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Festucetalia valesiacae communities and xerothermic vegetation complexes in the Central Alps related to environmental factors

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with 36 figures and 5 tables

Abstract. An important theme of this paper is to search for more generalities of pattern and diversity on the level of vegetation complexes. For this purpose the landscape sections chosen as investigation areas not only represent different mosaic habitats but have been selected according to climatic gradients and different human impact to test, e.g., hypotheses of correlations between vegetation structure and these gradients. As test areas dry physiotopes in the Central European Alps were chosen (Valle d'Aosta, Valais, Vinschgau [= Valle Venosta], Valtellina, Oberinntal/Engadin, Rhein near Chur). After a census of all plant communities present there and – if necessary – vegetation analysis with classical relevés, altogether about 150 vegetation-complex relevés, each covering landscape sections of about 0.5 ha, have been sampled. After classification and ordination of the vegetation-complex data sets it was possible to typify the complexes and to differentiate the valley regions by these complexes.

Using precipitation and temperature data for a CCA of the complex relevés it was possible to determine significant correlations with a meso-xerothermic and a meso-xerohygric gradient. This was the basis for deriving a landscape ecological differentiation of the valley areas. The DCA for the grassland communities and for the vegetation complexes results in a similar structure, but the individuality of the valley regions becomes much clearer in the vegetation-complex ordination.

Characteristic structures of plant species diversity and vegetation type diversity can be generalized on the one hand for the Festucetalia valesiacae communities and on the other hand for the dry grassland vegetation complexes. For both, significant positive correlations were found between humidity and high species/community diversity, which is consistent with the hypothesis of resource-limitation of phytodiversity. Mainly Trifolio-Geranietea communities contribute to the higher community richness of the more mesohygric complexes. The communities and complexes of the subcontinental, dry inner valleys show decreased species/community diversity but are rich in rare, stenoecious species and vegetation types. Vegetation complexes of the different valley regions (consisting mainly of corresponding but also of shared vegetation types) have a similar diversity pattern. Definable successional traits characterize xerothermic complexes of the different valleys. Shallow rocks are naturally free from forest, but many areas, especially in the more humid regions, are severely endangered by succession processes.

The inner-alpine dry vegetation is part of the Eurasian thermomontane vegetation complexes and has a high conservation value.

Keywords: vegetation pattern, multivariate methods, climatic gradients, species- and community diversity, resource-limitation of phytodiversity, successional pathways.

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Abbreviations and geographical names

Names and abbreviations of the valley regions which will be used (other names or translation in brackets). The geographical names regularly follow the official languages, in some cases (Vinschgau, Val Müstair, Engadin), one of the official languages of a valley region.

A = Valle d'Aosta (Vallée d'Aoste, Aosta valley): Italy
W = Valais (Wallis): Switzerland
V = Vinschgau (Valle Venosta): Italy with Münstertal/Val Müstair: Italy and Switzerland
P = Valtellina/Poschiavo: Italy; Poschiavo: Switzerland
I = Oberinntal/Engadin (Inn valley): Oberinntal (Upper Inn valley): Austria; Engadin: Switzerland, differentiated into Unterengadin (Lower Engadin) and Oberengadin (Upper Engadin)
R = Churer Rheintal (Rhein valley near Chur including Domleschg/Albula/Prättigau): Switzerland

Abbreviations of the grassland communities and of vegetation complexes and valley regions:
m = montane form, o = oreal form; [] = abbreviations valley regions; () complexes
ab = Astragalo onobrychidis-Brometum erecti (complex) m = montane, o = oreal form [I]
as = *Allium lineare* (= *A. strictum*)-*Stipa pennata* s.str. comm. (complex) [I]
cb = Centaureo bracteatae-Brachypodietum (complex) [P]$^{+}$
cc = Carici humilis-Chrysopogonetum grylli (complex) [P]
cf = Carici supinae-Festucetum valesiacae (complex) [V]
df = Diplachno serotinae-Festucetum valesiacae (complex) [P]
ds = *Dracocephalum austriacum-Stipa eriocaulis* subsp. *austriaca* comm. (complex) [I]
ea = Ephedro helveticae-Artemisietum vallesiacae (complex) [W]
hs = *Helianthemum***grandiflorum-Stipa eriocaulis* subsp. *austriaca* comm. (complex) [I]
mc = *Melica ciliata-Centaurea maculosa* comm. (complex) [P]
me = *Melica ciliata-Erysimum rhaeticum* comm. (complex) [V]
mk = Melico ciliatae-Kochietum prostratae (complex) [A]
ok = Onosmo pseudoarenariae-Koelerietum vallesianae (complex) [A]
pb = Pulsatillo montanae-Brometum erecti (complex) [A, W]
pc = *Petrorhagia saxifraga-Calluna vulgaris* comm. (complex) [P]
pf = Poo xerophilae-Festucetum valesiacae (complex) [V]
pk = Poo xerophilae-Koelerietum gracilis (complex) [I]
sa = *Saxifraga bulbifera-Stipa capillata* comm. (complex) [W]
sk = Stipo capillatae-Koelerietum vallesianae (complex) [W]
ss = Stipo capillatae-Seselietum variae (complex) [V]

ta = Tunico saxifragae-Artemisietum campestris (complex) m = montane, o = oreal form [P]
tb = *Thymus vulgaris-Bromus erectus* comm. (complex)
tc = Teucrio montani-Caricetum humilis (complex) [I]
tt = Tunico-Artemisietum-/Centaureo bracteatae-Brachypodietum complex (transition type) [P]
x = "Xero-Brometum" (= "Xerobrometum rhaeticum") [R]

Synonyms, which are important for the Syntaxa (old names in brackets): (*Centaurea bracteata*) = *Centaurea jacea* subsp. *gaudinii*, (*Diplachne serotina*) = *Cleistogenes s.*, (*Poa xerophila*) = *Poa molinerii*, (*Tunica saxifraga*) = *Petrorhagia s.*

+ actuel relevés: *Brachypodium rupestre* s.l. = *rupestre* s.str. and mainly subsp. *cespitosum* (Host) H. Scholz, det. H. Scholz, Braun-Blanquet relevés: *Brachypodium pinnatum* s.l. (including *B. rupestre*)

* = substitutes species epithet: example *Stipa*austriaca* = *Stipa eriocaulis* subsp. *austriaca*

col. = column in the tables, ch = character species, d = differential species, all = alliance, ord = order, cl = class, comm. = community

1 Introduction

For 30 years, mainly beginning with the publication of Tüxen (1973), methods of vegetation-complex analysis have been elaborated, and during this time results have accumulated. Review articles have been published, summing up the progress of the associated research regarding the analysis of vegetation-pattern generalities (reviews Schwabe 1991a, 1997a); case studies, e.g. for **different physiotope types** including river valleys, mires, grassland complexes, tundra vegetation, urban and ruderal habitats, have been published by various authors (see review Schwabe 1991 a, b), followed by more recent studies by Deil (1997, 2003), Köppler (1995), Köppler & Schwabe (1996), Goetze (2000), Schiller (2000). Raster-based studies were developed, e.g., by Zoller et al. (1978), Hegg et al. (1993) and Schmidtlein (2000, 2003).

These papers and others have shown that on the one hand, it is possible to detect definable types of vegetation complexes, while on the other hand, generalizations can be made regarding the spatial arrangements of vegetation types.

By now this has become the basis for a number of important insights, for example:

- in geomorphologically differentiated landscapes, there are combinations of micro-habitats and their specific vegetation types which, even in large transects of several hundred kilometres, have characteristic diversity patterns (see e.g. Köppler 1995, Schwabe 1999, Goetze 2000).
- anthropogenic influences often increase the diversity of vegetation types (this is expressed by the "intermediate disturbance hypothesis" of Connell & Slatyer 1977).
- vegetation complexes are often tools to answer questions concerning the mosaic structure of animal habitats. They often correspond closely to the habitats of animal species or groups of target animal species, a fact which has already been proven by studies of the bird species *Emberiza*

cia (Schwabe & Mann 1990), the day-flying butterflies *Parnassius apollo* and *Iphiclides podalirius* (Schwabe et al. 1992), dragonflies (Buchwald 1994a, 1994b, 1994c) and others; further examples are given in Kratochwil & Schwabe (2001).

As yet, however, little is known about generalities of pattern, heterogeneity and diversity concerning vegetation complexes. Moreover, there are deficiencies in the field of comparative analyses of defined vegetation complexes of large transects and their characteristics concerning general features such as phytodiversity at different spatial scales.

As model landscapes for the hypothesis and questions formulated below, Central Alpine dry physiotopes were chosen as investigation areas.

The main hypothesis is that in the inner-alpine dry regions, there are gradients of climatic factors and of human impact which can be correlated with the combination and diversity of plant species, the community structure and the vegetation pattern and its diversity.

The most important questions are as follows:

1. Do the floristic structure of the Festuco-Brometea communities and the community structure of the vegetation complexes reflect the gradients in a similar way, or will the two systems react differently to the specific gradients? (Chapters 4–7)
2. Do the vegetation complexes reflect possible successional traits? (Chapter 5.1)
3. Are there definable traits of ruderalization in the investigated vegetation complexes? (Chapter 5.2)
4. Are there correlations between diversity characteristics, environmental factors and human impact? Is there a resource-limitation of phytodiversity? (Chapter 6)
5. Are there correlations between ecological gradients and vegetation complexes? (Chapter 7)
6. Are there vegetation types and complexes with corresponding structural analogies in the different valley regions? (Chapter 7)
7. Are there possibilities for ecological differentiation of the valleys at the landscape level, based on the results so obtained? (Chapter 7.2).

2 Study area: physical and biogeographical background of the Central Alpine dry areas

2.1 Topography, geology and soil characteristics

The investigation area is surrounded by the highest summits of the Alps (e.g. Mont Blanc 4810 m a.s.l., Matterhorn 4478 m a.s.l., Piz Bernina 4049 m a.s.l., Ortler 3905 m a.s.l.). All investigated valley regions (Fig. 1) were once glaciated, and were formed and influenced by glacial dynamics of the last (Würm) glaciation (Welten 1982, Burga 1987, 1988, Burga & Perret 1998). Some parts of the valleys were especially subject to fluvial erosion and physicochemical weathering during the postglacial period;

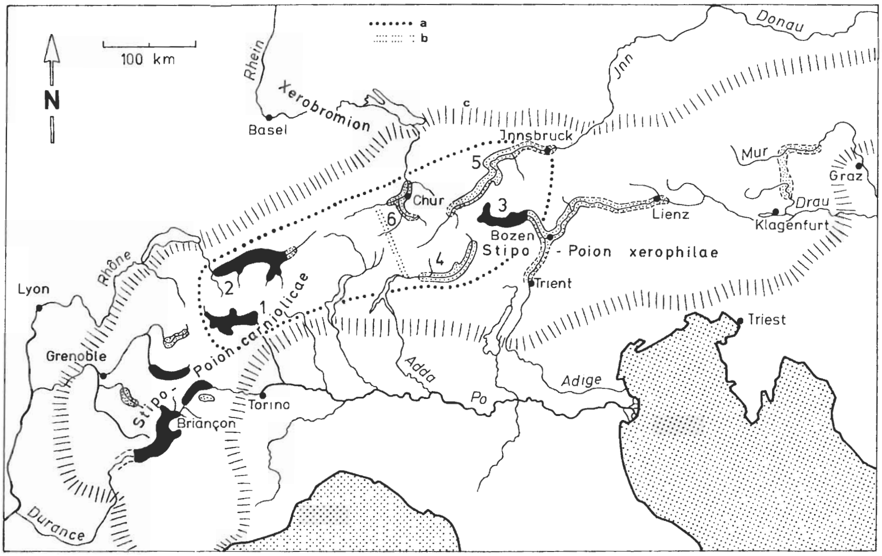


Fig. 1. The investigation area in the centre of all inner alpine dry areas. 1: Valle d'Aosta, 2: Valais/Wallis, 3: Vinschgau/Valle Venosta and Münstertal/Val Müstair, 4: Valtellina/Poschiavo, 5: Engadin/Oberinntal, 6: Rhein valley near Chur including Domleschg and Albula.
a: border of the investigation area, b: border between the Stipo-Poion carniolicae and the Stipo-Poion xerophilae (the Chur area lies in a transition zone between the latter alliance and the Xerobromion), c: border of the Alps. Black: valleys extremely; dotted: valleys less extremely dry areas according to Braun-Blanquet (1961).

these valley sections are characterized by steep slopes (e.g., parts of Poschiavo/Valtellina). Particularly in the Valle d'Aosta, there are still large moraine deposits in the submontane zone. The valley regions that have been shaped by glacio-fluviatile actions are located in the areas with the highest elevations and are orientated in the west-east or east-west direction, and hence have landscapes of high specificity. Each valley region has its own glacial and biogeographical history.

In the following, some generalities of the valley regions will be addressed (according mainly to Gwinner 1978, Labhart 1992, Schweizer 1991, Staub 1948, Zulauf 1963 and geological maps, named underneath the references). In Appendix I the geology of the vegetation complex relevés will be described for each plot area.

The investigation areas are mainly dominated by the following geological characteristics:
- Helvetian nappes (lower part of the Central Valais, south-facing slopes in the Rhein valley near Chur)
- Penninic nappes (parts of the Valais, Valle d'Aosta, Rhein valley near Chur/Domleschg, Inn valley)
- autochthonous crystalline zone and east-alpine nappes s.l. (Oberinntal/Engadin, Vinschgau, Valtellina).

The characteristics of the rock material are as follows:

- In the lower central Valais, there are gneisses (Follatères region), whereas in the sections further upstream limestone and base-rich schists predominate (in places there are loess deposits: e.g. Follatères, Saillon).
- The Valle d'Aosta contains mainly silicate rocks and partly calcareous schists (mostly with loess or moraine deposits); a special characteristic is the presence of large moraine deposits, even in the submontane zone; serpentine rock is very rare: Guyot (1935), Zulauf (1963).
- In the Vinschgau region, mainly silicate rocks and schists (partly with loess or moraine deposits) are found (Buschardt 1979, Rampold 1997, Strimmer 1974).
- In the Valtellina/Poschiavo region, again, there are silicate rocks; locally, base-rich dioritic rock and gabbro rock occur. The upper valley region near Bormio is characterized by limestone.
- The Oberinntal/Engadin is dominated by limestone and Bündner schists (rich in calcium carbonate); additionally, there are granite and amphibolite rocks in the upper parts of the Unterengadin and the Oberengadin (Schweizer 1991).
- The Rhein valley near Chur is dominated by limestone (south-facing slopes of the Calanda) and Bündner schist, with local concentrations of rock fall material and debris accumulation ("tumas" near Domat/Ems, Dolf 1974).

All in all, the geology is very diverse and partly influenced by base-rich glacial deposits and loess. It was not possible to find different valley regions with identical geological and petrographical characteristics. But even in silicate rock-dominated valley regions, there are small base-rich or even calcium carbonate-rich patches.

Some soil characteristics were already described in detail by Braun-Blanquet (1961). In the core areas of inner-alpine dry habitats, soils are mainly not fully developed, for various reasons: the substrates may be very recent (e.g. moraine, loess) and there may have been human degradation. Thus, on calcium-rich substrates various types of rendzina are found, on siliceous substrates ranker-type soils. Especially in the Valle d'Aosta, with a maximum of dryness from June to September, there are only poor eluviation processes in the soil; in summer, in the case of high evaporation, rising water percolation causes calcareous deposits. Therefore, white calcium-rich crusts exist in the soil to a depth of 30 to 40 cm (calcareous crust soil in the sense of Braun-Blanquet 1961). This "steppe-like inner-alpine dry soil" (Braun-Blanquet 1961) as an extreme form of rendzina soil mainly occurs in the Valais and in the Valle d'Aosta and in some parts of the Vinschgau. Often the profiles are disturbed or even amputated by landslips or talus deposits.

2.2 Climate

(The climate data refer to: Aistleitner 1998, Burga 1987, Fliri 1974, Florineth 1974a, Knoch & Reichel 1930, Schüepp 1962, Uttinger 1965, 1968, Pedrotti et al. 1974, Pichi-Sermolli & Chiarino-Maspes 1963, Schenk 1949, Walter & Lieth 1960)

– General characteristics, sunshine and wind

The inner-alpine situation characterized by orographic seclusion and a west-east or east-west direction of the climatically most "extreme" valleys,

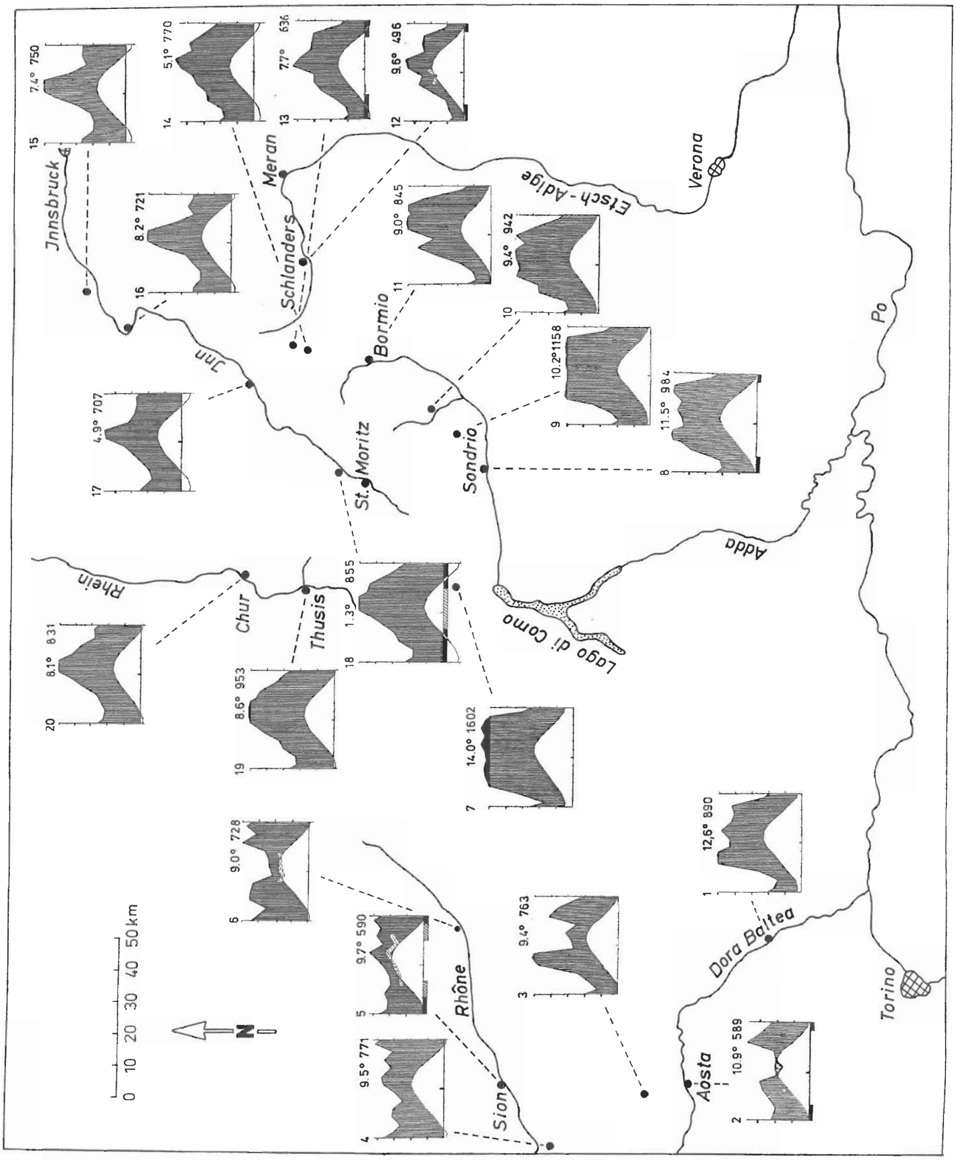


Fig. 2. Climate diagrams of the investigation area according to Walter & Lieth (1967); also included is one diagram of the insubric region (7: Chiavenna). 1–3: Valle d'Aosta (1 Ivrea, 2 Aosta, 3 Valpelline), 4–6: Valais (4 Martigny, 5 Sion, 6 Brig), 8–11: Valtellina, Poschiavo (8 Sondrio, 9 Teglio, 10 Brusio, 11 Bormio), 12–14: Vinschgau, Münstertal/Val Müstair (12 Schlanders/Silandro, 13 Taufers, 14 Santa Maria), 15–18 Engadin, Oberinntal (15 Imst, 16 Landeck, 17 Scuol, 18 Bever), 19–20: Rhein valley near Chur (19 Thusis, 20 Chur).

the Valle d'Aosta, Vinschgau and Wallis, causes an "intrinsic climate" with lower precipitation on the leeward sides, particularly in the centre of the valleys. Furthermore, there are large amplitudes of extreme annual temperature values, low humidity in the centre of the valleys, strong insolation of the slopes with southern and western exposure, and valley breezes that cause drying out.

The duration of sunshine is long; the following 30-year average values have been recorded: for Sion (Valais, 549 m) 2094 hours/a, for St. Moritz (Engadin, 1832 m, near plot I1) 1805 hours/a (in comparison with Zürich/Kloten, 431 m, 1532 hours/a) (Schüepp 1962). The valley breaks are characterized by more humid and less extreme conditions. Vineyards can be found in the Valle d'Aosta up to about 1200 m a.s.l.; here cultures of *Prunus dulcis* grow up to about 1100 m (Peyronel 1964), in the Valais up to 1100 m a.s.l. (Guyot 1935), and in the Vinschgau up to about 800 m a.s.l. (Rampold 1997). In parts of the valley mouth regions we find influences of insubrian climate (e.g. Valtellina). We define the term "insubrian" according to, e.g., Oberdorfer (1964): humid regions with high summer precipitation and milder winter temperatures in the southern Alps and the surroundings (see, e.g., the diagram of Chiavenna in Fig. 2).

Wind is an important factor, e.g. in the upper Vinschgau (Rampold 1997), in the Valais (Burnand 1976, Gams 1927, Yoshino 1964) and in the Oberinntal. South-Foehn influences can be observed in Innsbruck for 58 days a year (Fliri 1974).

– Precipitation (Fig. 2, 3)

Concerning precipitation values, there is no linear correlation between the vertical gradient of the inner-alpine dry regions and the precipitation. Normally, precipitation values are much higher in the valley mouth region and become lower in the leeward zones of the core areas.

According to Fliri (1974), the climatological stations in the Valle d'Aosta (Aymavilles, Aosta, Montjovet, Roisan, Valpelline), in the Valais (Sion), in the Vinschgau (Schlanders, Prad, Matsch, Taufers) and in the Oberinntal (Ried) are among the 20 localities having the lowest precipitation values in the whole Alps. The precipitation year-to-year variabilities are as follows: the Inn valley/Engadin: 14.5 %, Valais: 16.9 %, the Valle d'Aosta: 19.5 %, Vinschgau: 21.2 % and the basin of Bormio (Valtellina): 22.3 % (in comparison to the wet Isar-system: 13.1 %). The precipitation amounts reach their peak in October/November (Aosta), in August (Valais), in July/August (Vinschgau). The minimum values are reported for February and July (Valle d'Aosta), in April (lower Valais) and from January to April (Vinschgau) (Fliri 1974).

In the Valtellina region, the valleys extend from SSW to NNE. Moreover, this area is influenced by the strong gradients of the Lake Como region, characterized by insubrian climate even in the upper zones and influenced by the inner-alpine climate. The valley mouth regions of the Valle d'Aosta under submediterranean influence are characterized by even higher precipitation values and generally higher humidity rates than the inner valley areas.

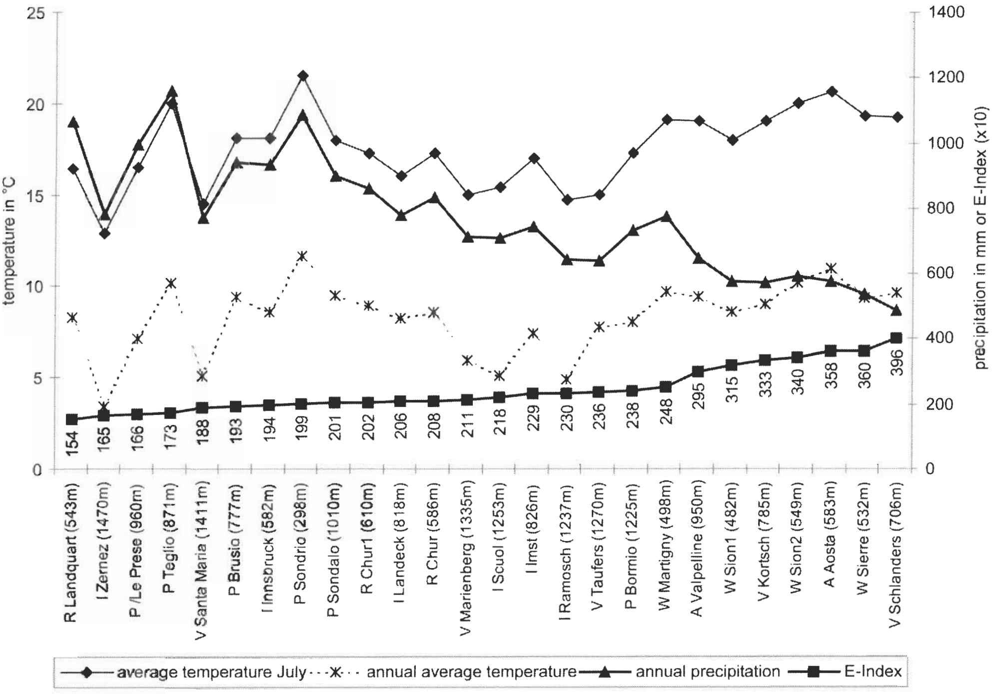


Fig. 3. Climatic data from selected stations (with details of valley region, locality and altitude a.s.l.) in the study area in relation to the Ellenberg Index (x 10); further explications in the text. Climatological data according to Burga (1987), Fliri (1974), Schüepp (1962), Uttinger (1965, 1968).

The same applies to the valley mouth region of the Valais, influenced by Lake Léman (higher humidity, less extreme temperature amplitudes).

– Temperature (Fig. 2, 3)

According e.g. to Ozenda (1988, Fig. 19), there should be a strong and linear correlation between the average annual temperature of a station and the sea level; the temperature decreases about 0.56/0.57 K per 100 m. Körner (2003) indicates as an average value a lapse rate of 0.60 K per 100 m for the Central Alps. According to Ozenda (l.c.) the deviations mostly should not exceed 1 °C. However, if these rules are applied to the inner-alpine dry areas, there will be severe deviations. As examples, the measured values for some stations of Valle d'Aosta, Vinschgau, Valtellina/Poschiavo and Rhein near Chur were compared with the projected values. About 1 °C deviation or more was found in the upper Engadin (Bever with its cold air lakes turned out to be colder than expected) and especially in Valtellina (Bormio and Sondalo characterized by stronger submediterranean influences and deviations up to 2 °C). In general, the special climate of the inner-alpine dry areas reduces the local rate of temperature decrease along the vertical gradient.

It should be taken into consideration that the minimum temperature values recorded in the valley bottom areas (e.g. station Bever, Fig. 2: 18) may not be representative of the plot areas. Nevertheless, the local climate, in which the plot areas are embedded, is reflected.

– Needle ice

Needle ice is an important factor in dry grassland ecosystems, as was previously observed by Kaiser (1926) and Reimers (1951). Lawler (1988) gives a worldwide overview showing that little attention has yet been paid to needle ice in dry grassland ecosystems. Körner (2003) and Veit (2002) discuss the phenomenon and refer to the alpine environment. Needle ice occurs if the soil is moist (not frozen), and very cold air (mostly in the night) comes into contact with the topsoil and causes cooling. Needles stand perpendicular to the soil surface, and in the course of a few days can grow up to 15 centimetres with different ice layers; the one-day layer is usually about 2–3 cm. The upper soil particles are integrated in the ice layer, plant individuals can be eradicated and on slopes microsolifluction is reinforced by needle ice. In Chapters 4.2.1 and 4.2.2 we shall describe the effects of needle ice in the pioneer communities of Valle d'Aosta and Valais.

2.3 Some aspects of vegetation history and human impact

The work of Burga & Perret (1998) presents a comprehensive history of the vegetation in Switzerland and its surroundings. Some taxa of dry grassland already existed in the late glacial period (as indicated by pollen or macrofossils): for instance, *Artemisia*, *Ephedra distachya* type, *Centaurea scabiosa*, *Helianthemum nummularium*, *Onobrychis montana*, *Plantago media*, *Sanguisorba minor*, *Saponaria ocymoides* and *Arenaria serpyllifolia.* The Chenopodiaceae and *Artemisia* species characterized by high pollen percentages and a clear peak in the late glacial period are of special interest. It is not possible to differentiate the pollen types of Chenopodiaceae (B. Ammann, in litt.). *Bassia prostrata*, e.g., has a disjunct area, being scattered in the Ebro basin and in the Valle d'Aosta. Its main distribution area is in the steppe region of eastern Europe, including the Pannonicum (Schwabe 1995). Zoller (1995) proposes the hypothesis that, concerning the Engadin, species of the steppe vegetation found the best dispersal conditions in the late-glacial period, when *Artemisia* was dominant.

During the postglacial forest-dominated periods, particularly species of dry grassland were gradually vanishing, though some probably survived in rock habitats or moraine/debris-slide habitats in the montane zone. In the Valais region, there is one pollen profile near the present Festucetalia valesiacae communities of Mont d'Orge near Sion (Lac du Mont d'Orge/ Sion 640 m a.s.l.). Human impact began there with the Neolithic Period (about 7000 BP).

Another pollen profile next to the Astragalo-Brometum complex in the Lower Engadin (Chanoua, Ardez: near our plot areas I11–13) was studied by ZOLLER & ERNY-RODMANN (1994) and ZOLLER et al. (1996). In the Lower Engadin region the first evidence of human impact was found at the beginning of the late Neolithic Period about 3600 BC (ZOLLER et al. 1996). At that time, "Lärchwiesen" (*Larix* meadows), which still occur today e.g. in the Upper Engadin and Poschiavo, were already present. Since the Bronze Age (about 3750 BP), in some cases earlier, the forest vegetation has been seriously declining in most if not all of the investigated valley regions, due to the impact of livestock (especially sheep, goats) and even fire.

During the last centuries, nearly all habitats of the inner-alpine dry vegetation, except some rock habitats, have been profoundly influenced by livestock. Nowadays, only a few of the investigated landscape sections are still being grazed, mainly in the Vinschgau (cattle grazing), in the Val Müstair/Münstertal (goats, cattle), and to a lesser extent in Poschiavo/Valtellina (cattle, goats) and the Lower Engadin (goats). The vanishing influence of livestock is, to some degree, documented by the comparison of the actual relevés and the relevés of BRAUN-BLANQUET (1961); see Chapter 4.2, 5.1.

2.4 State of knowledge: phytogeographical and phytosociological investigations in the Central Alpine dry areas

The classical studies of GAMS (1927) and BRAUN-BLANQUET (1961) have already focussed on the botanical research history of the Valais (GAMS l.c.) and the inner-alpine dry vegetation in general (BRAUN-BLANQUET l.c). The monograph written by BRAUN-BLANQUET (1961) is the most important phytocoenological basic work, particularly concerning the Festuco-Brometea communities. It comprises all regions with inner-alpine dry vegetation, including the western valley regions in France and Italy (Durance, Romanche, Maurienne/Tarentaise, Susa), the eastern parts in Austria (Puster and upper Drau valley, Kärnten, upper Mur valley in the Steiermark) and the southern parts in Italy (Trento, Bolzano, Eisacktal).

According to BRAUN-BLANQUET (1961), the inner-alpine dry regions are characterized by different alliances of the Festuco-Brometea. The alliance Stipo-Poion carniolicae with its western distribution (Valle d'Aosta and Valais in our investigation area), and in the eastern part, the Stipo-Poion xerophilae (Vinschgau, Valtellina, Inn region in our investigation area) are part of the order Festucetalia valesiacae. According to BRAUN-BLANQUET (l.c.), the Rhein area near Chur still shows great floristic similarities to the Central European Xerobromion (Brometalia erecti). BRAUN-BLANQUET (l.c.) includes the latter in the Brometalia, whereas ROYER (1987, 1991) proposes to assign it to the Festucetalia valesiacae. Most of BRAUN-BLANQUET's sample areas still exist and were available for actual phytosociological relevés.

Even though BRAUN-BLANQUET (l.c.) worked out the relationship between Festuco-Brometea communities and several forest communities (especially of the Ononido-Pinion alliance), as well as some other plant communities, vegetation complexes were not treated. Some aspects of vegetation complexes are included in the classical work of GAMS (1927), presenting a synusial approach to the famous vegetation of "Les Follatères" (Valais), and in the publication of FREY (1934), about the "Walliser Felsensteppe" (rock steppe of the Valais: see Chapter 4.3.2).

3 Methods

3.1 The physiotope concept, screening of the investigation area, distribution and size of plot areas

The plot areas for the vegetation complex relevés were chosen according to the **physiotope concept** (physiotope = geotope sensu THANNHEISER 1992). According to NEEF (1981), the physiotope is defined as follows: "in landscape science a topographical unit in which, as a result of the previous development, certain homogeneous stable conditions in the substance regime prevail (nutrient regime, water regime, air regime of the soil)".

In filigree landscapes, as in the case of rock-/moraine-dominated habitat complexes, such physiotopes form the type of a microgeomorphological catena in the sense of THEURILLAT (1992) or "small-patch landscapes" (FORMAN 1995). The concept of delimiting plot areas for vegetation-complex relevés in accordance with physiotope borderlines was already introduced and discussed, e.g., in the review given by SCHWABE (1997a), and in the textbook of KRATOCHWIL & SCHWABE (2001). The physiotope-based vegetation-complex relevés are linked to the **topical scale**, the comparison of different valley regions is done according to the **chorical scale**.

To minimize the varying parameters, the investigated valley regions were chosen with reference to the following points of view:
- central topographic position in the Alps
- occurrence of gradients of dryness and continentality between the valleys and within the valley
- occurrence of south-/southwest-/southeast-facing slopes
- representation of managed plot areas (grazing), if management is still practised.

To minimize the varying parameters of the plot areas the following criteria were used for the selection:
- rock- or loose sediment-dominated habitat complexes with mainly open dry grassland or pioneer vegetation **including areas of naturally non-forested dry habitats**. Sometimes, the latter may be concentrated in small rock areas. In the case of moraine habitats, some subhabitats can occasionally be absent.
- only south-/southeast-/southwest exposure (in two cases in the valley bottom shallow northeast exposure as well)
- (nearly) no fertilizer application.

The six valleys were chosen on the basis of these specified criteria, and in each valley, 9–30 plot areas were selected for analysis. About 350 possible plot areas were chosen from topographic maps 1 : 25,000. After field screening, 151 were chosen. Ground truthing turned out to be the only suitable method to find such plot areas, because there were many disturbance factors such as huts, fireplaces, high-voltage lines, chair lifts, and heavily fertilized areas. The plot areas were – if possible – distributed evenly in the areas of the valley slopes with southern or western exposure. In the case of the Valais (only the area between Martigny and Raron was chosen as comparable to the Valle d'Aosta) and the Rhein valley near Chur (only remnants and many fertilized habitats) it was not possible to study more than 13 (Valais) or 9 (Rhein) plot areas. Concerning the Valle d'Aosta (31 plot areas), Vinschgau (35), Valtellina (33) and Inn/Engadin (30) the data base is very comprehensive. Most of the plot areas are situated in the submontane, medium-montane and oreal zones; in the Valtellina region there are plots in the colline zone, in the Engadin in the subalpine zone as well (see Appendix I).

Only when differentiated physiotope types were present, such as moraine and rock physiotopes, several plot areas close to each other were selected, for instance in the centre of the Valle d'Aosta. There are also some valley sections without any plot areas, because the investigated physiotope type is lacking there; this can happen, for example in constricted sections of a valley.

Concerning **altitudinal gradients** of the xerothermic vegetation, investigations were concentrated in the Valtellina and the Engadin area. The Oberinntal/Engadin is especially suitable for the study of such gradients in the main valley from 750 m up to about 2000 m a.s.l. In other valleys, such as Valais and the Valle d'Aosta, clear gradients can mainly be observed in branch valleys (e.g. Valais: Visper valleys, Valle d'Aosta: Valle di Cogne). Branch valleys were studied in the Valle d'Aosta: Valpelline valley, Vinschgau: Münstertal/Val Müstair, and in the Valtellina valley region: Poschiavo. In all cases, the main valleys are also characterized by an altitudinal gradient of the xerothermic vegetation.

The plots of the investigated habitat types have a minimum area of approximately (0.3) 0.5 ha (SCHWABE 1999). Nearly all vegetation-complex plot areas in this study range between 0.3 and 1 ha. Some areas are smaller than 0.3 ha and are merely fragments; in these cases it was not possible to find larger plot areas (in the vineyard region and the upper valley of Valtellina: 7 plot areas and in the Rhein valley near Chur: 6 plot areas, see Appendix 1). That is, 2/3 of the latter vegetation-complex plot areas are more or less fragments, and therefore these remnants of former larger areas have to be interpreted in a special way. An example of the boundary of a plot area is given for A4 (Valle d'Aosta, Morgex: 1000 m a.s.l.) in SCHWABE et al. (1992: Fig. 5).

3.2 Phytosociological relevés

3.2.1 Sampling at the plant community level

The quality of vegetation-complex relevés depends on an exact knowledge of the relevant vegetation types. The work of BRAUN-BLANQUET (1961) and numerous special regional (mostly at least 30 years old) publications are valuable sources of information about plant communities. Nevertheless, anthropo-zoogenic impact has changed in the meantime, new community types such as therophyte-dominated communities (see Chapter 3.2.2), fringe and shrub communities have been described, and methodological standards have changed. Therefore, about 500 new relevés were made. In this paper, we focus on Koelerio-Corynephoretea and especially on Festuco-Brometea communities, also taking into account publications presenting relevés, e.g. those of DELARZE (1986, 1988) and THEURILLAT (1992).

The classical relevés were restricted to the vegetation-complex plot areas; in the ordination diagrams, they were indicated with an additional a, b, c (see Appendix 2). Nearly all vegetation-complex plots include localities of several classical phytosociological relevés. The cover-abundance scale follows BARKMAN et al. (1964). The cover-abundance data were not indicated in Table 3, but included in the ordination and the cluster diagram. Presence classes correspond to DIERSCHKE (1994: 192). We would like to point out that, e.g. in the Melico-Kochietum complex of the Valle d'Aosta, classical relevés of the Onosmo-Koelerietum were taken (because small areas of the latter association are present in this complex) and that this is possible in other complex types as well.

In this study we focus on the vegetation complexes using – whenever possible – the correct nomenclature for the syntaxa. However, there are still some types which have not yet been described. They are provisorily termed "communities" or stands.

3.2.2 Treatment of therophyte-dominated ephemeral vegetation and Fulgensietum patches

Especially the submontane stands in the Valle d'Aosta and the Valais, which are rich in bases, are characterized by a specific ephemeral vegetation, flowering early in March/April. BRAUN-BLANQUET (1961) included these therophyte communities in his Festuco-Brometea relevés. GAMS (1927) considered these communities to be synusia. KORNECK (1975) was the first to introduce a strict separation of the therophyte communities occurring in the Valais and the Valle d'Aosta, which now belong to the class Koelerio-Corynephoretea. The stands of the Fulgensietum fulgentis, which are very characteristic elements especially of the moraine stands in the Valle d'Aosta and the loess stands in the Valais, were also included in the Festuco-Brometea communities by BRAUN-BLANQUET (1961).

Fig. 4. Example of a well-definable microhabitat (shallow soil in a rock niche) with the **basiphytic** Clypeoletum jonthlaspi as a therophyte-dominated vegetation type (enlarged format: habitus of fruiting *Clypeola jonthlaspi*). Valais (plot area W8, 530 m a.s.l., 8.4.1991).

Normally, therophyte-dominated communities grow in microhabitats that are nearly devoid of other phanerogams (Fig. 4). Stands characterized by fine ground, slow creeping of wet soil in winter and spring, needle ice effects or anthropogenically initiated compaction of soil are often covered with large patches of therophytes. There are only scattered individuals of chamaephytes and hemicryptophytes. These stands were regarded as communities on their own (parts of mosaic complexes in the sense of MÜLLER 1970). As they are part of vegetation-complex relevés, the spatial relationship to the Festuco-Brometea communities is documented.

