.	.	.	11	6	2	+	7	20	.	.	1	.	+	7	12	20	32	2	9	21	19	2	9	+	10	2	2
Chaerophyllum villarsii	.	.	6	7	12	+	1	4	15	4	.	2	.	.	10	3	.	5	**49**	20	3	3	1	5	4	.	.	.
Persicaria vivipara	.	.	.	12	1	.	.	.	.	.	.	.	.	.	.	5	36	1	4	10	.	.	.	.	.	.	.	.
Poa alpina	.	.	.	17	7	+	.	9	.	.	.	.	.	.	.	37	**44**	6	.	7	3	2	.	1	.	.	.	.
Pinus mugo agg.	27	.	.	5	5	2	2	.	.	.	.	.	.	.	.	21	7	5	2	31	5	9	.	.	.	.	.	.
Gentiana pannonica	.	.	.	4	3	2	.	.	.	2	.	.	.	.	.	33	4	5	.	+	3	.	1	3	.	.	.	.

According to TWINSPAN indicator species (Table 3) and species groups (Table 1), moisture, nutrient regime and altitude appeared to be most relevant for the floristic differentiation on the third level of classification (see also Table 2). Group 000 had a distinct character due to an extreme water surplus.

On acid substrates, the nutrient-poor group 00 was further split according to differences in the water regime. Wet sites (group 000) were indicated by taxa of the genus *Sphagnum*. The corresponding communities nearly lacked species typical of fresh moder such as *Luzula luzuloides* and *Avenella flexuosa*. The nutrient-rich sites of group 01 were divided into

Table 2. Means of environmental variables, stand parameters, species richness and unweighted Ellenberg indicator values per plot for TWINSPAN clusters (* = cluster with less than 5 samples included). Cluster boundaries on the first two levels of division are indicated. Mean values for variables of clusters of the higher levels of division are calculated from the original plot data matrix. Environmental variables and stand parameters are available only for a part of the samples.

TWINSPAN 2nd level clusters

	00	01	10	11
Number of samples	1261	641	548	576
Mean altitude (m)	1434	1187	1317	974
Mean inclination (°)	23	24	28	23
Mean cover of tree layer (%)	62	70	61	71
Mean cover of herb layer (%)	56	54	60	59
Mean cover of cryptogam layer (%)	34	13	14	15
Mean maximal tree height (m)	25	29	23	28
Mean species number	19	27	46	42
Average Ellenberg indicator values				
Light	5.3	4.8	5.6	4.8
Temperature	3.5	4.1	3.8	4.5
Continentality	4.2	3.7	3.9	3.7
Humidity	5.2	5.4	5.0	5.3
Reaction	3.4	4.3	6.1	6.0
Nitrogen	3.4	4.8	4.1	5.2
No. of samples with geologic data	612	399	270	275
Silicate	503	322	17	60
Base-rich silicate	50	42	5	22
Carbonate	29	14	230	163
Not specified	30	21	18	30

TWINSPAN 3rd level clusters

	000	001	010	011	100	101	110	111
Number of samples	86	1175	229	412	249	299	427	149
Mean altitude (m)	1141	1438	1403	1069	1435	1214	1030	783
Mean inclination (°)	8	24	25	24	26	30	24	20
Mean cover of tree layer (%)	60	63	69	70	64	59	73	63
Mean cover of herb layer (%)	73	55	62	50	56	63	66	41
Mean cover of cryptogam layer (%)	47	34	11	13	17	12	18	6
Mean maximal tree height (m)	20	25	28	29	24	23	30	25
Mean species number	18	19	31	24	46	46	41	45
Average Ellenberg indicator values								
Light	5.7	5.3	4.9	4.8	5.4	5.7	4.6	5.2
Temperature	3.6	3.5	3.7	4.3	3.6	4.0	4.4	4.9
Continentality	4.7	4.2	3.7	3.8	3.8	3.9	3.7	3.8
Humidity	6.2	5.2	5.7	5.2	5.3	4.8	5.4	4.9
Reaction	3.4	3.5	4.6	4.1	5.8	6.3	5.8	6.5
Nitrogen	3.3	3.5	4.9	4.7	4.4	3.7	5.3	4.7
No. of samples with geologic data	7	605	132	267	131	139	202	73
Silicate	6	497	99	223	9	8	53	7
Base-rich silicate	–	50	14	28	4	1	20	2
Carbonate	–	29	9	5	112	118	107	56
Not specified	1	29	10	11	6	12	22	8

