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Vegetation complexes of flowing-water habitats and their importance for the differentiation of landscape units

Angelika Schwabe
Institut fur Biologie 11, Lehrstuhl fur Geobotanik der Albert-Ludwigs-Universität Freiburg i.Br., D-7800 Freiburg i.Br., Fed. Rep. of Germany

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Abstract

An inductive method for recognizing vegetation complexes is presented. These complexes can be used to define landscape units. The method is demonstrated with regard to the river and rivulet valleys of the Black Forest in south-western Germany. It is based on surveys of locally occurring plant communities in homogeneous landscape units, using a cover-abundance scale for the areal extension of each community. The communities have first been established on the basis of the usual releves of small homogeneous plots.

The surveys are called sigma relevés (sigma = Greek for sum), Sigma relevés can be arranged in tables by the usual classification method in order to establish vegetation complexes. Characteristic and differential communities can be elaborated to characterize the vegetation complexes. The specific spatial distribution of each complex reflects certain physical-geographical and anthropo-geographical characteristics. Some applied aspects can be included for each vegetation complex, for example, lists of woody species typical for a landscape unit. From the point of view of water economy such a survey is useful since many efforts are being made to plant woody species in accordance with natural conditions along river and rivulet embankments.

Introduction

Hardly any other habitat reflects its physical-geographical and anthropo-geographical characteristics to the remarkable extent that rivers, rivulets and their embankments do. For example, inferences may be drawn from the pattern of yearly run-off on snow cover, snow retention, and on the storage capacity of the basin (Keller 1979). Further, while the geomorphology of embankments is highly dependent upon the relief, rock type and annual run-off, it also depends on the type of land use of the adjoining areas. Flowing water habitats are also readily influenced by pollution.

There is considerable knowledge about the ecological indicator value of macrophytes in river systems; for example, studies have shown the importance of macrophytes as pollution indicators (*e.g.*, Kohler 1971; Kohler and Schiele 1985; Kohler and Zeltner 1974 for different regions in Bavaria and Monschau-Dudenhausen 1982 for the northern Black Forest).

Detailed knowledge of the role of different ecological factors may, of course, be achieved by experimental methods. However rivers and their valleys form a unique system, which are distributed linearily on the landscape mosaic. The rivers are also a key point in the landscape from the perspective of environmental management.

The comprehensive work of Haslam (1987) has shown that it is difficult to differentiate types of 'river landscapes' only by means of mapping macrophyte species, especially in mountain areas with high velocity and poverty in macrophytes. A comprehensive approach to riverine systems may profit from a classification which considers the totality of the landscape and the interactions between the rivers and land. This type of classification is best determined by inductive methods which build from specific features of the landscape to a general understanding.

The first step is to describe the corridors, patches and patterns of the running watercourses and their embankments, as suggested by Golley (1987): 'First we may look into nature, study the patterns as patches, corridors, and so forth'. These patterns consist in the sense of vegetation ecology, neither of individual plants, nor single plant communities, but the vegetation complexes. In an analogical sense, the individuals represent the letters, the communities the words, and the complexes the sentences in a landscape description. In the same way, pedologists describe soil communities and soil landscapes (Schlichting 1970). The sentences specified by the vegetation complexes must be deciphered. The following explanation will show how the description of patches and patterns of a flowing water habitat can be understood by virtue of the concept of vegetation complexes.

The concept of vegetation complexes

This concept is derived from the Central European tradition of the study of plant communities. Phytosociological investigations of many decades have resulted in detailed knowledge of the environmental indicator value of plant species and plant communities. In many cases plant communities of riverine areas can be defined by means of simultaneous hydrochemical measurements and knowledge of the annual variation of the discharge.

However, the landscape-ecological relevance of the vegetation of running waters and their embankments can only partly be investigated by studies of the individual plant species or even 'ecological groups' of those plant species (species concept) or plant communities (community concept). To lump indicator values of many individual plant species per embankment section, in the sense of Ellenberg (1974, 1979), would mix up species of very different microhabitats and rarely allow any conclusion. Which microhabitats coexist is not a matter of chance; there is a limited number of combinations of habitats shown by the plant communities which repeat themselves in nature. From a pedological viewpoint these microhabitats form pedocomplexes.

The spatial association of different plant communities and knowledge of their indicator values could allow us to recognize 'site communities', which are recurring mosaic patterns. In this study these mosaics of plant communities of river and rivulet sections were examined and characterized. Such a study of the sum of plant communities is described as 'sigma sociology' (sigma = Greek for sum), a proposal of W. Haber (see *e.g.*, Beguin *et* al. 1979). The subject of sigma sociology is also referred to as the study of vegetation complexes. We consider vegetation complexes as spatially associated plant communities within a relatively homogeneous part of the landscape, that can be arranged into individual stands either concretely or abstractly.