Therophytes can also occur in gaps between the dominant chamaephyte-/hemicryptophyte vegetation. Often the longer-lived plant individuals provide "safe sites" for the germination of single therophyte individuals or whole cohorts. This type is regarded as part of the Festuco-Brometea community.

3.3 Sampling of vegetation complexes

In all plot areas, samples were taken in different seasons including the early spring (end of March/April), late spring (May/June) and summer (August).

A standardized questionnaire was devised, including space for topographical, vegetation-type data and classical relevés. Additionally, the complete inventory of woody species was recorded to give evidence of successional stages (Chapter 5.1).

The cover/abundance ratings of the existing vegetation types, proposed by Wilmanns & Tüxen (1978) and Schwabe & Mann (1990), were used.

Upper limits for small stands are (see Kratochwil & Schwabe 2001: 131)

1 m²	Bryophyta/Lichenes communities rock fissure vegetation (1 m fissure with plant individuals)
1 m²	Koelerio-Corynephoretea communities
10 m²	grassland, fringe communities
100 m²	shrub communities
1000 m²	forest communities.

Contact vegetation and abiotic elements were registered as "x". The cover-abundance ratings for woody species were registered according to the scale of Barkman et al. (1964).

Since the treatment of microcoenoses and of single plant populations has not yet been standardized, we used the following criteria:

- The treatment of therophyte-dominated stands is introduced in Chapter 3.2.2.
- Plant species with espalier growth, often covering large areas as does *Juniperus sabina*, were estimated separately. The same applies to lianas such as *Hedera helix*.
- All vegetation types and vegetation stands that could be typified were taken into consideration (example Fig. 5).

It was not possible to include the Bryophyta- and Lichenes-synusia and -communities. This would be a research project for a whole group of specialists. The publication of Buschardt (1979), who studied the lichen species in some of the Central Alpine valleys, has shown that there are many systematically problematic species groups, e.g. *Diploschistes*. Only selected types, such as the Fulgensietum fulgentis, were estimated, but not included in the diversity calculation in Chapter 6.

Table 4 shows the presence data of the complex relevés completed by additional cover/abundance data. Table 5 is ordered according to the same structure and presents the woody species, especially taking into consideration the succession potential. Additionally, cluster analysis and DCA were elaborated with the same material (Chapter 4, 5).

Most of the work concerning the sampling of vegetation complex relevés was done in the years 1991, 1992 and 1994; additional observations were recorded in 2000 and 2002.

3.4 pH values

pH values were measured in H_2O dest. with fresh earth taken from 1–5 cm soil depth. In the evening of the sampling day soil material and water were suspended in the proportion 1 : 2.5, as recommended by Steubing & Fangmeier (1992) and Bogenrieder (1993), and the suspension was measured after 2 hours with an electrometrical pH-meter (Behr company). Each value refers to 6 samples with only slight variance. The measurements were all made in early summer. Comparisons of the values in the Vinschgau between May and August revealed no differences.

3.5 Flower phenological data

Data on the flowering periods of Koelerio-Corynephoretea-, Festuco-Brometea- and Trifolio-Geranietea species were recorded in all plot areas during the whole investigation period; additional data from Delarze (1986) and Strimmer (1974) were included.

3.6 Indices for the calculation of climatic characteristics

There are many indices with which it is possible to calculate gradients of continentality/oceanity or of aridity/humidity. The Gams index (Gams 1931, 1932 a, 1932b, Michalet 1991) was checked with negative results. The main problem is that there are no linear correlations between precipitation and sea level in the inner Alps. The aridity index ("Indice d'Aridité") of De Martonne (see e.g. Lauer 1952 and Schweizer 1991) was calculated for July; the more moderate conditions will only be taken into account to a lesser extent.

An index of great ecological significance had been proposed by Ellenberg (1963, 1996), and already used to differentiate Festucetalia valesiacae climates from Brometalia climates and to determine the composition of *Fagus-/Quercus-/Pinus sylvestris*-proportions in natural forests. The index is defined by the quotient of the average July temperature (°C) and the average annual precipitation (mm), and explains very well the floristic gradients of the forest communities. Kuhn (1973), who studied the importance of dry periods in Switzerland, examined the index and stated that it is of high significance. For the Festuco-Brometea area in Central Europe, the following correlations were determined: in regions of Central Europe where the quotient is below 30, Brometalia communities occur, whereas if it is higher there are Festucetalia valesiacae communities. This proportional similarity does not apply to the Alps (see Fig. 3); here E-index > 30 is restricted to the climatically extreme valley regions, the Valle d'Aosta, Valais, and Vinschgau. In the investigation area, Festucetalia valesiacae communities occur between E-index 15 and 40. In many cases, values higher than 30 correlate with dry periods in the year (Kuhn 1973). Climatological stations showing high index values (e.g. Aosta 34, Sion 32) are also characterized by dry periods in summer (Kuhn l.c.). In Fig. 3, we present climatological stations of the investigation area and their relevant Ellenberg indices. In Chapter 7.1, the phytocoenological data are correlated with the elements of the Ellenberg indices.

The aridity index for July and the Ellenberg index detect the climatically extreme valley regions characterized by hot-summer, dry conditions:

the Valle d'Aosta, Valais and Vinschgau. The striking differences between the aridity indices of, e. g., Schlanders and Aosta are caused by the different annual distribution of precipitation in the Vinschgau and Valle d'Aosta (see above). Both indices are only rough approaches, which do not reflect mesoclimatic conditions of the local climate.

3.7 Multivariate methods

A multivariate data analysis was carried out with the help of the PC-ORD Software Package (version 4.17) (McCune & Mefford 1999). For comparison of all classical relevés of Festuco-Brometea communities and of all vegetation-complex relevés of the different valley regions, we used the Detrended Correspondence Analysis (DCA) and the cluster analysis (see below). To detect probable correlations with environmental variables, the Canonical Correspondence Analysis (CCA) was used. (Transformation of the Braun-Blanquet/complex-relevé scale: r = 1, + = 2, 1 = 3, 2m = 4, 2a = 5, 2b = 6, 3 = 7, 4 = 8, 5 = 9.)

– DCA

The DCA (Hill & Gauch 1980) as an eigenanalysis ordination technique and based on reciprocal averaging (Hill 1973) was used as the gradient length of axis and clearly exceeds 2 SD. Only in the case of a gradient length of < 2 SD or < 1.5 SD is the Principal Components Analysis (PCA) recommended (Jongman et al. 1987, ter Braak & Prentice 1988). Further advantages of the DCA are: elimination of the arch (horseshoe) effect by detrending (relevant if the eigenvalue of the first axis is much higher than that of the second one), SD scaling (4 SD total species/community turnover, 1–1.5 SD half species/community turnover), higher reliability even in the case of heterogeneous data sets (e.g. ecological gradients: Ejrnaes 2000), and a better basis for interpretation especially in the case of high species/community numbers (see e.g. Oksanen 1983, Kenkel & Orloci 1986, Kent & Ballard 1988).

In our data set (species, plant communities), the results in the case of downweighting of rare species/communities were not convincing (in contrast e.g. to Oksanen 1983), probably because especially rare species and communities are the most specific stenoecious taxa/vegetation types in our data set. Therefore we used the DCA without downweighting. The axes were rescaled, the number of segments was 30.

– CCA

Temperature data, annual precipitation data and pH values were taken as environmental variables. The data sets for annual and July temperatures both follow a normal distribution, and the data on precipitation show only a slight asymmetry. Therefore, we did not transform the data logarithmically (ter Braak 1986). The CCA analysis follows Hill's method (SD scaling: Hill 1979). Furthermore, as preferred by Palmer (1993), the site scores as well as the choice of linear combination scores were optimized (optimization of vegetational similarity of sites: optimal adaptation concerning environmental variables). The significance of the axis was checked by a Monte Carlo Test (null hypothesis is no relationship between matrices).

– Cluster analysis
WARD's method (hierarchical grouping), which is based on minimizing increases in error sum of squares (WARD 1963, ORLOCI 1967, WISHART 1969) was applied as linkage method. According to McCUNE & GRACE (2002) WARD's method is an effective and useful tool. The Euclidean (Pythagorean) distance serves as distance measure. The objective function E (WISHART 1969) in the diagram is the "sum of error sums" of squares from each centroid to the items in that group. The dendrogram is also scaled by the percentage of information remaining.

3.8 Nomenclature of taxa and syntaxa

3.8.1 Taxa

Besides older floras (see Chapter 2.4) there are extensive and excellent floras from the last 40 years for the investigation area (HESS et al. 1967 ff., PIGNATTI 1982, POLATSCHEK 1997 ff. and ZOLLER 1964). The progress made especially in the field of floristic exploration has been summarized by MONTACCHINI (1988) for the Valle d'Aosta and by POLDINI (1988) for the Vinschgau (Valle Venosta). In this study the nomenclature of vascular plant species follows AESCHIMANN & HEITZ (1996). Exceptions are Poaceae: CONERT (1998) and *Brachypodium* (SCHOLZ 1968), *Rosa*: HENKER in WEBER (2003), *Centaurea* and *Onosma* (PIGNATTI 1982). The nomenclature of Bryophyta follows DIERSSEN (2002) and that of Lichenes, WIRTH (1995).

It was not possible to differentiate all critical taxa within the framework of this study, especially in the case of some types of the *Festuca ovina* complex and *Thymus*. Voucher specimens of some critical groups were kindly identified by specialists: *Brachypodium, Stipa*: H. SCHOLZ, Berlin; *Thymus*: W. GUTERMANN, Wien. For the comparisons with the BRAUN-BLANQUET relevés, it was necessary to adapt the nomenclature to those used in our study. In some cases subspecies that were differentiated by BRAUN-BLANQUET (1961) have meanwhile been put together. In other cases it was hardly possible to determine the synonyms at the species level (e.g. *Thymus* sectio *serpyllum*, see JALAS 1970: "extreme complexity of the pertinent synonomy").

In the following we list such cases:

- *Brachypodium* was recorded as *B. pinnatum* agg. by BR.-BL.; H. SCHOLZ differentiated *B. rupestre* s.l., *B. rupestre* s.str. and *B. rupestre* subsp. *cespitosum.* In the Valtellina valley region mainly *B.*cespitosum* occurred. *B. pinnatum* was not found.
- *Erysimum canescens* and *E. helveticum*, which were differentiated by BR.-BL., have since been united to *E. rhaeticum* (AESCHIMANN & HEITZ 1996, PIGNATTI 1982).

- *Galium mollugo* subsp. *corrudifolium*, which showed high presence according to the records of Br.-Bl., doesn't exist in the investigation area according to newer results. It is very likely that *Galium lucidum*, which occurs with high presence in the current relevé material, was meant instead (see also Hess et al. 1967 ff.).
- *Koeleria eriostachya* was frequently recorded by Braun-Blanquet (1976) for the dry grassland vegetation of the Lower and Upper Engadin. We were not able to detect *Koeleria eriostachya* in our plot areas. According to Conert (1998) and Welten & Sutter (1982) this species had seldom been recorded for the subalpine-alpine zone of the Engadin (1600–2300 m a.s.l.).
- *Onosma tauricum* subsp. *cinerascens*, *O. t.* subsp. *helveticum* and *O. tridentinum*, which were differentiated by Br.-Bl. have, according to Pignatti (1982), meanwhile been united to *Onosma pseudoarenaria*.
- "*Stipa pennata*" has to be differentiated into *Stipa pennata* s.str. (seldom), and mainly *Stipa eriocaulis* subsp. *eriocaulis* (recorded for our plot areas in Valle d'Aosta) and subsp. *austriaca* (recorded for our plot areas in Valtellina, Vinschgau, Inn/Engadin, Rhein near Chur, once in Valle d'Aosta); for *Stipa* see also Martinovsky (1965) and Moraldo (1986). In the Valais no specimens were sampled; evidently, however, besides *Stipa eriocaulis* subsp. *austriaca* there are transition types between subsp. *eriocaulis* and subsp. *austriaca* (Theurillat, in litt.). Conert (1998) and Aeschimann & Heitz (1996) only give records for subsp. *austriaca* in Switzerland.

3.8.2 Syntaxa

Most of the communities have already been described by other authors, and in some cases we present new types as rankless "communities". Furthermore we will make suggestions for nomina inversa. The nomenclature of plant communities mostly follows Braun-Blanquet (1961), additionally Korneck (1975), Mucina et al. (1993a, 1993b), Royer (1987), Theurillat (1992), Mucina & Kolbek (1993a, 1993b, 1993c). A list of the recorded vegetation types is not printed separately, but is integrated in Table 3. This table is ordered according to formation types.

4 Results

4.1 Flower phenological and area-geographical characteristics

– Flowering time

For the understanding of diversity patterns, phenological processes are important. According to Körner (2000), the length of the vegetation period may be one of the driving forces for high diversity.

The main flowering time of particular species is not identical in the investigated valley regions, but there are always species groups with synchronous flowering. The following-up phases are described and named according to characteristic species of the inner-alpine dry habitats. In general, even in the dry summer period, the phenological diversity of flower phases is large. In the following, we summarize the phases (Table 1), and give a survey of the flowering periods.

Table 1. Flower-phenological phases, diagnosis of the distribution area, life forms of entomophilic species as well as *Carex*, *Stipa pennata* and *S. eriocaulis* in the inner alpine dry areas, which are included in Tables 2, 3 (according to field observations in the years 1990 to 1995 and data of Strimmer 1974 and Delarze 1986; phenophases sensu Dierschke 1989, 1995). ++ Species with disjunct, (sub-continental) area, +++ endemic taxa for distinct regions in the Alps. Phenological data refer only to the investigated dry grassland complexes; valley regions according to the abbreviations defined above. Plant life forms: T = therophytes, B = biennial hemicryptophytes, H = hemicryptophytes, C = chamaephytes, G = geophytes. Chorotype of area according to Hess et al. 1976 ff. (H), Oberdorfer et al. 2001 (Od), Pignatti 1982 (Pg), *Stipa:* Conert 1998 (Co). Further abbrev.: mod. = moderate. Additional phenophases with lower importance in brackets.

Pre-spring (I): *Bulbocodium* phase (submontane zone: February)
Beginning of prime spring (II): *Carex humilis-Pulsatilla montana* phase (submontane zone: March)
End of prime spring (III): *Alyssum alyssoides-Carex liparocarpos* phase (submontane zone: April)
Beginning of full spring (IV): *Euphorbia cyparissias-Globularia bisnagarica* phase (submontane zone: end of April/beginning of May)
End of full spring (V): *Lactuca perennis-Stipa eriocaulis* s.l. phase (submontane zone: May/beginning of June)
Beginning of first summer (VI) (main phase of flowering of non-therophytes): *Astragalus onobrychis-Onosma pseudoarenaria* phase (submontane zone: June)
End of first summer (VII): *Hyssopus officinalis-Sempervivum tectorum* phase (submontane zone: July)
Summer (VIII): *Allium lusitanicum-Peucedanum oreoselinum* phase (submontane zone: August)
Early autumn (IX): *Artemisia campestris-Odontites luteus* phase (submontane zone: end of August and September)
Transition to autumn (X).

Especially the base-rich dry habitats of the submontane areas are rich in early-flowering therophytes. These are mostly winter annuals (e.g. *Alyssum alyssoides*, *Arenaria serpyllifolia* agg., *Medicago minima*; Frey 1934: 110), some of which germinate in phenophase I (e.g. *Hornungia petraea*). The silicate areas are poorer in such species (e.g. *Veronica dillenii, Silene armeria*); both plant species have later flowering times (phenophases IV,V). In the oreal-subalpine zones, therophytes do not play an important role, even in base-rich habitats. The therophytes especially in the Valle d'Aosta and the Valais form their own plant communities, not only synusia (Chapter 3.2.2). According to the results obtained in our investigation area, this niche is typical of those two valleys. These submontane-montane habitats are nearly free from snow; a good indicator of heavy snow influences are the old culms of *Stipa capillata*, which lie on the ground in times of heavy snowfalls (e.g. in the Valle d'Aosta above 1000 m a.s.l.); in the submontane zone, they are still erect in spring.

In summer (phenophases VI–VIII), there are hardly any therophytes. Exceptions are *Crupina vulgaris* and the hemi-parasite *Odontites luteus.*

PRE SPRING (I)

Bulbocodium phase

G Bulbocodium vernum, south european-caucas (Pg), mesohygric stands

BEGINNING OF PRIME SPRING (II)

Carex humilis-Pulsatilla montana phase

H Carex humilis, (euras)cont-submed (Od)
T Cerastium pumilum, submed-subatl (Od)
T Clypeola jonthlaspi (W), med (Pg)
T Erophila verna, euras-med (Od)
T Hornungia petraea (A, W), submed(-subatl) (Od)
H Pulsatilla montana (A, W, V), southeast-eur, stepp (Pg)
T Saxifraga tridactylites II, (III), med-submed (-subatl) (Od)
T Veronica praecox, submed (Od)
T Veronica verna, euras(cont)(-submed) (Od)
T Viola kitaibeliana (W, A), med-caucas (Pg)
Species with longer flowering period:
H Potentilla cinerea II, III, europcont (Od)
H Potentilla pusilla II, III, europcont (Od)

END OF PRIME SPRING (III)

Alyssum alyssoides-Carex liparocarpos phase

C Alyssoides utriculata (A), northeast-med (Pg)
T Alyssum alyssoides (IV), submed (Od)
T Arenaria serpyllifolia agg. (IV, V), submed (Od)
T Arabidopsis thaliana, submed-euras(subocean) (Od)
H Biscutella laevigata s.l., eastprealp-submed (Od)
G Carex liparocarpos, southeast-eur (H)
G Carex supina (V), easteur-asiat (Pg) ++
H Erucastrum nasturtiifolium, southwest-eur(subatl) (Pg)
G Muscari comosum, med-submed (Od)
T Valerianella coronata (A), med (Pg)

BEGINNING FULL SPRING (IV)

Euphorbia cyparissias-Globularia bisnagarica phase

H Anthyllis vulneraria, submed-satl (Od)
H Astragalus monspessulanus (A, W, R), med (H)
C Dracocephalum austriacum (I, W, V), easteur-caucas,
 s.stepp (H, Pg) ++
H Euphorbia cyparissias, submed-(euras) (Od)
H Euphorbia seguieriana IV, (V) (A, W, V), cont(-submed) (Od)
C Globularia cordifolia, alp-prealp (Od)
H Globularia bisnagarica, submed(-med) (Od)
H Hippocrepis comosa, submed(subatl) (Od)
T Linaria simplex (A), med (Pg)
T Medicago minima (IV, V), med-submed-centralas.,stepp (Od,Pg)
H Oxytropis halleri III, (IV), centraleur-merid (Pg)
H Stipa pennata (= joannis) (W, I), cont (Od)
H Taraxacum laevigatum s.l., submed-euras (Od)
C Thymus vulgaris, westmed (Pg)
H Trinia glauca, submed-subatl (Od)
T Veronica dillenii, mod. cont(-submed) (Od)
montane belt:
H Aster alpinus, alp(altaic)-arct(cont) (Od)
species with longer flowering period:
H Erysimum rhaeticum s.l. V (VI), westalp (Pg) +++
H Saponaria ocymoides, westprealp (-submed) (Od)
B Tragopogon dubius, submed-mod. cont (pont) (Od,Pg)
mesohygric stands:
H Ranunculus bulbosus, submed-subatl (Od)

Table 1. (cont.)

END FULL SPRING (V)
Lactuca perennis-Oxytropis pilosa phase
C Alyssum argenteum (A), V, (VI), endem. Valle d'Aosta (Pg) +++
H Astragalus excapus (V) V, (VI), southeur-pont (Pg) ++
C Ephedra helvetica (A, W, V), alp (Pg) +++
H Hieracium pilosella (IV) V, eurassubocean (Od)
H Lactuca perennis (VI), submed (Od)
T Orlaya grandiflora, med-submed (Od)
G Orobanche alba, submed-euras (Od)
G Orobanche laevis (=arenaria), submed-westasiat-subpont (Pg)
C Oxytropis pilosa, cont(prealp) (Od)
H Scorzonera austriaca (W, V) VI eastsubmed(-cont) (Od) ++
T Silene armeria, submed(-subatl) (Od)
H Stipa eriocaulis subsp. austriaca, esp. central, eastern Alps (Co) +++
H Stipa eriocaulis subsp. eriocaulis, south. Alps (Co) +++
C Thymus vulgaris, westmed (Pg)
B Tragopogon dubius, submed-mod. cont (pont) (O,P)
T Trigonella monspeliaca (A), med (Pg)
H Veronica prostrata, europcont (Pg)
species with longer flowering period:
C Fumana ericoides (A, W, P) V, (VI), med (Pg)
C Fumana procumbens V, (VI), med-pont (Pg)
H Galium lucidum V, VI, submed (Od) B82
mesohygric stands:
H Lotus corniculatus V, VI, eurassubocean-submed (Od)
H Salvia pratensis, submed (-mod. cont) (Od)
H,C Veronica teucrium, eurascont(-submed) (Od)

BEGINNING EARLY SUMMER (VI)
Astragalus onobrychis-Onosma pseudoarenaria phase
G Anthericum liliago, (west)submed (Od)
H Asperula aristata (A, W), southalp-apennin (H)
H Asperula cynanchica (R), V, submed (Od)
H Astragalus onobrychis, eastsubmed-cont (Od)
C Astragalus vesicarius subsp. pastellianus (V)VI, s.l.=southeur-pont (Pg)
T Calamintha acinos VI, VII, submed-euras (Od)
H Carduus nutans s.l., submed-euras (Od)
H Centaurea scabiosa s.l. VI, VII, euras (Pg)
T Crupina vulgaris (A, rare W), southeur-westasiat (H)
H Echium vulgare, eurassubmed (Od)
H Inula montana (A), west-med (Pg)
H Jasione montana, subatl-submed (Od)
H Lactuca perennis, submed (Od)
H Lychnis coronaria (A, W, V), med-turan (Pg)
H Medicago falcata, euras(cont)-submed
H Ononis pusilla (A), med (Pg)
C Ononis natrix VI, VII, submed (Od)
C Onosma pseudoarenaria, southeasteur-southwestasiat (Pg)
G Orobanche purpurea, submed (Od)
G Polygonatum officinale, euras(cont) (Od)
H Veronica spicata VI, VII, euras(cont) (Od)
H Silene nutans, euras(cont)(-submed) (Od)
H Stachys recta VI, (VII), submed(-mod. cont) (Od)
C Telephium imperati (A, W, V), westmed (Pg)
H Thesium linophyllum, southeasteur (Pg)
C Thymus praecox, prealp (submed) (Od)
species with longer flowering period:
H Achillea tomentosa, southeur-southsib (Pg)
H Seseli libanotis, eurascont (-submed) (Od)
H Silene otites, (mod.)cont(-submed) (Od)
H Helianthemum nummularium s.l. VI ff., eur-caucas (Pg)
H Vincetoxicum hirundinaria VI ff., eurascont-submed (Od)
montane belt:
H, Ch Calamintha alpina, alp-prealp (submed)
C,H Dianthus*sylvestris VI, VII, eastprealp(-submed) (Od)
H Onobrychis montana, eur-caucas (Pg)
H Phyteuma betonicifolium, alp (Pg)
mesohygric stands:
H Astragalus glycyphyllos, eurassubocean-submed (Od)
C, H Dianthus carthusianorum, submed(-mod. cont) (Od)
H Geranium sanguineum, mod. cont-submed (Od)
H Trifolium alpestre, mod. cont-submed (Od)
H Trifolium medium, eurassubocean (-submed) (Od)
H Trifolium montanum, mod. cont-submed (Od)

END OF EARLY SUMMER (VII)
Hyssopus officinalis-Sempervivum tectorum phase
G Allium lineare (= A. strictum) (R, I), euras-cont (Od)
G Allium sphaerocephalon, submed(-subatl) (Od)
G Anthericum ramosum, submed-satl (Pg)
H Dorycnium germanicum, eastprealp(-osubmed) (Od)
C Hyssopus officinalis (A, W), submed-med-cont (Od)
C,H Linum tenuifolium, submed (Od)
H Ononis pusilla (A), med (Pg)
C Sedum album, (prealp-)submed-subatl (Od)
C Sedum rupestre s.l., mod. cont-submed (Od)
C Sedum sexangulare, mod. cont-osubmed (Od)
C Sedum telephium, eastsubmed-mod.cont (Od)
C Sempervivum arachnoideum, alp (Od)
C Sempervivum tectorum, prealp-alp (Od)
C Teucrium chamaedrys, submed-med (Od)
C Teucrium montanum, submed (Od)
B Verbascum lychnitis, submed-mod. cont (Od)
Species with longer flowering period:
H Achillea nobilis, submed-eurascont (Od)
H Centaurea maculosa, east-alp (Pg) +++
H Centaurea vallesiaca, west-alp (Pg) +++
H Leucanthemum adustum (montane), prealp-southeur (O,P)
H Petrorhagia saxifraga (VI)VII, VIII, submed (Od)
H Scabiosa columbaria (montane), submed-subatl (Od)
H Scabiosa gramuntia (VI), VII, VIII, southeur (Pg)
H Stipa capillata VII(VIII), cont(-submed) (Od)
H Thymus oenipontanus (=glabrescens) VII, (VIII), alp (Od) +++
mesohygric stands:
H Galium verum VII (VIII), euras-submed (Od)
montane belt:
H Astragalus leontinus (P, I), alp (Pg) +++
H Astragalus penduliflorus, alp(altaic)-arct(cont) (Od)
H Buphthalmum salicifolium, prealp(-submed) (Od)
H Campanula rapunculoides, mod. cont-submed (Od)
H Campanula spicata, alp, end (Pg) +++
C,H Kernera saxatilis, alp(-prealp) (Od)
H Oxytropis campestris, arc(cont)-alp(altaic),circ (Od)
H Phyteuma scheuchzeri, alp-end (Pg) +++
T,H Trifolium aureum (I), mod. cont(-submed) (Od)

SUMMER (VIII)
Allium lusitanicum-Peucedanum oreoselinum phase
G Allium carinatum subsp. pulchellum, submed-med (Od)
G Allium lusitanicum (= A. senescens subsp. montanum), cont (Od) ++
H Campanula bononiensis, mod. cont (Od)
H Chondrilla juncea, med-submed-cont (Od)
H Peucedanum oreoselinum (VII)VIII, mod. cont-submed(-med) (Od)
H Plantago serpentina (VII) VIII, prealp-alp (Od)
H Seseli annuum, mod. cont-europcont (Od)
H Seseli varium (V), pont (Pg)
montane belt:
H Gentiana cruciata, eurascont(-submed) (Od)
H Laserpitium halleri, alp (Pg) +++
H Laserpitium latifolium (I), prealp-mod. cont-submed (Od)
H Laserpitium siler, prealp (Od)
mesohygric stands:
H Bupleurum falcatum (W), eurascont-submed (Od)
H Origanum vulgare, euras-submed (Od)
H Peucedanum cervaria, eurascont-submed (Od)
H Prunella grandiflora, mod. cont-(-submed) (Od)

EARLY AUTUMN (IX)
Artemisia campestris-Odontites luteus phase
C Artemisia campestris (VIII), IX, eurascont (-submed) (Od)
C Artemisia vallesiaca IX, (X), eur-southsib (stepp) (Pg)
H Aster amellus, mod. cont (Od)
H Aster linosyris IX, (X), mod. cont-submed (Od)
H Eryngium campestre IX, (X), med-submed (Od)
H Hieracium sabaudum IX, (X), eur-caucas (Pg)
C Bassia prostrata, palaeotemp (stepp) (Pg) ++ C4 plant
T Odontites luteus (VIII), IX, (X), submed(- mod. cont) (Od)
H Pimpinella saxifraga, europ-caucas (Pg)
passing to autumn (X)

Crupina and *Odontites* germinate in phenophase II and finish the growing season in phase VI/VII (*Crupina*) and IX/X (*Odontites*). In most cases, *Crupina* only has 2–3 black achenes, which are rich in reserve substances, and has exceptionally large cotyledons, up to a length of 3 cm.

– Area-geographical characteristics

By combining the flower-phenological phases with area-geographical characteristics the subsequent four phases could be distinguished:

- Spring (phases I–III, submontane zone: February until April): Mainly in the Valais and Valle d'Aosta, this period is characterized by species with (sub-)mediterranean distribution. The other valley regions have flowering aspects with Eurasian and additional (sub-)continentally distributed species.
- Spring (phases IV–V, submontane zone: May/beginning of June): This is a phase of great importance for the species with (sub-)mediterranean distribution. The other species are divided into species with Eurasian, (sub-)continental and alpine distribution.
- Summer (phases VI–VII, submontane zone: middle of June to July): This is a phase of great importance for the species with Eurasian and alpine distribution. Additionally there are flowering (sub-)continentally and (sub-)mediterranean distributed plant species.
- End of summer, autumn (phases VIII–X, submontane zone: August to October): Species with (sub-)continental distribution like *Bassia prostrata* and *Artemisia* species (*campestris, vallesiaca*) are dominant; some Eurasian elements and a few (sub-)mediterranean elements are also present.

Discussion: Flowering time

There is no evidence that drought reduces season length (flowering phases from early spring to autumn), but there is a retardation (see below). At the beginning of the main growing season between February and March, one early flower-phenological phase quickly follows another, but in late spring and in summer there is a retardation of growth due to the dry and hot conditions. Frey (1934) realized that the growth advantage in the dry habitats of the submontane zone can be equalled or even surpassed by the more humid montane habitats in summer. Gams (1927) depicted this phenomenon in an onion-like presentation of phenological phases.

According to Dierschke (1989), there are symphenological groups in plant communities flowering simultaneously. Dierschke (1995) differentiated 10 flower-phenological phases/a for the complete flora of Germany (Dierschke 1995). It is remarkable that Koelerio-Corynephoretea-, Festuco-Brometea- and Trifolio-Geranietea communities of the Central Alps have developed flower-phenological phases that correspond quite well to the phases in Central Europe. Probably these species are mostly influenced by environmental factors such as photoperiod, light quality and quantity, and exposure to a period of cold (factors named by Levy & Dean 1998). Some molecular-biological results from the model organism *Arabidopsis thaliana* give hints that the molecular basis of this chronology is a multifunctional control system with combinatorial interactions between classes of floral genes (Theissen & Saedler 2001).

Discussion: Area-geographical characteristics
As was found in a Mesobrometum study (Kratochwil 1988), the number of area-geographical phenological phases is identical; the main differences, however, are the more important influences of the (sub-)mediterranean element even in phase III, the importance of (sub)alpine elements, and the strong dominance of (sub)continental elements in late summer and autumn.

4.2 Vegetation types of the different valley regions

In the following we list the composition of character- and differential species (in the case of communities the "diagnostic species composition") and indicate the line number of the species in Table 3; for the list of all plot areas, see Appendix 1.

4.2.1 Valle d'Aosta

Biological soil crusts and Koelerio-Corynephoretea communities
(Table 2, col. 1–4, 6, 7)

Especially the moraine physiotopes in the centre of the valley are rich in biological crusts. The Fulgensietum fulgentis, often covering several square metres, with *Fulgensia fulgens, Psora decipiens, Toninia sedifolia, Catapyrenium squamulosum, Collema tenax*/sp., and some accompanying Bryophyta such as *Mannia fragrans* and the basiphytic *Tortella inclinata* are found in microhabitats that are hot in summer and rich in fine soil. According to our investigations, pH values lie between 8 and 9. The habitat is free from phanerogams, as was already shown, e.g. by Reimers (1951) and Wilmanns (1959) for stands in Central Europe. The maximal net photosynthesis of the Fulgensietum in a xerothermic grassland complex near Würzburg/Germany was recorded in winter (but in Germany limited by low light intensities) and after rain events in summer (Hahn et al. 1989). *Diploschistes* crusts are frequent in the dry areas of the Central Alps. Buschardt (1979) published maps with his collection plots of the Fulgensietum lichens and *Diploschistes* species from the Valle d'Aosta.

Most of the Koelerio-Corynephoretea communities were characterized in the basic work of Korneck (1975). He described the Veronico vernae-Poetum concinnae from the Valle d'Aosta and the Valais, which is restricted to silicate habitats (Fig. 5), and the Trisetetum cavanillesii, which occurs in base-rich habitats (e.g. moraines). According to Korneck (l.c.), the Veronico-Poetum can mainly be found in gritty silicate rock habitats with high presence of *Cladonia foliacea*. However, this community type was also found in rock physiotopes; additionally, there were initial stages without *Cladonia* species at needle-ice habitats. If the habitats are richer in bases (pH 6.5–8) the *Poa perconcinna-Alyssum alyssoides* comm. (Fig. 6) substitutes for the Veronico vernae-Poetum, partly enriched by *Hornungia petraea.* Especially in rock physiotopes the early spring aspect of the *Poa perconcinna-Alyssum* comm. sometimes is characterized by liverworts such as

Table 2. Fulgensietum fulgentis and Koelerio-Corynephoretea communities. 1: Fulgensietum fulgentis (Valle d'Aosta 600–700 m a.s.l.), 2: Trisetetum cavanillesii (Valle d'Aosta 570–720 m a.s.l.), 3a: *Poa perconcinna-Alyssum alyssoides* community with *Hornungia petraea* (Valle d'Aosta 660–730 m a.s.l.), 3b: *Poa perconcinna-Alyssum alyssoides* community (Valle d'Aosta 510–1060 m a.s.l., Valle d. Cogne: 1 × 1900 m a.s.l.), 4: Veronico vernae-Poetum concinnae (Valle d'Aosta 600–700 m a.s.l.), 5: *Veronica dillenii-Veronica verna* comm. (Vinschgau 600–1020 m a.s.l.), 6: *Rumex acetosella-Polytrichum piliferum* comm. (Valle d'Aosta 600 m a.s.l.), 7: Sileno armeriae-Poetum bulbosae (Valle d'Aosta 610 m a.s.l.), 8: *Poa molinerii-Sedum album* comm. (Unterengadin 1400–1540 m a.s.l.). Presence in %, if < 5 relevés: absolute presence. Plot size 0.25–1 m^2.

column	1	2	3a	3b	4	5	6	7	8
valley region	A	A	A	A	A	V	A	A	I
no. of relevés	3	5	5	7	2	8	1	1	8
ch,d									
Psora decipiens	3	40	60	14	.			.	.
Fulgensia fulgens	3	40	80	.	.	.	.		.
Toninia sedifolia	3	.	20	.	.		.	.	.
Tortella inclinata	2	.	20	.	1	.	.	.	.
Diploschistes sp.	3	.	20	.	.	.	.	.	.
Collema tenax et sp.	2		.	.	.	.	.	.	.
Catapyrenium squamulosum	2	.	.	.	.	.	.	.	.
Pterygoneurum ovatum	2		.	.		.	.	.	.
Mannia fragrans	1	.	.	.	.	.	.	.	.
Linaria simplex		80	.	.			.	.	
Trisetum cavanillesii		40	.	.	.	.	.	.	.
Hornungia petraea	.	40	100	.	.		.	.	.
Cerastium pumilum		40	40	29	.	.	.		.
Alyssum alyssoides	.	100	60	100		80	.	.	25
Poa perconcinna		40	100	100	2	.		1	.
Veronica verna	.	60	.	43	1	90			25
Riccia ciliifera	.	.	.	.	2			.	.
Viola kitaibeliana	.		.	14	.	.	.	.	.
Asterella saccata	.	.	.	29	.	20	.	.	.
Arabidopsis thaliana	.		.	.	.	50	.	.	13
Veronica dillenii	.	.		.		100	.	.	13
Filago arvensis	.		.	.		40	1		.
Sedum annuum		.	.	.	.	30	.	.	.
Polytrichum juniperinum		.		.	.	20	.	.	.
Rumex acetosella		.	.			.	1	1	
Scleranthus perennis		.	.		.		1	.	.
Polytrichum piliferum	.	.	.		.	.	1	.	.
Jasione montana	.	.	.	.	.	.	.	1	.
Poa bulbosa	.	.		29		10	.	1	.
Silene armeria	.	.	.	.	.		.	1	.
Medicago minima		60	.	29	2	90		1	.
Erophila verna		40	40	57	1	20			
Myosotis stricta		40	20	29	.	10			.
Saxifraga tridactylites		40	20	29	.	.		.	
Trifolium arvense	.	.	.	.	1	80	1	1	.
Sempervivum arachnoideum		.	.	.	.	60	.	.	75
Sedum rupestre s.l.	.	.	.	.	1	30	.	1	
Scleranthus perennis	.	.	.	.	.	70	.	.	.

Table 2. (cont.)

Sedum album	.	80	60	71	1	.	1	.	100
Koeleria cristata		.	.	.	.	40	.	.	100
Poa molinerii	.	.	.	.	.	.	.	.	88
Melica ciliata	.	.	.	.	.	.	.	.	25
Cetraria aculeata	.	.	.	.	.	.	.	.	50
Phleum phleoides	.	.	.	.	.	.	.	.	38
Tortella tortuosa	.	.	.	.	.	.	.	.	38
Koelerio-Corynephoretea									
Arenaria serpyllifolia	.	100	80	86	1	100		1	50
Petrorhagia saxifraga		40	80	86	2	40	1	.	25
Sempervivum tectorum	.	.	.	29	1	.	1	1	13
Lithospermum arvense	.	40	.	14	.	40	.	.	13
Echium vulgare	.	.	.	14	.	10	.	1	13
Thymus praecox	.	.	.	14	1	10	.	.	50
Holosteum umbellatum	.	.	20	29	1	.	.	.	.
Calamintha acinos	.	.	.	86	1	.		.	63
Erodium cicutarium	.	.	.	.	1	70	.	1	.
Syntrichia ruralis	1	.	.	.	.	.	.		25
Sedum sexangulare	.	.	.	.	.	20	.	.	38
Androsace septentrionale	.	.	.	14	.	.	.	.	.
Silene conica	.	.	.	14	.	.	.	.	.
Herniaria glabra	.	.	.	14	.	.	.	.	.
Micropus erectus	.	.	.	.	.	10	.	.	.
Cerastium semidecandrum	.	.	.	.	.	20	.	.	.
Sedum dasyphyllum	.	.	.	.	.	30	.	.	.
Filago germanica	.	.	.	.	.	10	.		.
Festuco-Brometea									
Potentilla pusilla	.	.	20	14	1	70	1	.	88
Bassia prostrata juv.	.	40	20	14	.	.	.	.	.
Stachys recta	.	.	40	14	1	.	.	.	.
Helianthemum nummularium	.	.	20	14	.	.	.	.	13
Fumana procumbens	.	40	60	.	.	.	.	.	.
Crupina vulgaris	.	40	.	29	.	.	.	.	.
Silene otites	.	.	20	14	.	.	.	.	.
Carex liparocarpos	.	.	.	14	.	10	.	.	.
Globularia bisnagarica	.	.	20	.	.	.	.	.	.
Koeleria vallesiana	.	.	20	.	.	.	.	.	.
Centaurea maculosa	.	.	.	.	.	10	.		.
Festuca valesiaca	.	.	.	.	.	.	.	1	.
Festuca rupicola	.	.	.	.	.	.	.	.	25
Bromus erectus	.	.	.		.	.	.	.	25
Onobrychis montana	.	.	.	.	.	.	.	.	13
Other species									
Teucrium chamaedrys	.	40	20	29	.	10	.	.	25
Artemisia campestris	.	40	.	14	1	.	.	1	88
Nostoc sp.	1	60	.	14	.	.	.	.	13
Encalypta vulgaris	1	.	20	43	.	10	.	.	.
Racomitrium canescens	.	.	.	14	.	30	.	.	13

Additional species: 1: *Barbula acuta* 1; 2: *Papaver* sp. 40; 3 a: *Dianthus*sylvestris* 20, *Minuartia* sp. (sterile) 20; 3b: *Biscutella laevigata* s.l. 14, *Bryum argenteum* 29, *Carex caryophyllea* 29, *Minuartia mutabilis* 57, *Muscari comosum* 29, *Saponaria ocymoides* 14, *Tragopogon dubius* 14; 4 A: *Muscari comosum* 1, *Ceratodon purpureus* 1; 5: Acrocarpi 10, *Chenopodium album* 30, *Cladonia pyxidata* 10, *Erysimum rhaeticum* 10, *Euphorbia cyparissias* 10, *Hypochaeris radicata* 10, *Saponaria ocymoides* 10, *Scabiosa triandra* 10, *Vicia hirsuta* 20, *Viola tricolor* 40; 6 A: *Bryum argenteum* 1, *Galium lucidum* 1; *Ceratodon purpureus* 1, *Tragopogon dubius* 1; 8: *Achillea millefolium* 13, Acrocarpi 25, *Allium lusitanicum* 25, *Allium oleraceum* 25, *Cladonia pyxidata* 50, *Cladonia* sp. 50, *Dianthus*sylvestris* 50, *Erigeron alpinus* 13, *Euphorbia cyparissias* 38, *Galium lucidum* 13, *Hieracium pilosella* 13, *Medicago falcata* 25, *Minuartia* sp. (sterile) 13, *Peltigera rufescens* 25, *Peucedanum oreoselinum* 13, *Polygonatum officinale* 13, *Rhinanthus glacialis* 13, *Stipa*austriaca* 25, *Thuidium abietinum* 25.