TWINSPAN 5th level clusters

	1*	2	3	4	5	6	7	8	9	10	11	12	13
Number of samples	34	35	17	122	154	694	205	56	54	49	70	91	127
Mean altitude (m)	1119	–	1179	1626	1636	1468	1083	1425	1401	1357	1420	1179	1182
Mean inclination (°)	10	–	4	26	24	23	23	25	28	24	22	22	23
Mean cover of tree layer (%)	60	–	60	57	50	65	69	65	74	70	69	72	70
Mean cover of herb layer (%)	73	–	72	68	64	52	55	57	61	68	59	55	50
Mean cover of cryptogam layer (%)	55	–	27	44	27	34	35	22	21	4	10	3	8
Mean maximal tree height (m)	21	–	19	24	22	25	26	27	30	30	29	30	29
Mean species number	8	22	28	33	30	15	14	37	30	31	27	24	21
Average Ellenberg indicator values													
Light	5.4	6.0	5.4	5.5	5.9	5.1	5.3	5.0	4.9	4.8	4.8	4.7	4.7
Temperature	3.2	3.9	3.7	3.3	3.4	3.4	3.8	3.7	3.7	3.8	3.7	4.4	4.1
Continentality	4.9	4.7	4.2	3.9	4.0	4.2	4.4	3.8	3.8	3.6	3.6	3.6	3.7
Humidity	5.6	6.7	6.3	5.6	5.2	5.2	4.9	5.8	5.6	5.6	5.5	5.3	5.3
Reaction	2.6	3.9	4.3	4.3	3.6	3.3	3.2	4.6	4.7	5.0	4.2	4.5	3.8
Nitrogen	2.5	3.7	4.5	4.1	3.3	3.4	3.2	4.9	5.1	5.4	4.6	4.9	4.4
No. of samples with geologic data	2	–	5	69	94	332	110	35	23	30	44	50	83
Silicate	2	–	4	40	76	279	102	26	18	22	33	44	69
Base-rich silicate	–	–	–	13	12	21	4	2	2	5	2	6	10
Carbonate	–	–	–	12	3	14	–	1	3	4	1	–	–
Not specified	–	–	1	4	3	18	4	3	–	2	5	2	2

	14	15	16	17	18	19	20*	21	22	23	24	25*	26	27	28*
Number of samples	165	29	67	45	82	55	123	117	59	90	203	134	49	49	51
Mean altitude (m)	889	1254	1502	1538	1338	1415	1304	1175	1093	971	1194	819	861	785	633
Mean inclination (°)	24	34	24	21	25	32	26	32	33	26	28	17	23	26	10
Mean cover of tree layer (%)	68	66	58	67	70	35	65	61	49	71	68	77	62	65	58
Mean cover of herb layer (%)	48	50	45	83	64	40	75	57	67	67	60	69	34	42	46
Mean cover of cryptogam layer (%)	21	17	6	33	25	50	23	10	8	4	15	25	10	4	7
Mean maximal tree height (m)	29	29	20	23	26	29	23	24	23	31	28	30	28	24	25
Mean species number	25	32	48	52	41	47	47	41	51	42	39	43	46	48	42
Average Ellenberg indicator values															
Light	4.8	5.4	5.5	5.8	5.0	5.4	5.7	5.5	6.1	4.8	4.7	4.4	5.0	5.1	5.4
Temperature	4.4	4.2	3.5	3.4	3.7	3.6	3.7	4.1	4.3	4.7	4.2	4.5	4.8	5.0	5.0
Continentality	3.8	4.0	3.8	3.8	3.9	3.8	3.9	3.9	3.9	3.7	3.7	3.6	3.8	3.7	3.9
Humidity	5.2	5.4	5.4	5.2	5.3	5.4	4.9	4.8	4.5	5.5	5.4	5.5	4.9	4.8	4.9
Reaction	4.1	4.4	6.0	5.6	5.6	6.0	6.0	6.4	6.8	5.8	6.0	5.7	6.2	6.8	6.5
Nitrogen	4.8	4.7	4.5	4.1	4.5	4.6	3.7	3.9	3.6	5.7	5.2	5.3	4.7	4.7	4.6
No. of samples with geologic data	110	88	46	22	33	30	41	66	32	50	96	56	21	42	10
Silicate	88	–	–	–	1	8	1	2	5	32	10	11	2	2	3
Base-rich silicate	10	2	–	1	2	1	–	1	–	10	8	2	2	–	–
Carbonate	3	–	46	20	29	17	33	61	24	6	77	24	14	37	5
Not specified	9	–	1	1	1	4	7	2	3	2	7	13	3	3	2

Table 3. TWINSPAN indicator species for the first three levels of division.