The approach was originally suggested by Schmithusen (1959), who created the concept of the landscape vegetation complex. Schmithusen was a geographer who looked for spatial relevance. His idea of the landscape vegetation complex was later adopted by Tuxen (1973) as a subject of vegetation science.

The early approaches of association complexes prior to 1973 are not discussed here (see *e.g.*, Westhoff and van der Maarel 1973; Aleksandrova 1973; Pignatti 1978; Béguin et al. 1979). There is no general methodological concept in these early studies and no attempt to make releves in the field – the latter was the important idea of Tuxen (1973).

In 1977 a Symposium on sigma sociology organized by the 'International Association of Vegetation Science' took place at Rinteln FRG, with nearly 40 contributions (see Tüxen 1978a).

The approaches to apply sigma sociology in vegetation ecological and landscape ecological research can be summarized as follows:

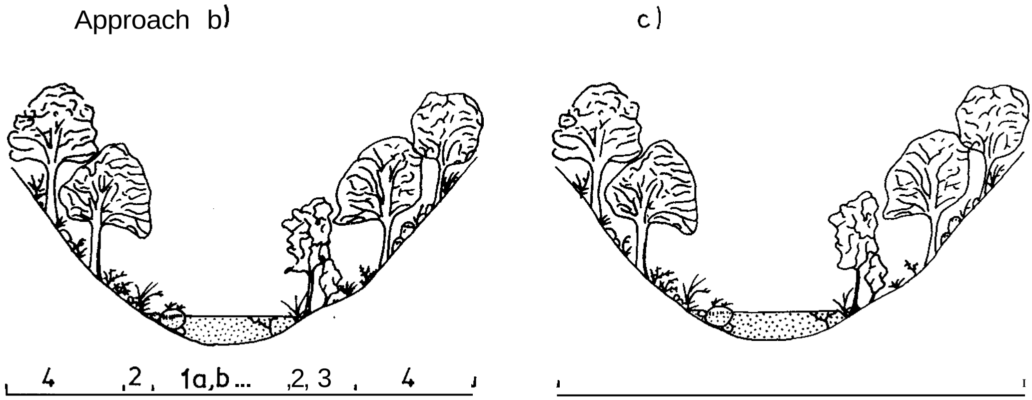

Fig. 1. Comparison of approaches (b) and (c) of sigma sociology (explained in the text) showing as an example a river valley section in regions with differentiated relief. (b). 1a, b ... Different sigma syntaxa of the riverbed and the litoral; **2.** Saliceto triandro-virninalis-Sigmetum; **3.** Stellario-Alneto-Sigmetum; **4.** Aceri-Fraxineto-Sigmetum (Sigma syntaxa according to Tüxen 1978b). (c) One relevé: after table work classified as Aceri-Fraxinetum-complex, Stellario-Alnetum subcomplex.

a. Combined deductive and inductive method, especially for mapping larger areas: Separation of areas of a defined size (*e.g.*, 1 km²), compilation of phytosociological units occurring in those marked areas (method applied by the 'Swiss School': *e.g.*, Béguin *et al.* 1975; Zoller *et al.* 1978; Béguin and Theurillat 1982, 1984).

b. Inductive method with application of sigma syntaxa (Sigmetum, Sigmion, Sigmetalia, Sigmetea): The releve areas of vegetation complexes are restricted to ecologically very homogeneous areas ('tesela' sensu Rivas-Martinez 1976, which refer to the squares of a chess-board). These areas do have the same potential natural vegetation. A system of sigma syntaxonomy is used and developed. Vegetation complexes of river valleys form geosyntaxa consisting of different Sigmeta (method applied, *e.g.*, by Rivas-Martinez 1976; Gehu 1977, 1987; Tüxen 1973, 1978b, 1979); see Fig. 1.

c. Inductive method without using a sigma syntaxonomy, units without syntaxonomical rank ('complexes'): Selection of geomorphological homogeneous units such as small V-shaped river Valley sections ('physiotopes' or 'tiles' – 'Fliesen' in the sense of Schmithusen 1948). These units can include different zones of potential natural vegetation if the relief is,largely differentiated (method applied by Pignatti 1978; Asmus 1987; Schwabe 1986/87; Asmus 1987); see Fig. 1.