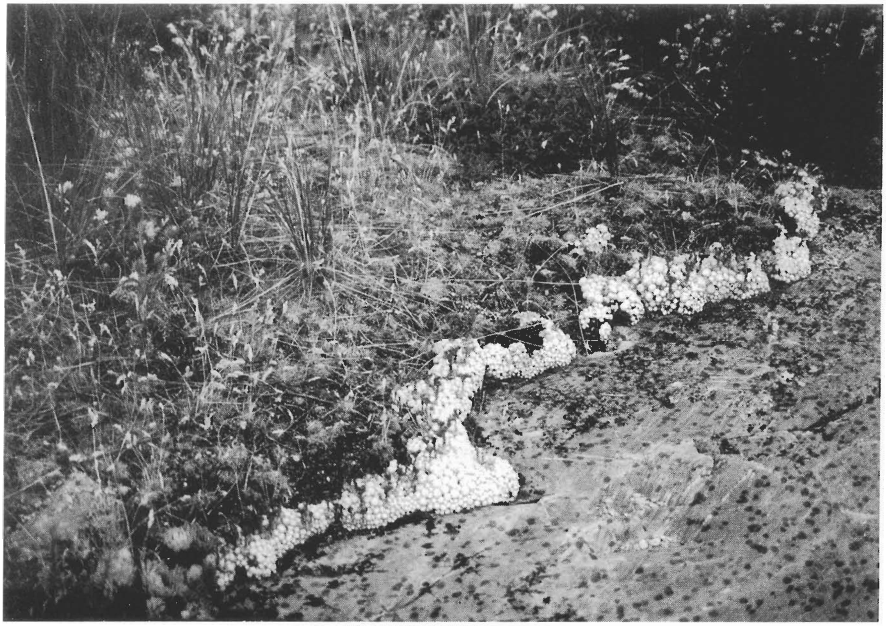


Fig. 5. Regular zonation at the edge of a silicate rock in the Valle d'Aosta (different types in the complex relevés); from right to left: *Sempervivum arachnoideum* stand (shallow, CAM plant), Veronico-Poetum concinnae (therophyte-/geophyte-dominated, using the moisture niche in spring), the hemicryptophytic/chamaephytic *Thymus vulgaris-Bromus erectus* comm. on deeper soil (plot area A27, 510 m a.s.l., 14.6.1992).

Asterella saccata (Fig. 7) with intensely green archegoniophores and *Mannia fragrans.* According to Giacomini (1952), these thallose liverworts are part of the continental-steppic bryophyte vegetation. Dierssen (2002) indicates that *Asterella saccata* occurs "along trails on steppe slopes". The vegetation period of these communities reaches its maximum at the end of March and in April, the therophytes being already dried up in May.

Additionally, the *Rumex acetosella-Polytrichum piliferum* comm. occurs on strongly acidic habitats (pH 4.9–5.8); species-poor *Rumex acetosella* stands are also found in subneutral habitats.

The Sileno armeriae-Poetum bulbosae Royer 1987 occurs in acidic habitats of the valley mouth region.

– Needle ice in the pioneer communities of Valle d'Aosta

In all the above-mentioned communities with the exception of the Sileno-Poetum needle ice could be observed in March/April. This was mapped by Schwabe et al. (1992) for two vegetation complex relevés (see Fig. 2, 3 in Schwabe et al. l.c.). The preconditions for the occurrence of needle ice are best during these months: changing diurnal/nocturnal frost action and moist soil. Some therophytes are favoured, namely those that are able to

Fig. 6. *Poa perconcinna-Alyssum alyssoides* comm. with *Hornungia petraea*, phenophase II (to the left: *Poa perconcinna*) (plot area A14, 700 m a.s.l., 29.3.1991).

germinate after this incident (e.g. *Arenaria serpyllifolia*), as well as the perennial CAM plant *Sedum album*. Although young rosettes of the CAM plant *Sempervivum tectorum* are often eradicated and translocated (Fig. 8) by combined cryopedological processes (needle ice and microsolifluction), sometimes they are able to take root again. Probably the seed bank is activated by needle ice turbation.

In the Fulgensietum fulgentis thalli are partly transported by needle ice solifluction. In Central Europe, where Fulgensietum patches are often very small, they may be severely disturbed by needle ice (WILMANNS 1959, 1989), However, they are locally supported by freezing processes as their habitats are free from phanerogamic vegetation (KAISER 1926, REIMERS 1951).

Xerothermic grassland communities

Thymus vulgaris-Bromus erectus comm. (syn. Thymetum angustanum Br.-Bl. 1961) (Table 3, col. 1)

Diagnostic species composition: (1) *Thymus vulgaris*, (2) *Fumana ericoides*, (3) *Alyssum argenteum* (serpentine), (6) *Melica ciliata*, (22) *Bromus erectus*, (48) *Oxytropis pilosa*, (170) *Koeleria vallesiana*, (174) *Centaurea valesiaca*, (176) *Stipa eriocaulis* s.str., seldom: one site (Chambave): (35) *Ephedra helvetica*. Ruderal species: (4) *Micropus erectus*.

(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/ Stipo-Poion carniolicae)

Fig. 7. *Asterella saccata* (with archegoniophores) in the shallow zone next to a rock area (right picture, left side): prime-spring aspect of the *Poa perconcinna-Alyssum alyssoides* comm. (plot area A12, 1050 m a.s.l., 25. 3. 1991). Left: dried-up *Asterella* archegoniophore (June).

This community reflects the decreasing inner-alpine character of the lower part of the Valle d'Aosta, e. g. by the presence of the Mediterranean *Thymus vulgaris*, which needs relatively mild conditions in winter. *Ephedra helvetica* can also be observed, as well as (at serpentine rocks) the endemic *Alyssum argenteum*. *Fumana ericoides* is abundant. There is no relationship to specific pH values. According to Braun-Blanquet (1961), it is an indicator community for alkalinity, but we found a range from pH 5.8 to 5.8–7.9. Although Braun-Blanquet (1961) described the Thymetum angustatum as an association, we only distinguish a community. *Thymus* is widely distributed in the Mediterranean zone (e. g. Braun-Blanquet & De Bolòs 1957: Ebro region/Spain, Nowak 1987: Liguria/Italy, map of Pignatti 1981) and occurs in many different habitats, especially in fallow land.

In the DCA (Fig. 9) the relevés of this community are situated near the submediterranean-type ones of low Valtellina. A comparison with the relevés of Braun-Blanquet (l.c.) is not possible, since the heterogeneity of the sites is extremely high and too few relevés (7) are available.

Fig. 8. Cryopedological processes in the Onosmo-Koelerietum complex of the Valle d'Aosta. *Sempervivum tectorum* rosettes are eradicated and translocated by needle-ice/microsolifluction (plot area A1, 1100 m a.s.l., 3.4.1991).

Melico ciliatae-Kochietum prostratae Br.-Bl. 1961 (Table 3, col. 2)
Character and differential species: (6) *Melica ciliata*, (7) *Agropyron intermedium*, (8) *Hyssopus officinalis*, (9) *Bassia* (= *Kochia*) *prostrata* (C4 species), (10) *Caucalis platycarpos*, (43) *Ononis natrix*, (82) *Cleistogenes serotina* (C4 species), (170) *Koeleria vallesiana*, (172) *Ononis pusilla*, (174) *Centaurea valesiaca*, (175) *Crupina vulgaris*; ruderal species as e.g. (11) *Isatis tinctoria*; more consolidated stages with (15) *Onosma pseudoarenaria*.
(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/Stipo-Poion carniolicae)

This is the most specific and most extraordinary Festucetalia valesiacae community of all valley regions (photos in Schwabe 1995, Fig. 2, 7, 8). The next distribution spots of *Bassia prostrata* are in the Ebro basin and in the Austrian "Weinviertel" (Chapter 2.3 and Schwabe l.c.). This association has a very limited distribution, being found only in the dryest centre of Valle d'Aosta with about 500 mm annual precipitation, and is restricted to moraine habitats, rich in calcium carbonate. pH values range from 7 to 8.7. The substrate coverage by the community is 30–70%; disturbances by erosion are frequent. Chamaephytes, e.g. *Hyssopus officinalis* and *Fumana procumbens*, are important in preventing slippage of debris (Fig. 7 in Schwabe 1995). The dominance of chamaephytes is remarkable: they are able to root to a depth of more than 1 m (Chapter 4.3.1). There are ruderal stands of *Bassia prostrata*, which were described as *Artemisia absinthium-*

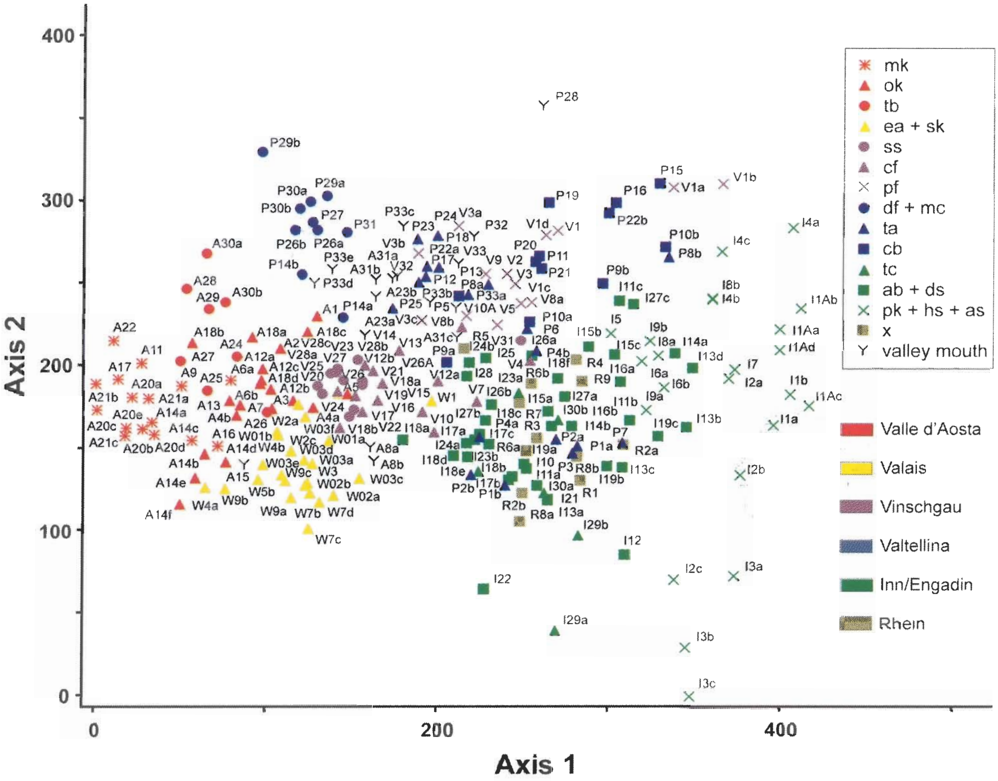


Fig. 9a. DCA of the entire data set of localities (species level); eigenvalues (λ) and gradient length (100 = 1 SD); axis 1: $\lambda_1 = 0.49$; gradient length = 4.2 SD; axis 2: $\lambda_2 = 0.27$; gradient length = 3.6 SD, axis 3: $\lambda_3 = 0.21$; gradient length = 2.5 SD. Coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space: axis 1: $r^2 = 0.46$, axis 2: $r^2 = 0.12$, axis 3: $r^2 = 0.04$; distance measure for original distance: Relative Euclidean. Symbols indicate different valleys and different valley regions.

Bassia prostrata comm. by SCHWABE (1995); this community is absent in the extreme moraine physiotopes.

In the DCA (Fig. 9), the Melico-Kochietum relevés mainly are ordered next to the mark zero of axis 1 (some relevés characterize more consolidated habitats and already include *Onosma pseudoarenaria*).

The comparison with the relevés of BRAUN-BLANQUET (1961) (Table 3, col. 2B) shows a remarkable similarity, although moraines were intensively grazed at that time. The current relevés revealed an increase of about 40–50% in presence of the C4-grass *Cleistogenes serotina*, as well as of *Stipa*eriocaulis, Galium lucidum* and the fluctuating therophyte *Crupina vulgaris*. *Carex liparocarpos* (BR.-BL.: presence class III), which is resistant to grazing, is lacking in our relevés.

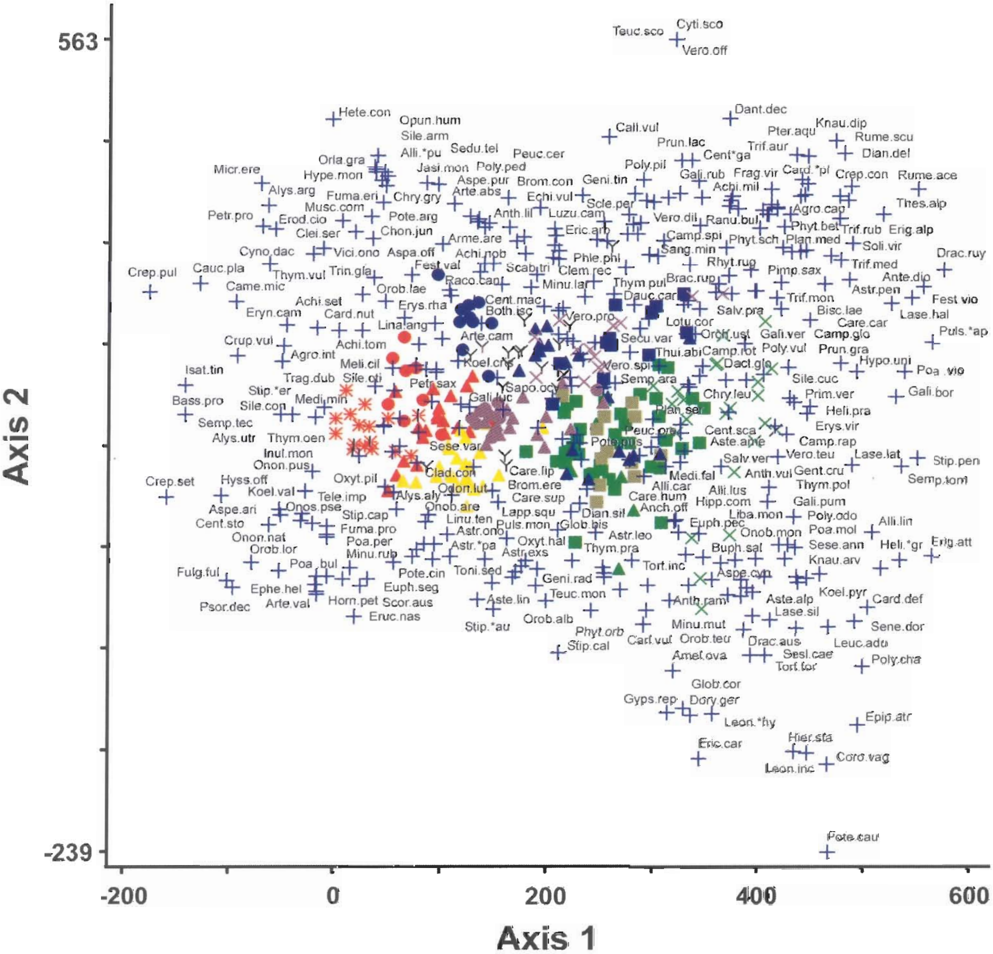


Fig. 9b. DCA of the entire data set of plant species (abbr. see Appendix 3); for all other information see Fig. 9a.

Onosmo pseudoarenariae-Koelerietum vallesianae Br.-Bl. 1961 nom. invers. propos. (Table 3, col. 3a, b)

Character and differential species: (15) *Onosma pseudoarenaria*, (16) *Inula montana*, (20) *Alyssoides utriculata* (only 3a), (36) *Artemisia vallesiaca*, (170) *Koeleria vallesiana*, (172) *Ononis pusilla*, (188) *Festuca valesiaca*, (203) *Minuartia rubra* (=*fastigiata*); 3a: (17) *Psora decipiens*, (19) *Fulgensia fulgens* s.l.; d acidic habitats O.-K. phleetosum: (58) *Koeleria cristata*, (162) *Phleum phleoides*, (163) *Potentilla argentea*, (164) *Achillea tomentosa*, (165) *Polytrichum piliferum*, (166) *Jasione montana*, (176) *Stipa eriocaulis* s.str.; montane zones: (25) *Vicia onobrychioides*.

class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/Stipo-Poion carniolicae)

At older moraines with less severe disturbance processes and in rocky habitats the Onosmo-Koelerietum builds up a chamaephyte-dominated grassland community, characterized by *Onosma pseudoarenaria*, *Inula montana*, *Artemisia vallesiaca* and others. The Onosmo-Koelerietum is restricted to the inner valley at altitudes up to 1150 m a.s.l. The A14–16 relevés belong to the moraine complex, while the others characterize rocky complexes often with small loess and moraine deposits, quite similar to the physiotope pattern in the Valais. The "artemisietosum vallesiacae Br.-Bl. 1961" is mostly associated with basic to subneutral/weakly acidic conditions; pH values range from 6.2 to 8.8. Especially loess/moraine material is covered by the *Stipa capillata* variant of the "artemisietosum". Acidic rocks without loess influence occur as well (e.g. A18). Especially in the more humid montane regions, processes of topsoil acidification can be observed; in this case the community includes acidophytic species such as *Phleum phleoides*, *Potentilla argentea*, *Jasione montana.* Sometimes deep-rooted basiphytic species, e.g. *Hyssopus officinalis*, grow together with the shallow-rooted acidophytic *Potentilla argentea.* These acidic sites (pH 4.9–6.2) are characterized by the Onosmo-Koelerietum phleetosum.

The Onosmo-Koelerietum is related to the Ephedro-Artemisietum vallesiacae in the inner Valais, which is outlined in the DCA (Fig. 9). Both communities are ordered more or less parallel to axis 1. The relevés of the "phleetosum" are ordered next to the Valtellina and Vinschgau plots.

A comparison between the Onosmo-Koelerietum relevés of Braun-Blanquet (1961) (Table 3, col. 3a, bB) and the present ones shows, as in the case of the Melico-Kochietum, that the principal floristic structure is identical. Remarkable features are the decrease of *Ononis pusilla* in the present relevés and the increase of the grazing-sensitive grass *Bromus erectus,* although it still exhibits low cover-abundance (*Bromus* 7.8 % versus 56 %, with main occurrence in the montane zone).

Communities of the valley bend region and of more humid habitats

Pulsatillo montanae-Brometum erecti Br.-Bl. 1961 nom. invers. propos., *Trinia glauca* vicariant (Table 3, col. 4S)

Character and differential species: (22) *Bromus erectus*, (23) *Pulsatilla montana*, (24) *Dianthus carthusianorum*, (25) *Vicia onobrychioides*, (73) *Trinia glauca*, (102) *Carex humilis*, (217) *Thuidium abietinum*; other more mesophytic species as (153) *Salvia pratensis*, (154) *Anthyllis vulneraria*, (155) *Trifolium montanum*, (254) *Silene nutans*, (279) *Ononis repens*, (284) *Thesium bavarum*; acidic habitats: (164) *Achillea tomentosa*, (165) *Polytrichum piliferum*, (168) *Armeria arenaria.*

(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/Stipo-Poion carniolicae)

This community occurs in the Valle d'Aosta as a local vicariant with *Trinia glauca*. The community characterizes more humid sites in the montane area (A8, A23), especially in the zone of the valley mouth (A 31). Even in plot areas with basic bedrock material the topsoils are weakly acidic due to the more humid conditions (pH-range: 5.8–6.9). The diagnostic species composition shows the similarity to meso-xerophytic communities of the Cirsio-Brachypodion and even the Brometalia.

In the DCA (Fig. 9) the core relevés (8 a,b, 23 a,b, 31a–c) are ordered with a remarkable distance from the other relevés, they lie next to the valley mouth of Valtellina and the montane Vinschgau relevés. The Pulsatillo-Brometum was not studied by Braun-Blanquet (1961) in the Valle d'Aosta, but in the Valais.

4.2.2 Inner Valais (from Martigny to Raron)

Biological soil crusts and Koelerio-Corynephoretea communities

Biological soil crusts as well as therophyte-dominated Koelerio-Corynephoretea communities are quite similar in structure to those found in the Valle d'Aosta, but basiphytic species and communities are more important. Buschardt (1979) presents a map of his investigation areas of Fulgensietum species; the areas correspond to our plots. A peculiarity of the base-rich habitats is the presence of the Clypeoletum jonthlaspi (Fig. 4), stands of which were described and documented by Korneck (1975). The Clypeoletum often grows below rocks, is imbedded in rocky habitats, or is found in the vicinity of trampled paths. The fluctuation of the population size of *Clypeola jonthlaspi* during different years is high. Concerning the area "Les Follatères", in 1991, there were hundreds of individuals, whereas in 1992, hardly any individual was found. Shallow rock ridges of the silicate area "Les Follatères" are characterized by the Sileno armeriae-Poetum bulbosae Royer 1987. Especially in this mainly acidic area the Veronico vernae-Poetum concinnae is present.

Gams (1927) and Frey (1934) have already studied the therophytes of the dry grassland complexes in the Valais. Gams (l.c.) proposed the name "steppic midgets" for the characterizing plants.

– Needle ice in the pioneer communities of the Valais
In all the above-mentioned communities with the exception of the Sileno-Poetum needle ice could be observed in March/April, e.g. in the Clypeoletum jonthlaspi (Fig. 4). In the case of cryopedological processes the therophyte *Hornungia petraea* often is able to react with intensified root growth (Fig. 10).

Xerotherm grassland communities

Ephedro helveticae-Artemisietum vallesiacae Br.-Bl. 1961
(Table 3, col. 6)

Character and differential species: (2) *Fumana ericoides*, (8) *Hyssopus officinalis*, (15) *Onosma pseudoarenaria*, (34) *Scorzonera austriaca*, (35) *Ephedra helvetica*, (36) *Artemisia vallesiaca*, (37) *Erucastrum nasturtiifolium*, (170) *Koeleria vallesiana*, (173) *Poa perconcinna*, (174) *Centaurea valesiaca.*

(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/ Stipo-Poion carniolicae)

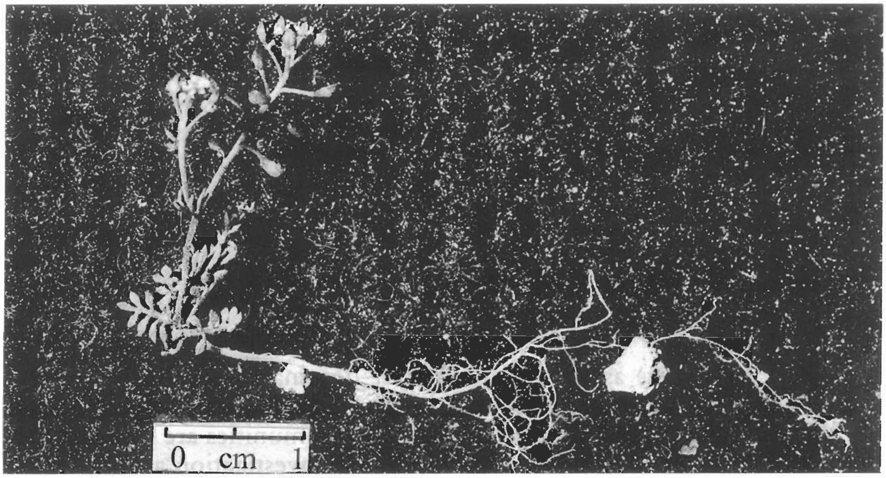


Fig. 10. *Hornungia petraea* from a needle-ice microhabitat in the Valais (Stipo-Koelerietum complex) with microsolifluction. By means of intensified root growth the individual was able to compensate for the microslide (plot area W6, 610 m a.s.l., 7.4.1991).

Fig. 11. Ephedro-Artemisietum vallesiacae (Valais) in phenophase V (end of full spring) with ovulate *Ephedra helvetica*, flowering *Scorzonera austriaca* and (in the background left) *Artemisia vallesiaca* (plot area W8, 530 m a.s.l., 10.6.1991).

The rock habitats, which are extremely shallow and mostly bear naturally forest-free stands, are characterized by this chamaephyte-dominated community. It is rich in relict species such as *Ephedra helvetica* and *Scorzonera austriaca* (Fig. 11). The substrate is basic, with pH values ranging from 7.6 to 8.1. *Ephedra helvetica* and *Fumana ericoides* are very slow-growing species (Zoller 1949); nevertheless, in the Valais (not in the Valle d'Aosta and not in the Vinschgau) *Ephedra* is able to grow in ruderal habitats as well.

In the DCA (Fig. 9) the Valais reléves are ordered next to the Onosmo-Koelerietum with a clear shift in the direction of less extreme conditions (axis 1 between 40 and 80).

The floristic similarity between the historic (Table 3, col. 6a, bB) and the actual species composition is high. Differences especially lie in the high presence of Fulgensietum species in the older relevés (for methodical reasons, see Chapter 3.2.2), and of *Centaurea scabiosa* (4 % versus 40 %) and *Bromus erectus* (15 % versus 60 %) in the newer ones. Both species are not resistant to grazing. *Erucastrum nasturtiifolium* (presence 40 %) was not recorded by Braun-Blanquet (l.c.).

Stipo capillatae-Koelerietum vallesianae Br.-Bl. 1961
(Table 3, col. 7a, bS)

Character and differential species: (39) *Stipa capillata* (dom.), (170) *Koeleria vallesiana*, (173) *Poa perconcinna*, (174) *Centaurea valesiaca*; d pot. fringe/forest stands: (41) *Peucedanum oreoselinum*; d mesothermic conditions compared to the Ephedro-Artemisietum: (40) *Hippocrepis comosa*; Subass. stipetosum calamagrostis: (43) *Ononis natrix*, (44) *Stipa calamagrostis*, (45) *Galeopsis ladanum*, (95) *Brachypodium rupestre* s.l.
(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/Stipo-Poion carniolicae)

This association is typical of habitats situated in areas with loess, moraine material or schists, characterized by less extreme conditions than the Ephedro-Artemisietum; often loess mantles occur. Floristically it is weakly characterized, mainly by the dominance of *Stipa capillata* and lack of most of the rock-specific chamaephytes of the Ephedro-Artemisietum (exception: *Scorzonera austriaca* is present with 30 %). The vertical structure, however, is totally different from the Ephedro-Artemisietum, especially owing to the dominance of grasses (*Stipa capillata*, partly *Stipa calamagrostis*). According to Frey (1934) and the permanent plot investigations of Delarze & Werner (1985), *Stipa* species are favoured by fire. *Stipa capillata* forms pure stands with physiognomic similarity to crop fields after fire. Probably all sites are potential forest stands; *Peucedanum oreoselinum*, which is not present in the Ephedro-Artemisietum, suggests the potential development of fringe/forest stands.

Debris stands are characterized by a subtype of the Stipo-Koelerietum, which includes the debris-tolerant species *Stipa calamagrostis* and *Ononis natrix* (Table 3, col. 7b). It is proposed to associate this type with the Stipo-Koelerietum as "stipetosum calamagrostis" (see also the concept of Mucina & Kolbek 1993a for the Oberinntal, Chapter 4.2.5). The pH values range from 7.9 to 8.

In the DCA (Fig. 9) the relevés of the Stipo-Koelerietum are not well distinguished from the Ephedro-Artemisietum, which underlines the floristic (but not the structural) similarity.

Comparisons of the Stipo-Koelerietum relevés with Braun-Blanquet (1961) (Table 3, col. 7a–cB), show that the floristic similarities are likewise high. All character species for this association that are listed by Braun-Blanquet (1961), e.g. *Carex liparocarpos* and *Aster linosyris*, also occur in the present relevés of the Ephedro-Artemisietum with similar presence.

Communities of the valley bend region near Martigny

Saxifraga bulbifera-Stipa capillata comm. (syn.: Saxifrago bulbiferae-Stipetum capillatae Delarze 1986) (Table 3, col. 5D)

Diagnostic species composition: (23) *Pulsatilla montana*, (27) *Orchis morio*, (28) *Anacamptis pyramidalis*, (29) *Saxifraga bulbifera*, (30) *Centaurium erythraea*, (31) *Cruciata pedemontana*, (32) *Bulbocodium vernum*, (39) *Stipa capillata*, (58) *Koeleria cristata*, (148) *Stipa pennata* s.str. (= *S. joannis*), (162) *Phleum phleoides*.

(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/Stipo-Poion carniolicae)

In the valley bend region near Martigny ("Les Follatères"), and therefore influenced by the air humidity of the Lac Léman region, there is a more mesophytic community with species such as *Ranunculus bulbosus, Galium verum, Orchis morio, Orchis ustulata, Euphorbia cyparissias* and *Carduus nutans*, which had been described as Saxifrago-Stipetum capillatae by Delarze (1986). Due to the very local occurrence of this vegetation type, we prefer to regard it only as a rankless community. This community includes *Stipa pennata* s.str. in a habitat different from those occupied north of the Alps: in the Valais and Engadin the more mesothermic habitats, in the Upper Engadin areas of the subalpine zone (in the Follatères even partly shaded sites) are colonized, whereas e.g. in Germany the dryest sites in the Xerobromion complex are characterized by this *Stipa* species (Witschel 1987). According to Rychnovská & Úlehlová (1975) the relatively high rates of water loss of *Stipa pennata* s.str. are close to those associated with the strategies of mesophytic grasses. The substrate is acidic (pH 5.6, but locally loess occurs with pH values between 7 and 8). The relevés of Delarze (l.c.) were not included in the ordination diagram.

Pulsatillo montanae-Brometum erecti, *Aster linosyris* vicariant (Table 3, col. 8S)

Diagnostic species composition and syntaxonomical rank: see p. 364, additionally (158) *Aster linosyris*; absence of (25) *Vicia onobrychioides*.

As in the Valle d'Aosta, this community occurs in more humid stands. The floristic structure is similar, with the exception of the occurrence of *Aster linosyris* (Valais) and *Trinia glauca* (Valle d'Aosta). In the DCA (Fig. 9), the W1 relevé, which represents this association, is ordered next to the Engadin/Rhein relevés.

4.2.3 Vinschgau

Biological soil crusts and Koelerio-Corynephoretea communities (Table 2, col. 5)

Silicate habitats dominate in the Vinschgau, and some areas include loess or moraine. There are mostly fragmentary stands of the Fulgensietum fulgentis, always without *Psora decipiens*. The therophyte vegetation is poor in comparison with the diverse stands of Valle d'Aosta and Valais. As in the silicate areas of Valle d'Aosta, the *Rumex acetosella-Polytrichum piliferum* comm. can often be found. A very characteristic therophyte-dominated community is the *Veronica dillenii-Veronica verna* comm. Habitats that are not extremely acidic are also characterized by *Alyssum alyssoides*. The frequency of gritty substrates is high; therefore a variety of succulent-dominated communities, mainly without syntaxonomical rank, occur. Colourful stands are formed by *Sempervivum arachnoideum*, which grows in nearly all plot areas. These are the first stands of higher plants in a gradient (Fig. 5 from the Valle d'Aosta) beginning on the bare grit. Species-rich, typical stands of the Scleranthо-Semperviretum arachnoidei Br.-Bl. 1955 in the narrow sense, like those in the Engadin, were not recorded in the plots, although the association occurs in the upper Vinschgau and in the Val Müstair.

– Needle ice in the pioneer communities of the Vinschgau
In all the above-mentioned communities needle ice could be observed in March/April; in particular, *Arenaria serpyllifolia* patches with seedlings partly eradicated are typical in these microsites.

Xerothermic grassland communities

Stipo capillatae-Seselietum variae Br.-Bl. 1936 (Table 3, col. 10S)
Character and differential species: (15) *Onosma pseudoarenaria*, (34) *Scorzonera austriaca*, (35) *Ephedra helvetica*, (39) *Stipa capillata*, (47) *Saponaria ocymoides*, (48) *Oxytropis pilosa*, (49) *Seseli varium*, (82) *Cleistogenes serotina* (C4 species), (102) *Carex humilis*, (117) *Stipa*austriaca*, (178) *Centaurea maculosa*, (188) *Festuca valesiaca*; acidophytic species (d): (58) *Koeleria cristata*, (162) *Phleum phleoides*, (164) *Achillea tomentosa*.
(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/Stipo-Poion xerophilae)

The "Edelvinschgau", with the core area between Schlanders (Silandro) and Naturns (Naturno), where fruits such as *Prunus armeniaca* are grown, is characterized by slopes with solid silicate rocks. pH values range from 5.4 to 6.6 (7.0). Some small loess covers have even higher pH values. To a lesser extent, there are stands with moraine and debris material. At present there is no longer any influence of grazing. The rock habitat complexes are covered by this association, which is characterized, e.g., by the tall herb *Seseli varium*, growing up to about 1 m and with mainly pontic distribution.

A relict species is *Ephedra helvetica* (one site near Schlanders), another one *Scorzonera austriaca*. Acidotolerant plant species such as *Koeleria cris-*

tata, *Phleum phleoides* and *Achillea tomentosa* show high presence (as also in the other grassland types of the Vinschgau). *Carex humilis, Pulsatilla montana* and *Bromus erectus*, which are restricted to the more mesohygric Pulsatillo-Brometum in the Valle d'Aosta (precipitation maximum in October), occur in the Stipo-Seselietum with a presence of 92 %, 33 % and 42 %.

Regarding the DCA (Fig. 9), the Stipo-Seselietum relevés are ordered on the right of the Onosmo-Koelerietum, following the meso-xerothermic gradient of axis 1. One relevé, which marks a transition type in the valley mouth region, is positioned next to the following types. Apart from this exception, the relevés form a very homogeneous agglomeration.

The comparison with the relevés of BRAUN-BLANQUET (1961) shows (Table 3, col. 10a, bB) that the floristic structure of character and differential species is very similar; some species which are preferred by livestock show high presence in the recent material, for instance *Lactuca perennis* (92 % versus 4 %), *Tragopogon dubius* (50 % versus 0), *Asparagus officinale* (58 % versus 0). *Saponaria ocymoides* (67 % versus 4 %) also increased.

Carici supinae-Festucetum vallesiacae Br.-Bl. 1936 nom. invers. propos. (Table 3, col. 11)

Character and differential species: (51) *Achillea nobilis*, (52) *Carex supina*, (53) *Astragalus excapus*, (54) *Astragalus vesicarius* subsp. *pastellianus*, (60) *Plantago serpentina*, (61) *Veronica prostrata*, (102) *Carex humilis*, (110) *Astragalus onobrychis*, (178) *Centaurea maculosa*, (188) *Festuca valesiaca*; d grazed areas: (56) *Lappula squarrosa* (epizoochorous); additional acidophytic species (d): (58) *Koeleria cristata*, (162) *Phleum phleoides*; rocky material: (117) *Stipa* austriaca*; fine material (partly with loess): (39) *Stipa capillata*.
(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/Stipo-Poion xerophilae)

In the central Vinschgau the south-facing slopes are characterized mainly by schists and high anthropozoogenic impact (the so-called "Leiten"). Additionally, there are some rock complexes. pH values reach from 5.8 to 7.2, and lie mainly between 6 and 7, but locally are higher (loess!). Parts of the schists, including phyllite/biotite/mica, are weakly calcareous (BUSCHARDT 1979). The "Leiten" are still mainly grazed by cattle (in former times by cattle, sheep and goats). The characteristic mosaic of fine ground, dry erosional channels, and bedrocks is characterized by the Festuco-Caricetum supinae with the relict species *Carex supina*, and *Astragalus excapus;* both species are characterized by continental disjunct distribution (next occurrences in the north-east: Pannonicum (Burgenland, Niederösterreich). The very rare steppic *Carex stenophylla* with disjunct distribution could not be recorded in our plot areas. *Astragalus*pastellianus* (= *A. "venostanus"*) ist very characteristic for fine-grain substrate; according to PIGNATTI (1982) the south-European-Pontic *A. vesicarius* s.l. is polymorphic and has the tendency to differentiate local ecotypes. The bedrock areas in particular are covered by *Stipa*austriaca*, whereas *Stipa capillata* is dominant in the zone at the bottom of the slope containing colluvial transported material, richer in bases. Ecophysiological investigations of FLORINETH (1974b) in this community have shown that the two *Stipa* species and *Festuca valesiaca* have high transpiration rates and hardly any strategies to reduce water loss, but compensate this with an extensive, deep (80 cm) root system (in July 1778 g below- versus 270 g/m^2 above-ground phytomass dry weight). The floristic structure is characterized by the livestock influence, so that in parts the community looks like a short lawn with many small trails trampled parallel to the slope by the grazing animals. The trails are partly covered by gappy vegetation with high presence of *Plantago serpentina.* The livestock impact facilitates the growth of non-palatable plants such as *Carex supina, Festuca valesiaca, Achillea nobilis, Astragalus excapus*. The current boundary between Stipo-Seselietum and Carici-Festucetum is identical with that specified on the map of BRAUN-BLANQUET (1936, 1961): the Stipo-Seselietum replaces the Carici-Festucetum downstream from Schlanders (plot 21, 900 m a.s.l.).

In the DCA (Fig. 9), the Festuco-Caricetum relevés are connected to the right side of the Stipo-Seselietum, following the meso-xerothermic gradient of axis 1. The left-right difference of the plots reflects the altitudinal gradient or more mesothermic conditions. The plot area at the far right is the one with the highest altitude (V4: 1350 m a.s.l.).

A comparison with BRAUN-BLANQUET (1961) (Table 3, col. 11B) is not very useful, as his material includes few or none of the rocky habitats (e.g. *Fumana procumbens, Teucrium montanum* and *Allium sphaerocephalon* with low presence). It is astonishing that *Veronica prostrata*, which is enriched by grazing (today 46 %), is totally lacking in the historic material, whereas it is named as a character species in the Poo xerophilae-Festucetum valesiacae.

Poo xerophilae-Festucetum valesiacae Br.-Bl. 1961 (Table 3, col. 12)

Character and differential species: (51) *Achillea nobilis*, (53) *Astragalus excapus*, (58) *Koeleria cristata*, (60) *Plantago serpentina*, (61) *Veronica prostrata*, (62) *Hieracium velutinum*, (162) *Phleum phleoides*, (163) *Potentilla argentea*, (164) *Achillea tomentosa*, (165) *Polytrichum piliferum*, (178) *Centaurea maculosa,* (179) *Poa molinerii* (= *xerophila*), (188) *Festuca valesiaca*, more mesophytic species (d): (22) *Bromus erectus*, (59) *Pimpinella saxifraga*, (95) *Brachypodium rupestre*, (139) *Cerastium arvense* subsp. *strictum*, (141) *Phyteuma betonicifolium*, (153) *Salvia pratensis*, (217) *Thuidium abietinum*, (254) *Silene nutans*, (155) *Trifolium montanum*, (261) *Galium verum*, (263) *Achillea millefolium*, (273) *Ranunculus bulbosus.*

(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/ Stipo-Poion xerophilae)

This community, which typically occupies more humid habitats, occurs in the upper montane zone between 1000 and 1500 m a.s.l. There are larger areas, especially in the Münstertal/Val Müstair.

The community is only weakly characterized. pH values lie between 6 and 6.9. Many of the plot areas are still grazed by cattle and, near Taufers (Münstertal), by goats. If the community lies fallow, especially *Brachypodium rupestre* and *Pteridium aquilinum* increase.

In the DCA (Fig. 9), the plot areas are ordered next to the silicate plots of the montane zone of Poschiavo/Valtellina, conforming closely to the "mesothermic direction" of axis 1. Two relevés from Sta Maria/Val Müstair (Switzerland) that are separated in the DCA reveal a fragmentary oreal form of this community.

The comparison with BRAUN-BLANQUET (1961) (Table 3, col. 12a, bB) suggests that the grazing pressure was higher at that time; for instance, *Centaurea scabiosa* and *Phyteuma betonicifolium* are absent in the older relevés.