Level 1		Level 2		Level 3	
0	*Avenella flexuosa* *Luzula luzuloides*	0	*Vaccinium vitis-idaea* *Pleurozium schreberi*	0	*Molinia caerulea* agg. *Alnus incana* *Sphagnum capillifolium* *Sphagnum palustre*
				1	*Homogyne alpina* *Avenella flexuosa* *Luzula luzuloides* *Larix decidua*
		1	*Senecio nemorensis* agg. *Athyrium filix-femina* *Rubus idaeus* *Hieracium murorum* and *H. bifidum*	0	*Viola biflora* *Stellaria nemorum* *Calamagrostis villosa* *Luzula sylvatica* *Homogyne alpina*
				1	*Fagus sylvatica*
1	*Fragaria vesca* *Daphne mezereum* *Calamagrostis varia* *Acer pseudoplatanus* *Mercurialis perennis*	0	*Vaccinium vitis-idaea* *Melampyrum sylvaticum* *Homogyne alpina* *Aster bellidiastrum* *Sesleria albicans*	0	*Viola biflora* *Luzula sylvatica* *Oxalis acetosella*
				1	*Carex alba* *Polygala chamaebuxus* *Erica carnea* *Buphthalmum salicifolium*
		1	*Senecio nemorensis* agg. *Mycelis muralis*	0	*Athyrium filix-femina* *Lamiastrum galeobdolon* agg.
				1	*Carex alba* *Lonicera xylosteum* *Cyclamen purpurascens* *Berberis vulgaris* *Melica nutans*

mesic-cool sites (group 010) and a negatively characterized, drier and warmer group of sites (group 011).

On base-rich substrates, nutrient-poor sites were divided into mesic-cool (group 100) and dry-warm (group 101) sites. The nutrient-rich subgroup (11) was split into analogous vicariants. Mean altitudes of the subgroups were well separated (Table 2). The ecological profile of the indicator species (Table 3) of the division on the third level was fairly similar in both groups (10 and 11). *Viola biflora* (group 100) and *Athyrium filix-femina* (group 110) indicate humid conditions, whereas *Carex alba* (groups 101 and 111) is typical for (sub)xeric sites. On poorer soils (group 10), some pronounced thermophilous elements were absent (e.g. *Clematis vitalba*) and species with an optimum in the higher montane to subalpine belt (e.g. *Homogyne alpina* and *Aster bellidiastrum*) were much more frequent, reflecting that relevés are on average located at higher altitudes as compared to group 11.

Ordination

Ordination parameters are listed in Table 4. Except for the outlier group in the upper left part of the ordination diagram, no clear discontinuities were visible in the sample and species

Table 4. Parameters of the detrended correspondence analysis (DCA).

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalue	0.417	0.301	0.219	0.170	24.865
Gradient length	4.495	4.373	3.573	3.998	
Cumulative % variance explained	1.7	2.9	3.8	4.5	

Table 5. Correlations of species richness and unweighted average Ellenberg indicator values per plot with DCA axes as calculated by CANOCO (inter-set correlations). Values exceeding 0.5 are printed in bold.

Variables	Axis 1	Axis 2	Axis 3	Axis 4
Soil reaction	**0.9390**	0.0324	**-0.5396**	0.0701
Temperature	**0.5801**	**0.6971**	0.2024	-0.0734
Nutrients	0.4035	**0.6367**	-0.1832	-0.0477
Light	0.0344	**-0.6513**	-0.3037	-0.4494
Humidity	-0.3901	0.3139	-0.3330	-0.1188
Continentality	-0.4351	-0.2205	0.1785	0.0102
Species richness	**0.6870**	-0.1011	**-0.5198**	-0.1476

ordinations (Figs. 1 and 2). The exclusion of the outlier group (which corresponds to the TWINSPAN clusters 2 and 3) had only weak effects on the ordination pattern.

Axis 1 showed the strongest correlation with Ellenberg values for soil reaction (Table 5). Species richness and the values for temperature closely followed this trend. Nutrient values displayed the same pattern, but with a weaker correlation. Values for humidity and continentality were negatively correlated with axis 1, probably due to the low water retention capacity of carbonate soils and their rarity in the inner continental parts of the Alps. Axis 2 showed a positive correlation with values for temperature and nutrients and a strong negative relationship with light values. Axis 3 was obviously influenced by the outlier group, since the correlations changed when the respective samples were excluded.