Approach c. is employed in this study, because it is nearly impossible to differentiate zones of potential natural vegetation in small river valleys. We even think that the hierarchical construction of sigma syntaxa is unnecessary at this moment and has prevented this subject from being vigorously pursued, especially with regard to landscape ecological questions.

Description of the area and methods

The Black Forest was selected in its entirety for this research project. The Black Forest is a Variscian folded mountain range in southwestern Germany, consisting of gneiss, granite and sandstone. The area covers approximately 6000 km², with a maximum length of 160 km and a width of 50 km. As a result of distinctly marked differences in (1) the relief of the western and eastern sides; (2) the effects of the Wuerm glaciation, and (3) elevation and other factors we would expect to observe a series of landscape patches ('tiles') for the rivers and rivulets found in the various sections. These patches would be characterized by geomorphological, geological and anthropo-geographical factors.

The following method was adopted (Table 1): Phytosociological releves were taken after a thorough reconnaissance of the vegetation of numerous rivulet and river valleys in order to describe and characterize the plant communities

Table 1. Methodical steps concerning the investigation of vegetation complexes.

CLASSICAL PHYTOSOCIOLOGY	SIGMA-SOCIOLOGY (INVESTIGATION OF VEGETATION COMPLEXES)	SPATIAL DISTRIBUTION OF UNITS, CARTOGRAPHICAL REPRESENTATION
numerous traversings of river and rivulet valleys ↓	search for homogeneous sigma sociological sample plots ↓ →	selection of sigma sociological sample plots, homogeneously distributed in the area in question ↓
search for homogeneous sample plots ↓	sigma sociological relevés of plant communities, association fragments and certain chosen plant species ↓ →	distribution of communities in the sigma sociological sample plots ↕
relevés ↓		
table, determination of communities ← (→ search for homogeneous sigma sociological sample plots)	sigma table, determination of sigma communities →	distribution of vegetation complexes within the sigma sociological sample plots

Table 2. Scale for estimating the cover-abundance-ratings of plant communities (partly herbages, species) with reference to Wilmanns and Tüxen **1978.**

+	= 1 – 5 small stands or standard plots, cover < 5 %
1	= 6–50 small stands or standard plots, cover < 5 %
2	= > 50 small stands or standard plots, cover < 5 % or cover 5–25 %
3	= any number, cover more than 1/4 - 1/2 of the reference area
4	= any number, cover more than 1/2 - 3/4 of the reference area
5	= any number, cover more than 3/4 of the reference area

(upper limit for small stands: Bryophyta/Lichenes-communities, 1 m^2; Therophyte/Hemicryptophyte-communities of low high, 10 m^2; grassland/tall herbaceous/shrub-communities, 100 m^2; forest communities, 1000 m^2)

Concerning cover rates below 5 % a big stand is separated in the adequate number of small stands ("standard plots").

(step I). Altogether some 80 communities of association rank were distinguished which belong to 16 phytosociological classes. **A** documentation with 40 phytosociological tables including ca. 600 releves is found in Schwabe 1987: 35–281. Most of them are included in the community list of Table 4.

Then, about 200 homogeneous areas representing landscape units distributed over the entire Black Forest, belonging to six different regional natural units, were selected. Each plot had a length of approximately 150–200 m and included the episodically flooded area or – in V-shaped valleys – the area geomorphologically formed by the rivulet. The plot size varied between 150 m × 10 m and 200 m × 100 m, depending on the width of the river. The plot sizes within one type (*e.g.*, V-shaped valleys) were nearly identical.

All existing vegetation types had been compiled by means of a standardized inquiry paper *(step* 2). The distribution of the plots 1–207 is shown in Fig. 8.

The cover and abundance of plant communities, including fragmentary associations, was estimated in these plots according to a 6-part scale (see Table 2). Additionally the occurrence of woody species in each area was estimated. The distribution of some aquatic mosses and the genus *Lemanea* (Rhodophyceae) was also included on the sigma releves. Tables 2 and **3** show the estimate scale and present an example of a sigma relevé.

Table 3. Relevé example of a sigma releve (without geological, geomorphological, hydrological dates).