Communities of the Vinschgau valley mouth region

Melica ciliata-Erysimum rhaeticum comm. (Table 3, col. 9S)

Diagnostic species composition (provisional because of small database): (6) *Melica ciliata*, (58) *Koeleria cristata*, (162) *Phleum phleoides*, (178) *Centaurea maculosa*, (184) *Scabiosa triandra*, (188) *Festuca valesiaca*, (192) *Erysimum rhaeticum*; more mesophytic species (d): (22) *Bromus erectus*, (59) *Pimpinella saxifraga*, (273) *Ranunculus bulbosus*.
(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/ Stipo-Poion xerophilae)

In the region of the valley mouth there is a community with more mesophytic species, which has to be studied in greater detail. Silicate rock and debris form the substrate with the pH value 6.5. In the DCA (Fig. 9), this type is situated next to the relevés of the mouth of Valle d'Aosta and is included in the Valtellina relevés.

4.2.4 Valtellina/Poschiavo

Koelerio-Corynephoretea communities

Therophyte-dominated communities are poorly developed in the Valtellina valley region. In the very acidic parts of the low Valtellina, the *Rumex acetosella-Polytrichum piliferum* comm. occurs.

The **Sileno** armeriae-Poetum bulbosae Royer 1987 characterizes rocky structures or stone walls in the vineyard region, and is an element of the Diplachno-Festucetum complex. The therophyte *Silene armeria* has its sociological core in Koelerio-Corynephoretea communities, but also has high presence in the gappy Diplachno-Festucetum as a differential species. Typical features are *Sedum rupestre* stands and the **Sedetum montani** Br.-Bl. 1949, which cover microhabitats with shallow soil on silicate rocks, and have already been sampled by KNAPP (1953: p. 81) in the Diplachno-Festucetum complex of the Valtellina region. As it was not possible to differentiate sterile *Sedum rupestre* s.str. and *Sedum montanum*, both types were summarized as "*Sedum rupestre* s.l. stands".

Xerothermic grassland communities

Diplachno serotinae-Festucetum vallesiacae Br.-Bl. 1961 (Table 3, col. 15)

Character and differential species: (6) *Melica ciliata*, (24) *Dianthus carthusianorum*, (81) *Sedum telephium*, (82) *Cleistogenes* (= *Diplachne*) *serotina* (C4 species), (83) *Silene armeria*, (84) *Orlaya grandiflora*, (85) *Heteropogon* (= *Andropogon*) *contortus* (C4 species), (86) *Opuntia humifusa* (alien species), (87) *Allium carinatum* subsp. *pulchellum*. Further acidophytic species (d): (162) *Phleum phleoides*, (165) *Polytrichum piliferum*, (166) *Jasione montana*, (178) *Centaurea maculosa*.

(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/ Stipo-Poion carniolicae)

This association characterizes the dry grassland of the vineyard region of the lower Valtellina region, and often covers only fragmentary stands between the managed land parcels. The gappy association is restricted to the (edaphically) hottest habitats of the whole valley. The areas are not managed, but might well be irregularly influenced by burning. The stands are acidic with pH 4.5–6.5, mainly between 5 and 6. There is no relict species such as in comparable habitats in the Valle d'Aosta, Valais and Vinschgau.

In the DCA (Fig. 9), the Diplachno-Festucetum is ordered next to the right of the *Thymus vulgaris-Bromus erectus* comm. of Valle d'Aosta. The group: *Heteropogon, Opuntia, Orlaya* is also depicted in Fig. 9b.

The comparison with the relevés of BRAUN-BLANQUET (1961) (Table 3, col. 15B) shows a high similarity. The main difference is that there is now a high presence of the alien species *Opuntia* (63% versus 10%) and of the grazing-intolerant species: *Dianthus carthusianorum* (50% versus 0), *Erysimum rhaeticum* (63% versus 10%) and *Asparagus officinalis* (50% versus 0).

Tunico saxifragae-Artemisietum campestris Br.-Bl. 1961 (Table 3, col. 17a, cS)

Character and differential species: (22) *Bromus erectus*, (58) *Koeleria cristata*, (91) *Phyteuma scheuchzeri*, (92) *Campanula spicata*, (102) *Carex humilis*, (154) *Anthyllis vulneraria*, (184) *Scabiosa triandra*, (288) *Artemisia campestris*.

Festuca valesiaca form (silicate, middle-montane zone): (162) *Phleum phleoides*, (178) *Centaurea maculosa*, (188) *Festuca valesiaca*.

Aster alpinus-form (limestone, oreal zone): (89) *Aster alpinus*, (90) *Tortella inclinata*, (93) *Astragalus leontinus*, (104) *Sesleria caerulea*, (111) *Onobrychis montana*, (112) *Laserpitium siler*, (210) *Teucrium montanum*.

Rock areas: (117) *Stipa*austriaca*, (213) *Fumana procumbens*.

(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/ Stipo-Poion carniolicae)

In the dry zone of the inner Valtellina the Tunico-Artemisietum represents the typical dry grassland community. It covers silicate, partly base-rich rock areas (e.g. gabbro with hornblende), and in the upper valley part Triassic limestone of the Ortler zone. The association is only weakly characterized, and marks a transitional type between the dry habitats of the

Diplachno-Festucetum and the more humid conditions of the Centaureo-Brachypodietum. Indicator species of relatively high humidity are, e.g., *Bromus erectus, Anthyllis vulneraria* and *Phyteuma scheuchzeri*. The latter as well as *Campanula spicata* also occur in the following association. Only a few plot areas are still grazed (by cattle or goats); the others lie fallow. We distinguish two altitudinal-edaphic forms (see above); pH values lie between 5 and 6.7 (a) and 7 to 7.6 (b). In the oreal limestone zone of the upper valley near Semogo the Tunico-Artemisietum stands, which lie fallow, are characterized by *Laserpitium siler* facies. The same successional phase can be recorded in the oreal Rhein region near Chur (plot area R1).

In the DCA (Fig. 9), the relevés are added on the right side of the Diplachno-Festucetum, leading to the Centaureo-Brachypodietum, and lying next to the montane Vinschgau relevés (Koelerio-Festucetum). The plot areas of the oreal *Aster alpinus*-form on limestone are ordered next to the Astragalo-Brometum (Inn) and "Xero-Brometum" (= "Xerobrometum rhaeticum") (Rhein). This reflects the narrow floristic connections between the upper Valtellina and Engadin, pointing to historical traits between these regions concerning their postglacial vegetation history (see also FURRER 1914, BRAUN-BLANQUET 1961).

Comparing the Tunico-Artemisietum, *Aster alpinus*-form with the montane-oreal Astragalo-Brometum of the Lower Engadin, *Silene otites* is lacking in the Engadin, and specific influences of the southern Alps are present in the Valtellina relevés (*Phyteuma scheuchzeri, Campanula spicata*), while *Astragalus onobrychis* and *Asperula cynanchica* have high presence in the Astragalo-Brometum. *Astragalus leontinus* (presence 50%) only very seldom occurs in the Engadin in the Seslerio-Caricetum sempervirentis (ZOLLER 1964).

The community had been characterized by high grazing pressure in former times. Already FURRER (1914) described the over-exploited community pastures (grazed by cattle, sheep, goat). Nearly 50 years later, BRAUN-BLANQUET (1961) described the dry grassland of Bormio (translated: "over-exploited, clear-grazed poor grassland ... These pastures present a pitiful sight ..."). BRAUN-BLANQUET (l.c.) distinguishes two subassociations: a: "festucetosum vallesiacae" and b: "brometosum erecti" (Table 3, col. 17a–cB). They represent, on the one hand, altitudinal forms (a: middle-montane, b: oreal), and on the other hand, edaphic differences and lower (a) or higher (b) grazing pressure. The high grazing pressure in former times is reflected by a *Veronica prostrata* variant of the "brometosum" in the historical relevés. Nowadays, the differentiation into the altitudinal forms and the edaphic differences are represented by (a) *Festuca valesiaca, Centaurea maculosa* and some acidophytic species and by basiphytic species as listed above (b). The *Veronica prostrata* subtype only very locally occurs, where pastures are still grazed. *Bromus erectus* occurs in both subtypes.

Centaureo bracteatae-Brachypodietum Br.-Bl. 1961 nom. invers. propos. (Table 3, col. 18)

Character and differential species: (22) *Bromus erectus*, (58) *Koeleria cristata*, (59) *Pimpinella saxifraga*, (91) *Phyteuma scheuchzeri*, (92) *Campanula spicata*, (95) *Brachypodium rupestre* s.l. (especially *B. cespitosum*), (98) *Galium rubrum*, (99) *Centaurea jacea* subsp. *gaudinii* (= C. *bracteata*), (100) *Prunella laciniata*, (102) *Carex humilis*, (135) *Helicto-*

trichon pratense, (154) *Anthyllis vulneraria*, (162) *Phleum phleoides*, (217) *Thuidium abietinum*, (223) *Rhytidium rugosum*, (268) *Agrostis capillaris*.
(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/Stipo-Poion carniolicae)

More humid and acidic to subneutral stands (pH 4.5–7) mainly occur in tributaries to the Adda valley and less extremely insolated habitats of the main valley. They were already described by Brockmann-Jerosch (1907) as "*Brachypodium pinnatum*-Typus". Nearly all areas lie fallow and are enriched with fringe species such as *Silene nutans, Geranium sanguineum, Trifolium alpestre* and others, except plot P21 (goats). *Brachypodium cespitosum/rupestre* s.l. has high presence and will extend the cover ratings in the future, if the areas are not grazed. In the lower regions, *Centaurea jacea* subsp. *gaudinii* occurs in fringes, and, according to Becherer (1966a), represents a frequent species, e.g., of bush formations. This weakly characterized association corresponds to the Poo xerophilae-Koelerietum gracilis in the acidic montane zones of the Engadin and the Poo-Festucetum of the Vinschgau/Val Müstair.

In the DCA (Fig. 9), the relevés – together with Vinschgau relevés of the Poo-Festucetum – nearly mark the marginal points of axis 1 in the upper part. These upper parts mainly include the acidophytic plant communities.

The comparison with the relevés of Braun-Blanquet (1961) (Table 3, 18B) shows differences with respect to species that are favoured in fallow land, e.g. *Phyteuma scheuchzeri*.

Communities of the valley mouth regions and of special habitats

Petrorhagia saxifraga-Calluna vulgaris comm. (Table 3, col. 13S)
Diagnostic species composition: (65) *Genista tinctoria*, (66) *Calluna vulgaris*, (67) *Cytisus scoparius* juv., (68) *Teucrium scorodonia*, (69) *Veronica officinalis*, (230) *Petrorhagia saxifraga*; acidophytic species: (162) *Phleum phleoides*, (165) *Polytrichum piliferum*, (166) *Jasione montana*.
(class/order: Festuco-Brometea/Festucetalia valesiacae/Stipo-Poion carniolicae)

In the acidic, forest-dominated (especially *Castanea sativa*) slopes of the lower valley (between 750 and 900 m a.s.l.), rocky habitats are covered with this vegetation type, combining heathland elements (e.g. *Cytisus scoparius* juv.) and Festucetalia valesiacae species. pH values are considerably acidic (4.4–4.9). The evergreen species *Teucrium scorodonia* and *Cytisus scoparius* are sensitive to cold winters, need humidity and grow in a subatlantic-west-submediterranean area. Bolzon (1921) has described these species for northern Italy as "insubric species".

In the DCA (Fig. 9), one relevé (P28) marks the highest values of axis 2 (about 350), which also indicates the lowest pH value (4.4) of the whole data set. In Fig. 9b *Teucrium scorodonia, Veronica officinalis* and *Cytisus scoparius* juv. are ordered next to this plot area. The other relevé (P32) is ordered next to the acidic, montane Vinschgau relevés.

Carici humilis-Chrysopogenetum grylli Meyer 1976 (Table 3, col. 14S)

Character and differential species: (71) *Globularia bisnagarica*, (72) *Linum tenuifolium*, (73) *Trinia glauca*, (74) *Asperula purpurea*, (75) *Polygala pedemontana*, (76) *Erica arborea* juv., (77) *Clematis recta* juv., (78) *Chrysopogon gryllus*, (79) *Bromus condensatus*, (82) *Cleistogenes serotina* (C4 species), (84) *Orlaya grandiflora*, (85) *Heteropogon contortus* (C4 species), (95) *Brachypodium rupestre* s.l. (especially *B. cespitosum*), (98) *Galium rubrum*, (102) *Carex humilis*, (153) *Salvia pratensis*, (154) *Anthyllis vulneraria*.

(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/Diplachnion; the position of the Diplachnion is uncertain)

In the warm and humid valley mouth region near Lago Como (about 400 m a.s.l.) there is a grassland community with Festucetalia valesiacae species and insubric influence; pH values reach 6.9. The plot areas lie fallow. In the insubric core region near Lugano, Koch (1943) recorded the Andropogenetum grylli with high presence of *Polygala pedemontana* and including plant species such as *Calluna vulgaris* and *Pteridium aquilinum*. This acidophytic community is not identical with our type. The same applies to the relevés of Hofer (1967) taken from the insubric region. He presents very complex relevés, combining open grassland stands of *Erica arborea* and *Calluna*. *Chrysopogon* is present in our relevés; in the insubric region it is restricted to hot-summer habitats (Meyer 1976). The occurrence of *Bromus condensatus*, an endemic southeastern alpine species, in the insubric region and western Balkan peninsula is remarkable. Our community belongs to the Carici humilis-Chrysopogenetum grylli fumanetosum ericoidis described by Meyer (1976) for the insubric region. Meyer (1977) compared the Carici-Chrysopogenetum with related communities of the insubric region and its surroundings in a presence degree table and with the help of an affinity analysis, and worked out that it belongs to the Diplachnion.

In the DCA (Fig. 9), the extraordinary and really different structure of this community is not reflected by axis 2, but in axis 3 the relevés are totally separated (value 250); the next Valtellina relevés (P26–P30) are ordered to the point 180 of axis 3.

Melica ciliata-Centaurea maculosa comm. (Table 3, col. 16S)

Diagnostic species composition: (6) *Melica ciliata*, (7) *Agropyron intermedium*, (178) *Centaurea maculosa*, (188) *Festuca valesiaca*, (288) *Artemisia campestris*.

(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/Stipo-Poion carniolicae)

One stand in the Valtellina area (P14, Migióndo near Sondalo; 900 m a.s.l.) is quite similar to the moraines in the Valle d'Aosta, bearing a species-poor and gappy community. The substrate of the steep slope consists of debris material, modelled by fluvial processes. No relict species or any species with slow dispersal mode is present. pH values lie in the subneutral range (6.6).

In the DCA (Fig. 9), the relevés (P14) are ordered next to the Valle d'Aosta-relevés.

4.2.5 Oberinntal/Engadin

Koelerio-Corynephoretea communities (Table 2, col. 8)

Although this region includes some habitats rich in bases and in particular calcium carbonate, the therophyte vegetation is not as diverse as it is in the Valais and the Valle d'Aosta; with only a few exceptions, this valley region is not affected by submediterranean climatic influences.

Alyssum alyssoides- and *Arenaria serpyllifolia* colonies are present. In very shallow microhabitats of limestone rocks, a pioneer community could be recorded comprising in particular *Sedum album* and *Poa molinerii*; *Sempervivum arachnoideum, Calamintha acinos* and *Thymus praecox* also have a high presence (*Sedum album-Poa molinerii* comm.). According to our relevé material and our observations, *Poa molinerii* mainly is a Koelerio-Corynephoretea species as well as the related species *Poa perconcinna* and *Poa badensis*. This community is restricted to microsites richer in bases, whereas the typical Scleranthо-Semperviretum arachnoidei Br.-Bl. 1955 characterizes silicate rocks and is rich in acidophytic species. Braun-Blanquet & Sutter (1982) propose a wide view of the Scleranthо-Sempervivetum including a "leptocladietosum" without *Scleranthus* and without *Sempervivum arachnoideum*. Like Korneck (1975), we consider only typical stands with *Sempervivum arachnoideum* and mostly acidophytic differential species to be part of the association. In the silicate region of the Lower Engadin, there are typical stands of the *Rumex acetosella-Polytrichum piliferum* comm. and of the Scleranthо-Sempervivetum arachnoidei.

– Needle ice in the pioneer communities of the Oberinntal/Engadin
Needle ice could be observed at the end of April; *Alyssum alyssoides*- and *Arenaria* colonies germinated in needle ice microsites in the Oberinntal and Lower Engadin (both seed bank species according to Thompson et al. 1997).

Xerothermic grassland communities

Preface: A comparison of the relevés of Kielhauser (1954a) and Braun-Blanquet (1961) with the current relevés is hardly possible in these long and geologically complicated valley sections. In the Oberinntal, many areas that were recorded by Kielhauser (l.c.) have since undergone spontaneous succession. Furthermore, the rocky sites, e.g. in the Astragalo-Brometum complex, were not recorded in detail by Braun-Blanquet (l.c.). Only in the case of the Poo-Koelerietum (restricted silicate zone of the Engadin) is comparison appropriate.

Teucrio montani-Caricetum humilis Br.-Bl. 1961 (Table 3, col. 19)
Character and differential species: (41) *Peucedanum oreoselinum*, (89) *Aster alpinus*, (95) *Brachypodium rupestre* s.str., (102) *Carex humilis*, (103) *Globularia cordifolia*, (104) *Sesleria caerulea*, (105) *Leontodon incanus*, (106) *Dorycnium germanicum*, (107) *Erica carnea*, (108) *Leontodon*hyosuroides*, (156) *Asperula cynanchica*, (157) *Anthericum ramosum*,

(210) *Teucrium montanum*; d debris material: (44) *Stipa calamagrostis*; d rocky areas: (117) *Stipa*austriaca*, (213) *Fumana procumbens*.

(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/ Stipo-Poion xerophilae)

The differentiation between the Teucrio-Caricetum, which occurs on more or less solid limestone habitats (partly with moraine) and the following Astragalo-Brometum, which is restricted more or less to schists, does not always turn out to be very sharp. In Table 44 of Braun-Blanquet (1961), *Astragalus onobrychis* also has a high presence in this association (II in the "brometosum" and V in the "linetosum"; the latter was regarded as "Lino-Andropogenetum" ass. prov. by Kielhauser 1954a). In the overall view of Table 3, it is above all the species group indicating solid limestone and prealpine distribution which is characteristic. There are many floristic relations to the Erico-Pinetea communities, in which it is imbedded (e.g. *Erica carnea, Dorycnium germanicum*). *Pulsatilla oenipontana* is detected as character species by Mucina & Kolbek (1993a), but currently, due to succession processes and the increase of the urban area near Innsbruck, there are hardly any stands of *Pulsatilla oenipontana* in the Teucrio-Caricetum humilis (Unterasinger & Erschbamer 2002 and Erschbamer, pers. comm.). The remnant populations east of Innsbruck decreased from 1761 individuals (year 1995) to 181 in the year 2000 (Unterasinger & Erschbamer l.c.); the seedbank of these stands is already rich in ruderal species (Erschbamer & Scherer 1999). If the limestone is decaying and moving on the steep slopes, *Stipa calamagrostis* is present. The range of pH values lies between 7.3 and 8. The floristic inventory of the stands of the Oberinntal, which are all very threatened by succession processes, had been compiled by Pokorny & Strudl (1986).

In the DCA (Fig. 9), there are close connections to the Astragalo-Brometum and the Rhein relevés. The relevés from the dolomite area near Silz, including *Globularia cordifolia*, *Erica carnea* and others, are marginally ordered at the low part of axis 1; there, the basiphytic types are concentrated. The corresponding community of the oreal zone in the Upper Engadin (*Helianthemum*grandiflorum-Stipa*austriaca* comm.) has roughly the same position according to axis 2, but is shifted – in the course of the meso-xerothermic gradient – to the right (axis values about 250 versus 350).

Astragalo onobrychido-Brometum Br.-Bl. ex Kielhauser 1954 (Table 3, col. 20a, b)

Character and differential species: (22) *Bromus erectus*, (95) *Brachypodium rupestre*, (110) *Astragalus onobrychis*, (111) *Onobrychis montana*, (153) *Salvia pratensis*, (154) *Anthyllis vulneraria*, (156) *Asperula cynanchica*, (179) *Poa molinerii*, (296) *Medicago falcata*; montane form: (39) *Stipa capillata*, (102) *Carex humilis*, (114) *Salvia verticillata*, (178) *Centaurea maculosa*, p.p. *C. stoebe* s.l., (188) *Festuca valesiaca*, (184) *Scabiosa triandra*, (209) *Bothriochloa* (= *Andropogon*) *ischaemum* (C4 species); especially fallow land: (115) *Libanotis montana*.

montane-oreal form: (155) *Trifolium montanum*, (217) *Thuidium abietinum*, (293) *Centaurea scabiosa* s.l.; especially fallow land: (112) *Laserpitium siler*, (113) *Veronica teucrium*, (115) *Libanotis montana*.
d debris material: (44) *Stipa calamagrostis*; d rocky areas: (117) *Stipa*austriaca*.
(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/ Stipo-Poion xerophilae)

This is the characteristic community of the "Unterengadin geological window", although it also grows on moraine or fluviatile debris material, always with fine-grain material, rich in bases. pH values range from 6.9 to 8.1.

A montane form with *Stipa capillata* is to be found up to Ramosch (Lower Engadin, 1350 m a.s.l.); in the Oberinntal, *Bothriochloa ischaemum* and *Salvia verticillata* are present. In Ramosch there are succession stages of the Astragalo-Brometum with *Genista radiata* (see p. 407). pH values range from 7.3 to 8.4.

In the montane-oreal zone above 1350 m a.s.l., mesophytic species have a higher presence (*Trifolium montanum, Centaurea scabiosa* s.l. and others). Some plot areas of the montane-oreal form are characterized by high presence of *Libanotis montana*, *Veronica teucrium* and *Medicago falcata*, especially if they lie fallow. In the Lower Engadin, there are efforts to reintroduce grazing regimes with goats.

In both altitudinal forms a "brachypodietosum rupestris" can be detected, which characterizes the stands in small slope depressions, and which is enriched in the fallow areas as well. The convex culminations are often covered by the "typicum", the concave forms of the slopes by the "brachypodietosum".

If the slopes are very steep and enriched in debris material, *Stipa calamagrostis*, often together with *Stipa capillata*, becomes increasingly important. The type was decribed as "Achnathero-Stipetum capillatae" by MUCINA in MUCINA & KOLBEK (1993a) for the Oberinntal. As we did in the Valais (Stipo-Koelerietum), we consider Astragalo-Brometum types with *Stipa calamagrostis* to belong to the "stipetosum calamagrostis"; if the Festuco-Brometea elements vanish, to the Stipetum calamagrostis. Relevé I22 marks a transitional type between the "stipetosum" and the Stipetum calamagrostis, and includes *Gypsophila repens.* It is separated in the DCA, which is indicated by *Stipa calamagrostis* and *Gypsophila* in Fig. 9b. and occurs next to the Teucrio-Caricetum.

The floristic inventory of the Oberinntal areas was elaborated by POKORNY & STRUDL (1986); like the Teucrio-Caricetum, the stands of the Astragalo-Brometum are also endangered.

In the DCA (Fig. 9), the Astragalo-Brometum is directly added to and partly intermingled with the limestone relevés of the Tunico-Artemisietum (Valtellina) and the Rhein relevés.

*Dracocephalum austriacum-Stipa*austriaca* comm. (Table 3, col. 23S)
Diagnostic species composition: (22) *Bromus erectus*, (89) *Aster alpinus*, (111) *Onobrychis montana*, (112) *Laserpitium siler*, (113) *Veronica teucrium*, (117) *Stipa*austriaca*, (118)

Dracocephalum austriacum, (136) *Koeleria pyramidata*, (144) *Allium lineare*, (154) *Anthyllis vulneraria*, (179) *Poa molinerii*, (180) *Allium lusitanicum*, (214) *Lactuca perennis*, (255) *Polygonatum odoratum*, (293) *Centaurea scabiosa* s.l., (296) *Medicago falcata*.
(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/Stipo-Poion xerophilae)

In the area of the Tasna limestone near Ardez there is a gappy community, including the disjunct species *Dracocephalum austriacum*, further stands of which are situated in the Vinschgau and in the Valais. According to BRAUN-BLANQUET (1961), such stands are included in the Astragalo-Brometum, but in our material it is more similar to the other rock-restricted communities, such as the Teucrio-Caricetum humilis (e.g. sharing *Sesleria caerulea* and *Aster alpinus*) and the *Helianthemum*grandiflorum-Stipa*austriaca* comm. *Astragalus onobrychis* and *Brachypodium* are lacking; rock-specific species present here include, e.g., *Allium lineare* and *Lactuca perennis*. pH values range from 6.9 to 7.6. We preliminarily regard this type as a community with very local distribution.

In the DCA (Fig. 9), the plots are situated next to the Teucrio-Caricetum and the Rhein relevés.

Poo xerophilae-Koelerietum gracilis Br.-Bl. 1961 (Table 3, col. 21)

Character and differential species: (58) *Koeleria cristata*, (59) *Pimpinella saxifraga*, (60) *Plantago serpentina*, (95) *Brachypodium rupestre* s.l., (130) *Carlina acaulis*, (131) *Trifolium aureum* (= *agrarium*, = *strepens*), (132) *Crepis conyzifolia*, (133) *Dianthus deltoides*, (135) *Helictotrichum pratense*, (136) *Koeleria pyramidata*, (139) *Cerastium arvense* subsp. *strictum*, (140) *Solidago virgaurea*, (141) *Phyteuma betonicifolium*, (143) *Laserpitium halleri*, (154) *Anthyllis vulneraria*, (155) *Trifolium montanum*, (162) *Phleum phleoides*, (165) *Polytrichum piliferum*, (179) *Poa molinerii*, (180) *Allium* lusitanicum (= *montanum*), (190) *Veronica spicata*.
(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/Stipo-Poion xerophilae)

In the restricted silicate zone with mainly gneisses between Guarda and Brail (Lower and Upper Engadin), there is a community characterized by a close similarity to the Poo-Festucetum valesiacae of the Val Müstair. Among the differentiating species is *Festuca valesiaca*, which grows in the Val Müstair. The occurrence of *Helictotrichon pratense* is very characteristic for the Poo-Koelerietum. pH values are moderately acidic to subneutral (4.7–6.6). Acidophytic and oreal species such as *Laserpitium halleri* (species of Festucion variae s.l.) and *Crepis conyzifolia* (Nardion) can be observed. Some of the stands are still grazed (by cattle), some lie fallow. The grazed ones are rich in *Trifolium aureum*, the fallow plots are enriched by, e.g., *Laserpitium halleri* and *Astragalus penduliflorus*.

In the DCA (Fig. 9), the relevés are mostly ordered between 350 and appr. 400 of axis 1, which marks the plot areas far away from the Melico-Kochietum. Additionally, they lie next to the montane silicate areas of the Tunico-Artemisietum (Valtellina) and Val Müstair in the upper part of axis 2.

In the relevés of Braun-Blanquet (1961), *Crepis conyzifolia* occurs with r, *Laserpitium halleri* with II and *A. penduliflorus* is absent. In contrast, *Trifolium aureum* is assigned presence IV (versus currently 20 %) (Table 3, col. 21B).

Festuco-Brometea communities of the Upper Engadin above Brail (1650 m a.s.l.)

Preface: According to Braun-Blanquet (1976), stands of the Centaureo-Gentianetum cruciatae mainly occur in the Upper Engadin, but are also present in the Lower Engadin. This association is listed by Mucina & Kolbek (1993a) as Gentiano cruciatae-Centaureetum alpestris nom. inv. (local character species are *Gentiana cruciata, Centaurea scabiosa* subsp. *alpestris*). This community has a wide ecological amplitude and includes Mesobromion-like stands (*Bromus erectus-Brachypodium* variant) as well as rock stands (*Stipa pennata* s.l. variant); we specified it in Table 3, col. 22a-cB. We especially detected the Mesobromion-like types at the base of rock physiotopes and added it to the vegetation complex relevés as contact vegetation (see Table 4 and below). For the dolomite stands, we propose the differentiation of a new community (see below).

*Helianthemum*grandiflorum-Stipa*austriaca* comm. (Table 3, col. 25S)

Diagnostic species composition: (89) *Aster alpinus*, (102) *Carex humilis*, (103) *Globularia cordifolia*, (104) *Sesleria caerulea*, (105) *Leontodon incanus*, (111) *Onobrychis montana*, (112) *Laserpitium siler*, (117) *Stipa*austriaca*, (120) *Helianthemum nummularium* subsp. *grandiflorum*, (121) *Gypsophila repens*, (122) *Laserpitium latifolium*, (123) *Coronilla vaginalis*, (124) *Hieracium staticifolium*, (125) *Polygala chamaebuxus*, (135) *Helictotrichon pratense*, (136) *Koeleria pyramidata*, (154) *Anthyllis vulneraria*, (155) *Trifolium montanum*, (156) *Asperula cynanchica*, (179) *Poa molinerii*, (270) *Rhinanthus glacialis* s.l. (= *aristatus*).
Comment: *Koeleria cristata* reaches the altitudinal limit at about 1700–1800 m a.s.l. (Zoller 1974) and is there replaced by *Koeleria pyramidata. Koeleria eryostachya,* which was recorded by Braun-Blanquet (1961) in a similar community with high presence (see Chapter 3.8.1), could not be found. There are only a few clear records of this plant species in the Engadin region as yet (Welten & Sutter 1982, Conert 1998).
(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/ Stipo-Poion xerophilae)

In the area of dolomite rock stands, we studied a community characterized by floristic similarities to the Teucrio-Caricetum humilis (e.g. with *Leontodon montanus, Globularia cordifolia* but without the differential species *Dorycnium germanicum*). The Erico-Pinetea species *Coronilla vaginalis* is present. *Helianthemum*grandiflorum* underlines the oreal-subalpine character and the floristic connections to the Seslerietalia communities. pH values range from 7.9 to 9.2.

In the DCA (Fig. 9), the plot areas lie – referring to axis 2 – more or less on the same level as the Teucrio-Caricetum. The separated plot I2 marks a stand which is not as shallow as the others.

Allium lineare-Stipa pennata s.str. comm. (Table 3, col. 24S).

Diagnostic species composition: (59) *Pimpinella saxifraga*, (60) *Plantago serpentina*, (120) *Helianthemum nummularium* subsp. *grandiflorum*, (135) *Helictotrichon pratense*, (136) *Koeleria pyramidata*, (139) *Cerastium arvense* subsp. *strictum*, (140) *Solidago virgaurea*, (141) *Phyteuma betonicifolium*, (142) *Senecio doronicum*, (143) *Laserpitium halleri*, (144) *Allium lineare* (=*strictum*), (145) *Thymus polytrichus*, (148) *Stipa pennata* s.str. (= *joannis*), (150) *Festuca violacea*, (151) *Pulsatilla apiifolia*, (155) *Trifolium montanum*, (162) *Phleum phleoides*, (165) *Polytrichum piliferum*; d Festucion variae s.l.: (146) *Astragalus penduliflorus*, (147) *Poa violacea*, (149) *Dracocephalum ruyschiana*.

(class/order/alliance: Festuco-Brometea/Festucetalia valesiacae/Stipo-Poion xerophilae)

In the small silicate area next to Samedan/Celerina (1780–1900 m a.s.l.), there are still extraordinarily dry grassland communities, forming the transition to the Festucion variae s.l. The silicate rocks are not too poor in bases (orthogneisses), allowing the growth of plants such as *Aster alpinus*. The pH value is 5.8/5.9. With the floristic combination of *Stipa pennata* s.str., *Allium lineare, Pulsatilla apiifolia* and *Dracocephalum ruyschiana* it practically represents a unique type.

In the DCA (Fig. 9), this community is separated on the extreme right side of axis 1, defining the endpoint of the meso-xerothermic gradient.

4.2.6 Churer Rheintal with Prättigau, Albula and Domleschg

Xerothermic grassland community

"Xero-Brometum" Beger 1923 (syn.: "Xerobrometum rhaeticum" Br.-Bl. 1959) (non Xerobrometum Braun 1915) (Table 3, col. 26)

Character and differential species: (22) *Bromus erectus*, (23) *Pulsatilla montana*, (40) *Hippocrepis comosa*, (58) *Koeleria cristata*, (71) *Globularia bisnagarica* (= *elongata*, = *punctata*), (90) *Tortella inclinata*, (95) *Brachypodium rupestre*, (102) *Carex humilis*, (104) *Sesleria caerulea*, (111) *Onobrychis montana*, (136) *Koeleria pyramidata*, (153) *Salvia pratensis*, (154) *Anthyllis vulneraria*, (155) *Trifolium montanum*, (156) *Asperula cynanchica*, (158) *Aster linosyris*, (159) *Allium carinatum*, (160) *Buphthalmum salicifolia*, (187) *Potentilla pusilla*, (210) *Teucrium montanum*.

Rock habitats: (117) *Stipa*austriaca*; seldom: (48) *Oxytropis pilosa*, (144) *Allium lineare* (= *strictum*), (336) *Astragalus monspessulanus*; fallow land: (157) *Anthericum ramosum*; oreal form: (112) *Laserpitium siler*.

(class/order/alliance: Festuco-Brometea/sensu ROYER 1987: Festucetalia valesiacae/Stipo-Poion xerophilae; syntaxonomical rank not clear)

Up to now, there has not been agreement concerning the syntaxonomical status and the rank of this association. BEGER (1923) described the "Xero-Brometum" (with abundant *Brachypodium pinnatum,* which probably is *B. rupestre*) in the second part of his Schanfigg-monograph (area near Chur). He was – according to our data – the first to publish relevés with cover/abundance data. Later, BRAUN-BLANQUET (1959) elaborated 28 relevés in a monographic paper and named the association "Xerobrometum rhaeticum". The whole nomenclature of the "Xerobrometum" s.l. has to be revised (see also MUCINA & KOLBEK 1993a, RENNWALD et al. 2000). The association holds a transitional position between Brometalia and

Festucetalia valesiacae. Character species of the latter order are only weakly represented, e.g. by *Potentilla pusilla.* Most similarities can be detected if the association is compared with limestone and Bündner schist areas of the Oberinntal/Engadin, because in all these areas, there are *Bromus erectus, Carex humilis, Teucrium montanum, Globularia cordifolia, Sesleria caerulea, Libanotis montana* and others. Royer (1987) proposes to include this association in the Stipo-Poion xerophilae. Concerning the Festucetalia valesiacae communities, the association is rich in more mesophytic species, e.g. *Koeleria pyramidata, Salvia pratensis, Trifolium montanum.* This corresponds to climatically less extreme conditions of the northern Alps. Nevertheless, some very xerophytic species such as *Stipa*austriaca, Oxytropis pilosa, Allium lineare* occur. pH values range from 6.7 to 8.5. Site-specific subtypes are differentiated by *Stipa capillata, Stipa*austriaca* and a typical, more oreal form, characterized by *Laserpitium siler,* can be distinguished. The "Xero-Brometum" can mostly be found on secondary stands which had been conserved by grazing pressure. The most impressive "Xero-Brometum" stand R6 has traditionally been grazed by sheep; in the last decades it has been mown and cleared from shrubs (Trepp in litt. 15.2.1992). The rocky areas with *Stipa*austriaca* and *Allium lineare* are potentially free from forest.

In the Rhein area, there are very special geological structures, the so called "tumas" or "tomas" built up by rock slide material (Malm limestone) and intermingled with moraine material, which forms hills of debris (Dolf 1974). The "Xero-Brometum" stands of these tumas are especially rich in *Teucrium chamaedrys.*

In the DCA (Fig. 9), the Rhein relevés are intermingled with those of the Astragalo-Brometum, but if axis 3 is depicted, they are separated (they are vertically distinct from the other plot areas).

A comparison with the Braun-Blanquet relevés (l.c.) shows that some fringe species such as *Vincetoxicum officinale, Anthericum ramosum* and *Peucedanum oreoselinum* (at higher altitude *Laserpitium siler*) have a higher presence than in the old relevés, which also applies to *Buphthalmum salicifolium.*

4.3 The vegetation complexes

4.3.1 Valle d'Aosta (map: Fig. 12)

Thymus vulgaris-Bromus erectus comm. complex (A30, 29, 28, 27, 26, 25, 24; Table 4, 5, col. 1)

The more humid zone in the valley bend region is characterized by submediterranean influence. Communities which include steppic elements decrease. An extreme subtype of this complex is restricted to serpentine rock stands (A30, A29), with the *Notholaena marantae-Asplenium septentrionale* comm. in rock fissures. Serpentine habitats often are characterized by the drought-resistant fern *Notholaena marantae.* According to

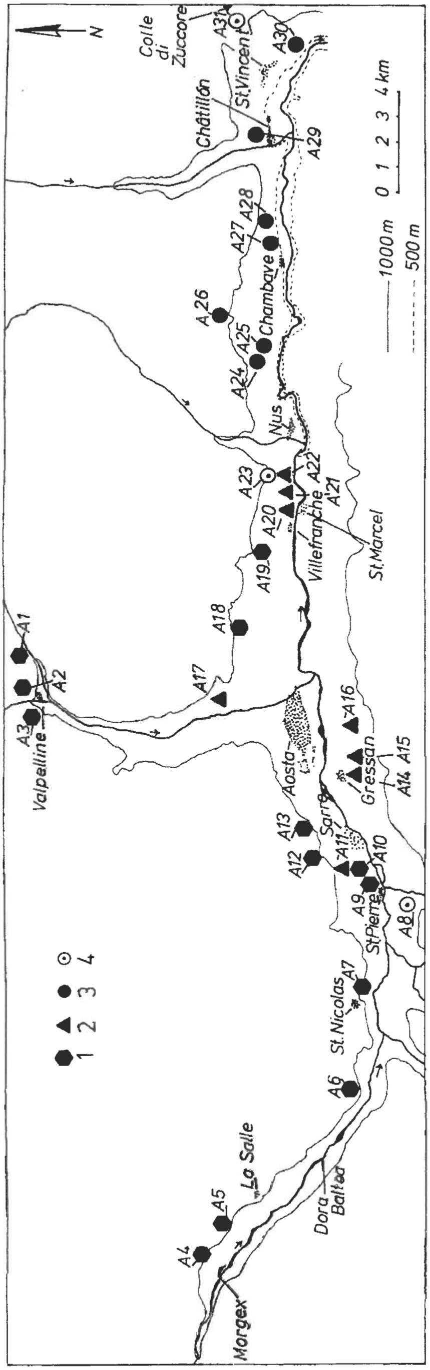


Fig. 12. Investigation area in the Valle d'Aosta, topographical location and vegetation complex type of the plot areas. Complex types: 1 ok, 2 mk, 3 tb, 4 pb.

Pichi-Sermolli & Chiarino-Maspes (1963), the wintergreen fern *Notholaena* occurs in Italy in mild-winter areas with between 9 °C and 16.9 °C mean annual temperature and 458 mm to 1780 mm mean annual precipitation, and therefore has a certain climatic amplitude, but it is strongly heliophilous, calcifugal and poorly competitive. There are some fringe communities in this complex (e.g. Trifolio-Geranietum alpestris, *Peucedanum oreoselinum* fringe, shaded habitats: *Salvia glutinosa* fringe); the mild-winter/more humid conditions are underlined by the occurrence of *Hedera helix* espaliers, lacking in the Melico-Kochietum- and Onosmo-Koelerietum complex. As in the whole valley, the Prunetum mahaleb (see Müller 1986), *Lonicera etrusca* vicariant, occurs in abundance. Remnants of the Quercetum pubescentis s.l. characterize the contact vegetation of the plot areas. *Colutea arborescens* and *Hippocrepis emerus* form small shrubs or occur as scattered individuals with high presence, underlining the more submediterranean and mild-winter character of the valley region (in comparison with the upper valley parts).

In the DCA (Fig. 13) the core of this complex is ordered between the Onosmo-Koelerietum complex and the submediterranean types of Valtellina and the Ephedro-Artemisietum complex of the Valais. The latter includes *Hedera*, the frequent presence of which is probably due to subatlantic influences with higher summer precipitation (see Chapter 2.2). The cluster analysis (Fig. 14) lists all relevés in a separate branch next to the Valais plot areas.

Melico-Kochietum complex (A 11, 14, 15, 16, 17, 20, 21, 22; Table 4, 5, col. 2)

This complex is restricted to the moraine habitat complexes (Fig. 15.1–4), and includes a species rich therophyte vegetation and soil crusts. The Melico-Kochietum has high presence; more consolidated sites are covered by the Onosmo-Koelerietum artemisietosum vallesiacae (typicum and *Stipa capillata* variant). Fringe communities are lacking; the Prunetum mahaleb, *Lonicera etrusca* vicariant, occurs with high presence. The moraine physiotopes are embedded in *Quercus pubescens* stands, nevertheless the core areas are naturally free from forest. *Celtis australis* and *Prunus dulcis* are the most characteristic scattered woody plants.