DISCUSSION

DCA ordination and syntaxonomy

The first DCA axis is best explained by indicator values for soil reaction. The available data on geological substrate (Table 2) underline the importance of this ecological factor. Other numerical studies (e.g. OLANO et al. 1998, EWALD 1999, 2000) have also suggested the overriding role of acidity in controlling the species composition of the forest understorey in monospecific tree stands. This has already been taken into account in the syntaxonomy of fir forests. OBERDORFER (1992) distinguishes the acidic suballiance *Vaccinio-Abietenion* and the base-rich suballiance *Galio-Abietenion* (see also WALENTOWSKI 1998). WALLNÖFER (1993) made a similar distinction by separating the orders *Piceetalia excelsae* and *Athyrio-Piceetalia*, thus extending Oberdorfer's concept of the systematics of fir forests to fir and spruce forests.

In contrast to the first DCA axis, the second axis represents a more complex environmental gradient integrating the floristic effect of at least three site variables: temperature, nutrients and light (Table 5). Because of the strong positive causal interdependence between nutrient
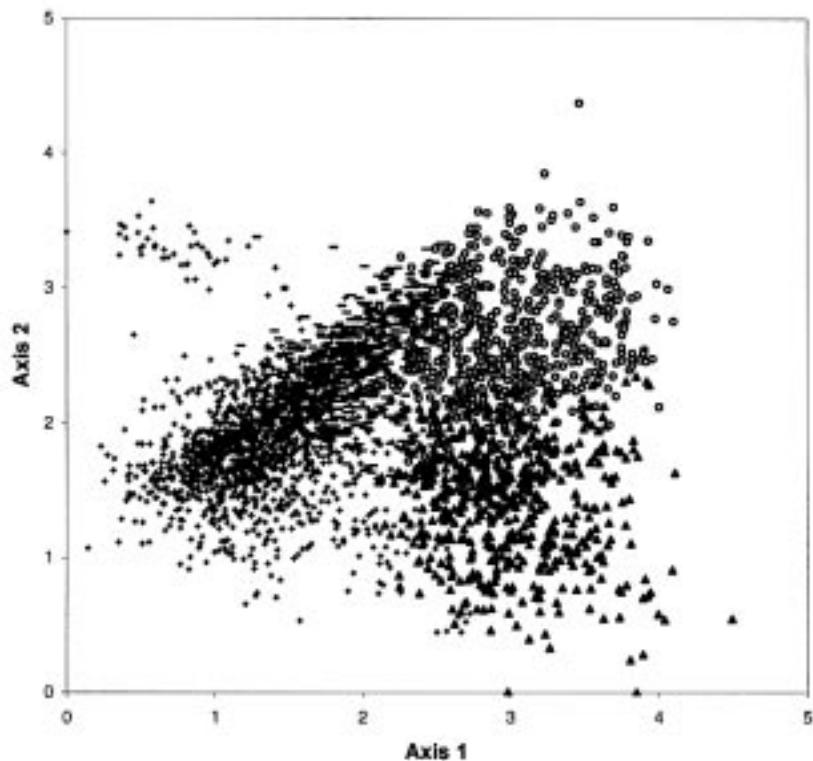
Fig. 1. DCA ordination of the samples on axis 1 and 2. TWINSPAN clusters of the second level of divisions are shown. + – cluster 00 (nutrient-poor silicate soils, cool sites); ‐ – cluster 01 (nutrient-rich silicate soils, warm sites); ▲ – cluster 10 (nutrient-poor carbonate soils, cool sites); O – cluster 11 (nutrient-rich carbonate soils, warm sites).

richness, favourable climatic conditions and shading, axis 2 might be interpreted as a site productivity gradient.