Estimation *of* plant communities or their fragments:
2 Urtica dioica-Calystegia sepium-community
2 Filipendula ulmaria-community
1 Phalaridetum arundinaceae
1 Phalarido-Petasitetum hybridi
+ Mentha longifolia-herbage
+ Convoivulo-Epilobietum hirsuti
+ Solidago gigantea-herbage
1 Rubus caesius-herbage
1 **Rubus** idaeus-herbage
+ Sambuco-Salicion-brush (fragment)
2 Stellario nemorum-Alnetum glutinosae

Estimation of woody species (incl.Rubus-species)	
2 Alnus glutinosa	+ Fraxinus excelsior
1 Rubus caesius	+ Prunus padus
1 Rubus idaeus	+ Sambucus nigra
+ Acer pseudoplatanus	+ Salix fragilis
+ Acer platanoides	+ Salix caprea

Location: River Nagold/ Wildberg, 390 m above sea level

The 200 sigma relevés were compiled in the form of a large synthesis table (Schwabe 1987) after evaluation of the data, and according to the approved phytosociological methods (see, *e.g.*, Mueller-Dombois and Ellenberg 1974) their character and differential communities were determined *(step 3)*.

The next *step (4)* was to summarize the relevks which show the types defined by the 'blocks' of character and differentiating species and to determine the constancy. The constancy table of all vegetation complexes (Table 4) represent in each column the typified complexes. The following classes are used:

r present in less than 5% of the compared plots;
\+ present in 5–10% of the compared plots;
I present in 11–20% of the compared plots;
II present in 21–40% of the compared plots;
III present in 41–60% of the compared plots;
IV present in 61–80% of the compared plots;
V present in 81–100% of the compared plots

In the case of less than **5** relevés Arabic numbers 1–4 are used which mark how often the community is represented. The exponents specify the amplitude of cover-abundance-ratings of the occurring communities. Accompanying communities of constancy below 20% are not taken into account.

The constancy table could as well be based on the material of nearly 600 'classical' phytosociological relevks as on over 200 sigma relevés. Altogether 15 well defined major vegetation complexes exist for the river and rivulets of the Black Forest; in addition there are some subcomplexes (see Table 4).

Furthermore it is possible *(step* ***5)*** to develop a key for mapping these vegetation complexes. The 'blocks' of character and differential communities are outlined in this key (Fig. 2).

The vegetation complexes and their spatial distribution patterns

After evaluation of the data it was possible to show the distribution patterns of all plant communities and all woody species (Table 1). Maps of the distribution of approximately 80 communities and 30 woody species were prepared for the area studied (for example, see Fig. 8, all maps are published in Schwabe 1987).

On the other hand, the spatial distribution patterns of vegetation complexes also can be worked out *(step 6)*. These patterns show that it is possible to divide the 15 vegetation complexes into four groups which are concentrated in definable landscape units. These groups with their own distribution pattern are called 'complex groups'.

The following groups can be differentiated:

Type 1: Vegetation complexes of developed and anthropogenically disturbed river sections;
Type 2: Alluvial fringing forests of mild winter climate;
Type 3: Forest valleys and steep slope sites;
Type 4: Regions characterized by locally cool or cold winter climate.

Each type has some characteristic vegetation complexes spatially replacing each other, *e.g.*, according to altitude or edaphic differences. Some characteristics of the complex groups are included in the following list:

a. Complex group No. 1: Developed and anthropogenically disturbed river sections (see Fig. 2, columns 1–3; Fig. **3;** and Fig. 7) This group consists of vegetation complexes without woody plants belonging to river sections which are greatly disturbed by man. However, relations to the natural

Table 4. Constancy table of the vegetation complexes based on 205 sigma relevés (abbr. see Fig. 2, further explanations in the text).