The DCA (Fig. 13) shows the same xerothermic gradient in axis 1 as in the case of the communities. The xerothermic core of the Melico-Kochietum complex is also concentrated next to the zero point of the axis. In the cluster analysis (Fig. 14) the core areas of this complex are separated, but the connection with the Onosmo-Koelerietum complex is very close, especially because there are already elements of the latter complex in the Melico-Kochietum complex, showing a successional gradient.

Onosmo-Koelerietum vallesianae complex (silicate rock: A 18, 19; silicate and base-rich fine soil: 2, 3, 4, 5, 6, 7, 9, 10, 12, 13; poor, fragmentary stand 1100 m a.s.l.: A1) (Table 4, 5, col. 3)

Table 5. Occurrence of woody species in the vegetation complex relevés.

column	1	2	3	4	5	6	7	8	9	10	11
valley region	A	A	A	A	W	W	W	V	V	V	V
complex type	tb	mk	ok	pb	sa	ea	sk	me	ss	cf	pf
number of complex relevés	7	8	13	3	1	8	4	2	12	13	8
above sea level: from ...m	510	600	620	680	600	530	580	650+	600	850	1000
to ...m	1050	900	1150	1380		760	700	700	1000	1350	1500
Indic. (former) grazing											
Berberis vulgaris	V +-2	V 1-2m	V 1-2m	2 +-2m	2m	V +-2m	4 +-1	2 +-1	V +-2m	V 1-2m	V +-2m
Juniperus communis	III +-2m	IV +-2m	V +-2m	3 +-1	+	IV +-1	4 +-1	2 1	V +-2a	V 1-2m	V +-2m
Early successional species											
Betula pendula	I +	I 1	II +	2 +	1	.	2 +-1	2 1	I +	II +-2m	II +-1
Buddleja davidii	.	.	.		.	.	.	.		.	
Colutea arborescens (ind. submed.)	V +	II +-1	I +	1 +		I	2 +	1 +	V +-1	I +	I +
Cornus mas	.	I +	I +		2m		.	1 1		.	
Cornus sanguinea	I +	I +	+ 1		1	II +	3 +	1 +	.		
Cotinus coggyria	.				.		1 1		.	.	
Crataegus monogyna	II +	II +	I +	1 1	.	I +	2 +	2 +	III +-1	+ +	II +
Cytisus nigricans		.			.	.		.		.	.
Erica arborea (ind. submed.)		.			.	.		.	.		.
Euonymus europaeus	I +		.		+	I +	1(+)		+ +		
Frangula alnus	.	.	.	.	.			1 +			
Hippocrepis emerus (ind. submed.)	III +	.	+ +	2 +-1	.	II +-1	2 +-1	1 +	II +-1		
Hippophae rhamnoides	I 2a	I 2a	II +		.	II +	2 +	.	III +-1	V +-2a	II +-1
Larix decidua	II +-1	I +	II +-1	1	.		.	.	I +	II 1	V 1
Ligustrum vulgare	V +-1	II +-1	II +-1	1 1	v	III +-1	4 +-1	1 +	IV +-1	IV 1-2m	II +-1
Pinus sylvestris	II 1	II 1	III +-2m	2 1	.	.	3 +-2a	.	III +-1	II +-1	II +-1
Prunus mahaleb	V +-2m	IV +-1	V +-2m	2 +	1	IV +-1	4 +-1	1 +	IV +-1	IV +-2m	III 1-2m
Prunus spinosa	II 1	II (+)	II +	2 1	+	IV +	4 +-1	1 1	II +-1	II +-1	IV +-2m
Prunus spinosa, crooking growth				.	.	.		.	.	.	.
Rhamnus cathartica		.	I +		.	.					
Rubus idaeus					.	.	.	.			.
Rubus ulmifolius	II +	.	II +	1 +	+	I +		1 1	IV +-1		I +
Sambucus nigra	.			.	.			.			
Sambucus racemosa	.			.	.			.		+ +	I +
Cytisus scoparius	.				.			.			.
Viburnum lantana				2 +	+	I +	1 +	.			I 1
-- -- Rosa											
Rosa agrestis	III +-1	I +	I +	2 +-2m	+	II +	.	.	IV +-1	V +-2m	III +-2m
R.canina	I +-1	II +	IV +-2m	1 +	1	IV +-1	3 +-1	1 +	II +-1	I 1	I 1
R.chavinii			+ +	.		.	.	.	.	.	.
R.cinnamomea	.			.	.			.	.	.	.
R.coriifolia (rh = rhaetica)				.	.			.		.	
R.glauca (rubrifolia)				.	.						
R. jundzillii	.	.		.	.	.			+ +		
R.micrantha		.	II +-1	1 1	.			.	I 1	+ 2m	
R.montana	.				.				.		
R.pendulina	.	.			.	.	.	.	.		
R.pendulina x pomifera			.		.	.	.	.	.		.
R.rubiginosa (eglanteria)			I +-1		.	I +			II +-1	III +-1	I 1
Rosa spec.		I +	.	2 +	.	I		1 +	+ 1	+ 2m	II +-2m
R.tomentosa	I +		.	1 +	.					+ +	II +
R.villosa (=pomifera)				.	.			.			
R.vosagiaca (glauca,dumalis)	.	.		.	.	.	.	.		.	.
Middle successional species											
Acer campestre	.	.	.		.	.	1 +	.	.	.	
Acer opalus		.			+	.	.	.	.	.	.
Acer pseudoplatanus		.	.		.	.				.	
Alnus incana, root sucker			.		.	.					.
Castanea sativa	III +	III +	II +	1 +	(v)	.	.	2 +	III +	.	.
Celtis australis (ind. submed.)	IIII +-2m	IIII +-1	III +-2m		.	.	.	2 1-2m	III +-2m	.	.
Corylus avellana (higher hum.)			I +	1 2a	.		1 +	2 1	.	.	III +
Fraxinus excelsior	I +	IV +	IV +-1	2 +	+	I +	1 +	.	II +	II +-1	III +-1
Fraxinus ornus (eastmed.p=planted)					.			2 +-1	IIII +-2a	.	.
Lonicera xylosteum			+ +	.	.		1 +			I +-1	I 1
Ostrya carpinifolia	.	I +p		.	.			.	.	.	
Populus tremula	.		II +	2 +	.		1 +				
Prunus avium	II +	II +-1	II +	1 1		II +	2 +		+ +	II +-1	III +-1
Prunus cerasus				.	.		.	.			
Prunus padus	.				.	.	.	.	.	I +	II +
Robinia pseudacacia	II 1	II +	+ +	1 (1)	.		.	1 +	II +-1	.	
Sorbus aria	.	I +	IV +-1	2 +-1		I +	2 +-1	1 +			I +
Sorbus aucuparia	.			.	.	.		.		+ +	II +
Ulmus minor	IIII +-1	IV +-1	I +	1 +	.	IV +-1	2 +	1 +	II +		

Table 5. (cont.)

12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
P	P	P	P	P	P	P	P	I	I	I	I	I	I	I	R
pc	cc	df	mc	tam	tao	tt	cb	tc	abm	abo	ds	hs	pk	as	x
2	1	5	1	4	9	6	5	4	8	4	4	6	2	2	9
750+	400	400	900	620	1000	710	950	800	750	1350	1400	1480	1750	1800	600
900		600		900	1700	1100	1350	1050	1350	1550	1570	1620	1800	1900	1450
1 +	+	II +	1	2 +-1	V +-2m	V +-2m	IV +-2m	2 2m	V 2m	4 +-2m	4 1-2m	V +-2m	1 1		IV +-1
2 1-2m	2m	I +	+	2 +-1	III +-2m	IV +-1	II 1	2 +-2m	V +-2a	4 +-2a	1 +	V +-2m	1 1		III +-2m
2 1-2m	.	II +	.	1 1	I +	V +-1	IV +-2m		IV +-2m	2 +-1	2 +-1	II +-2m			II +-2m
	.	I +								.					
	1		2m					1 1	I 1			.			.
.	.	.							.	.					
	2m		.			.		1 1	II +						IV +-1
.		.	.		.										
		II +		1 1	II +	IV +	IV +-1	2 +-1	III +-1	2 +					I 1
		I 1	.	2 +-1			I +			.					
	2m	I 2m		.						.	.		.		
	.		.	.					II +		.				.
	.					I +	.	2 +-1	.	.				.	I +
	.					III 1	I 1					.			I +
	.		1		II 1-2m	II +		2 +-2m	II 1-2m		.	.	.		I +
1 +	.			1 +	III +-1	III +	IV 1	1 1	IV +-1	1 +	1 +	IV 1-2m	1 1	2 1	II +-2m
.	2m	II +-1		2 +				.	II 1-2m			.	.	.	V +-2m
1 1	.	.	.	2 1	V +-1	IV +-1	II +-1	4 2m	V +-2a	.		IV +	1 +	1 +	III +-1
.	.			2 +-2m					.	.	.				
.	+	III +			I +	II +-1	III +-2m	1 2m	II +-2m	4 +-1	.	.		.	IV +-2m
.	.	I +	2m	3 1	I 2m	II 1-2m		.				.			.
	.	.	+	1 +		II +	II +	1 1	IV +-1	4 +-1		II +			
	.	.			I +	.	I 1			1 1	.	V +	.		
2 1	.	V 1	2m	4 +-1		IV +-1	III +				.				
					I (+)		I (+)				.				
		.			I +						1 +	III +			
2 2m		I 1			.	I 1				.	.			.	.
		.					.	2 +-2m	III +-1	2 +				.	II + 1
	+	I +			II 1-2m	I +	II +-2m		.			.	.	.	
1 +		II +		3 +	II +	IV +-1	III +-1		IV +-1	3 +-1	1 1	II +-1	.		II +
.						.									
.		.			I 2m		I 1	.				II 1		.	.
					I +	.					2 +rh	I +		.	
					I +				I +	2 +	3 +-1	IV +-1		.	
		.		1 +	II +	I +	II +-1			1 1		.		.	
1 +		I +	1	2 +	IV +-1	V +-2m	V 1-2m		III +-1			.	.		
.			.	.	II 1-2m		II 1		.		.			.	
		.	.				.		.	.			1 +	1 +	
			.								.	I +			.
	.					.		.	III +	1 1	.	.		.	I +
		.				I +		1 +	III +	1 +	.			.	II +-1
		.			II +	.	I 1	.							I +
	.	.			.		.		I 1	1 1	4 1-2m	IV +-1	1 1	1 1	
	.			.	.	.		.	II +-1		2 +	IV +	.	.	.
			.					.				.		.	
	.			.			.			.					I 1
.								.		.	.	.			
						.				.	.				II +
	.	.				.		.		.		I +	.		
2 1-2m	.	II +	.	3 1		IV +		.	I +				.		
		V 1-2m		1 (+)	.	.	.	.			.		.		.
1 1	1				III +	IV +-2m	III 1-2m	2 1-2m	II +	2 +-1				.	V +-2m
1 +			+		II +	III +-1	II 1	1 +	III +	.			.	.	IV +-1
	(+)	IV +-1	.					1 2m		.			.		.
				.				1 1	IV +	.	1 +		.	.	
	.		.	1 +					.		.	.	.	.	.
1 1	.		.	2 1	III 1	I 1	I +		II +		1 1	III +-1			.
1 +	.	I (+)		3 +-1		I +	I +	1 +	II +					.	II +-1
			2m					.	.			.	.	.	.
.	.	.	.		.	.			I +	1 +	1 +	IV +-1	.	.	.
1 +		II +-1	+	1 1	.				I +						
.					I +		II +	1 +	II +		.				III +-1
.				.	I +	I +	I +	.	III +	1 +	2 +	V +-1		1 +	
.		II +		.	.		.	2 +-1	II +-1			.	.	.	.

Table 5. (cont.)

column	1	2	3	4	5	6	7	8	9	10	11
valley region	A	A	A	A	W	W	W	V	V	V	V
complex type	tb	mk	ok	pb	sa	ea	sk	me	ss	cl	pf
number of complex relevés	7	8	13	3	1	8	4	2	12	13	8
above sea level: from ...m	510	600	620	680	600	530	580	650+	600	850	1000
to ...m	1050	900	1150	1380		760	700	700	1000	1350	1500
Late successional species											
Picea abies	.		.	.	.	.	.		.	I +-1	I 1
Pinus cembra	.			.	.		.		.	.	
Quercus petraea	.	.		.	.	.		.	.	.	.
Quercus pubescens (et x petraea)	V +-2a	IV	V +-1	2 +-1	1	IV +-1	4 +-1	1 1	III +-2m	I +-1	
Quercus pubescens x petraea	.		.	.	.		.	.			.
Tilia cordata	.		.	.	.	.	.	.	.	.	.
Other species								.	.	.	
Amelanchier ovalis	.	I +	I +-1	2 1	.	.	1 +	.	II 1	IV +-2m	II +-1
Clematis alpina	II +-1	II +	II +-1	.	.	.	.	.		I +-1	.
Clematis recta	.		.	.	.		.	.		.	.
Clematis vitalba	II +-1	IV +	III +-1	.	.			1 +	I +		.
Cotoneaster integerrimus	.	.	+ +	.	.	II +		.	I +	.	II +
Cotoneaster tomentosus		.	.		.	.	.		.	.	.
Daphne alpina	I +	I +	.	.	.	.	.	.		.	.
Ficus carica (from gardens)	I +		.	.	.	I +	.	.		.	.
Hedera helix (ind. mild winter)	III +			1 +	+	IV +	1 +	2	II +		
Humulus lupulus	.	.	.	.	.		.	.	.		
Juglans regia	I +	II +	I +		.	.			.	.	I +
Juniperus nana	.	.	.	.	.	.	.		.	.	.
Juniperus sabina (thermomont.)			IV +-2a	1 +	.	II +-2b	3 +-2a	.	I +	.	I 1
Lonicera etrusca (ind. submed.)	III 1-2m	I 1	III +-2m	1 +	.		.	.			.
Malus domestica (from gardens)	.		I +	.	.						.
Pinus nigra	.	.			.	.		.	+ 1	II +-1	.
Prunus (=Amygdalus) dulcis	III +-2m	IV 1-2m	II +-2m		.	II +	.		.	.	
Pyrus pyraster	I +			.	.		.	.		+ 1	
Rhamnus alpina	.			2 +-1	.		.	.		.	.
Rhamnus pumilus	.	.		.	.		1 +	.	I +		.
Rhamnus saxatilis	.	.	.		.	.	.		.		.
Ruscus aculeatus (ind. submed.)	.	.	.	.	.	.	.		.		
Tamus communis (ind.mild winter)	I (+)		.	.	1	.	.		.	.	
Viscum album var. pini	.			.	.			.		.	.
Vitis vinifera, remnants of cult.	II +	I +	II +	.	(+)	I +	.	.		.	.

This complex characterizes the rock-dominated physiotopes in the dry and hot-summer centre of the valley in the submontane-montane and in the montane zone (620 to 1050 m a.s.l.). The Onosmo-Koelerietum is also found in the successional gradients of moraines, where it is restricted to the consolidated moraine stands (see above). Fine soil, rich in bases and especially calcium, occurs in almost every plot area, but is intermeshed with rocky silicate stands. Additionally, local "calcification" in silicate complexes can be observed (Zulauf 1963: 122). Rock fissure vegetation such as the Sedo dasyphylli-Asplenietum ceterach, rock grit vegetation such as *Sedum rupestre* s.l. stands and dominants with espalier growth such as *Globularia cordifolia* and *Juniperus sabina* are very characteristic. Biological soil crusts like Fulgensietum occur, and pioneer communities like the silicate-specific Veronico vernae-Poetum concinnae are present. The latter is completely lacking in the moraine physiotopes. The montane stands of the complex are locally enriched with fringe communities composed of *Laserpitium siler* and *Origanum vulgare*. However, the Prun-

Table 5. (cont.)

12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
P	P	P	P	P	P	P	P	I	I	I	I	I	I	I	R
pc	cc	df	mc	tam	tao	tt	cb	tc	abm	abo	ds	hs	pk	as	x
2	1	5	1	4	9	6	5	4	8	4	4	6	2	2	9
750+	400	400	900	620	1000	710	950	800	750	1350	1400	1480	1750	1800	600
900		600		900	1700	1100	1350	1050	1350	1550	1570	1620	1800	1900	1450
.	.	.	.		I 1	II +	III +-2m	.	II +	1 +		II +	1 +	2 1	II +
.	.	.	.	.		.	.	.	.			.	.	.	.
1 +	.	.	.	.	I +	.	I +		I +	.		.	.	.	II +
1 1	2m	V 1-2m	.	4 +-2m	.	.	I +		.	.	.	.	.	.	I 1
.	.	.	.	2 1		IV +-1	.	.	I 1	.		.		.	.
.	.	.	.	.	I +	II +-1		1 1	.	.	.	.	.	.	I +
.		.	.		.	.				.	.	.	.	.	
.	+	I +		2 +-1	III +-2m	IV 1	II +-1	2 2m	IV +-2m	3 +-1	4 1	III +-1	.	.	II 2m
	.		.	.	.		II +-1	1 +	I +	.	.	.	.	.	.
	1			.			.	.	I 1	.	.	.	.	.	.
	+	V +	.	1 1		.	.	.	III +-1		.				III +-1
.		.	.	.	II +-1		.	1 +	II +	2 1-2m	3 1-2m	I 1	.	2 +	II +-1
	.	.	.	.	II +-1		.	.	.		.	.		.	.
	.		.	.	.	.	.	.	.	.		.		.	.
.	.	IV +-2m	.	2 (+)	.	.		.	.	.	.	.	.	.	
	.	IV +	.	.	.	I +		.	.	.	.	.	.		II +
.	.	.	.	.	.	.			.	I +	.	.	.	.	.
.		I +	.	2 +	.	II +			I (+)	.	.	.	.	.	II +
.	.	.	.	.	.		.	.	.	.	.		.	1 +	.
.	.	.	.		II +	.	.	2 +	II +-2m	1 +	.				.
.	.	.	.		.	.	.	.	.		.	.	.		.
.	.		.	.	I +		.	.	I +		.	.			.
.	.	.	.	.	.	I +	.	.	.		.	.		.	.
.	.	.	.	.	.		.	.	.		.	.	.	.	.
	.	.	.	.		.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	I +	.		.	IV +-1	3 +-1	2 +-1	I +	2 1-2		
.	.	.	.	.	.	.	.	1 +	.	.	.	.	.	.	
.	+	.	.	.	.		.	.	.	.	.	.	.	.	
.	2m	IV +		.	.	I (+)	.	.		.	.				I(+)
.		.	.	.	.	.	.	1 2m	II +-1	.	.	.	.	.	I 1
.	.	IV +-1		3 +	.	.	.	.	.	.	.	.	.	.	.

etum mahaleb, *Lonicera etrusca* vicariant, is abundant. The submontane-montane subtype of the Onosmo-Koelerietum complex is embedded in *Quercus pubescens* stands, the montane subtype in the Ononido-Pinion zone (Varese 1996). The more elevated plots of this complex coincide with the altitudinal border of vineyards (1188 m a.s.l. near Morgex). *Quercus pubescens* (+ × *petraea*) and *Sorbus aria* are the most characteristic scattered woody plants. The thermomontane character of A4–A7 is underlined by species such as *Juniperus sabina* and the butterfly *Parnassius apollo*.

In the DCA and in the cluster analysis (Fig. 13, 14) this complex is directly associated with the Melico-Kochietum complex, following the meso-xerothermic gradient in axis 1, as in the case of the communities. A9 marks an extreme rock complex near St. Pierre, and has the same position in the DCA as the moraine physiotopes. Two relevés with strictly silicate habitats (A18,19) are separated in the DCA and in the cluster diagram.

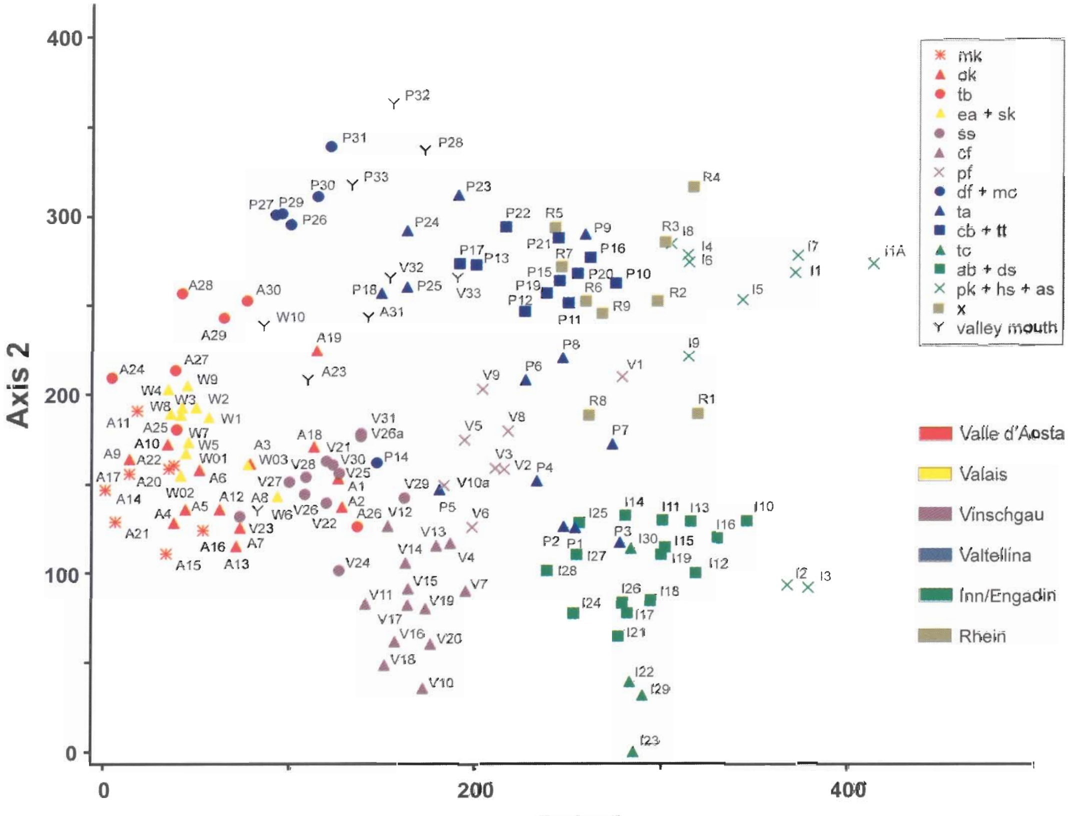


Fig. 13a. DCA of the entire data set of localities (community level); eigenvalues (λ) and gradient length (100 = 1 SD); axis 1: $\lambda_1 = 0.53$; gradient length = 4.3 SD; axis 2: $\lambda_2 = 0.39$; gradient length = 3.8 SD, axis 3: $\lambda_3 = 0.35$; gradient length = 3.5 SD. Coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space: axis 1: $r^2 = 0.23$, axis 2: $r^2 = 0.11$, axis 3: $r^2 = 0.05$; distance measure for original distance: Relative Euclidean. Symbols indicate different valleys and different valley regions.

Pulsatillo montanae-Brometum erecti complex (A8, A23, A31; Table 4, 5, col. 4)

This complex characterizes **the transition** between xeromontane and more mesothermic complexes. There are some fringe communities (e.g. Geranio-Trifolietum alpestris, *Vicia onobrychis* fringe) and shrubs such as *Corylus avellana* and *Viburnum lantana*. In the DCA (Fig. 13) the plot area of the montane zone of the valley mouth (A31: Colle di Zuccore, 1300 m) is separated from the other Aosta plots and ordered next to Valtellina,

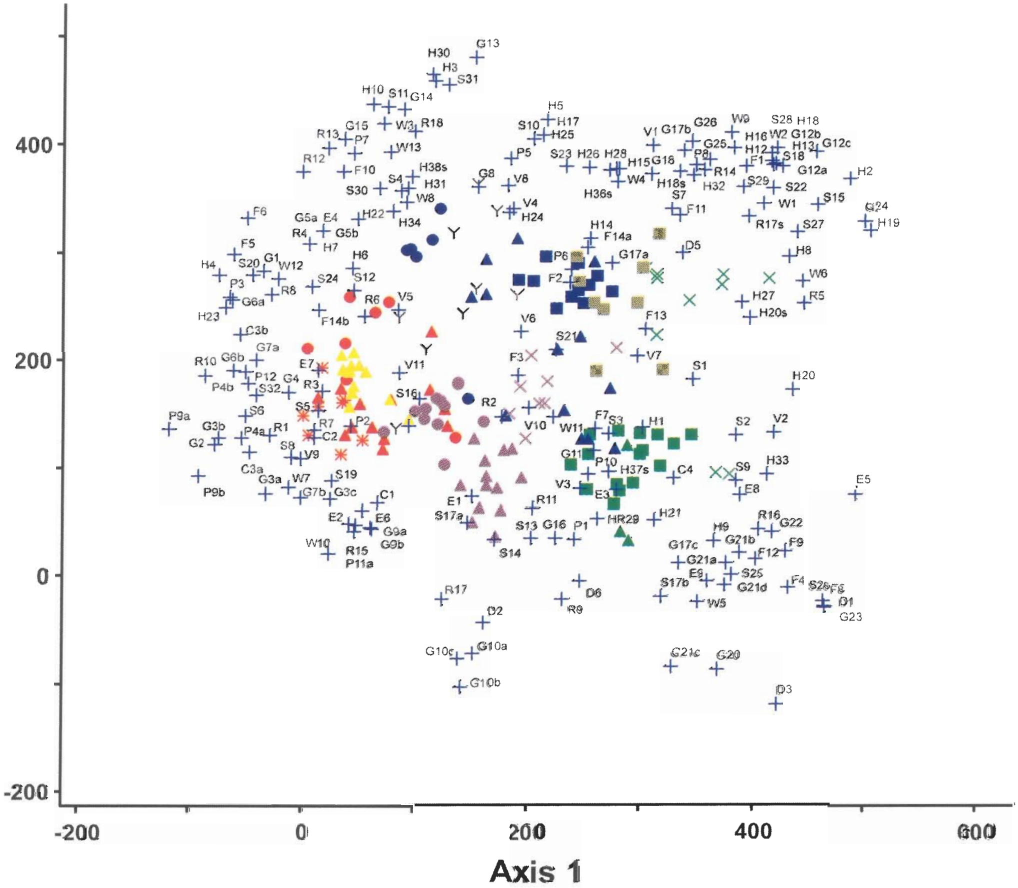
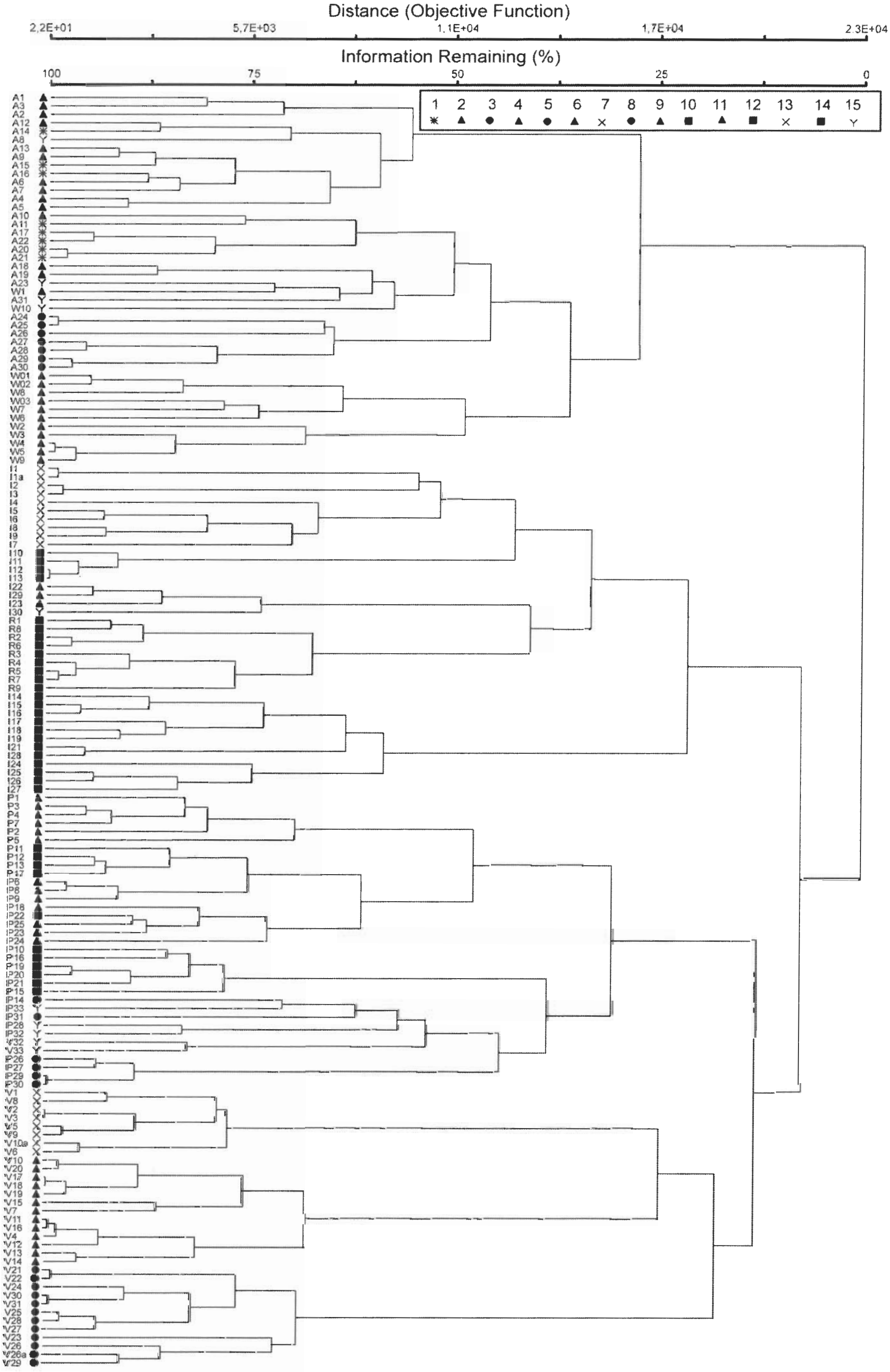


Fig. 13b. DCA of the entire data set plant communities (vegetation complexes), abbr. see Table 4 "code"; for all other information see Fig. 13a.

whereas the other plots of this complex are marginal in the axis 1 gradient. In the cluster diagram A31 is ordered next to the valley bend region in the Valais (W10: Les Follatères).

4.3.2 Inner Valais (from Martigny to Raron) (map: Fig. 16)

Preface: All plot areas lie – according to the investigations of BURNAND (1976) – in the *Quercus pubescens* zone with high solar radiation; at about 700 m a.s.l. there are transitions to the Ononido-Pinion. None of the areas is still grazed. According to GAMS (1927) and FREY (1934), grazing pressure by goats and sheep played an enormous role at that time, e.g., the Follatères village Fully kept 1058 goats in the year 1906 (GAMS 1927).


Distance (Objective Function)
2,2E+01
5,7E+03
1,1E+04
1,7E+04
2,3E+04
Information Remaining (%)
100
75
50
25
0
1 ✱
2 ▲
3 ●
4 ▲
5 ●
6 ▲
7 ×
8 ●
9 ▲
10 ■
11 ▲
12 ■
13 ×
14 ■
15 Y
A1
A3
A2
A12
A14
A8
A13
A9
A15
A16
A6
A7
A4
A5
A10
A11
A17
A22
A20
A21
A18
A19
A23
W1
A31
W10
A24
A25
A26
A27
A28
A29
A30
W01
W02
W8
W03
W7
W6
W2
W3
W4
W5
W9
I1
I1a
I2
I3
I4
I5
I6
I8
I9
I7
I10
I11
I12
I13
I22
I29
I23
I30
R1
R8
R2
R6
R3
R4
R5
R7
R9
I14
I15
I16
I17
I18
I19
I21
I28
I24
I25
I26
I27
P1
P3
P4
P7
P2
P5
P11
P12
P13
P17
P6
P8
P9
P18
P22
P25
P23
P24
P10
P16
P19
P20
P21
P15
P14
P33
P31
P28
P32
V32
V33
P26
P27
P29
P30
V1
V8
V2
V3
V5
V9
V10a
V6
V10
V20
V17
V18
V19
V15
V7
V11
V16
V4
V12
V13
V14
V21
V22
V24
V30
V31
V25
V28
V27
V23
V26
V26a
V29

Ephedro-Artemisietum complex (W2, 3, 4, 5, 8, 9, 01, 02) (Table 4, 5, col. 6)

This complex type is characteristic of the rocky habitat complexes in the region between Saillon and Raron, and is mainly composed of the gappy Ephedro-Artemisietum. The rocky substrate mostly is rich in calcareous material; moreover, loess and moraine material occur – often in small patches. Apart from the dominant Ephedro-Artemisietum, in small areas the loose material is covered by the Stipo-Koelerietum vallesianae. The vegetation complex has a high presence of the Fulgensietum, of therophyte communities such as the Clypeoletum jonthlaspi, of rock grit communities such as stands of *Sedum album* or *S. rupestre*, *Sempervivum tectorum*, and of populations with espalier growth such as *Globularia cordifolia.* Bare and overgrown rocks occupy 20–50% (average 35%). Fringe communities are rare, whereas shrub communities such as the Prunetum mahaleb and small groups of *Berberis vulgaris* and single shrubs/trees of *Prunus dulcis* occur frequently. As in the *Thymus vulgaris-Bromus erectus* comm. complex in the Valle d'Aosta, *Hedera helix* is present. In the Mont d'Orge area Stipo-Koelerietum patches are progressively covered by *Ulmus minor* clones. All investigated plots are partly potentially non-forested stands. The two photos of the Ephedro-Artemisietum complex near Ardon – a) September 1932 (taken by H. Frey, see Frey 1934) and b) July 1992 – document that the core of the rock areas remained free from forest vegetation, although locally the Quercetum pubescentis s.l. increased (Fig. 17a, b).

In the DCA (Fig. 13) this complex follows the Onosmo-Koelerietum complex in the meso-xerothermic gradient and has partly the same level on axis 1. In the cluster analysis (Fig. 14) all Valais complex relevés are ordered together in one branch with the exception of W10 ("Les Follatères"). Ephedro-Artemisietum complex and Stipo-Koelerietum complex form two subgroups.

– Remarks concerning the "Felsensteppe"

The Ephedro-Artemisietum complex is more or less identical with the "Felsensteppe" ("steppe of the rock areas"), which had been described by Frey (1934) in his classical work. The term "Felsensteppe" had already been used by Schröter (in Stebler & Schröter 1892: 21 ff.). Although the dry grassland complexes are not restricted to the rocky areas, (see Braun-Blanquet 1961), it is very difficult to detect the really "steppic" habitats (i.e., naturally non-forested dry grasslands, which are cold in win-

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Fig. 14. Cluster analysis of the complete data set of vegetation complexes (Ward's method: measure for distance: Euclidean). Symbols indicating vegetation complexes or complex groups refer to the symbols of Fig. 13. 1 mk, 2 (with valley symbol A) ok, 3 (with A) tb, 4 (with W) ea + sk, 5 (with V) ss, 6 (with V) cf, 7 (with V) pf, 8 (with P) df, 9 (with P) ta, 10 (with P) cb + tt, 11 (with I) tc, 12 (with I) ab + ds, 13 (with I) pk + hs + as, 14 (with R) x, 15 valley mouth regions.

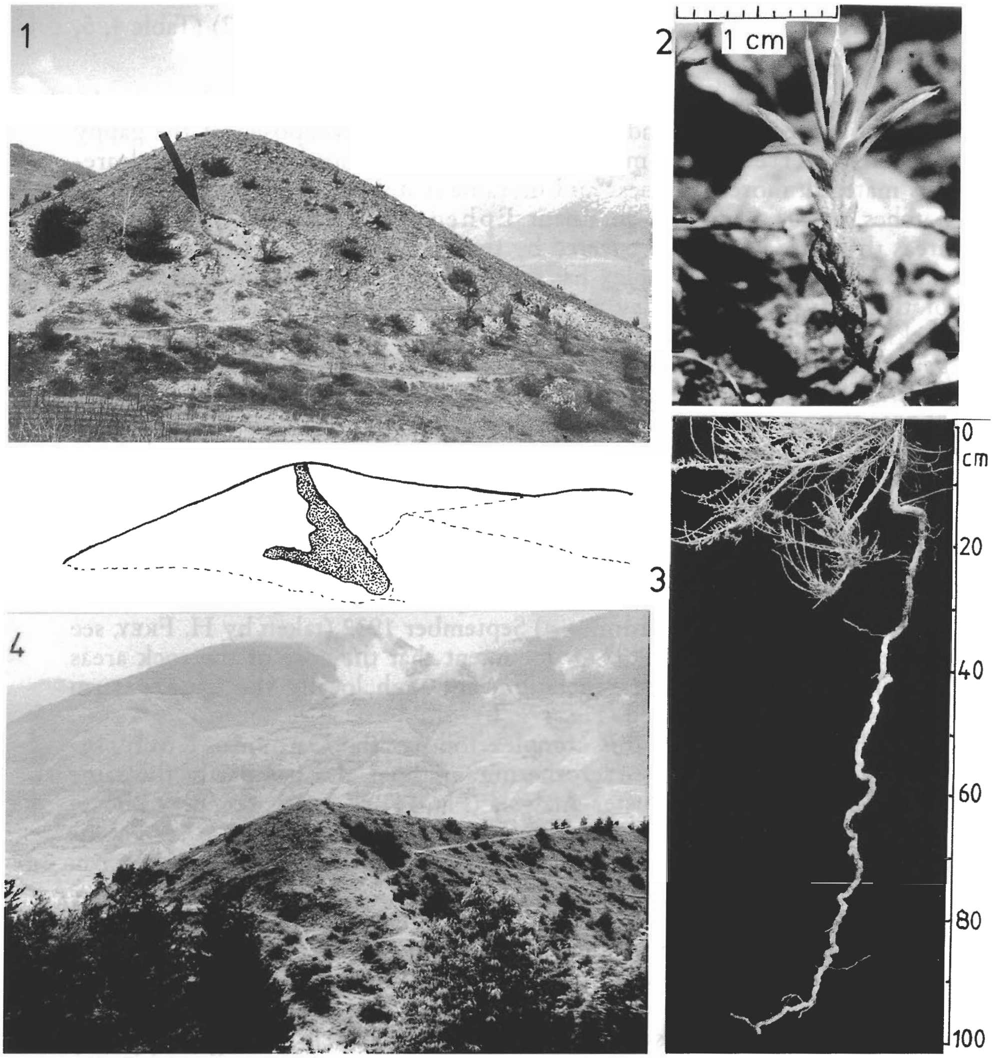

Fig. 15. 1–4. The moraine "Gargantua" next to Gressan (A14, 700 m a.s.l.) with the Melico-Kochietum complex on the south-facing side. The arrow (15.1: left, top) indicates the core of the complex with seedlings of *Bassia prostrata* (15.2: right top). The root system of this chamaephyte (15.3: right, bottom) extends down to 100 cm and more (root profile from a slope near plot area A17). 15.4 (left, bottom): Southeastern exposure of the moraine "Gargantua". In this special perspective of the June aspect the main distributions of the (meanwhile dried-up) therophyte communities are visible. In the middle, left: schematic depiction of 15.4, therophyte areas are indicated (dotted zone).

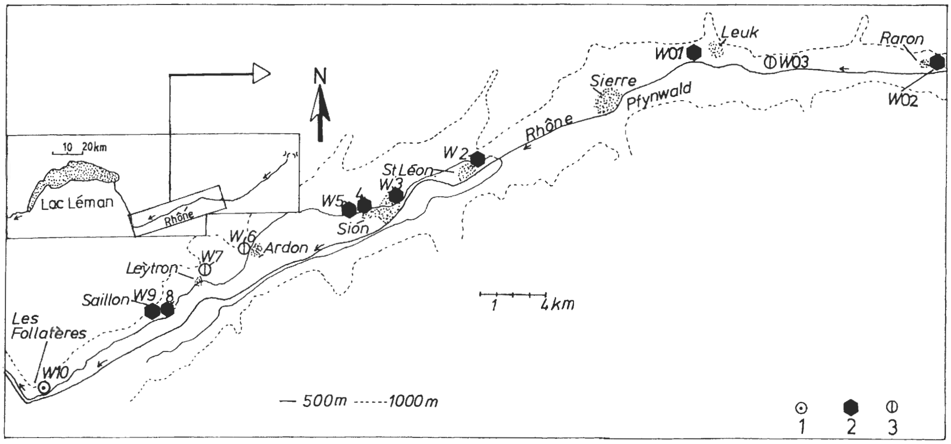

Fig. 16. Investigation area in the Valais, topographical location and vegetation complex type of the plot areas. Complex types: 1 sa, 2 ea, 3 sk.