Interestingly, early syntaxonomy mainly classified Alpic fir and spruce forests according to the altitudinal gradient. BRAUN-BLANQUET et al. (1939) assigned all montane fir and spruce forests of the Alps to the suballiance *Abieti-Piceenion* and subalpine spruce forests to the suballiance *Rhododendro-Vaccinienion*. The *Abieti-Piceenion* is differentiated by the low frequency of dwarf shrubs and subalpine species on the one hand, the regular occurrence of species of broad-leaved forests (class *Querco-Fagetea*) and of *Abies alba* on the other. OBERDORFER (1992) still follows this concept: warmer sites with fir-dominated communities are put into the *Galio-Abietenion* and the *Vaccinio-Abietenion*, whereas the cooler spruce forests are assigned to the *Vaccinio-Piceenion*, irrespective of nutrient regime and soil reaction. The presupposition of a strong correlation between climate (*Abies alba* versus subalpine species) and nutrient status (*Querco-Fagetea* species versus dwarf shrubs) obviously corresponds with the results of DCA and TWINSPAN. However, the respective ecological species groups actually show a considerable amount of uncoordinated variation:
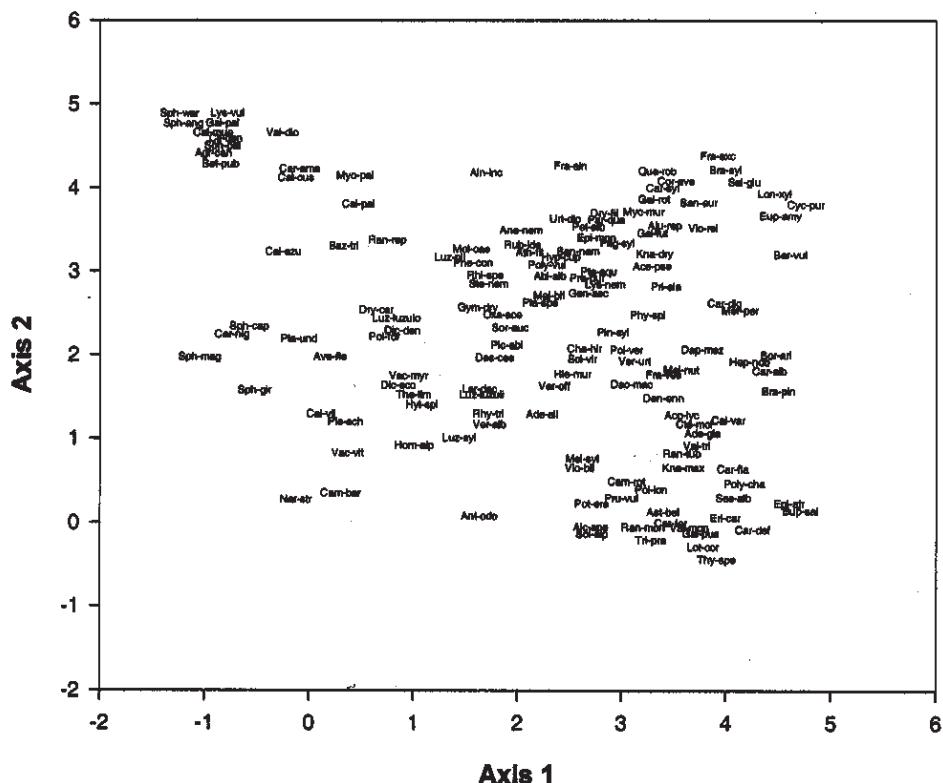
Fig. 2. DCA ordination of the species on axis 1 and 2. All species with more than 39% frequency in any TWINSPAN cluster (see Table 1) are shown. Several species positions were slightly adjusted to avoid overlapping. Taxon names are abbreviated by the first three letters of the genus name and epithet except for *Luzula luzuloides* = Luz-luzulo and *Luzula luzulina* = Luz-luzuli. See Table 1 for full names.

very poor sites are not restricted to high altitudes and subalpine spruce forests might be very rich in nutrient-demanding species (see also ZUKRIGL 1973).

TWINSPAN classification and syntaxonomy

Numerical classification cannot replace the traditional syntaxonomic methodology including manual table-sorting, the interpretation of sample and species groups using "external" information as well as the definition and delimitation of associations (DIERSCHKE 1994, GLAVAČ 1996). Nevertheless, numerical classification methods constitute a valuable tool for syntaxonomy as they help to define syntaxonomic units in a reproducible way (WILLNER 2001). In comparison with other classification algorithms, TWINSPAN additionally offers the advantage of interpreting clusters as divisions of floristic and ecological gradients and assessing their relative importance.

EXNER (2001) recently proposed a new system of fir and spruce communities for Central Europe, covering large areas outside the Alps. Because of the different geographical context,

this classification is neither directly comparable with the results of the present study nor with existing syntaxonomic systems of the Austrian Alps. In the following, we discuss our results with respect to the system of WALLNÖFER (1993), although some names used there are not in accordance with the International Code of Phytosociological Nomenclature (WEBER et al. 2000). We furthermore compare our results with those of EXNER (2001).