	Complex type	Tanacetum-Convolvuletalia-comm.-complex			Polygonum cusp.-comm. complex		Urtica-/Filip.-comm.-complex	Querco-Ulmetum-complex	Stellario-Alnetum complex		Carpinus-Fraxinus-comm.-complex		Aceri-Fraxinetum-complex				Alnus vir.-Ath.-comm.-complex	Salic. pentandro-cin.-complex	Alnetum incanae-complex	Acer-So.auc.-comm.-complex	Salicetum fragilis-c.	Abieti-Fagetum-complex	Luzulo-Abietetum-c.	Galio-Abietetum-complex
		1a	1b	1c	2a	2b	3	4		5_2 13,3	6a	6b	7a	7b	7c	7d	8	9	10	11	12	13	14	15
Ch,D1	Solidago gigantea-herbage	V^{+-1}	1^{+}			1^{+}				r^{+}			I+	++										
	Aster lanceolatus-Senecion fluv.-comm.	III^{+-2}	1^{+}							r^{+}														
	Tanacetum-Convolvuletalia-comm.	V^{+-3}	1^{+}						++															
	Saponaria-Convolvuletalia-comm.	IV^{+-1}		1^{1}																				
	Arrhenatherion-(frgm.)-comm.	IV	.																					
Ch2	Polygonum cuspidatum-comm.	V^{+-2}		1^{3}	V^{2-3}	3^{3-4}			$+^{1}$	1	II^{+-2}	I^{1}	I^{+-2}						$+^{+-2}$					
	Polygonum sachalinense-comm.					2^{+-3}							$+^{2}$											
Ch4	Querco-Ulmetum								1^{3}															
Ch5	Stellario nemorum-Alnetum glutinosae		1^{2}		II^{+-1}	43	I^{+}	1^{1}	V^{2-4}	V^{1-4}_{2-3}	V^{+-3}		V^{1-2}	2^{+-1}	I^{+}		II^{2-3}				II^{1}	1^{1}		3^{1-2}
	-- , Acer pseudoplatanus-Fraxinus-form									r														
Ch6	Carpinus-Fraxinus-comm.			1^{3}			I+	1^{2}		r	V^{1-5}	V^{3-4}		4^{1-2}										
Ch7	Aceri-Fraxinetum												V^{1-3}	4^{3-4}	V^{1-5}	V^{2-4}								
Ch8	Alnus viridis-Athyrium f.-f.-comm.									1						V^{+-3}	V^{2-4}							
Ch9	Salix x multinervis-comm.									r^{2}			$+^{1}$				I^{+}	V^{1-4}	II^{+}					
	Salicetum pentandro-cinereae																	III^{1-3}	$+^{2}$					
Ch10	Alnetum incanae																		V^{2-5}		I^{+}			
D	Carduus personata-comm.									r^{+-1}			I^{+}		$+^{1}$				III^{+-1}					
D	Rosa pendulina-Lonicera nigra-comm.																		II^{+-2}					
Ch11	Acer ps.pl.-Sorbus auc.comm.(w.Alnus viridis)																			4^{+-3}				
Ch12	Salicetum fragilis						I^{+}		I^{+-1}	r^{1}	++	I							$+^{2}$	1^{1}	V^{1-3}			
Ch13	Abieti-Fagetum				I^{1}	2				+	I	II		3	III	V						4^{2-4}		
Ch14	Luzulo-Abietetum									+					:+			▪-▪	II^{+}	$+^{+}$		1^{+}	3-4 ;+-1	
D	Polytrichum commune-cushion				I+	1^{+}					+								+				4^{+-1}	
D	Sphagnum squarrosum-cushion									r^{+-1}														
Ch15	Galio-Abietetum												1						+					3^{3-4}
Differential communities of altitude																								
sub-mont. reg.	Impatiens glandulifera-comm.	V^{+-3}		1^{2}	IV^{+-3}	2^{+-2}	III^{2}	1^{+}	IV^{+-3}	I^{+-2}	III^{+-3}	III^{+}	II^{+-2}	1^{1}					$+^{+}$		I^{1}			
	Arrhenatheretum alopecuretosum	$+^{+-3}$		1^{2}	IV^{2}	1	III^{2}	1	IV^{2-3}	II^{+-3}	IV^{+-2}	I^{2}	I				I		+					
	Urtica-Convolvulus sepium-comm.	IV^{+-2}	1^{2}	1	II^{1}		I		IV^{+}	I	II	II^{2}												
	Convolvulo-Epilobietum hirsuti	II	1^{+}						I^{+}	r^{+}											I+			
	Humulus lupulus-Sambucus nigra-comm.	.		1^{+}				1^{+}	II^{+}		II^{+-1}	II^{+-1}												
	Senecioni-Brometum racemosi					1			I^{+}		I^{+}	I^{+}			$+^{1}$									
	Rubus caesius-colony	II^{+}	1^{+}				I^{+}		$+^{+}$		$+^{+}$	II^{+}												
	Lythrum salicaria-herbage	IV^{+}		1^{+}			I^{+}		II^{+}		I^{+}													
	Iris pseudacorus-herbage	I					I		II		r													
mon-tane reg.	Chaerophyllo-Ranunculetum aconitifolii	I^{+}			III^{+-1}	2^{+}	I^{2}	1^{+}	II^{+-1}	V^{+-3}	III^{+-2}	III^{+-2}	IV^{+-2}	3^{+-2}	V^{+-2}	III^{2-3}	V^{1-2}	V^{+-2}	V^{+-2}	4^{+-3}	V^{+-1}	4^{+-2}	1^{1}	2^{2}