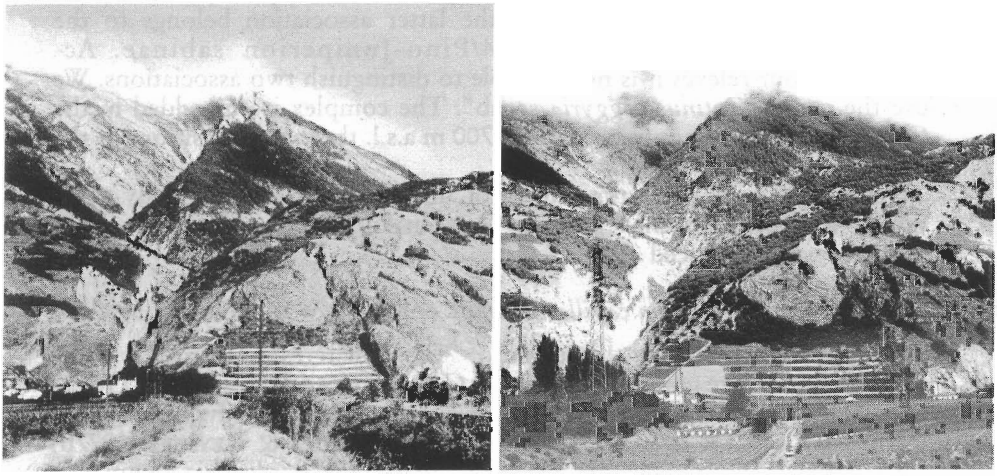

Fig. 17a, b. The "Felsensteppe" (steppe of the rock areas) near Ardon/Valais. Left (17a): photo taken in 1932 (Frey 1934), right (17b): photo taken in 1992. For further explanations, see text.

ter and very hot in summer); therefore, Theurillat (1991) introduced the term "pelouses pseudo-steppiques" ("pseudo-steppic grassland"). In a comprehensive sense this would mean: "pseudo-steppic vegetation complex". Compared with the "Steppenheide" ("steppe heath") of Gradmann (1933, 1950), which had been studied e.g. by Köppler (1995) and Köppler & Schwabe (1996) the "Felsensteppe" is free from fringe communities. In contrast, the core of the steppe heath is defined by the richness of Geranion sanguinei communities (Müller 1962).

Stipo capillatae-Koelerietum vallesianae complex (W6, 7, 03) (Table 4, 5, col. 7)

The Stipo-Koelerietum complex without or with only small patches of Ephedro-Artemisietum occurs in habitat complexes with higher percentages of loose material, which are rich in bases. The complex grows on potential forest sites, with the exception of some rock and slipping debris patches. Formerly this complex was more widespread; at that time these habitats were grazed and/or burned, and leafy shoots were cut for use as livestock fodder (Frey 1934). The complex is rich in communities characteristic of debris material, such as the Stipo-Koelerietum stipetosum calamagrostis and the Stipetum calamagrostis.

Fringe communities like the *Origanum vulgare* comm. occur, and *Juniperus sabina* espaliers emphasize the thermomontane character of the complex. A very special characteristic of this complex is the eastern Mediterranean shrub *Cotinus coggyria*. In the surroundings of Getwing (W03, 700 m a.s.l.) the shrub forms a community described by Rivas-Martinez & Géhu (1978) as Pruno mahaleb-Cotinetum coggyriae (Berberidion), and in the case of *Juniperus sabina*-dominance as Cotino-Juniperetum sabinae. According to the authors, the latter association belongs to the Pino-Juniperetea Riv.-Mart. 1964/Pino-Juniperion sabinae. According to our relevés it is not possible to distinguish two associations. We use the name "*Cotinus coggyria* scrub". The complex is embedded in the Quercetum pubescentis zone; at 700 m a.s.l. there are transitions to the Ononido-Pinion zone.

In the DCA (Fig. 13) the relevés of this complex are marginally positioned (to the right of the Ephedro-Artemisietum complex); the cluster analysis was introduced above.

Saxifraga bulbifera-Stipa capillata comm. complex (W10) (Table 4, 5 col. 5)

This type is restricted to the region of "Les Follatères". The area is especially rich in fringe communities of the Geranion sanguinei, e.g. Geranio-Trifolietum alpestris Müll. 62, which has already been documented by Eijsink & van Gils (1979) and van Gils & Keysers (1977b) for the Valais. Due to the vicinity effect of the vineyards, this complex is the one with the greatest number of ruderal communities (referring to all complex relevés); 7 communities are recorded. With the exception of some rock habitats the area is probably potential forest land. There are occurrences of Fulgensietum (small sites with loess!), rock fringe vegetation such as Sedo dasyphylli-Asplenietum ceterach, therophyte communities such as Veronico-Poetum concinnae, and ruderal stands. Widespread stands of the Pruno-Ligustretum form the typical shrub vegetation. Quercetum pubescentis s.l. stands form the contact forest vegetation; in one case a small forest consisting mainly of the subatlantic-submediterranean *Ilex aquifolium* occurs (Béguin 2001).

In recent times Delarze (1986, 1988), Delarze & Werner (1986), Werner (1988) studied the flora and vascular plant vegetation. Geissler et al. (1993) found a remarkable bryophyte flora (210 species, mostly with Mediterranean distribution). It is a silicate complex (partly pH between 5.5 and 6.5 with local occurrence of loess [pH 7.3–8.4]).

In the DCA (Fig. 13) the plot W10 is linked to the Valtellina plots and is next to the Pulsatillo-Brometum complex of Valle d'Aosta. In the cluster analysis (Fig. 14) it is ordered together with the Aosta relevés, especially together with those at the valley mouth (A31).

4.3.3 Vinschgau (map: Fig. 18)

Preface: All sites of the Stipo-Seselietum- and Carici-Festucetum complex studied here were classified as "formazione steppiche" (between Naturns and Tartsch) in a map worked out by BÉGUINOT (1934). But there is no doubt that only the rocky areas would be naturally free from forest (see also STRIMMER 1974). Especially forest clearance, e.g. to supply the saltworks of Hall/Tirol, burning and intensive grazing favoured the heliophilous plant species. According to GRABHERR (1949), who analysed historical archive documents, a special form of burning perennial herbs "Stauden-Brandwirtschaft" in the 18th/19th century favoured the expansion of pseudosteppic vegetation. Between 1951 and 1965 an afforestation program was carried out and 900 ha of the unique pseudosteppic vegetation complexes were planted with mainly the not indigenous *Pinus nigra* (FEICHTER & STAFFLER 1996, STAFFLER 2002).

Stipo-Seselietum variae complex (V31, 30, 29, 28, 27, 26, 26a, 25, 24, 23, 21, 22) (Table 4, 5 col. 9)

This complex is restricted to the "Edelvinschgau" (see p. 369). The habitats, which are mainly dominated by silicate rocks, are characterized by the gappy Stipo-Seselietum grassland, and differentiated e.g. by the silicate-specific rock fissure community Asplenietum septentrionali-adianti-nigri and by *Sedum rupestre/montanum* and *Sempervivum arachnoideum* stands. The *Notholaena marantae-Asplenium septentrionale* comm. seldom occurs (compare Chapter 4.2.1). Fulgensietum fulgentis only occurs locally in microhabitats with loess partitioning (see Chapter 4.2.3). The number of therophyte communities is relatively low. As in the highly xerothermic complexes of the other valley regions, fringe communities are almost entirely absent (one occurrence of *Campanula bononiensis* fringe). There is a high diversity of shrub communities. *Berberis* and *Juniperus* give hints of former grazing influence. *Quercus pubescens*-, *Colutea*- and *Hippocrepis emerus* shrubs present three characteristic elements of the *Quercus pubescens* forests. *Fraxinus ornus* mainly occurs as an isolated small tree, and is an indicator for the eastern-Mediterranean biogeographical influences (Orno-Ostryon region). The region in the lower Vinschgau is not too cold in winter in the area with southern exposure, which is indicated e.g. by the occurrence of *Rubus ulmifolius, Hedera helix* and *Celtis australis.*

In the DCA (Fig. 13), nearly all relevés of this complex are ordered next to the silicate-dominated plots of the *Bromus erectus-Thymus vulgaris* comm. complex and the Onosmo-Koelerietum complex (Valle d'Aosta). Two moraine plots of the complex without rock fissure vegetation

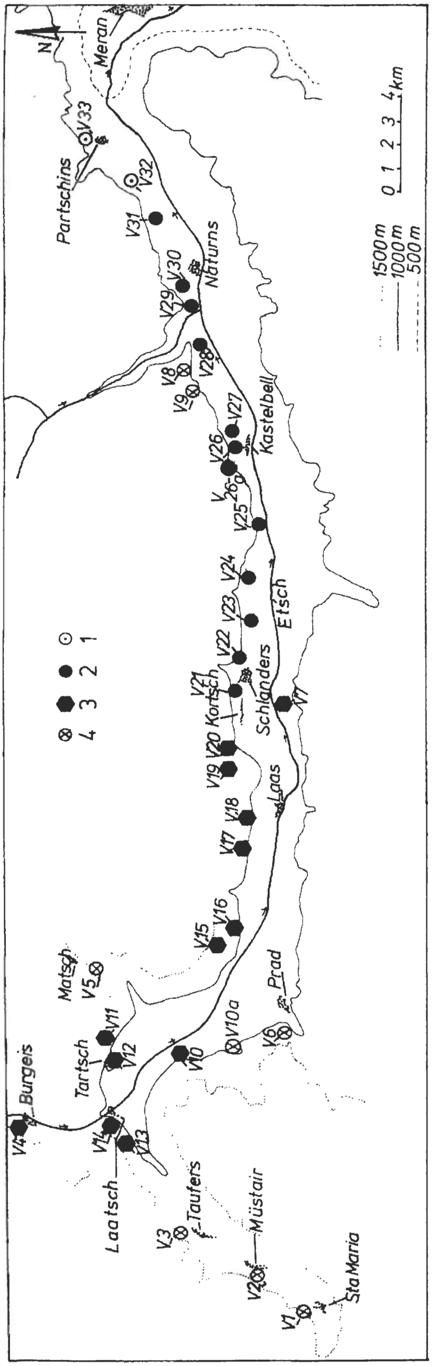

Fig. 18. Investigation area in the Vinschgau and Val Müstair, topographical location and vegetation complex type of the plot areas. Complex types: 1 me, 2 ss, 3 cf, 4 pf.

are ordered separately (V23, 24). In the cluster analysis (Fig. 14), all 12 complex relevés are ordered in a separated branch.

Carici supinae-Festucetum valesiacae complex (V4, 7, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20) (Table 4, 5, col. 10)

The "Vinschgauer Leiten" (Fig. 19) are characterized by this complex type. As in the Stipo-Seselietum complex, various therophytic communities are rare. *Alyssum alyssoides* stands are frequent and cover microhabitats, which are richer in bases. The Fulgensietum fulgentis is restricted to fine-grain microhabitats, mostly with loess particles; pH values locally reach 8.3. The rock fissure vegetation shows the silicate character of the "Leiten" (e.g. with Asplenietum septentrionali-adianti-nigri) and there are also some silicate-specific pioneer communities (*Veronica dillenii* comm., *Rumex acetosella-Polytrichum piliferum* comm.). The characteristic grassland community dominates the complex with its subtypes. The shrub inventory is mainly characterized by browsing-resistant shrubs comprising, e.g., *Berberis, Juniperus* communities and those *Rosa* species that have high contents of volatile ethereal oils (*Rosa agrestis, R. eglanteria*). The browsing-resistant Hippophao-Berberidetum occurs with high presence. Browsing-sensitive species, e.g. *Prunus avium*, are mainly found in the

Fig. 19. Grazed Carici supinae-Festucetum valesiacae complex in the central Vinschgau (Valle Venosta). The browsing-resistant *Juniperus communis, Berberis vulgaris* as well as *Rosa* species dominate the shrub inventory. Slope-parallel cattle paths can be seen (plot area V20, 1030 m a.s.l.).

shelter of resistant ones. Fringe communities only occur in shaded habitats. The occurrence of *Pinus nigra* (partly even irrigated) is attributed to the afforestation projects (see above).

The extreme climatic condiditons are reflected by extreme minima of −22 °C and maxima of 34.5 °C (Laas 532 m a.s.l., Wilhalm & Scholz 2000); the maxima in the slope areas are even higher. In general, this complex determines the subcontinental core of this inner-alpine valley, submediterranean elements being concentrated in the Stipo-Seselietum complex.

In the DCA (Fig. 13), the relevés are clearly separated on the right side of the Stipo-Seselietum complex, following the meso-xerothermic axis. In the cluster analysis (Fig. 14), the plot areas are separated in one branch.

Koelerio gracilis-Poetum xerophilae complex, *Festuca valesiaca* vicariant (V1, 2, 3, 5, 6, 8, 9, 10a) (Table 4, 5 col. 11)

As already mentioned, higher humidity in this complex causes the occurrence of, e.g., Brometalia species. The pH values of the acidic stands range from 5.5 to 6.5. As in the other montane complexes, there are fringe communities such as *Astragalus glycyphyllos* fringe and mesophytic shrubs such as *Corylus avellana*.

In the DCA (Fig. 13), the complex follows the Festuco-Caricetum complex to the right side. There are narrow connections to the montane silicate relevés of Valtellina and in the case of the Val Müstair to the silicate Engadin relevés, the latter lying at the other side of the Fuorn pass. In the cluster analysis (Fig. 14), the relevés are ordered together with a clear distinction from the Carici-Festucetum complex.

Melica ciliata-Erysimum rhaeticum comm. complex (V32, 33) (Table 4, 5 col. 8)

Closely resembling the insubric Valtellina plot areas, this complex of the valley mouth shows the transition between xeromontane and mesohygric-insubric types. The complex is rich in fringe communities, in woody species of the Quercetalia pubescentis as well as in mesophytic shrubs such as *Corylus avellana*. *Celtis australis*, *Castanea sativa* and *Hedera helix* are also characteristic woody species.

In the DCA (Fig. 13), the two relevés are ordered next to the insubric Valtellina relevés and the valley mouth relevé of the Valle d'Aosta (A31). In the cluster analysis (Fig. 14) the relevés are intermingled with the insubric Valtellina plot areas.

4.3.4 Valtellina/Poschiavo (map: Fig. 20)

Diplachno serotinae-Festucetum valesiacae complex (P26, 27, 29, 30, 31) (Table 4, 5 col. 14)

The complex is restricted to edaphic dry habitats in the vineyard region in the potential Orno-Ostryion zone; there are often only fragments of

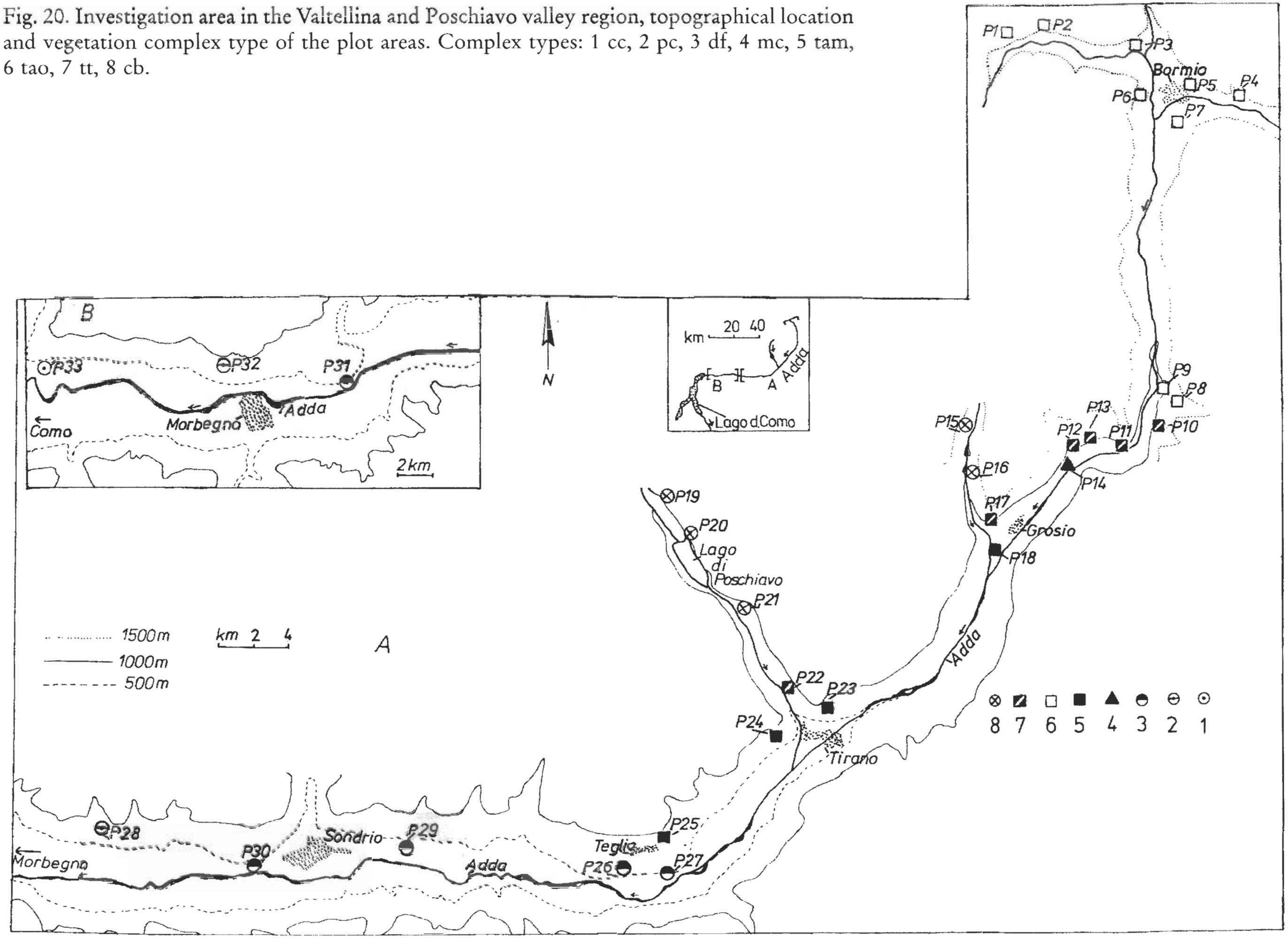

Fig. 20. Investigation area in the Valtellina and Poschiavo valley region, topographical location and vegetation complex type of the plot areas. Complex types: 1 cc, 2 pc, 3 df, 4 mc, 5 tam, 6 tao, 7 tt, 8 cb.

this complex. A large number of different rock fissure vegetation types is present; they are exclusively acidophytic, like the Asplenietum septentrionalis-adianti-nigri. As in the valley mouth regions of the Valle d'Aosta and Vinschgau, the frost-sensitive *Notholaena marantae-Asplenium septentrionale* comm. can be observed. Pioneer communities such as the acidophytic Sileno armeriae-Poetum bulbosae Royer 1987 and the *Rumex acetosella-Polytrichum piliferum* comm. are to be found. In contrast to the corresponding types of Valle d'Aosta and Vinschgau, fringe communities are present. *Celtis australis*, *Ficus carica*, *Hedera helix* and *Quercus pubescens* are very characteristic woody plant species.

All relevés lie together in the DCA (Fig. 13), nearly at the same level of axis 1 as the corresponding Stipo-Seselietum complex (Vinschgau). Together with the acidophytic *Petrorhagia-Calluna* comm. complex, it is ordered in the upper part of axis 2. In the cluster analysis (Fig. 14), the core areas are ordered together in a subbranch of the Valtellina relevés.

Tunico-Artemisietum complex (montane form, acidic substrate: 620–900 m a.s.l., P18, 23, 24, 25; montane-oreal form, base-rich substrate: 1000–1700 m a.s.l., P1, 2, 3, 4, 7; subtype on subneutral substrate: P4, 5, 8, 9) (Table 4, 5 col. 16, 17)

Fig. 21. Tunico-Artemisietum complex, oreal form, in the limestone area of the upper Valtellina valley. The aspect is characterized by *Laserpitium siler* and *Stipa eriocaulis* subsp. *austriaca* (plot area P1, 1700 m a.s.l.).

This is the core complex of the inner alpine Valtellina region. The dryest and hottest areas of the montane zone and the montane-oreal zone near Bormio (Fig. 21) are characterized by this complex (with the exception of type P14, see below). A transition type to the Centaureo-Brachypodietum complex corresponds to the next complex type. In the upper valley near Bormio, on limestone material, there are thermomontane-oreal elements such as *Juniperus sabina* espaliers, oreal-alpine elements (e. g., *Arctostaphylos uva-ursi* espaliers) and typical basiphytic espaliers (e. g., *Globularia cordifolia* and *Rhamnus pumila*). On debris material, the Rumicetum scutati and the Stipetum calamagrostis are frequent. Additionally, there is an extraordinarily rich shrub flora with, for instance, many different *Rosa* species including *R. coriifolia, R. glauca, R. micrantha, R. montana*. The montane form still lies in the Orno-Ostryion zone, the montane-oreal form in the Ononido-Pinion/Erico-Pinion zone (Credaro & Pirola 1975). The complex is rich in different fringe communities.

In the DCA (Fig. 13), the plots in the limestone area are ordered next to the Astragalo-Brometum complex of the Engadin; the other plots (including the transitional type mentioned below) lie next to the Diplachno-Festucetum complex (next to the valley mouth relevés of the Vinschgau). In the cluster analysis (Fig. 14), all Valtellina relevés are ordered together, including the two relevés of the Vinschgau valley mouth region. The limestone relevés are separated, whereas the acidic plot areas of the Tunico-Artemisietum complex and the transition type are ordered close together.

Tunico-Artemisietum-/Brachypodio-Centaureetum complex (transition type) (P10, 11, 12, 13, 17, 22); Brachypodio-Centaureetum bracteatae complex (P15, 16, 19, 20, 21) (Table 4, 5 col. 18)

The community structure is – with the exception of the dominant grassland community and the lack of basiphytic espaliers – very similar to the previous one. But there are some important communities indicating higher moisture and lack of extreme dryness: the higher humidity is indicated by the mesohygric *Corylus* shrub, *Rubus idaeus* and *Pteridium aquilinum* stands and *Knautia dipsacifolia* fringe; these communities are nearly lacking in the typical Tunico-Artemisietum complex.

In the DCA (Fig. 13), especially the Brachypodio-Centaureetum complex is ordered on the right side of axis 1 (in comparison with the other Valtellina plot areas), showing the highest grade of mesothermic/mesohydric conditions in this valley region. In the cluster analysis (Fig. 14), the Centaureo-Brachypodietum complex is separated and is ordered next to the valley mouth relevés of Valtellina (for further details, see above).

Petrorhagia saxifraga-Calluna comm. complex (P28, 32) (Table 4, 5 col. 12)

This complex type is embedded in the montane Quercetalia roboris-petraeae zone of the lower Valtellina valley between Morbegno and Sondrio. *Teucrium scorodonia* fringe, *Pteridum aquilinum-, Cytisus scoparius-*

and *Calluna* stands, and *Castanea sativa* selvae complete the structure of an insubric complex type with only weak connections to inner-alpine dry vegetation complexes.

In the DCA (Fig. 13), it is ordered marginally at the upper point of axis 2. In the cluster analysis (Fig. 14), the relevés are ordered next to the Vinschgau valley mouth relevés.

Carici humilis-Chrysopogenetum grylli complex (P33) (Table 4, 5 col. 13)

This insubric-submediterranean type (Fig. 22) is extraordinary in the proportion of the *Erica arborea* shrub, and the *Teucrium scorodonia* fringe. *Clematis recta* and *Tamus communis* occur as single lianas. *Erica arborea* shrubs can be found in Valtellina up to Sondrio, but have their main area in the valley mouth region (Becherer 1966a, 1966b). Similar types, but nearly without Festucetalia valesiacae species, occur in the insubric zone near Chiavenna.

In the DCA (Fig. 13), this type lies between the Diplachno-Festucetum and the *Petrorhagia-Calluna* comm. complex. The same applies to the cluster analysis (Fig. 14).

Fig. 22. Carici humilis-Chrysopogonetum grylli complex in the valley mouth region of Valtellina. Carici-Chrysopogonetum (with *Heteropogon contortus*) and *Erica arborea* scrub are the most characteristic elements of this vegetation mosaic (plot area P33, 400 m a.s.l.).

Melica ciliata-Centaurea maculosa comm. complex (P14) (Table 4, 5, col. 15)

This complex with steep slopes up to 80° and fine-grain debris is very poor in communities; debris-indicating types such as Stipetum calamagrostis and *Hippophaë* shrub occur here.

In the DCA (Fig. 13), the relevé is totally separated from the other Valtellina complexes, lying next to the Stipo-Seselietum complex of the Vinschgau. In the cluster analysis (Fig. 14), it is integrated in the valley mouth relevés.

4.3.5 Oberinntal/Engadin (map: Fig. 23)

Teucrio montani-Caricetum humilis complex (I22, 23, 29, 30) (Table 4, 5 col. 20)

The complex is typical for the mainly solid limestone (partly dolomitic) habitats in the Oberinntal between Zirl and Ried and is characterized by some communities that are restricted to limestone rock habitats, such as the Potentillo caulescentis-Hieracietum humilis, and typical espaliers (*Globularia cordifolia, Rhamnus saxatilis*). *Juniperus sabina* espaliers underline the thermomontane character. Only in one plot area (I30) is there a variety of fringe communities, e.g. *Origanum-* and *Geranium sanguineum* fringe; *Amelanchier ovalis* and *Cotoneaster integerrimus* represent very typically scattered scrubs in rocky areas. The complex is embedded in the Erico-Pinetum s.l. zone. A remarkable fact is the isolated occurrence of *Fraxinus ornus* in this complex (I30), which is likely to be based on climatic influences of the "foehn-climate" (see Chapter 2.2) as well as biogeographical connections with the Vinschgau.

In the DCA (Fig. 13), the dolomite and very dry areas I29, I22, I23 are ordered separately at the beginning of axis 2. I30 (Zirl), with deeper soils and different fringe communities, is integrated into the Astragalo-Brometum complex. In the course of the meso-xerothermic gradient of axis 1, the Inn/Engadin relevés of this complex together with the following relevés form a triangle, which lies clearly separated on the right ("more mesothermic") side of the Carici-Festucetum complex (Vinschgau). In the cluster analysis (Fig. 14), the 4 plots are ordered next to those of the *Dracocephalum austriacum-Stipa*austriaca* comm. complex, which is likewise restricted to solid limestone.

Astragalo-Brometum complex (montane form: 750–1350 m a.s.l., I17, 18, 21, 24, 25, 26, 27, 28; oreal form: 1350–1550 m a.s.l., I14, 15, 16, 19) (Table 4, 5 col. 21, 22)

The montane form of this complex can be detected between Roppen (slope of the Inn, Fig. 24) and Ramosch (Lower Engadin). The physiotope is dominated by fine soil material of Bündner schists or other fine grid material,

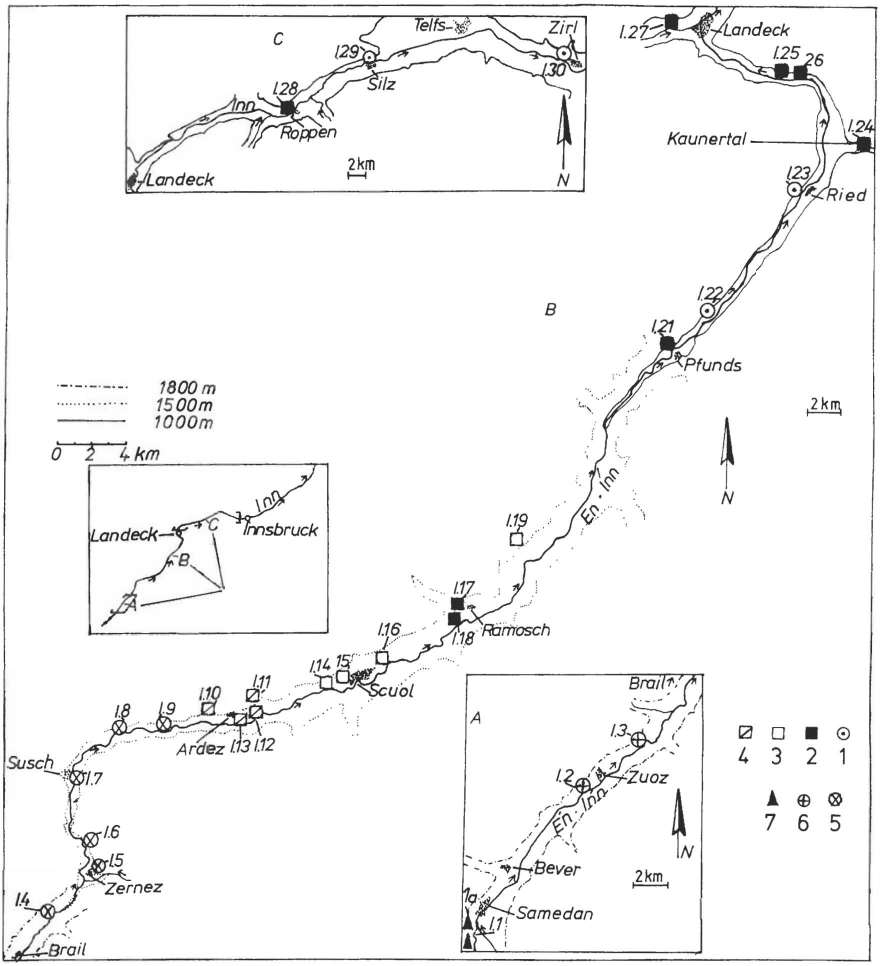

Fig. 23. Investigation area in the Oberinntal and Engadin, topographical location and vegetation complex type of the plot areas. Complex types: 1 tc, 2 abm, 3 abo, 4 ds, 5 pk, 6 hs, 7 as.

which is always rich in calcium carbonate. A fragmentary *Alyssum alyssoides* comm. occurs, and Stipetum calamagrostis and Rumicetum scutati are present. The steep slopes are in some cases intermingled with small areas of solid rocks and rock grit (occurrence of the *Poa molinerii-Sedum album* comm. in gritty areas) and of debris. The upper border of the montane form mainly corresponds to the altitudinal limit of *Stipa capillata.* Fringe communities comprising *Origanum vulgare* or *Laserpitium siler* occur. In the Engadin plots the Onopordetum acanthii is present. A typical espalier shrub is *Rhamnus saxatilis* (only Oberinntal); characteris-

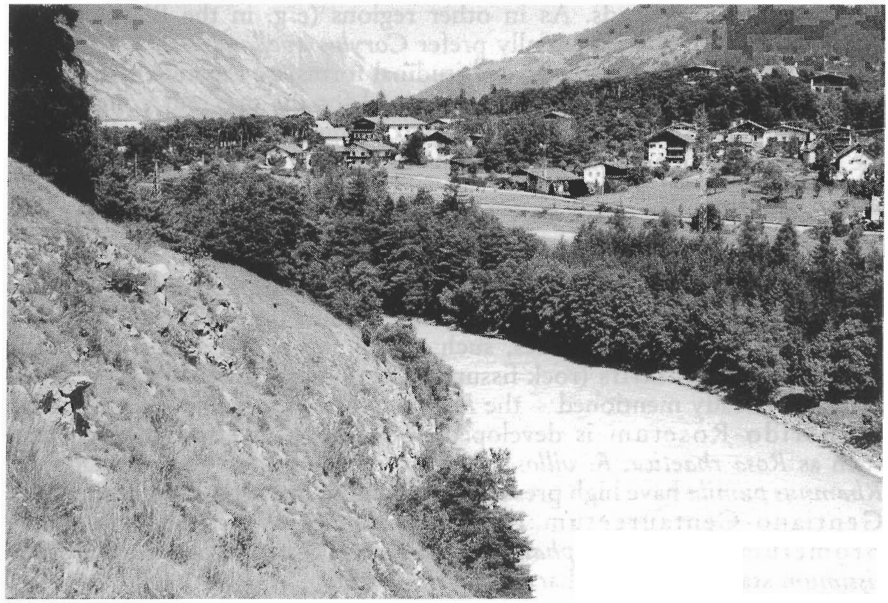

Fig. 24. Montane Astragalo-Brometum complex in the Tyrolean Oberinntal (plot area I28, 750 m a.s.l.).

tic shrub communities are *Hippophaë* pioneer stands and – especially in the Engadin – the Berberido-Rosetum. Plot areas that are very hot in summer (especially between Kaunerberg: Oberinntal and Ramosch: Lower Engadin) are embedded in the Ononido-Pinetum zone (Mucina & Kolbek 1993a, Zoller 1995), having different transitions to the Erico-Pinetum s.l.

In Ramosch the extremely steep, very hot-summer slopes are covered by *Genista radiata* stands. Other occurrences of this plant species, the centre of distribution of which is in the mountains of the Balkan peninsula, are in the oreal belt south of Bozen (Peer 1983, 1984). Fortini et al. (1999) studied *Genista radiata* in the central Apennine where it occurs – as in the Engadine – on calcareous slopes with southern exposure, and regard it as a mesoxerophilous, heliophilous and calcicolous Berberidion species; in the Carpathian Mountains, it is linked to the Genisto radiatae-Pinetum nigrae (Coldea 1991).

The oreal form of the Astragalo-Brometum complex is differentiated by the contact vegetation of the Gentiano cruciatae-Centaureetum (see p. 381), insolated *Laserpitium latifolium* fringes (Trifolio-Laserpitietum latifolii in the sense of Mucina & Kolbek 1993c, which includes the Trifolio-Seselietum libanotis of van Gils & Gilissen 1976), lack of the Hippophao-Berberidetum, occurrence of insolated *Rubus idaeus* stands on debris, the Corylo-Populetum, and lack of *Fraxinus excelsior and Clematis vitalba.* In the oreal form, there are grazing/browsing experiments with goats in this community to protect or re-develop the diversity of these stands. As in other regions (e.g. in the Black Forest, SCHWABE 1997b), goats especially prefer *Corylus avellana.*

In the DCA (Fig. 13), the two altitudinal forms are separated from each other; the principal structure is as described for the previous complex. In the cluster analysis (Fig. 14), this complex forms a separate branch next to the limestone plot areas of the upper Valtellina.

*Dracocephalum austriacum-Stipa*austriaca* comm. complex (I10, 11, 12, 13) (Table 4, 5 col. 23)

Closely related to the Astragalo-Brometum complex, but restricted to the limestone rock areas near Ardez, this complex type is characterized by limestone-specific communities, such as the Potentillo caulescentis-Hieracietum humilis (rock fissures) and *Globularia cordifolia* espaliers, and – as already mentioned – the *Poa molinerii-Sedum album* comm. The Berberido-Rosetum is developed with a high diversity of *Rosa* taxa such as *Rosa rhaetica*, *R. villosa*, *R. vosagiaca.* Espaliers of the basiphytic *Rhamnus pumila* have high presence. A contact vegetation is built up by the Gentiano-Centaureetum. In the Engadin plot areas of the Astragalo-Brometum- and *Dracocephalum-Stipa* comm. complex, *Sisymbrium strictissimum* stands are very characteristic elements.

In the DCA (Fig. 13), this complex type is ordered close to the Astragalo-Brometum complex, and in the cluster analysis (Fig. 14) it is ordered next to the Teucrio-Caricetum complex.

Poo xerophilae-Koelerietum gracilis complex (I4, 5, 6, 7, 8, 9) (Table 4, 5 col. 25)

This silicate-restricted complex type is similar to the corresponding type in the Val Müstair. The rock areas are not too acidic (gneisses, partly hornblende). This is why *Saxifraga paniculata* stands occur as indicators of locally subneutral up to basic conditions. The same applies to debris material (occurrence of the Rumicetum scutati). The typical therophyte community of acidic stands is – as in the Vinschgau/Val Müstair – the *Rumex acetosella-Polytrichum piliferum* comm. The Sclerantho-Sempervivetum arachnoidei is well developed. Higher humidity is indicated by *Epilobium angustifolium* stands, by isolated *Rubus idaeus* stands (debris material) and *Prunus padus* shrub. *Larix decidua* and *Sorbus aucuparia,* which are typical of the oreal-subalpine region, have high presence.

In the DCA (Fig. 13), the plot areas are clearly separated and ordered nearly at the extreme marginal point of axis 1 (300–400). They are ordered next to the silicate Valtellina and Vinschgau relevés. In the cluster analysis (Fig. 14), the relevés are likewise clearly separated.

*Helianthemum*grandiflorum-Stipa*austriaca* comm. complex (I2,3) (Table 4, 5 col. 24)

The large limestone rock areas near Madulain and Zuoz in the Upper Engadin are covered by a complex which shows structural similarities to the

Teucrio-Caricetum complex. The typical limestone-restricted communities, for example the Potentillo caulescentis-Hieracietum humilis, as well as *Kernera saxatilis* stands and *Globularia cordifolia* espaliers are present. The debris material is covered by *Calamagrostis varia* stands and, on dolomitic marl, *Leontodon*hyosuroides* stands. *Pinus sylvestris* rejuvenates in small groups.

In the DCA (Fig. 13), this extraordinary complex type is ordered – together with the following one – at the most marginal points of axis 1 (appr. 400). In the cluster analysis (Fig. 14), this type is clearly separated.

Allium lineare-Stipa pennata s.str. comm. complex (I1, 1a) (Table 4, 5 col. 26)

This complex type is restricted to the subalpine belt. The stands of the characteristic grassland community grow together in one complex with *Pinus cembra-* and *Picea abies* stands (Fig. 25) and a few hundred metres away from the *Sphagnum fuscum* rich bogs in the large Larici-Pinetum cembrae area of the Staz Forest. The complex marks the transition to Festucion variae complexes with *Laserpitium halleri* stands and *Astragalus penduliflorus* fringe.

The inventory of shrub and tree species is restricted in this zone. Besides the two species mentioned above, there are also *Larix decidua, Pinus sylvestris, Cotoneaster integerrimus, Juniperus nana*, *Rosa pendulina* and *Sorbus aucuparia.*

Fig. 25. *Allium lineare-Stipa pennata* s.str. comm. complex in the subalpine Larici-Pinetum cembrae zone of the Oberengadin (plot area I1, 1800–1900 m a.s.l.).

In the DCA (Fig. 13), this type lies at the extreme right margin of the xerothermic-mesothermic gradient of axis 1 and therefore marks the end of the gradient, which begins with the Melico-Kochietum complex of the Valle d'Aosta. In the cluster analysis (Fig. 14), the type is clearly separated.

4.3.6 Churer Rheintal with Prättigau, Albula and Domleschg (map: Fig. 26)

"Xero-Brometum" complex (Table 4, 5 col. 27)

The "Xero-Brometum" complex is mainly embedded in the Ononido-Pinion and Erico-Pinion zone (Hegg et al. 1993), and in some cases includes *Quercus pubescens.* Often the Mesobromion is part of the com-

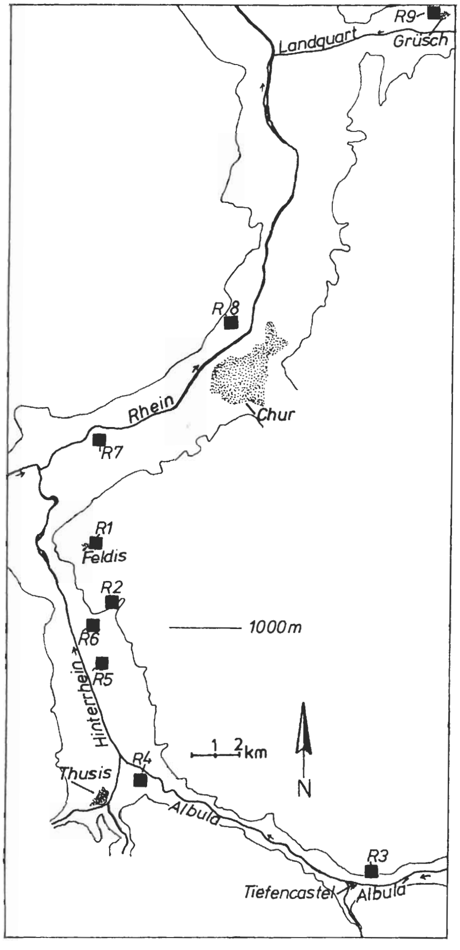

Fig. 26. Investigation area in the Rhein region near Chur, topographical location and vegetation complex type of the plot areas. Complex type: x.