The TWINSPAN cluster 1 closely corresponds to *Sphagno girgensohnii-Piceetum*. The differential species *Sphagnum magellanicum* shows high frequency and fidelity. Clusters 2 and 3 resemble *Equiseto sylvatici-Abietetum*, characterized by *Caltha palustris*, *Cardamine amara* and *Valeriana dioica*. Although Wallnöfer assigns the *Equiseto-Abietetum* to the base-rich alliance *Abieti-Piceion* (*Athyrio-Piceetalia*), TWINSPAN puts it into the acidophilous group, which mostly corresponds to *Piceion excelsae* (*Piceetalia excelsae*). EXNER (2001) suggests that spruce forests on relatively nutrient-poor moist soils should be separated from *Equiseto-Abietetum* and assigned to the association *Equiseto-Piceetum* (see JIRÁSEK 1996) (*Piceion excelsae* s.str. = *Eu-Vaccinio-Piceenion*; EXNER 2001).

Clusters 4 to 6 consist of subalpine spruce forests which closely resemble *Larici-Piceetum*. Highly frequent differential species of the *Larici-Piceetum* are *Calamagrostis villosa* (species group 111) and *Homogyne alpina* (species group 110). They are almost missing in cluster 7, which corresponds to *Luzulo nemorosae-Piceetum*. Cluster 4 shows a slight tendency towards the nutrient-rich associations *Veronico latifoliae-Piceetum* and *Adenostylo alliariae-Abietetum* due to the frequent occurrence of *Veratrum album*, *Viola biflora* and *Adenostyles alliariae*. Following EXNER (2001), this community can be considered to be the same as *Athyrio alpestris-Piceetum* (see also JIRÁSEK 1996).

Clusters 8 to 11 consist of higher montane to subalpine spruce forests. In terms of Wallnöfer's typology, clusters 8 to 10 represent a transitional community between the nutrient-poorer *Larici-Piceetum* (*Piceetalia excelsae*) and the nutrient-richer associations *Veronico-Piceetum* and *Adenostylo alliariae-Abietetum* (*Athyrio-Piceetalia*), characterized by *Adenostyles alliariae*, *Saxifraga rotundifolia*, *Viola biflora* (species group 011), *Veratrum album* (species group 100) and *Stellaria nemorum* (species group 101). Additionally, nutrient-demanding species, which are typical for *Athyrio-Piceetalia* associations in general, e.g. *Fragaria vesca*, *Veronica urticifolia* and *Lamiastrum galeobdolon* agg. are frequent. Interpreting the *Adenostylo alliariae-Abietetum* as a mesic, nutrient-rich higher montane to subalpine community (EXNER 2001) obviously corresponds better to the TWINSPAN result than limiting the association to forests with an understorey rich in hygrophilous species and dominated by tall herbs (WALLNÖFER 1993). Clusters 8 to 10 can thus be easily assigned to this association. Cluster 11 belongs to *Larici-Piceetum*.

Clusters 12 to 15 primarily correspond to *Luzulo nemorosae-Piceetum*. However, cluster 15 has a transitional character pointing towards the nutrient-richer *Galio rotundifolii--Piceetum*. As compared to cluster 7, *Fagus sylvatica* is more frequent.

Interestingly, TWINSPAN separates clusters corresponding to the same association in Wallnöfer's system (*Larici-Piceetum* and *Luzulo nemorosae-Piceetum*) already on the second level of divisions. This considerable differentiation is better reflected by splitting acidophilous fir and spruce forests of high altitudes into the nutrient-richer *Larici-Piceetum* s.str. and a nutrient-poorer association (*Calamagrostio villosae-Piceetum*; EXNER 2001).

[38]

Similarly, the acidophilous communities of the montane belt might be split into the nutrient-richer *Luzulo nemorosae-Piceetum* s.str. and a nutrient-poorer association (*Bazzanio-Piceetum*; EXNER 2001). The TWINSPAN indicator species *Senecio nemorensis* agg. and *Hieracium murorum* and *H. bifidum* (clusters 8 to 15) are important differential species of both the *Larici-Piceetum* and *Luzulo nemorosae-Piceetum* against the nutrient-poorer associations *Calamagrostio villosae-Piceetum* and *Bazzanio-Piceetum* (EXNER 2001).