	Knautia dipsacifolia-Aegopodion-comm.	+			III^{+}	2^{+-1}	I^{1}		II^{+-1}	IV^{+-2}	III^{+-1}	II^{+-1}	IV^{+-1}	3^{+-1}	V^{+-1}	III^{+-1}	V^{+-1}	V^{+-1}	IV^{+-1}	4^{+}	III^{+}	2^{+-1}	1^{+}	
	Athyrium filix-femina-colony	$+^{+}$			III^{+-1}	3^{+}			III^{+-1}	III^{+-1}	III^{+-1}	II^{+-2}	III^{+-2}	3^{+-2}	IV^{+-1}	III^{+}	V^{+} I^{+}	II^{+}	I^{+-1}	1^{+}		4^{+-2}	3^{+-1}	
	Caltha palustris-colony				III	1^{+}	I+		+	IV^{+}	I^{+}	IV^{+}	V^{+-1}	4^{+}	III^{+}		III^{+}	IV^{+-1}	V^{+}	4^{1}	III^{+}	4^{+}	1^{+}	
	Senecio fuchsii (nemorensis)-herbage				II^{+}	2^{+}			$+^{+}$	II^{+}	I^{+}	II^{+}	III^{+}	2^{+-1}	I^{+-2}	I^{+-1}	I^{+} I	II^{+-1}	III^{+-1}	1^{+-1}	II^{+}	1^{+-2}	2^{+}	
	Epilobium angustifolium-herbage				I^{+}	2^{+}	II^{+}			II^{+-2}	$+^{+-2}$	II^{+}	III^{+}	3	IV	IV		III^{+-1}	IV^{1-2}	2^{+}	IV^{2}	2	2^{1}	3^{1-2}
	Stachyo-Impatientetum				I^{+}	2				II^{+-3}	I^{+}	II^{+}	III^{+-3}	4^{+-3}	II^{1-4}	III^{+-3}	III^{+}	II^{+}	I	1	I	1-2	4^{3-4}	3^{3}
	Luzula sylvatica-comm.				I^{1}	2^{+}				$+^{+}$	I^{+}	II^{+-2}	V^{+-1}	1^{+}	II^{+-2}		I+		I^{+}	1^{+}		;+-2	4^{+-2}	1^{+}
	Adenostyles all.-Athyrium filix-f.-comm.				I^{1}					I^{+}	r^{+}	IV^{+}	I^{+-1}		II		II^{+}	II	II	2	IV	2^{+}	2^{+}	
	Geranio-Trisetetum, moist unit						II			II^{+-2}	$+^{+}$	I^{+}	I^{+-1}		III^{1-2}	I^{2}	III^{+}		II^{+-2}			1^{1}	1^{+}	1^{+}
	Petasites albus-colony									I^{+}	$+^{+}$	I^{+}	$+^{+-3}$		II^{+}			III^{+}						
	Chrysosplenietum oppositifolii									+	+		II^{+} I^{+}	2^{+}										
	Rubus idaeus-colony		1^{1}		I^{+}	3^{+}	I^{+}		III^{+-1}	V^{+-2}	IV^{+-2}	IV^{+-1}	IV^{+-2}	3^{+-1}	V^{+-2}	III^{+-1}	V^{+-2}	IV^{+-1}	V^{+-2}	3^{+-2}	III^{+-1}	4^{1-2}	4f	1^{2}
	Sambuco-Salicion frgmt.		1^{+}			1^{+}	I^{+}		$+^{2}$	r^{+-2}	$+^{2}$	II^{1-2}	I^{1}	1^{1}	I^{+} I^{1}	V^{+-2}	I^{+-2}	II^{+}	I^{+-1}	2^{+-1}	I^{+}	1^{+}		1^{+}
	Corylus avellana-shrub									II	r^{2}		II^{1}	2^{1}	$+^{+-2}$		II^{+-1}	I+	I^{2} I^{+}	1^{+}		3^{+}	1^{+}	,+-1
	Piceo-Sorbetum aucupariae									$+^{+}$			I^{+}		II^{+-1} I		II^{+}		II^{+-2}	1^{+}	I^{1}			
	Pure Lonicera nigra-colony									$+^{1}$	r^{+}		$+^{+}$	2^{+}										
	Pure Rosa pendulina-colony									r														
D comm. of valleys with swamp- and fen-veg., eastern Black For.															$+^{+}$		I^{+}	III^{+-1}	II^{+}	1^{+}			1^{+}	2^{+}
	Equisetum sylvaticum-comm.						I^{+}										I^{1}	III^{+-1}		1	I			
	Juncetum acutiflori						I												+		I			
	Juncetum filiformis						I										I	III	I	3				
	Caricetum fuscae/Parn.-Car. fuscae						I			r^{+}							I^{1}	I		1^{+}				
	Caricetum rostratae																I^{+}	II^{+}	$+^{+}$	2^{+}				
	Ran. flammula-Agrostis can.-pion.-comm.																I	I	+		II			
	Epilobio-Juncetum effusi																:+	I1	+					
	Carex panicea-Molinietalia-comm.																	II^{+}		1^{+}				
	Juncus bulbosus-comm.																							
D comm. in reg. with low velocity of runn. waters															$+^{1}$									
	Scirpetum sylvatici					1	III^{+-1}		I	II^{+-1}	I^{+-2}		$+^{1}$			I^{+}	III^{+-2}	IV^{+-1}	II^{+-2}	4^{+-1}	III^{+}	2^{+}		2^{1}
	Glycerietum fluitantis, typical ""it					1^{+}	IV		$+^{1}$	I^{+}							IV	III^{+}	III^{+}	4^{+}	III^{+}	1^{+}		1^{1}
	Glycer. fluit., Veronica beccabunga-facies						III^{+}			$+^{+}$	r						I^{+}	I^{+}	I^{+}	3^{+}	I^{+}		1	