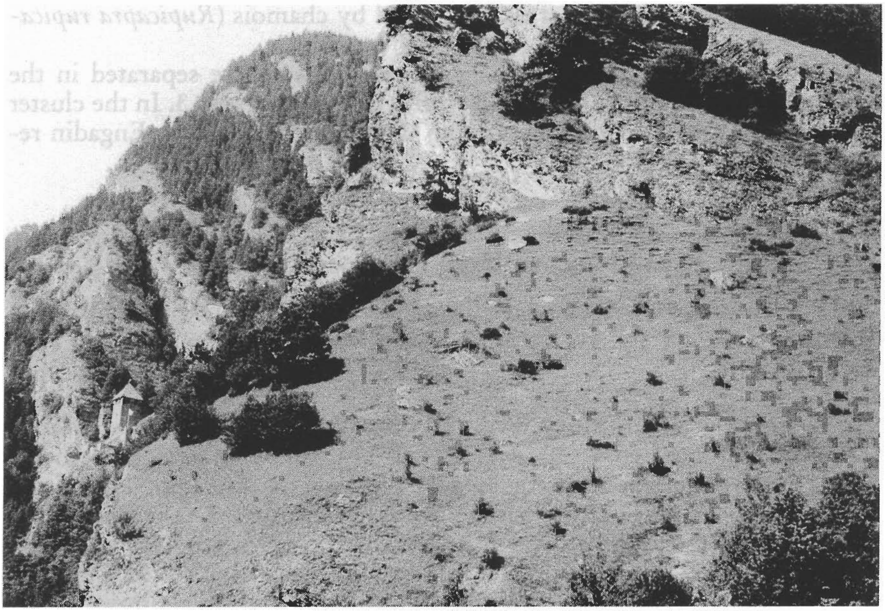

Fig. 27. "Xero-Brometum" complex in the Rhein area near Chur. Convex structures and rocky parts are covered by the "Xero-Brometum" (with *Allium lineare*) (plot area R6, 750 m a.s.l.).

plex and slight depressions are colonized by this community, whereas convex structures and rocky parts are colonized by the "Xero-Brometum" (Fig. 27). The Fulgensietum fulgentis (partly with *Psora decipiens*) and characteristic rock espaliers with *Globularia cordifolia* occur. Fringe communities (*Origanum vulgare* fringe, *Geranium sanguineum* fringe, in the oreal form: *Laserpitium siler* fringe) as well as mesophytic shrub communities comprising, e.g., *Corylus avellana* are characteristic. The mesophytic tree species *Fraxinus excelsior* often can be found as scattered shrubs or trees. Shrub communities are widespread (Pruno-Ligustretum, *Corylus avellana* bushes). There is an increase of this formation in comparison with old photos of BRAUN-BLANQUET (e.g. Solavers: Prättigau, photo according to BRAUN-BLANQUET 1948ff.). The tumas are edaphically dry and rich in vegetation of gritty soils, e.g. *Sedum album* stands and *Alyssum alyssoides-Melica ciliata* stands.

Many of the plot areas of the "Xero-Brometum" which were documented by BRAUN-BLANQUET (l.c.) meanwhile have vanished: they have been fertilized, they lie fallow, they have become built-up areas and some of them have been afforested. Remnants can be found on the southwest-facing slopes of the Calanda mountains in the *Pinus sylvestris*-dominated zone, characterizing very shallow, naturally open habitats, and in the Domleschg (Fig. 27). Other remnants are grazed by sheep (R9). In autumn/winter/spring some of the plot areas are grazed by chamois (*Rupicapra rupicapra*).

In the DCA (Fig. 13), the Rhein complex relevés are separated in the same way as those of the "Xero-Brometum" by the axis 3. In the cluster analysis (Fig. 14), all relevés lie next to the Oberinntal/Lower Engadin relevés.

4.4 Ordination and classification of the plant communities and the vegetation complexes: a comparison

In the following we will compare the results of the multivariate ordination for the community and vegetation complex level comprehensively:

– DCA

Concerning the **community level** (Fig. 9), all Festucetalia valesiacae relevés are ordered in a broad band, mainly following axis 1, from the Melico-Kochietum to the subalpine types of the Engadin. This meso-xerothermic axis will be analyzed in detail in Chapter 7.1. The differentiation from axis 2 (meso-xerohygric axis: Chapter 7.1) is not very clear. Regarding the **vegetation-complex level** (Fig. 13), there is an obvious individuality of nearly each valley region. Valle d'Aosta and Valais however are quite similar and the hygric gradient (Chapter 7.1) between Vinschgau and Valtellina/Poschiavo is reflected.

– Cluster analysis (for the vegetation complex level Fig. 14, for the community level not printed)

The results of the cluster analysis as a polythetic approach reflect a very differentiated picture. At the community and the complex level, the data set is separated into the Valais plus Valle d'Aosta and the other valley regions. Even when the community-level results proved similar to those for the complexes, the latter are more differentiated. That means, the results are comparable but the cluster analysis of the complexes again gives more detailed information about the individuality of the valley regions.

On the basis of these findings we are able to answer question 1 (Chapter 1). Although all data sets show clear and corresponding results with respect to the supposed temperature gradient on different complex levels, the supposed hygric gradient can be worked out especially with the help of the complex level (the factors "temperature and hygric gradient" will be validated in Chapter 7.1). This is mainly caused by the occurrence of fringe communities and mesophytic shrub communities as indicators of more humidity. Therefore, in the case of our systems, a more distinct individuality is reflected for the specific valley regions by using the vegetation complex approach.

There have previously been hardly any comparisons between DCA ordinations on the community and the complex levels. Schiller (2000) studied the effects of organic and conventional agriculture on the vegetation of agricultural and grassland fields and their borders. Compared with the inner-alpine physiotopes, these communities and vegetation complexes are much poorer in species and communities. SCHILLER (l.c.) elaborated DCA diagrams of communities and complexes and derived similar gradients in both approaches; in these community-poor systems with high anthropogenic impact, there was no clear advantage of the DCA: "vegetation complexes".

5 Vegetation dynamics

5.1 Successional processes

– Comparison with historical relevés

The comparison with the historical relevés of BRAUN-BLANQUET (1961) has shown (Chapter 4.2) in the case of the extremely dry conditions of the Melico-Kochietum-/Onosmo-Koelerietum stands (Valle d'Aosta), the Ephedro-Artemisietum-/Stipo-Koelerietum stands (Valais) and the Stipo-Seselietum stands (Vinschgau) that there are hardly any successional processes. As already mentioned, all these stands have been grazed and have since been abandoned. Some grazing-sensitive plant species are more frequent in the current than in the historical relevés, e.g. *Bromus erectus* (Onosmo-Koelerietum, Ephedro-Artemisietum), *Centaurea scabiosa* (Ephedro-Artemisietum), *Lactuca perennis* (Stipo-Seselietum), but the principal floristic structure is nearly identical. Some prostrate growing and weakly competitive species, which are favoured by grazing, as *Veronica prostrata* (Tunico-Artemisietum) and *Trifolium aureum* (Poo-Koelerietum gracilis), had a higher presence in the historical relevés.

As already mentioned above, only those grassland communities that occur in more humid, especially fallow areas are characterized by fringe species (including *Brachypodium rupestre* s.l., see WILMANNS 1981). Therefore, successional stages of those species mainly occur in the Poo xerophilae-Festucetum valesiacae (V), in the Carici-Chrysopogetum, the oreal Tunico-Artemisietum and Centaureo-Brachypodietum (P) as well as in all dry grassland types of the Inn/Oberinntal and Rhein valley near Chur. The comparison with the historical relevés has shown that species favoured in fringe communities have a higher presence in the current relevés; these include, e.g., *Phyteuma betonicifolium* (Poo-Festucetum valesiacae), *Phyteuma scheuchzeri* (Centaureo-Brachypodietum), *Astragalus penduliflorus* (Poo-Koelerietum), *Vincetoxicum officinale, Anthericum ramosum, Peucedanum oreoselinum* and *Buphthalmum salicifolium* ("Xero-Brometum").

Brachypodium rupestre facies, which are always rich in a distinctive litter layer, may remain fallow land for a long time and hinder the rejuvenation of woody species. This phenomenon, which KRAUSE (1974) called (translated) "persistence of grasses and grass-like stands", also applies to other clonal grasses.

– Occurrence of woody species
All shrubs and trees were recorded separately in the vegetation-complex relevés. The grazed areas of each vegetation complex are always characterized by shrub species, especially by those with defence strategies against browsing (see below). Only on small patches, which are potentially free from forest, shrub species are nearly absent. Table 5 shows the complete shrub inventory of all investigated vegetation-complex plots. The table is classified in 4 functional species groups: 1. *Berberis vulgaris* and *Juniperus communis*, which indicate (former) grazing influences and are present in all complexes with the exception of the subalpine complex "as" (Upper Engadin); 2.–4. three successional groups (early, middle and late successional species). Differential and characteristic shrubs, which have already been named in Chapter 4.3, are marked with frames.

There is a remarkably high diversity of shrub species (about 90 species in all valley regions), especially in the montane areas of the Lower Engadin (48 in the Astragalo-Brometum complex, with a high diversity of *Rosa* species) and the Valle d'Aosta (44 in the Onosmo-Koelerietum complex). The corresponding complex in the Vinschgau (Carici supinae-Festucetum complex), which is heavily grazed and browsed, only comprises 29 shrub species. In the Carici-Festucetum complex palatable shrubs, such as *Sorbus aria* or *Cotoneaster integerrimus*, can seldom be found or are entirely absent, whereas *Rosa* species with high contents of volatile substances occur (e.g. *R. micrantha, R. rubiginosa*).

Moreover, *Pinus sylvestris* is abundant in nearly all complex types (confirming the "inner-alpine *Pinus sylvestris* zone"). The same applies to *Quercus pubescens*, which often occurs in the Valle d'Aosta and the Valais, as well as to *Fraxinus ornus* in Valtellina and Vinschgau (only once in the Oberinntal).

Browsing-resistant shrubs, such as *Berberis vulgaris, Juniperus communis, Crataegus monogyna* are abundant. *Prunus mahaleb* and *Prunus spinosa* (less browsing-resistant, absent in the case of intensive grazing), show a clear differentiation of occurrence depending on the summer humidity: *Prunus mahaleb* can be found in the Valle d'Aosta, Valais and Vinschgau, and in the dryest region of Valtellina, whereas *Prunus spinosa* occurs in the more humid plot areas with an upper limit about 1400/1500 m a.s.l. in the Engadin.

The extremely hot-summer and dry plot areas contain no mesophytic species. Most of these species grow in the montane areas and in the valley mouth regions. *Corylus avellana* and *Populus tremula* are suitable indicator species for these more mesophytic conditions. The characteristic community is the Corylo-Populetum, which grows in the more humid montane areas, as was described by KIELHAUSER (1954b) concerning the Oberinntal and by BRAUN-BLANQUET (1975) concerning the Engadin and the Rhein valley near Chur. All vegetation-complex types include species of early, middle and (less diverse) late successional species.

Regarding question 2 in Chapter 1, vegetation complexes do reflect possible successional traits. The results concerning the successional traits of the mesophytic woody species outline the areas having a high potential for progressive shrub development. These are those of the Rhein region near Chur, the Lower Engadin and Oberinntal, the valley bend regions of all investigated valleys, Poschiavo and the montane zone of Valtellina and the upper Vinschgau/Val Müstair. Therefore, nearly all dry grassland complexes of these regions will be reduced in size by succession, because for most of them there are no management concepts (for Switzerland: Gigon, pers. comm.). Very locally extensive grazing is used as a management method of stopping or even regressing succession processes. In parts of the areas without mesophytic woody species long-term succession processes will take place; the shallow rocky core areas will be free from forest.

5.2 Ruderalization trends

Grades of ruderalization (Table 4, types R1–18 + HR29) can be assessed by analyzing the occurrence of ruderal vegetation types in the vegetation-complex relevés (see Fig. 32).

Communities that are abundant in ruderal habitats are especially likely to be found in the following complex types:

1. complexes embedded in the vineyard region; mainly the types "sa", "ea" (Valais), sometimes "ok" (Valle d'Aosta) and "df" (Valtellina) (the latter with *Opuntia humifusa* stands). The maximum of 7 ruderal communities is reached in complex type "sa" ("Les Follatères").
2. complexes on loose substrates such as moraines or weathered schists; mainly the types "mk" (Valle d'Aosta) and "ab" (montane form). The C4 species *Bassia prostrata* has a large ecological amplitude and occurs in Festucetalia valesiacae communities as well as in ruderal stands (Schwabe 1995).

A single ruderal plant species that had been recorded but is not included in Table 4 is *Isatis tinctoria*. Although it occurs in the Valle d'Aosta (tb: III^{+}, mk: IV^{+-2}, ok: III^{+-2m}) and in the Valais ("ea": III^{+-2}, sk: 2^{+-1}), this archaeophytic plant species can hardly be found in (nearly) natural, e.g. rock, habitats. Concerning *Cirsium eriophorum*, there are ruderal stands in "tb", "ss", and in all Inn complex types with the exception of "tc" and "hs". In the subalpine complex "as", this plant species occurs in a (nearly) natural habitat: rocky debris material.

No specific traits of ruderalization can be differentiated in the investigated vegetation complexes (question 3, Chapter 1). The results in Table 4 and Fig. 32 show that ruderal communities play only a minor role in the inner-alpine dry vegetation. With the exception of *Opuntia* (see below) there is nearly no ruderal community or ruderal species that has invaded the plot areas with higher abundance. Only in one complex is there a cover percentage of 5–15 % (*Agropyron intermedium* ruderal stand in "ok"); each of the other ruderal communities remains below 5 % cover.

In comparison with the relevés of Braun-Blanquet (1961), *Opuntia humifusa* has increased (in the Diplachno-Festucetum 10 % versus 63 %, see p. 373). Nowadays, nearly all vegetation-complex relevés of the Diplachno-Festucetum complex include *Opuntia*, although the percentage cover is still low. It is not clear whether this indicates an "invader problem" or is a result of edge effects caused by areas that are too small and fragmented.

The low extent of occurrence of ruderal communities may be explained by the fact that the stands are too dry, with insufficient amounts of available N and P. There are no studies on the mineralization rates of, e.g., nitrogen in those habitats. The investigations of Leuschner (1989) in a Xerobrometum near Rouffach (Alsace) showed that the stands of this community are not really poor in N, but rather in available N, which is limited by water stress in summer. In Festucetalia valesiacae communities in Germany there are ruderalization processes (Mahn 1986), especially in loose material such as sand and loess (Stroh et al. 2002).

6 Aspects of diversity

6.1 Species diversity in Festuco-Brometea communities (Fig. 28)

The number of species occurring in the extremely dry habitats of Valle d'Aosta and Valais ranges from 24 to 28 and is even higher in almost all other valley regions. Exceptions are the *Melica ciliata-Centaurea maculosa* comm. with 19 species (debris stand Valtellina) and the Teucrio-Caricetum humilis with 27 species. Highest diversity values are reached in the predominantly fallow stands of the Centaureo-Brachypodietum (Valtellina/Poschiavo), with 40.3 species.

The Shannon index is very high in nearly all vegetation types (between 3.14 in the Melico-Kochietum and 3.66 in the Centaureo-Brachy-

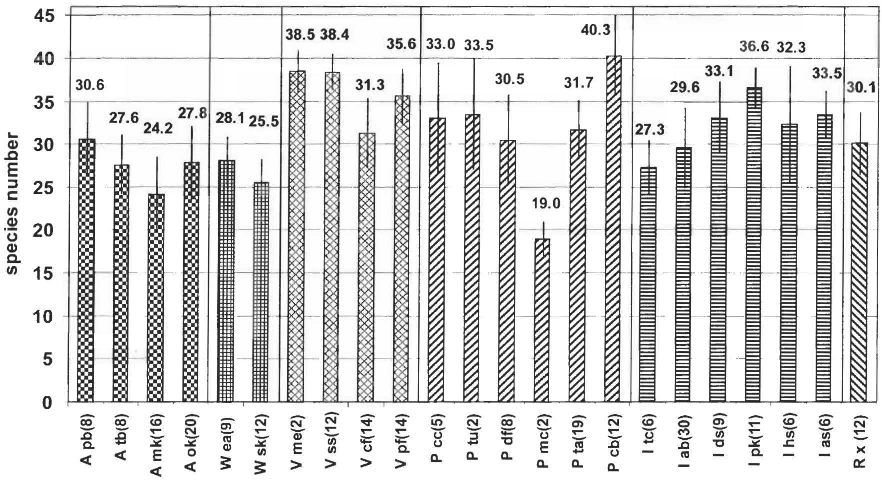

Fig. 28. Average species number of Festuco-Brometea communities according to the relevés of Table 3. Relevé numbers are indicated in brackets. Error bars: mean deviation from the average species number.

podietum), whereas the value in the debris stand in Valtellina (mc) is lower (2.91). FISCHER (1982) found for the "Kaiserstuhl" in southwestern Germany values of 2.83 and 3.03 in Brometalia communities. High values are also obtained for evenness: between 0.98 (e.g. Melico-Kochietum) and 0.99 (e.g. Centaureo-Brachypodietum); Kaiserstuhl 0.79 to 0.82 (FISCHER l.c.); other Brometalia stands in Germany: 0.55–0.81 (HAEUPLER 1982).

Examinations of the relations between species number and annual precipitation (Fig. 29) have shown that there is a significant correlation. The data also reveal a significant correlation between large numbers of species and lower pH values (Fig. 30).

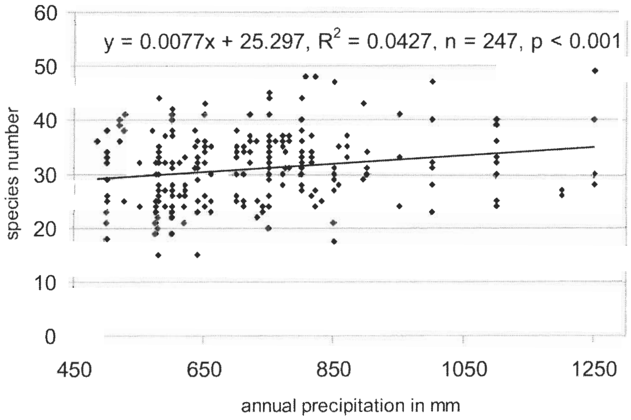

Fig. 29. Correlation between species number and annual precipitation.

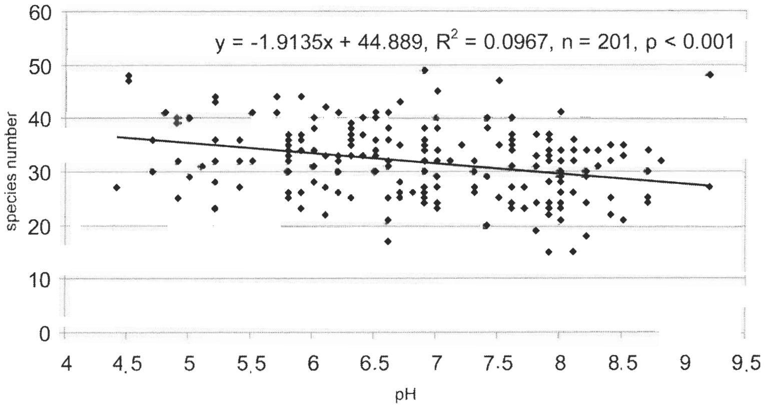

Fig. 30. Correlation between species number and pH values.

A comparison with the average species numbers of BRAUN-BLANQUET (1961) is difficult, although the plot size was adapted to those of BR.-BL. (about 50 m^2). This is due to different methodological standards, since the Koelerio-Corynephoretea communities and the Fulgensietum fulgentis were separated in the current relevés (see Chapter 3.2.2). This separation has caused a lower abundance of those species especially in the types "mk" and "sk"; for the other types there is essentially no consequence.

In the following we list the results of the comparison: current and BRAUN-BLANQUET relevés:

Melico-Kochietum 24.2 versus 27.4 (BR.-BL.) = **−3.2**, Onosmo-Koelerietum (27.8/27.5) = **+0.3**, Ephedro-Artemisietum (28.1/29.6) = **−1.5**, Stipo-Koelerietum (25.5/28.7) = **−3.2**, Stipo-Seselietum (38.4/34.5) = **+3.9**, Carici-Festucetum (31.3/26.0) = **+5.3**, Poo-Festucetum (35.6/36.6) = **−1.0**, Diplachno Festucetum (30.5/30.5) **(identical)**, Centaureo-Brachypodietum (40.3/41.07) = **−1.4**, Poo-Koelerietum (36.6/34.4) = **+2.2**.

The average data are quite similar with the exception of types "mk" and "sk" (see above) and the Vinschgau relevés "ss" and "cf".

In Chapter 1 the question was raised, if there are correlations between diversity characteristics and environmental factors.

The results are consistent with the hypothesis that good water availability may enhance plant species richness, as shown e.g. by PIGNATTI & PIGNATTI (1999). According to these authors, an optimal combination of warm temperatures and good water availability leads to a high species abundance (**resource-limitation of phytodiversity**).

Middle-montane plot areas with more precipitation and – according to WIESER et al. (1984) and KÖRNER (2003) lower evapotranspiration rates – show the highest species numbers; such conditions are found, e.g., in the submontane zone of the Vinschgau. These silicate rock complexes, with 38.4 species in the Stipo-Seslerietum, have a summer maximum of precipitation higher than that in the Valle d'Aosta. Accordingly, they include more "mesophytic" species such as *Carex humilis* (presence 92 % in ss) and *Euphorbia cyparissias* (presence 67 % in ss), which are absent in the extremely summer dry communities of Valle d'Aosta. Additionally, in the lower Vinschgau regions, the species pool is very large, including (sub)mediterranean species, relict species (more than in Valle d'Aosta), indicators of disturbance, acidophytic and (weakly) basiphytic species. The results comply with the hypothesis: "Communities are more diverse in less extreme habitats" (compiled e.g. in SCHAEFER 1999).

The most extremely xerophytic communities, in the Valle d'Aosta and Valais (tb, mk, ok, ea, sk), show a relatively small species diversity and include different stenoecious species, often characterized by disjunct distribution. This is in accordance with the fact that extreme environments are colonized by fewer species ("THIENEMANN's rule", see e.g. SCHAEFER 1999).

The significant relationship between large numbers of species and low pH values might be caused by the fact that humid conditions are correlated with more acidic plot areas (e.g., in the Centaureo-Brachypodietum with 40.3 species). Higher precipitation will lead to acidification processes in the topsoil. This would be compatible with the "resource-limitation hypothesis" (see above).

The results of the following authors, working in Festuco-Brometea communities, correspond to our results:

In the data material of Jandt (1999), who worked in the Kyffhäuser and Harz region in central Germany, there are differences in the species richness, when a) Stipetum capillatae (average 32.9 species) and b) Adonido-Brachypodietum (average 40.7 species) are compared. pH values differ slightly (a: average 7.8, b: 7.4), but are lower in the more species-rich type, just as in the case of the inner-alpine vegetation types. In the most western stands of Festucetalia valesiacae communities near Mainz, Korneck (1974) identified in "Rheinhessen" in the Allio-Stipetum capillatae an average of 34.5 (mean of different subtypes), in the Adonido-Brachypodietum of about 40.1 (mean of different subtypes). In general the edaphically more humid stands of the Adonido-Brachypodietum stands are richer in species.

6.2 Community diversity of vegetation complexes

In general, the diversity of vegetation types (without cryptogam communities and without adjoining plant communities) follows the same pattern as the species diversity (Fig. 31). The highest diversity is again reached in the montane-oreal zone (exception: Vinschgau). The oreal Vinschgau complex ("pf") comprises about 14 types of vegetation. Differences can be observed in the case of the lower Vinschgau (type "ss"), which shows high species numbers but moderate vegetation-type diversity. In the Rhein region near Chur, most of the areas are fragmentary (see p. 410), so that only the maximal value (from the largest area) is likely to be suitable for comparison with other data.

The differentiation of the vegetation types according to their formations in Table 4 shows that there are more pioneer communities in the complex types with submontane distribution, especially in the base-rich plot areas. Moreover, there is an obviously higher number of fringe communities in

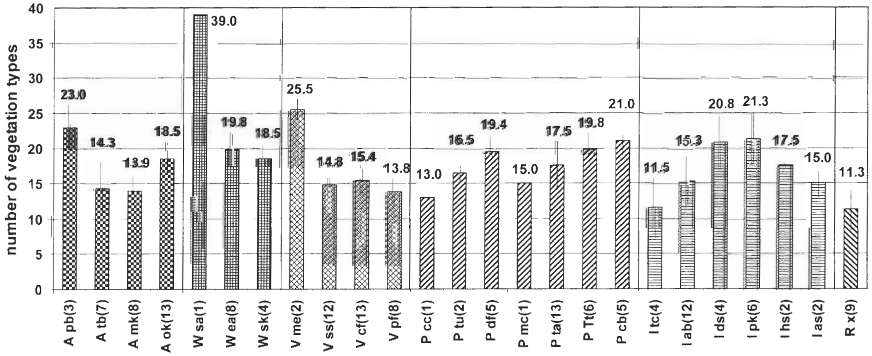

Fig. 31. Numbers of vegetation types according to the relevés of Table 4. Relevé numbers are indicated in brackets; error bars: mean deviation from the average species number.

the more humid areas. The ruderal communities were most numerous in the vineyard regions and in complexes restricted to loose material (Fig. 32).

The correlation between the total number of vegetation types and the annual precipitation was investigated for the complexes as well (Fig. 33). There is a significant correlation between high annual precipitation and high numbers of vegetation types (but only p = 0.015). Concerning pre-

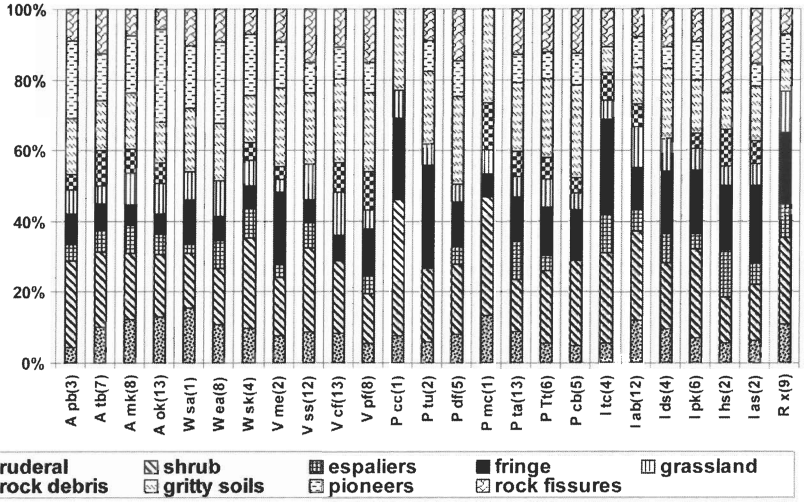

Fig. 32. Proportion of vegetation types in the vegetation complex relevés (according to numbers of vegetation types). Abbr.: rock debris etc. means: vegetation of rock debris, gritty soils, rock fissures.

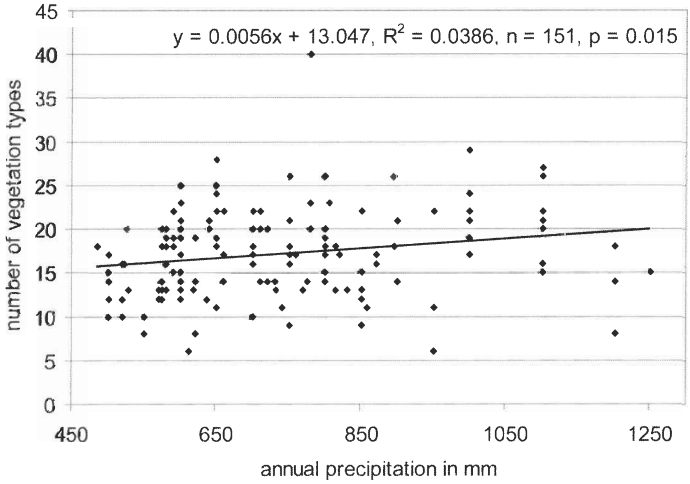

Fig. 33. Correlation between number of vegetation types and annual precipitation.

vailing pH values and amounts of vegetation types, there is a significant correlation, with trends similar to those in the species data (Fig. 34).

The main reason for a correlation between numerous vegetation types and relatively high moisture content (or humidity owing to lower evapotranspiration rates, see above) is the occurrence of fringe communities in the dry grassland complexes, which are mainly restricted to the valley mouth regions and the montane-oreal complex types. According to studies in the Karst region of former Yugoslavia carried out by van Gils et al. (1975), grassland cannot be invaded by fringe communities if the soil is very shallow and dry. The same applies to the extreme Xerobrometum stands of Central Europe (Müller 1962, 1966, Wilmanns 1988).

Van Gils & Keysers (1977a) already stated that Geranion communities can be characterized as communities of perhumid to subhumid climates. According e.g. to the investigations of Dierschke (1974, 1977) in Central Europe, the Trifolio-Geranietea communities are thermophilic. In the core areas of the inner-alpine dry vegetation they are restricted to mesoclimatically more humid (e.g. shaded) and relatively mesothermic habitats (example for relative stenotopy as defined e.g. by Schaefer 2003). In the montane-oreal zone of the less extreme valleys, in the valley mouth regions or under insubric influence they occur in habitats similar to those occupied in Central Europe.

Concerning question 3 in Chapter 1 the results can be interpreted in the following way:

Some of the principal aspects of diversity in inner-alpine vegetation complexes have already been introduced by Schwabe & Kratochwil (1994). The total number of vegetation types in the extremely dry inner-alpine valleys decreases in their centre. The relatively low values in the lower Vinschgau ("ss") regions are mainly due to the absence of a rich pioneer vegetation (acidic substrate). In the case of the Carici-Festucetum- and

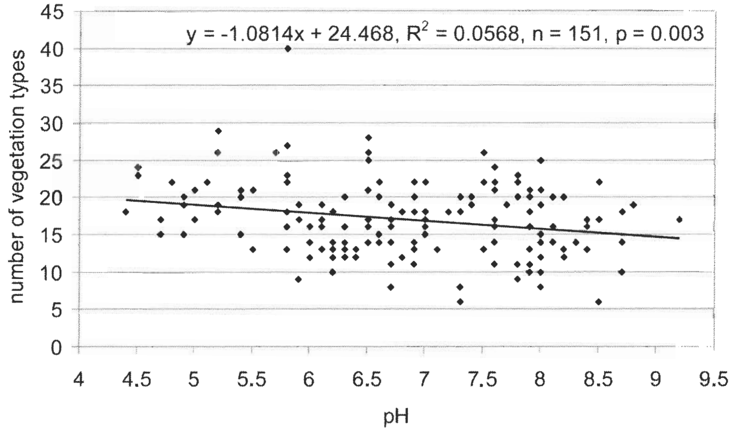

Fig. 34. Correlation between number of vegetation types and pH values.

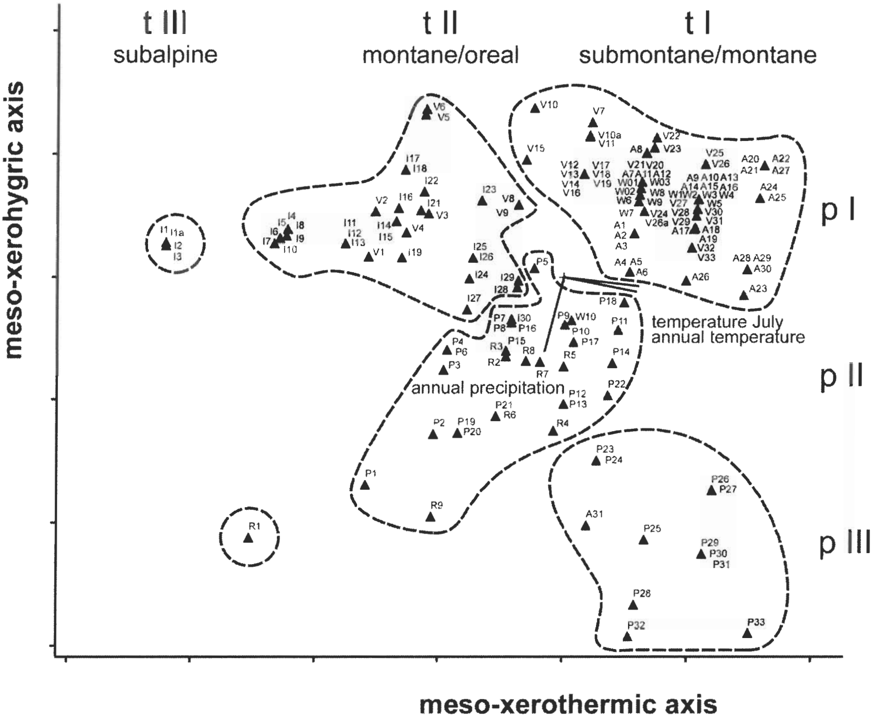

Fig. 35. CCA of the entire data set of localities (community level) in correlation with the average temperature of July, average temperature of the year and the average of annual rainfall; allocation to 3 temperature (t) and 3 precipitation (p) degrees (I = low, II = medium; III = high).
Eigenvalue axis 1: $\lambda_1 = 0.47$; axis 2: $\lambda_2 = 0.34$, axis 3: $\lambda_3 = 0.16$; Monte Carlo test results of vegetation complexes – environment correlation: axis 1: $p_1 = 0.002$; axis 2: $p_2 = 0.002$, axis 3: $p_3 = 0.002$. The vegetation complexes are primarily correlated in the first axis with July temperature and annual temperature (r = 0.99, r = 0.97), in the second axis with annual precipitation (r = −0.96). Coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space: axis 1: $r^2 = 0.14$, axis 2: $r^2 = 0.04$, axis 3: $r^2 = 0.002$; distance measure for original distance: Relative Euclidean.

the Poo-Festucetum complex of the Vinschgau the main cause is likely to be the strong anthropo-zoogenic influences (grazing/browsing) which, e.g., reduce the diversity of shrub communities.

7 Vegetation complexes and environmental factors: a synthesis

7.1 Multivariate ordination

The CCA (Fig. 35, 36) combines the vegetation-complex relevés with the climatic data which, in the case of the average July temperature and the

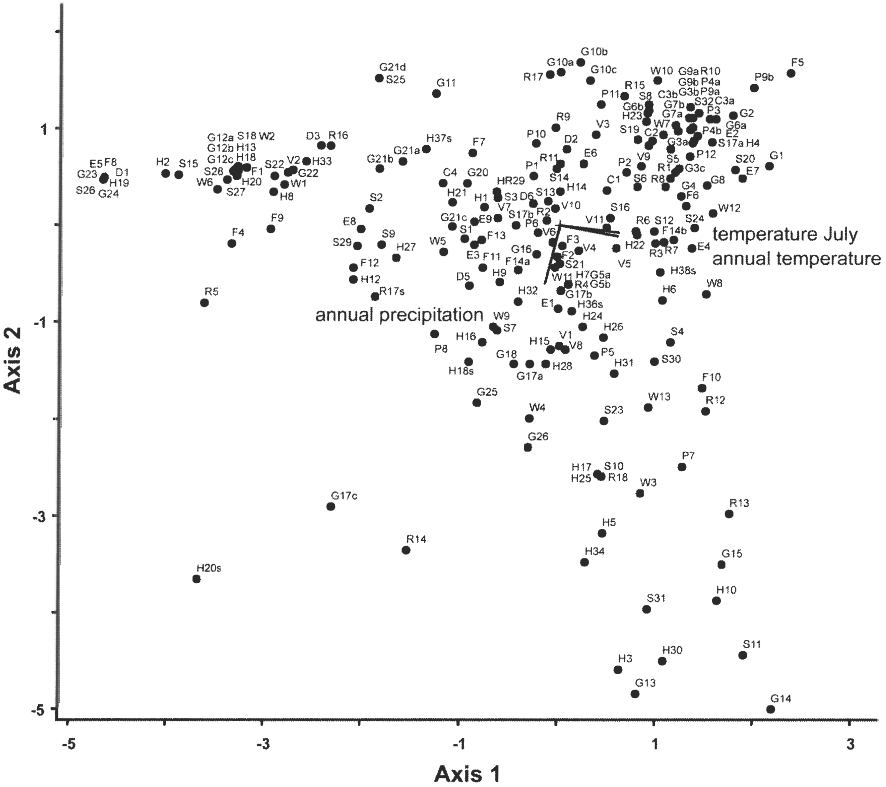

Fig. 36. CCA of the entire data set of plant communities (vegetation complexes) in correlation with the average temperature of July, average temperature of the year and the average of annual rainfall; for all other information see Fig. 35.

annual precipitation, are part of the ELLENBERG index as well. The gradient of annual temperature occupies nearly the same position between axis 1 and 2 as the July temperature. The structure presented in the DCA ordinations is repeated mirror-symmetrically in the CCA. There is a clear temperature gradient, with a decrease between the Aosta/Valais/ the lower and middle Vinschgau and the Engadin relevés. The subalpine types of the Engadin ("hs", "as") form a separate group. According to the precipitation gradient, the valley regions are classified from the valley mouth regions and the insubric zone, with high precipitation values, to the dry Vinschgau/ Valle d'Aosta/Valais plot areas. Valley mouth regions characterized by higher humidity are separated from the core plot areas of the associated valley (e.g. W10: "Les Follatères" lies next to the central Valtellina relevés (near Sondalo); A31 next to the valley mouth relevés of Valtellina). In Chapter 4.4, the gradient of axis 1 was provisorily characterized as a meso-xerothermic one and axis 2 as a meso-xerohydric gradient; the CCA tests the significance of the correlations. In the following chapter we develop a scheme, including the vegetation-complex data as well as the precipitation and temperature data, to define certain complex groups.

7.2 Vegetation complex groups

7.2.1 Differentiation according to environmental gradients

Complex groups can be determined on the basis of the results concerning the complex structure and the environmental gradients. Complex groups include vegetation complexes that have a structural similarity as defined by Schwabe (1989) and that substitute for one another spatially. According to Table 4 the characteristic grassland vegetation types of the corresponding complexes belong to the same order, Festucetalia valesiacae; some of the vegetation types are identical.

The grades of semi-aridity/humidity combined with the characteristics of the July/annual temperature and probably the potential evapotranspiration rate (Wieser et al. 1984) are linked to special features of the complex groups and their corresponding types in the different valleys.

According to the results taken from the CCA (Fig. 35, 36) the plot areas can mainly be ordered as follows (for the Ellenberg index, see Chapter 2.2 and Fig. 3).

a) temperature types (according to the average July and annual temperatures)
  - tI: xero-submontane/montane
  - tII: xero-montane/oreal
  - tIII: xero-subalpine.

b) precipitation types of xero-vegetation complexes (mm/a)
  - pI: low (in relation to the altitude): 485–600(700), oreal-subalpine belt: –800
  - pII: intermediate: 750–1000
  - pIII: higher (in relation to xero-vegetation complexes): about 1000–1200 mm

Group 1
tI: xero-submontane/montane, pI

Rock habitat complexes: submontane(s)/montane(m) zone with summer (semi-)arid conditions

Types: A: tb (s), ok (m), W: ea (s-m), sk (s-m), V: ss (s), cf (m)

Ellenberg index: appr. 30–40 (42)

Climatic indicators: Fringe communities are not present or have little importance, the xerophytic Prunetum mahaleb is abundant, in the case of basic conditions: species-rich therophyte vegetation.

s: indicators for mild-winter conditions: e.g. *Hedera helix* espaliers, for mild-winter/warm-summer conditions: *Notholaena marantae-Asplenium septentrionale* comm. in A: *Lonicera etrusca.*

Habitat complexes on moraine or loose material: submontane zone with summer (semi-)arid conditions
Types: A: mk, P: mc
Ellenberg index: 32–42, Ellenberg value not representative: P: mc edaphically characterized
Climatic indicators: nearly no fringe communities, no mesophytic shrub communities, species-rich therophyte vegetation.

Group 2
tII: xero-montane-oreal, pI

Types: V: pf, I: tc, ab, ds, pk
Ellenberg index: 26–19 (16)
Climatic indicators: fringe communities, *Rubus idaeus*- and *Epilobium angustifolium* stands, *Corylus avellana* and *Picea abies* occur, no indicators of mild-winter conditions, no or poor therophyte vegetation.