Clusters 16 to 22 show high frequencies of *Erico-Pinetea* species such as *Sesleria albicans*, *Polygala chamaebuxus* and *Erica carnea* (species group 000). Clusters 16 to 19 can be assigned to the subalpine association *Adenostylo glabrae-Piceetum*. A slight tendency towards the association *Adenostylo alliariae-Abietetum* rich in tall-herb species is visible in cluster 16. According to the moderate frequency of *Erico-Pinetea* elements and the high portion of *Veronica urticifolia*, cluster 18 tends to *Veronico-Piceetum*. Clusters 20 to 22 closely correspond to the montane *Calamagrostio variae-Piceetum*. Chorological differentiations within this group are indicated by species which are very rare or missing in the northwestern Alps such as *Euphorbia amygdaloides*, *Cyclamen purpurascens*, *Helleborus niger*, *Dentaria enneaphyllos* and *Cirsium erisithales* and the southern Alpic element *Anemone trifolia* (species group 001). Eastern and southern Alpic species are restricted to clusters 21 and 22. Accordingly, EXNER (2001) proposes the delimitation of geographical vicariants.

Cluster 23 nicely fits the description of *Galio-Piceetum*, a montane nutrient-rich association over silicate substrates. Cluster 24 might be assigned to the montane limestone association *Adenostylo glabrae-Abietetum*, slightly tending to the subalpine *Adenostylo alliariae-Abietetum* as indicated by *Adenostyles alliariae*, *Saxifraga rotundifolia* and *Viola biflora*. In cluster 25, calcicolous species have rather moderate frequencies, suggesting a transitional position between *Galio-Piceetum* and *Adenostylo glabrae-Abietetum*. Clusters 26 to 28 are related to *Calamagrostio variae-Piceetum*, mainly representing a thermophilous variant of submontane to lower montane sites. In correspondence with TWINSPAN, EXNER (2001) separates these communities from the montane *Calamagrostio variae-Piceetum* s. str. (clusters 20 to 22). Geographical differentiation is indicated by the southern Alpic species *Anemone trifolia* (species group 001) in clusters 26 and 28. According to EXNER (2001), three geographically vicariant associations can be distinguished.

On the whole, all clusters can be more or less accurately described by means of Wallnöfer's system. However, several clusters obviously represent transitional types between associations. Out of 13 Alpic spruce and fir associations, only 8 are more or less reproduced by one or several TWINSPAN clusters. Five associations do not clearly coincide with any TWINSPAN cluster. According to EXNER (2001), these associations cannot be retained in the sense of Wallnöfer (*Bazzanio-Piceetum*, *Adenostylo alliariae-Abietetum*) or must be completely abandoned (*Asplenio-Piceetum*, *Veronico-Piceetum* and *Carici--Piceetum*). Three associations are split on the second level of divisions (*Larici-Piceetum*, *Luzulo nemorosae-Piceetum* and *Calamagrostio variae-Piceetum*), which suggests that they should be further divided (see EXNER 2001). Besides, putting the *Carici albae-Piceetum* and the *Asplenio-Piceetum* into the montane alliance *Abieti-Piceion* was a clear misclassification.

The differential species combination of these associations includes important diagnostic species of the *Chrysanthemo-Piceion*.

Syntaxonomic orders are fairly well reproduced by TWINSPAN. The *Piceetalia excelsae* on acid soils and the *Athyrio-Piceetalia* on base-rich carbonate and silicate substrates are more or less separated by the first TWINSPAN division. Accordingly, the corresponding diagnostic species are well separated on the first level of division (see also Table 3, Fig. 2). Almost all diagnostic species mentioned for the *Piceetalia excelsae* (e.g. *Avenella flexuosa*, *Luzula luzuloides*, *Calamagrostis villosa*) belong to species group 11, except for *Calamagrostis arundinacea* (species group 101) and *Luzula luzulina* (species group 100). The diagnostic species combination of the *Athyrio-Piceetalia*, including *Daphne mezereum*, *Mercurialis perennis* and *Calamagrostis varia*, is entirely reproduced within the TWINSPAN species group 00.

On the level of alliances, the correspondence between TWINSPAN results and Wallnöfer's typology is considerably weaker. Within the acidophilous sample group 0, three alliances can be discerned: Cluster 1 belongs to the *Betulion pubescentis* (*Piceetalia excelsae*), and clusters 2 and 3 can be assigned to *Abieti-Piceion* (*Athyrio-Piceetalia*). Despite a strong tendency towards the *Chrysanthemo-Piceion* (*Athyrio-Piceetalia*), clusters 8 to 10 might be assigned to the *Piceion excelsae* (*Piceetalia excelsae*). Clusters 4 to 7 and 11 to 15 belong to the *Piceion excelsae* (*Piceetalia excelsae*).