Veronica beccabunga-colony	I^{+}	.	.			.	.	I^{+}	r^{+}	r^{+}	.	.	.			.	I^{+}	.		.	.		
Cardamine amara-Stellaria ulig.-comm.	.	.	.			I^{+}	.	.	.	.	.	.	.			.	I^{+}	II^{+}	2^{+}	.	.		
Montienion-frgmt.-comm.	.	.	.							.	.	.				I^{+}	II^{+}	.	2^{+}	I^{+}	.		
Selected aquatic cryptogams																							
Fontinalis antipyretica-colony	III	1	.	I		II	1	+	I	II	IV	I				.	.	I	1	III	.	1	1
Lemanea spec.-colony	.	.	.			I	1	I	I	I	II	II	1	II	∀	II	.	II	.	I	.		
Fontinalis squamosa-colony	+	.	.				1	+	+	I		I		I		.	.	II	.	.	.		
Waterplant(s)-(comm.)																							
Callitriche hamulata-colony	I^{+}	.	.		1^{+}	II^{+-1}	1	II^{+-1}	$+^{+-2}$	I^{+}	.	$+^{+}$	.			I^{2}	II^{+-3}	I^{+-2}	.	IV^{+-1}	1^{+}	.	1^{2}
Ranunculetum fluitantis	$+^{1}$	1^{+}	.				.	I^{1}	.	r^{+}	.	.	.			.	.	III^{+}	.	.	.		.
Ran.pelt.-col.and hybrid-pop.(p.p.cf.)	II^{+-1}	.	.			.	.	$+^{1}$	r^{2}	r^{1}	.	.	.			.	.	.	.	.	.		.
Ran.trich.col.and hybrid-pop.(p.p.cf.)	$+^{+}$	.	.			.	.	II^{1-2}	.	.	.	.	.			.	.	.	.	.	.	.	.
Pioneer comm.of eutrophic habitats																							
Agrostis*prorepens(-Ran.repens)-comm.	IV^{+}	.	1^{+}	III^{+}		III^{+}		III^{+}	II^{+}	II^{+}	II^{+}	1^{+}		.	I^{+}	.	III^{+}	II^{+}	2^{+}	III^{+}	1^{1}	1^{+}	1^{+}
Equisetum arvense-colony	III^{+}	.	1^{+}						.	II^{+}	.			$+^{+}$	.	.	.	$+^{+}$	.	.	.	.	.
Polygonum hydropiper-comm.	II^{+}	.	1^{+}	I^{+}		II^{+}		II^{+}	$+^{+}$	++	II^{+}	++		.	.	.	.		.	I^{+}	.	.	.
Rorippo-Agrostietum prorepentis	I^{+-1}	.	.											.	.	.	.		.	I^{+}	.	.	.
Agropyro-Rorippetum austriacae	I^{+-1}	.	.				.	.	.					.	.	.	.	.	.	.	.	.	.
Other tall-herb.-and reed-comm.with high constancy																							
D3 Urtica-Herden(without Urt.-Conv.-comm.)	II^{+-2}	.	.	III^{1-2}	2^{+-1}	IV^{1-3}	1^{1}	I^{1-2}	IV^{+-3}	IV^{1-2}	III^{+-1}	V^{+-3}	1^{+}	III^{+-2}	III^{+-1}	III^{+-1}	III^{+-3}	III^{+-}	3^{+-1}	V^{1-3}	3^{+-1}		2^{2}
D3 Filipendula ulmaria-comm.	II^{+-2}	1^{2}	.	IV^{+-2}	3^{+}	V^{1-3}	.	III^{+-2}	V^{+-3}	III^{+-2}	IV^{+}	III^{+-2}	1^{+}	II^{+}	IV^{1-2}	IV^{1-3}	IV^{1-3}	III^{+-2}	2^{1-2}	V^{1-3}	.		1^{2}