Group 3
tIII: xero-subalpine, pI

Rock habitat complexes: subalpine zone
Types: I: hs, as
Ellenberg index: 13–14 (the index does not reflect the specific subalpine conditions)
Climatic indicators: absence of plant species and communities with high sensitivity to cold-winter conditions (e.g. *Prunus spinosa*), mainly subalpine vegetation types and species: *Laserpitium halleri* stands, *Rosa pendulina* scrub, *Juniperus*nana*, *Pinus cembra*.

Group 4
tII: xero-montane-oreal, pII

Rock habitat complexes: central valley regions with higher humidity
Types: P: ta, tt, cb, R: x (excluded is R1 with only a slight connection to the other plot areas; with an E-index 10.8, it is a transitional type to the Central European Brometalia complexes)
Ellenberg index: 25–18 (14: oreal plot areas P1, R9)
Climatic indicators: fringe communities (e.g. *Knautia dipsacifolia* fringe) and in some cases *Brachypodium rupestre* s.l. facies, more mesophytic shrub communities comprising, e.g., *Prunus spinosa* and *Corylus avellana*.
m: relatively mild-winter conditions with *Tamus communis*, *Tilia cordata*.

Group 5
tI: submontane/montane, p(II)III

Rock habitat complexes: valley mouth regions and connected habitats with higher humidity
Types: A: partly pb (A31), W: Sa (800 mm), V: me, P: cc, tu, df
Ellenberg index: below appr. 18–20, Valais (W10): 23.1, if higher (V32/33) more humidity due to deeper soil or special mesoclimate, which is not reflected by a climatic station
Climatic indicators: Occurrence of fringe communities in sunny habitats, additionally in "cc", "df": Mediterranean shrubs such as *Erica arborea*. Indicators of mild-winter/warm-summer conditions: A, P woody species: *Celtis australis*, *Rubus ulmifolius*, *Ficus carica*, *Tamus communis*, *Vitis vinifera*.

7.2.2 The individuality of the xerothermic vegetation complexes in the Central Alpine dry areas

– Valle d'Aosta (Fig. 12, 35, 36)
With the exception of complex type **"pb"** in the valley mouth region (**t1/pIII**) and in climatically/edaphically more humid sites, this valley region is characterized by a sequence of highly xerothermic/xerohygric conditions (**t1/p1**). In the case of the rock complexes there are indicator communities and complexes according to the altitudinal zones submontane (**"tb"**) and submontane/montane (**"ok"**). The montane plot areas of the complex "ok" already have sparse fringe vegetation. The climatically/edaphically most extreme type in the whole investigation area with low soil-water storage capacitiy is **"mk"** (**tI/pI**), covering moraines between 500 and 800 m a.s.l. It includes elements of the loess steppic vegetation, which is most closely adjacent towards the east in the Austrian "Weinviertel" and in Hungary (Schwabe 1995, Varga 1997). Probably species of "tb" (*Ephedra*), "ok" (*Artemisia vallesiana* and others) and "mk" (*Bassia prostrata*) have survived since late glacial times in this area.

– Valais (Fig. 16, 35, 36)
The investigated part of the Valais between Martigny and Raron can be differentiated as follows. The lemanian-influenced zone of Martigny corresponds to the valley mouth region of Valle d'Aosta: **"sa"** (Les Follatères: **t1/pII**). In the case of rock physiotopes, the xerothermic sites of the central valley region beween Saillon and Raron are covered by **"ea"** (tI/pI) or, if there are loose rock/loess sites, by the complex **"sk"** (**tI/pI**). Both are nearly as xerothermic/-hygric as the corresponding types in the Valle d'Aosta "tb"/"ok", despite the higher summer precipitation in the Valais (indicators *Carex humilis, Anthyllis vulneraria*, which occur in A only in **"pb"**). Mainly species of "ea" (e.g. *Ephedra, Scorzonera austriaca, Artemisia vallesiaca*) have probably survived in the Valais since late glacial times.

– Vinschgau/Val Müstair (Fig. 18, 35, 36)
In the lower and central Vinschgau there is a differentiation of complexes corresponding to the sequence in the Valle d'Aosta. In the valley mouth region the complex type **"me"** is characterized by fringe species and corresponds to the type "pb" in Valle d'Aosta. For "me" the higher humidity is not reflected by the temperature/precipitation data; probably the complex can be assigned to type **t1/pII**. The complex type **"ss"** corresponds to "tb" and **"cf"** to "ok" (all **tI/pI**). As in the Valais, both types are nearly as xerothermic/-hygric as the corresponding types in the Valle d'Aosta "tb"/"ok"; the higher summer precipitation minimizes the dryness (indicators *Carex humilis, Euphorbia cyparissias*).

In the montane/oreal zone of the Vinschgau/Val Müstair the complex type **"pf"** can be distinguished, with occurrences of *Brachypodium rupestre* facies and fringe communities (**tII/p1**).

Species of the types "ss" and "cf" (e.g. *Ephedra, Scorzonera austriaca, Carex supina*) have probably survived in this area since late glacial times.

– Valtellina/Poschiavo (Fig. 20, 35, 36)
In this valley region there is no clear bend of the valley like that, e.g., in Valle d'Aosta; therefore the gradients between the insubric zone and the inner-alpine conditions decrease gradually but the insubric climate influences large parts of the valley. The plot areas next to the "Lago di Como" are rich in submediterranean shrub communities, and partly in fringes (**"cc"**, **"pc"**, **"df"**: **tI/pIII**). The type **"ma"** (P14: **tI/pII**) is restricted to a debris habitat and has structural similarity with "mk". Inner-alpine conditions, but with relatively high humidity (exception Bormio: P5) and therefore a rich fringe vegetation, occur

in the zone of the complex type **"ta"** (montane type: **t1/pIII/II**, oreal type: **tII/pII**, for P5: Bormio: **tII/pI**, for the oreal P1: **tII/pIII**). More humid conditions, mostly in Poschiavo and one other branch valley, are characterized by the type **"cb"** with *Brachypodium rupestre* facies, rich fringe vegetation and mesophytic scrubs such as *Corylus avellana*. Type **"tt"** is a transition type between **"ta"** and **"cb"**.

The types "ta" and "cb" are structurally similar to those in the Rhein area near Chur ("x"), with the montane/oreal Engadin (ab) and the Vinschgau/Val Müstair (pf). In the complex types "ta: montane/oreal" and "cb/tt" the thermomontane *Parnassius apollo* is present, in "cc", "df", "ta: montane" and "mc" it is replaced by *Iphiclides podalirius* (map in Schwabe et al. 1992). As in the Lower Engadin, a species-rich scrub vegetation with highly diverse *Rosa* species is a notable feature.

No obviously relict species with disjunct areas are present, but there are xerophytic species with slow dispersal such as *Fumana procumbens.*

– Oberinntal/Engadin (Fig. 23, 35, 36)
Between Zirl (east of Innsbruck) and the Oberengadin there is a remarkable toposequence of complex types, beginning with the type **"tc"** (**tII/pI; I30: pII**). The following type **"ab"** (**tII/pI**) characterizes mainly the Bündner schist zone (partly with moraine) in the "Unterengadin geological window". The complex is differentiated into a montane form and an oreal form. The latter, in combination with types **"ds"**(**tII/pI**) and **"pk"**(**tII/pI**), characterizes the thermomontane core of the Inn valley. In this area the thermomontane species *Parnassius apollo* and *Emberiza cia* are frequent (the latter has its altitudinal limit in the Engadin in plot area I6: Mattes in Schwabe & Mann 1990). All complex types are associated with the montane-oreal conditions rich in fringe communities. Especially types "ab: montane-oreal" and "ds" comprise an abundant and diverse scrub vegetation (especially *Rosa*, comparable to the upper Valtellina, as mesophytic species: *Corylus avellana*). Thus they correspond mainly to "ta" (Valtellina) and additionally to "x" (Rhein near Chur).

An extraordinary finding is the occurrence of the complex types **"hs"** and **"as"** (both **tIII/pI**) in the subalpine zone. The type "hs" (dolomitic rock area) corresponds to the montane type "tc". Due to the limited species pool in this zone, especially type "as" includes few fringe communities and scrubs. The xerophytic Festuco-Brometea vegetation is being progressively replaced by the Festucion variae s.l. in these silicate areas.

Species of the types "ds" and "as" (e.g. *Dracocephalum austriacum*: only "ds", *Allium lineare*) have probably survived in this area since late glacial times (possibly also *Stipa pennata* s.str.).

– Rhein near Chur including Domleschg/Albula (Fig. 26, 35, 36)
The complex type **"x"** (**tII/pII; R1, R9: tII/pIII**) is characterized by fringe communities and mesophytic scrubs with *Corylus avellana*; two of the plot areas (R9: oreal and R1: Prättigau) only marginally reflect the inner-alpine conditions. As already mentioned, the community structure is quite similar to the oreal Valtellina relevés.

Species of this type (*Allium lineare*) have probably survived in this area since late glacial times, whereas *Astragalus monspessulanus* is probably a relict from warmer post glacial periods.

8 Summarizing discussion and outlook

Chapter 7.1 has shown that the central question, whether there are correlations between ecological gradients and vegetation complexes (question 5, Chapter 1), can be answered affirmatively. The multivariate analysis of temperature, precipitation and vegetation complex data leads to a comprehensive view of a highly differentiated data set. The great significance of fringes and mesophytic shrubs, which can only be shown on this spatial level, mainly leads to the clear correlations. As yet it remains impossible to compare these results with those from other authors.

In Chapter 7 the last questions (6., 7.) of Chapter 1 were answered affirmatively. In Chapter 7.2.1 a concept for the differentiation of structurally corresponding vegetation complexes is given. The latter replace one another depending on the hydrothermic conditions. In Chapter 7.2.2 the vegetation complex differentiation leads to a landscape-ecological differentiation of the valley regions.

The plant communities, such as the Festucetalia valesiacae communities, show slighter differences between the valley regions than do the vegetation complexes. The latter reflect the specificity of the valleys and their sections much better than single vegetation types. Especially the grades of humidity are reflected by the combination of Festucetalia valesiacae communities with humidity indicators: fringe communities and mesophytic scrubs. The historical impact of livestock is evident, e.g., in the structure of the scrub communities and the presence of single shrubs, among which unpalatable and spiny species are of particular importance. The succession potential is greatest where the humidity is comparatively high, as is demonstrated by mesophytic scrubs such as the Corylo-Populetum, fringe communities including *Brachypodium rupestre* s.l. facies.

In spite of the individuality of the valley regions, which is evident in the complex table, the ordinations and the cluster analysis, it is possible to detect generalities regarding the diversity pattern and to carry out landscape ecological differentiations for the xero-vegetation complexes of the valley regions investigated here.

The main hypothesis, namely that there are gradients of climatic factors and of human impact that can be correlated with the community structure as well as the vegetation pattern and its diversity, has been confirmed.

The inner-alpine dry vegetation studied here is part of the Eurasian thermomontane vegetation complexes, with target species such as *Juniperus sabina.* The *Juniperus sabina* espaliers have their main area in central Asia (map, see Ozenda 1988: 192). *Astragalus excapus, Oxytropis pilosa* and closely related taxa also correspond to the thermomontane type, as was pointed out long ago by Meusel (1939) for *Oxytropis.* In the thermomontane zone of tributary valleys of the Rhône valley (Zermatt) and the Valle d'Aosta the thermomontane vegetation, for instance, grows at altitudes as high as 2500 m, *Poa perconcinna* up to 2950 m a.s.l. (Richard 1985, 1992).

The areas are characterized by thermomontane animal species and their related taxa, e.g., the bird species *Emberiza cia, Monticola saxatilis, Alectoris graeca* (areas in Hagemeijer & Blair 1997) and the butterflies *Parnassius apollo* s.l. (in all investigated valleys in the montane zone; caterpillar feeding on *Sedum,* mainly *S. album), Plebejides pylaon* s.l. (oreal-subalpine zone of Valais, Vinschgau, Valle d'Aosta; caterpillar feeding in the Alps on *Astragalus excapus* and in Valle di Cogne on *A. centroalpinus* (according to LEPIDOPTEROLOGEN-ARBEITSGRUPPE 1988). VARGA (1989) gives numerous examples, especially of thermomontane Noctuidae.

Thermomontane species are defined as such when they are characteristic of the core areas of semiarid/arid high mountain areas (VARGA l.c., 1996, 1997) or corresponding edaphically very dry sites. There is no specific altitudinal belt for thermomontane species, communities and complexes in the region of the Alps, but specific micro- and mesoclimatic characteristics according to Fig. 35 (especially t1–3-p1). VARGA (1989) formulates the hypothesis that parts of the steppic fauna are also central components of the thermomontane fauna. In our investigation area there are such thermomontane elements, submediterranean and alpine elements, endemisms (e.g. *Alyssum argenteum*), and others which constitute specific communities and vegetation complexes.

Only rocks and edaphically extreme moraine areas are naturally free from forest. These were habitats in which the species with nowadays disjunct areas such as *Bassia prostrata* (moraines), *Ephedra helvetica, Dracocephalum austriacum, Scorzonera austriaca* (all rock areas) and others could survive since late glacial times. The actual structure of these habitats is a result of those traits of biogeographic history, but mainly of the anthropo-zoogenic impact, which had formed the complexes mainly since the Bronze age (Chapter 2.3). All these traits lead to a distinctive vegetation pattern in the valley regions with high conservation value. For the last 50 years the anthropo-zoogenic impact by livestock grazing/browsing has been progressively disappearing, some areas have been afforested (Vinschgau) or fertilized; therefore different types of the xerophytic vegetation complexes with their pattern are endangered.

The inner-alpine dry regions are a model system for the study of microgeomorphological catenae with their specific vegetation complexes, reflecting the prevailing historical, climatological and anthropo-zoogenic influences. Further research work, especially concerning cryptogam communities and biocoenological studies, would be very important.

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Appendix

Appendix 1. Additional data to the sample plots of the vegetation complex relevés. Column 1: Valley region, 2: number, 3: code locality, 4: m a.s.l. × 10, 5: size vegetation complex relevé in ha, 6: exposition, 7: locality and geology, 8: pH value Festuco-Brometea community, 9: code vegetation complex type.

1	2	3	4	5	6	7	8	9
						Valle d' Aosta (Vallée d'Aoste) (Italy)		
A	1	Lav	110	0.5	ESE	Valpelline valley/Lavod (granite, moraine)	6.9	ok
A	2	Che	115	0.5	S	Valpelline valley/Cheillon (granite, moraine)	8.5	ok
A	3	Val	110	0.5	SE	Valpelline valley above Valpelline (granite, moraine)	7.6	ok
A	4	Mor	100	0.5	SSW	Morgex/Villair (schistly calcareous, gneiss)	7.8	ok
A	5	Nab	115	0.3	SSW	La Salle/Châtelard (gneiss, moraine)	8.1	ok
A	6	Avs	105	0.3	SSW	above Avise (gneiss, moraine)	6.6	ok
A	7	Nik	95	0.5	SSW	below St.Nicolas/Lyveroulaz (schist: partly calcareous, debris)	8.8	ok
A	8	Aym	68	0.3	W	Aymavilles/below Issogne (calcareous schist, gneiss)	6.9	pb
A	9	Pie	62	0.5	S	St. Pierre/Mte.Torrette (gneiss, schist)	8.4	ok
A	10	Tor	65	0.3	S	Monte Torrette above Sarre (schist, gneiss)	6.9	ok
A	11	Foc	90	0.5	S	Fochat above Sarre (schist, moraine)	7	mk
A	12	VsS	105	0.5	SSE	below Ville sur Sarre (calcareous schist, moraine)	7.8	ok
A	13	Pal	90	0.5	SSE	Palue above Sarre (gneiss, moraine)	6.2	ok
A	14	Gr1	70	1	S	Gressan, Gargantua (moraine)	8	mk
A	15	Gr2	65	0.3	WE	Gressan (moraine)	8.2	mk
A	16	Cha	65	1	WNW	Charvensod (moraine)	8.7	mk
A	17	Roi	80	1	S	Roisan (moraine)	8.2	mk
A	18	Sor	90	0.5	S	Sorreley (above) (gneiss, moraine)	6.2	ok
A	19	Ver	85	0.3	S	Verney/Quart (gneiss)	4.9	ok
A	20	Chz	54	0.5	S	Chetoz/Quart (moraine)	8.7	mk
A	21	Qua	60	0.5	S	Quart/Villefranche (moraine)	8.2	mk
A	22	Mar	60	0.5	S	St.Marcel/Quart (green schist, moraine)	8.5	mk
A	23	PlQ	95	0.3	S	Planette/Quart (green schist)	6.3	pb
A	24	Pla	77	0.3	S	Plaisant between Nus and Chambave (schist)	7.3	tb
A	25	Nus	85	0.3	SSE	Nus Fogner (schist)	7.9	tb
A	26	Vey	105	1	S	Verrayes (schist, moraine)	6.8	tb
A	27	Chv	51	0.5	S	Chambave (green schist)	6.8	tb
A	28	Far	62	0.5	S	Farys/below St. Denis (green schist)	6.7	tb
A	29	Cht	62	0.3	S	Châtillon/below Merlin (serpentine rock)	5.9	tb
A	30	StV	60	0.5	SW	St.Vincent/ Mt. de Fourche (serpentine rock)	5.8	tb
A	31	Zuc		0.5	SW	below Pta. Zuccore (serpentine, schist)	5.8	pb
						Valais (Wallis) (Switzerland)		
W	0-1	Var	73	0.4	S	west of Varen (schist)	7.9	ea
W	0-2	Rar	76	0.4	S	Raron (limestone)	8.1	ea
W	0-3	Get	70	0.5	SSE	west of Getwing (calcareous schist, debris)	7.9	sk
W	1	ChW	68	0.3	S	west of Chelin (L'Ormy) (schist)	7.9	sk
W	2	Leo	57	0.5	S	above St. Léonard (schist)	8	ea
W	3	Tou	64	0.5	S	Sion Tourbillon (schist)	8	ea
W	4	Org	62	0.5	SSE	Mont d'Orge (schist)	7.9	ea
W	5	Pon	64	0.5	S	Pont-de-la-Morge (schist)	7.7	ea
W	6	Ard	61	0.5	SE	above Ardon (limestone)	7.8	sk
W	7	Ley	58	0.3	SW	Leytron La Barme (limestone)	8.	sk
W	8	Sai	53	0.5	S,W	Saillon ruin (limestone)	7.8	ea
W	9	Sar	54	1	S	Saillon between ruin and La Sarvaz (limestone, loess)	7.6	ea
W	10	Fol	60	1	SE	Les Follatères west of Branson (gneiss, locally loess)	5.6	sa
						Vinschgau (Valle Venosta), Münstertal (Val Müstair) (Italy, Switzerland) (gneiss, schist, locally loess)		
V	1	Stm	150	0.5	S	S.ta Maria between Pizzet and Büglios	6.3	pk
V	2	Müs	135	0.3	SSE	above Müstair	6	pk
V	3	Tau	139	0.5	SSW	Taufers, ruin Helfmirgott	6.3	pk
V	4	Bur	135	0.3	SSE	north of Burgeis	6.3	cf
V	5	Mat	148	0.5	S	Matsch above castle	5.5	pk
V	6	Pra	115	0.3	E	above Prad	6.2	pk
V	7	Göf	85	0.3	NE	above Göflan	6.6	cf
V	8	Juv	130	1,0	S	upper Juvalhof above Staben	6.9	pk
V	9	Sön	110	0.3	S	upper Schöneckhof above Tschars	6.7	pk
V	10	Söl	95	0.5	SSE	"Söles-Hof" south of Glurns	6.4	cf
V	10a	Lic	100	0.3	NE	above Lichtenberg	6.5	pk

Appendix 1. (cont.)

V	11	Glu	103	0.5	SSW	between Tartsch and Matsch, "Leiten"	6.7	cf
V	12	Tar	102	0.5	S	Tartscher Bühl	5.8	cf
V	13	Cal	115	0.5	SW	Calvenklause above sports field	5.9	cf
V	14	Laa	115	0.5	SSE	Calvenklause above Laatsch	5.8	cf
V	15	Spo	132	0.5	SW	above Spondinig, "Schludernser Berg"	6.7	cf
V	16	Eyr	100	0.5	S	Eyrs "Leiten"	7.1	cf
V	17	Laa	102	0.5	SSW	Laaser "Leiten"	6.1	cf
V	18	Lor	101	1,0	S	Laaser "Leiten" above Loretzhof	6.1	cf
V	19	Ali	104	1,0	S	Kortscher "Leiten" near Allitz	7.2	cf
V	20	Kor	103	1,0	S	Kortscher "Leiten"	6.2	cf
V	21	Aeg	90	0.5	S	Kortsch, Aegidius chapel	7	ss
V	22	Sil	75	0.7	SSW	Schlanders slope Schlandrauner valley	5.4	ss
V	23	Mar	78	0.3	S	above Marainhof	6	ss
V	24	Vet	95	0.5	SSE	Vetzan above Schloß Goldrain	6.2	ss
V	25	Lat	68	0.7	SSW	above Latsch	6.3	ss
V	26	Csi	65	0.7	S	above Kastelbell	6.4	ss
V	26a	Kas	100	1,0	SSE	between Galsaun and Kastelbell	6.1	ss
V	27	Tsa	65	0.7	SSW	Tschars and Galsaun	6.4	ss
V	28	Sta	62	1,0	S	Staben-Kochenmoos	6.6	ss
V	29	Sna	60	0.7	SSW	Schnalstal near Naturns	6.1	ss
V	30	Nat	62	1,0	SSE	Naturns	6	ss
V	31	Pla	62	0.5	S	above Plaus (Pardell)	6.4	ss
V	32	Rab	65	0.5	SSE	Rabland "Happichl"	6.5	me
V	33	Par	70	0.7	S	above Partschins	6.5	me
						Valtellina/Poschiavo (Italy, Switzerland)		
P	1	Sem	170	0.3	S	above Semogo/Valdidentro (limestone)	7	tao
P	2	Iso	160	0.7	S	above Isolaccia/Valdidentro (limestone)	7	tao
P	3	Pre	130	0.1	S	near Premadio (limestone)	7.6	tao
P	4	StN	150	0.3	S	S.Nicolo/Valfurva (gneiss)	7.6	tao
P	5	Bor	125	0.2	S	Bormio Eingang Valfurva (gneiss, moraine)	6.5	tao
P	6	SLu	140	0.4	SE	S. Lucia/Valdisotto (gneiss, moraine)	6.5	tao
P	7	Pia	120	0.2	W	Piatta/Valdisotto (limestone)	7.4	tao
P	8	Fro	125	0.3	S	Frontale/Rezzalasco (diorite)	6.7	tao
P	9	LeP	100	0.3	SSW	Le Prese below Turchi (diorite)	6	tao
P	10	Gra	110	0.4	SSW	above Grailé (Scala) (diorite)	7.4	tt
P	11	SAg	90	0.3	S	S. Agnese/Sondalo (diorite)	5.2	tt
P	12	Som	100	1,0	SSW	Sommacologna (gneiss)	5.2	tt
P	13	Son	100	0.2	SSW	Sondalo (gneiss)	7	tt
P	14	Mig	90	0.3	SSE	Migióndo (debris material)	6.6	mc
P	15	Fol	135	0.7	SSE	Folino east of Roasco valley (gneiss)	7.5	cb
P	16	Fus	120	0.5	SW	below Fusino, Roasco valley (gneiss)	4.5	cb
P	17	Rav	100	0.3	S,W	above Ravoledo (gneiss)	5.4	tt
P	18	CaV	620	0.3	SSE	Castello Visconti Venosta/Grosio (gneiss)	5	tam
P	19	Prd	105	0.5	SSE	above Prada/Puschlav (gneiss, moraine)	5	cb
P	20	Can	105	0.5	SSE	Cantone above Lago di Poschiavo (granite, debris)	4.5	cb
P	21	Bru	95	0.7	SSE	Brusio above Ginetto (Brusio granite)	4.8	cb
P	22	Ros	71	0.4	SSW	Roscellina (schist, crystalline basement)	6.5	tam
P	23	Ron	80	0.3	S	Roncaiola above Tirano (gneiss)	5.2	tam
P	24	Nov	85	0.5	SSE	Novaglia above Tirano (gneiss)	5.1	tam
P	25	Teg	90	0.5	SSE	Teglio (gneiss)	5.5	tam
P	26	StG	60	0.3	S	below S.Gervasio near Teglio (gneiss)	5.2	df
P	27	Tre	50	0.3	S	Tresenda (gneiss)	5.4	df
P	28	Pai	90	0.2	S	La Paiosa above Berbenno (gneiss)	4.4	pc
P	29	Pog	45	0.2	S	below Poggiridenti (gneiss)	4.9	df
P	30	Tri	45	0.2	S	below Triangia (Castellina) (gneiss)	4.9	df
P	31	Des	40	0.3	S	Desco east of Morbegno (gneiss, granite)	6.5	df
P	32	Mel	75	0.3	S	above Mello near Morbegno (gneiss)	4.9	pc
P	33	Mon	40	0.3	S	Montastero west of Dubino (gneiss)	6.9	cc
						Engadin (Engiadina)/Oberinntal (Switzerland, Austria)		
I	1a	Cr2	190	0.5	SSE	Cristolais near Samedan (granite, hornblende)	5.8	as
I	1	Cri	178	0.5	SSE	Cristolais near Samedan (granite, hornblende)	5.9	as
I	2	Zuo	180	0.4	SSE	between Zuoz and Madulain Quadrellas (dolomite)	7.9	hs
I	3	S-c	175	0.5	SSE	S-chanf above Serlas (dolomite)	9.2	hs
I	4	Brai	162	0.7	SSE	below Brail Prada d'Urezza (moraine)	5.2	pk
I	5	Zer	154	0.7	SSE	Zernez, Munt Baseglia (amphibolite)	5.8	pk
I	6	Clü	152	0.5	SSW	Zernez Clüs below Plattas (amphibolite)	6.6	pk

Appendix 1. (cont.)

I	7	Sus	148	0.5	SSW	Susch Chaschina (gneiss)	4.7	pk
I	8	Lav	148	0.5	SSW	east of Lavin (gneiss)	5.9	pk
I	9	Gua	148	0.4	SSE	Guarda (Gneis)	5.7	pk
I	10	Bos	154	0.5	S	between Bos-cha and Ardez (Pradasura) (limestone)	6.9	ds
I	11	Cha	157	0.7	S	between Ardez and Chanoua (limestone)	7	ds
I	12	Ste	145	0.5	S	Ardez "ruin Steinsberg" (limestone)	7.5	ds
I	13	Ard	140	0.2	S	Ardez below "ruin Steinsberg" (limestone)	7.6	ds
I	14	Fo2	135	0.5	SSE	Foppas, Tarasp (Bündner schist, moraine)	8.1	abo
I	15	Fo1	135	0.6	SS0	Foppas above station Scuol (Bündner schist, moraine)	8	abo
I	16	Sen	138	0.4	SSE	between Scuol and Sent below Chauennas (Bündner schist, moraine)	6.9	abo
I	17	Rao	135	0.4	SSW	Ramosch above Tschanüff, Val Sinestra (Bündner schist)	7.9	abm
I	18	Rau	130	0.3	WSW	Ramosch above Tschanüff (Bündner schist)	7.9	abm
I	19	Tsc	155	0.5	S	Tschlin southwest of village (Bündner schist)	7.4	abo
I	21	Pfu	100	0.5	SSE	Pfunds-Stuben, slopes Stubner rivulet (Bündner schist)	8	abm
I	22	Laf	105	0.4	S	Lafairsch, Via Claudia (Bündner schist)	8	tc
I	23	Rie	930	0.7	SSE	Ried, steep slope north of Prauns (Bündner schist)	7.3	tc
I	24	Kau	100	0.5	SSE	Kauns, slope Faggenbach, Greitweg (Bündner schist)	8.4	abm
I	25	Flo	95	0.7	S	Fließ, slope below Fließ (micaceous schist)	8.4	abm
I	26	Flu	90	0.7	S	Fließ, slope above "Neuer Zoll" (micaceous schist))	8.2	abm
I	27	Lan	90	0.5	S	Landeck-Stanz, "Leiten" above Bruggen (quarz phyllite, moraine)	8.3	abm
I	28	Rop	75	0.5	S	Roppen undercut slope, Inn, debris material	7.3	abm
I	29	Slz	80	0.6	S	Silz slope below Grünberg (dolomite)	7.6	tc
I	30	Zir	80	0.7	S	Zirl ruin Fragenstein (dolomite)	7.3	tc
						Rhein near Chur and Domleschg/Albula) (Switzerland)		
R	1	Fel	145	0.2	S	Feldis (clay schist)	6.7	x
R	2	Tom	100	0.2	S	between Tomils and Scheid (Bündner schist)	6.7	x
R	3	Tie	95	0.2	S	between Tiefencastel and Brienz (Lias)	6.9	x
R	4	Cas	73	0.1	S	near S. Cassian/Sils (Bündner schist)	8.5	x
R	5	Pas	76	0.2	S	Paspels ruin, Alt-Sins (Bündner schist)	7.8	x
R	6	Rot	75	0.5	S	Scheidhalde above Rothenbrunnen (Bündner schist)	7.8	x
R	7	Ems	60	0.2	S	Ems Tuma Caste (debris material)	7.5	x
R	8	Hal	65	0.3	S	Haldenstein-Böfel (Calanda) (limestone)	8	x
R	9	Sol	72	0.7	S	above ruin Solavers, Grüsch/Prättigau (Bündner schist)	7.6	x

Appendix 2. Plot areas of the Festuco-Brometea relevés (all relevés are restricted to the plot areas of Appendix 1) and assignment to the vegetation types.

A1	ok	A25	tb	I14a	ab	P4b	ta	R1	x	V22	ss
A2	ok	A26	tb	I14b	ab	P5	ta	R2a	x	V23	ss
A3	ok	A27	tb	I15a	ab	P6	ta	R2b	x	V24	ss
A4a	ok	A28	tb	I15b	ab	P7	ta	R3	x	V25	ss
A4b	ok	A29	tb	I15c	ab	P8a	ta	R4	x	V26	ss
A5	ok	A30a	tb	I16a	ab	P8b	ta	R5	x	V26A	ss
A6a	mk	A30b	tb	I16b	ab	P9a	cb	R6a	x	V27	ss
A6b	ok	A31a	pb	I17a	ab	P9b	cb	R6b	x	V28a	ss
A7	ok	A31b	pb	I17b	ab	P10a	cb	R7	x	V28b	ss
A8a	pb	A31c	pb	I17c	ab	P10b	cb	R8a	x	V28c	ss
A8b	pb	I1a	as	I18a	ab	P11	cb	R8b	x	V31	ss
A9	mk	I1Aa	as	I18b	ab	P12	cb	R9	x	V32	me
A11	mk	I1Aa	as	I18c	ab	P13	ta	V1	pf	V33	me
A12a	ok	I1Ab	as	I18d	ab	P14a	mc	V1a	pf	W01a	sk
A12b	ok	I1Ab	as	I18e	ab	P14b	mc	V1b	pf	W01b	sk
A12c	ok	I1b	as	I18f	ab	P15	cb	V1c	pf	W02a	sk
A13	ok	I2a	hs	I19a	ab	P16	cb	V1d	pf	W02b	sk
A14a	mk	I2b	hs	I19b	ab	P17	ta	V2	pf	W03a	sk
A14b	ok	I2c	hs	I19c	ab	P18	ta	V3	pf	W03c	ea
A14c	mk	I3a	hs	I21	ab	P19	cb	V3a	pf	W03d	sk
A14d	ok	I3b	hs	I22	ab	P20	cb	V3b	pf	W03e	sk
A14e	ok	I3c	hs	I23a	tc	P21	cb	V3c	pf	W03f	sk
A14f	ok	I4a	pk	I23b	tc	P22a	ta	V4	cf	W1	pb
A15	pb	I4b	pk	I24a	ab	P22b	cb	V5	pf	W2a	ea
A16	mk	I4c	pk	I24b	ab	P23	ta	V7	cf	W2b	sk
A17	mk	I5	pk	I25	ab	P24	ta	V8a	pf	W2c	sk
A18a	ok	I6a	pk	I26a	ab	P25	ta	V8b	cf	W3	ea
A18b	ok	I6b	pk	I26b	ab	P26a	df	V9	pf	W4a	ea
A18c	ok	I7	pk	I27a	ab	P26b	df	V10	cf	W4b	sk
A18d	ok	I8a	pk	I27b	ab	P27	df	V10A	pf	W5a	sk
A20a	mk	I8b	pk	I27c	ab	P28	pc	V12a	cf	W5b	ea
A20b	mk	I9a	pk	I28	ab	P29a	df	V12b	cf	W7b	sk
A20c	mk	I9b	pk	I29a	tc	P29b	df	V13	cf	W7c	ea
A20d	mk	I10	ds	I29b	tc	P30a	df	V14	cf	W7d	ea
A20e	mk	I11a	ds	I30a	tc	P30b	df	V15	cf	W9a	ea
A21a	mk	I11b	ds	I30b	tc	P31	df	V16	cf	W9b	ea
A21b	mk	I11c	ds	P1a	ta	P32	pc	V17	cf	W9c	sk
A21c	mk	I12	ds	P1b	ta	P33a	cc	V18a	cf		
A22	mk	I13a	ds	P2a	ta	P33b	cc	V18b	cf		
A23a	pb	I13b	ds	P2b	ta	P33c	cc	V19	cf		
A23b	pb	I13c	ds	P3	ta	P33d	cc	V20	cf		
A24	tb	I13d	ds	P4a	ta	P33e	cc	V21	ss		

Appendix 3. Alphabetical list of species abbreviations in Fig. 9b and indication of lines in Table 3.

Achi.mil	263
Achi.nob	51
Achi.set	197
Achi.tom	164
Agro.cap	268
Agro.int	7
Alli.car	159
Alli.lin	144
Alli.lus	180
Alli.ole	305
Alli.pul	87
Alli.sph	215
Alys.aly	236
Alys.arg	3
Alys.utr	20
Anac.pyr	28
Anth.lil	309
Anth.ram	157
Anth.vul	154
Arab.hir	224
Aren.ser	235
Arme.pla	168
Arte.abs	313
Arte.cam	288
Arte.val	36
Aspa.off	342
Aspe.ari	171
Aspe.cyn	156
Aspe.pur	74
Aste.alp	89
Aste.ame	226
Aste.lin	158
Astr.*pa	54
Astr.exs	53
Astr.leo	93
Astr.mon	336
Astr.ono	110
Astr.pen	146
Bass.pro	9
Berb.vul	301
Bisc.lae	277
Both.isch	209
Brac.rup	95
Briz.med	266
Brom.con	79
Brom.ere	22
Bryu.arg	340
Bulb.ver	32
Buph.sal	160
Cala.aci	234
Cala.alp	343

Call.vul	66
Camp.glo	271
Camp.rap	267
Camp.rot	302
Camp.spi	92
Card.def	272
Card.nut	315
Card.pla	316
Care.car	312
Care.hum	102
Care.lip	182
Care.sup	52
Carl.aca	130
Carl.vul	333
Cauc.pla	10
Cent.gau	99
Cent.ery	30
Cent.mac	178
Cent.sca	293
Cent.val	174
Cera.*st	139
Chon.jun	311
Chry.adu	275
Chry.gry	78
Clad.con	325
Clad.pyx	319
Clad.sym	329
Clei.ser	82
Clem.rec	77
Conv.arv	314
Coro.vag	123
Crep.con	132
Crep.pul	13
Crep.set	12
Cruc.ped	31
Crup.vul	175
Cusc.epi	300
Cyno.dac	332
Cyti.sco	67
Dact.glo	262
Dian.car	24
Dian.del	133
Dian.sil	287
Dory.ger	106
Drac.aus	118
Drac.ruy	149
Echi.vul	238
Ephe.hel	35
Epip.atr	127
Eric.arb	76
Eric.car	107

Erig.ace	330
Erig.alp	278
Erig.att	128
Erod.cic	247
Erop.ver	252
Eruc.nas	37
Eryn.cam	222
Erys.rha	192
Erys.vir	205
Euph.cyp	291
Euph.seg	193
Euph.tat	198
Fest.ovi	297
Fest.rup	219
Fest.val	188
Fest.vio	150
Fulg.ful	19
Fuma.eri	2
Fuma.pro	213
Gale.lad	45
Gali.bor	281
Gali.luc	290
Gali.pum	276
Gali.rub	98
Gali.ver	261
Geni.tin	65
Gent.cru	269
Gera.san	258
Glob.bis	71
Glob.cor	103
Gyps.rep	121
Heli.*gr	120
Heli.num	207
Heli.prat	135
Hete.con	85
Hier.pil	289
Hier.sta	124
Hier.vel	62
Hipp.com	40
Hype.per	306
Hyss.off	8
Inul.mon	16
Isat.tin	11
Jasi.mon	166
Juni.com	318
Koel.cris	58
Koel.pyr	136
Koel.val	170
Lact.per	214
Lapp.squ	56
Lase.hal	143

Appendix 3. (cont.)

Lase.lat	122
Lase.sil	112
Leon.*hy	108
Leon.his	326
Leon.inc	105
Liba.mon	115
Lina.ang	317
Linu.cat	225
Linu.ten	72
Lotu.cor	294
Medi.fal	296
Medi.lup	220
Medi.min	231
Mela.arv	280
Meli.cil	6
Micr.ere	4
Minu.lar	204
Minu.mut	201
Minu.rub	203
Musc.com	221
Myos.str	250
Odon.lut	191
Onob.are	196
Onob.mon	111
Onon.nat	43
Onon.pus	172
Onon.rep	279
Onos.pse	15
Opun.hum	86
Orch.mor	27
Orch.ust	227
Orig.vul	256
Orla.gra	84
Orob.alb	320
Orob.gra	228
Orob.lae	194
Orob.spe	341
Orob.teu	202
Oxyt.cam	335
Oxyt.pil	48
Petr.pro	249
Petr.sax	230
Peuc.ore	41
Phle.phl	162
Phyt.bet	141
Phyt.sch	91
Pimp.maj	63
Pimp.sax	59
Plan.lan	310
Plan.med	264
Plan.ser	60
Poa .ang	299
Poa .bul	246
Poa .mol	179
Poa .per	173
Poa .pra	298
Poa .vio	147
Poly.cha	125
Poly.odo	255
Poly.ped	75
Poly.pil	165
Poly.vul	274
Pote.arg	163
Pote.cau	126
Pote.cin	195
Pote.pus	187
Prun.gra	216
Prun.lac	100
Psor.dec	17
Puls.*ap	151
Puls.mon	23
Ranu.bul	273
Rhac.can	338
Rhin.gla	270
Rhyt.rug	223
Rosa.spe	334
Rume.ace	167
Salv.pra	153
Salv.ver	114
Sang.min	211
Sapo.ocy	47
Saxi.bul	29
Scab.col	218
Scab.tri	184
Scle.per	248
Scor.aus	34
Secu.var	304
Sedu.acr	251
Sedu.alb	232
Sedu.rup	237
Sedu.sex	241
Sedu.tel	81
Semp.ara	240
Semp.tec	233
Semp.tom	245
Sene.dor	142
Sese.ann	199
Sese.var	49
Sesl.cae	104
Seta.vir	339
Sile.arm	83
Sile.cuc	327
Sile.nut	254
Sile.oti	189
Soli.vir	140
Stac.off	285
Stac.rec	208
Stip.*au	117
Stip.*eri	176
Stip.cal	44
Stip.cap	39
Stip.eri	183
Stip.pen	148
Synt.rur	323
Tara.lae	328
Tele.imp	200
Teuc.cha	292
Teuc.mon	210
Teuc.sco	68
Thal.min	265
Thes.alp	283
Thes.bav	284
Thes.lin	282
Thui.abi	217
Thym.oen	185
Thym.pol	145
Thym.pra	242
Thym.pul	303
Thym.ser	295
Thym.vul	1
Toni.sed	331
Tort.inc	90
Tort.tor	321
Trag.dub	308
Trif.alp	259
Trif.arv	239
Trif.aur	131
Trif.cam	244
Trif.med	257
Trif.mon	155
Trif.pra	337
Trif.rep	345
Trin.gla	73
Turr.gla	346
Verb.lyc	212
Vero.off	69
Vero.pro	61
Vero.spi	190
Vero.teu	113
Vero.ver	243
Vici.cra	324
Vici.ono	25
Vinc.hir	307