Within the base-rich sample group 1, corresponding to the order *Athyrio-Piceetalia*, the TWINSPAN division on the second level might be interpreted as the differentiation between the subalpine alliance *Chrysanthemo rotundifolii-Piceion* (clusters 16 to 22) and the montane alliance *Abieti-Piceion* (clusters 23 to 28) in the sense of WALLNÖFER (1993), reflecting the overriding role of temperature values on the second DCA axis (Table 5; see also Table 2). The diagnostic species of the *Chrysanthemo-Piceion* and the *Abieti-Piceion* are both spread over different TWINSPAN species groups, but remain well separated from each other. However, the TWINSPAN division better corresponds to the differentiation proposed by EXNER (2001), ranking the edaphic factors higher than the altitudinal gradient. Actually, none of the TWINSPAN indicator species of clusters 16 to 22 (see Table 3) are restricted to the higher montane and subalpine zone. *Homogyne alpina* is rather widespread on carbonate bedrock of the montane belt (see also EWALD 1997, WALENTOWSKI 1998). The differential species of the *Chrysanthemo-Piceion* are frequent in clusters 16 to 19, but become rare in clusters 20 to 22. In contrast to Wallnöfer, we separate the nutrient-poor alliance *Calamagrostio variae--Abietion* (clusters 16 to 22) on dry carbonate substrates regardless of altitude from the mesic and nutrient-rich communities (clusters 23 to 28, *Abieti-Piceion* s.str. = *Galio-Abietenion*; EXNER 2001). The differential species combination of the *Calamagrostio-Abietion* consists of *Erico-Pinetea* elements including *Sesleria albicans*, *Galium pusillum* agg., *Carduus defloratus* agg. and others, and this combination is reproduced by TWINSPAN within the first subgroup of species group 000.

We conclude that the major outlines of the syntaxonomic system presented by Wallnöfer are supported by TWINSPAN. However, the differentiation of alliances is only partly reproduced. The crucial syntaxonomic problem of the delimitation of associations is not adequately solved. The preliminary results of the Central European survey carried out by

EXNER (2001) apparently fit better to the patterns indicated by TWINSPAN on the scale of the Austrian Alps.

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APPENDIX

Authors of the data used for TWINSPAN (Table 1).

Author(s)	Source	Date of publication	No. of samples
AICHINGER	*Angew. Pflanzensoziol. (Wien)* 1: 21–68	1951	1
AICHINGER	*Carinthia* II 153/73: 227–292	1963	6
AMANN	Dipl. thesis, Univ. Innsbruck	1992	2
AMBERGER	Dipl. thesis, Univ. Agriculture, Wien	1991	1
BLAB	unpubl.		84
DANKL	Dipl. thesis, Univ. Agriculture, Wien	1996	3
EGGLER	*Pflanzendecke des Schöckls,* Graz	1952	7
ENGLISCH & STARLINGER	*FBVA-Berichte* 87: 25–54	1995	11
ENNEMOSER	PhD. thesis, Univ. Salzburg	1985	41
ESSL	unpubl.		1
ESSL	*Stapfia* 57: 1–265	1998	10
EXNER	unpubl.		68
FREIMANN	Dipl. thesis, Univ. Wien	1999	45
GRABHERR et al.	unpubl. (project *Hemeroby of Austrian forests*)		760
GUMPELMAYER	unpubl. manuscript, Univ. Innsbruck	[1967]	35
HAUPT	*Veröff. Tiroler Landesmus. Ferdinandeum* 63: 11–67	1983	22
HERBST	PhD. thesis, Univ. Salzburg	1980	33
HÖFLER & WENDELBERGER	*Verh. Zool.-Bot. Ges.* 100: 112–145	1960	18
JEGLITSCH et al.	*Mitt. Forstl. Bundes-Versuchsanst.* 112: 1–162	1975	41
JELEM	*Mitt. Forstl. Bundes-Versuchsanst.* 117: 1–164	1979	178
JELEM & KILIAN	*Forstl. Bundes-Versuchsanst.* 20: 1–93	1966	62
JELEM & KILIAN	*Mitt. Forstl. Bundes-Versuchsanst.* 93: 19–61	1971	29
JELEM & KILIAN	*Mitt. Forstl. Bundes-Versuchsanst.* 111: 1–167	1975	41
JELEM et al.	*Forstl. Bundes-Versuchsanst.* 14: 1–93	1964	54
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