Phalaridetum arundinaceae	V^{1-4}	1^{1}	1^{3}	IV^{+-2}	2^{1-2}	IV^{+-3}	1^{1}	IV^{+-3}	III^{+-3}	III^{+-2}	II^{+-1}	IV^{+-2}	1^{+}	$+^{+}$		.	III^{1-2}	III^{1-2}	2^{2}	V^{1-3}	.	.	.
Phalarido-Petasitetum hybridi	II^{+-2}	1^{1}	.	I^{+}	.	II^{2}	.	III^{+-2}	II^{+-4}	I^{+-4}	III^{1-3}	III^{+-4}	2^{+-1}	II^{1-2}	III^{2}	I^{2}	I^{+}	III^{1-2}	2^{2}	V^{+-3}	1^{+}		.
Other shrub-communities																							
Rubus fruticosus agg.-colony	II^{+-1}	.	.	IV^{+}	2^{+}	III^{+-1}	1^{+}	IV^{+-2}	I^{+-2}	IV^{+-2}	V^{+-2}	II^{+-1}	3^{+-1}	II^{+-2}	II^{+-1}	.	.	$+^{1}$	.	.	3^{+-1}	3^{+-1}	
Sal.triandrae/Salix viminalis-comm.	.	.	.	.	1^{2}	.	.	I^{1-2}	$+^{+-2}$	.	.	$+^{1}$	.	$+^{2}$		.	.	.	.	I^{2}	.	.	.
Salix purpurea-alliance-comm.	.	.	.	.	.	I^{+}	.	$+^{1}$	$+^{+-2}$	r^{1}	.	.		.		.	.	I^{+}	.	I^{1}	.	.	.
Salix cinerea-shrub						.	.	I^{+-2}	.	$+^{+-1}$		.				.	.	$+^{+}$	.	.	.	.	.
Viburnum opulus-shrub						.	.	.	.	I^{+}	I^{+}	.				.	.	.	.	.	.	.	
Other comm. Lysimachia vulgaris-herbage	III^{+}		1^{+}			II^{+}	.	II^{+}	I^{+-1}	II^{+}	II^{+}	I^{+}	.		.		.	$+^{+}$	1^{+}	I^{+}	.	.	
Mimulus guttatus-colony	III^{+}			III^{+}	2^{+}	.	.	$+^{+}$	I^{+-1}	I^{+}	.	$+^{+}$		.		I^{+}		I^{+}	.	II^{+}	.	.	
Angelico-Cirsietum oleracei	$+^{1}$					.	.	$+^{+}$	r^{+-1}	r^{+}	I^{+}	.	.		.	.	.	$+^{+}$		.	.	.	.
Digitalis purpurea-herbage				I^{+}	1^{+}		.	.	$+^{+}$			.		$+^{+}$		.	.	$+^{+}$			2^{+}	3^{+}	
Epilobio-Geranietum robertiani						.		$+^{+}$	r^{1}	¿+		$+^{1}$ 2-11		$+^{1}$	.	.	.			.	.	.	
Impatiens parviflora-colony						.		.	r^{+-1}	I^{+-1}							.	$+^{+}$		.	.		
Polygonum bistorta-comm.						.	.	.	.							I^{+}	.	$+^{+}$		.	.		

VEGETATION COMPLEXES:
1 TANACETUM-CONVOLVULETALIA-COMM.-COMPLEX
- 1a TYPICAL SUBCOMPLEX
- 1b STELLARIO-ALNETUM-SUBCOMPLEX
- 1c CARPINUS-FRAXINUS-COMM.-SUPCOMPLEX

2 POLYGONUM CUSPIDATUM-COMM.-COMPLEX
- 2a TYPICAL SUBCOMPLEX
- 2b STELLARIO-ALNETUM-SUBCOMPLEX

3 URTICA-FILIPENDULA-COMM.-COMPLEX WITHOUT TILLERING

I QUERCO-ULMETUM-COMPLEX

5 STELLARIO-ALNETUM-COMPLEX
- 5a1 SUBMONTANE FORM
- 5a2 MONTANE FORM

6 CARPINUS-FRAXINUS-COMM.-COMPLEX
- 6a STELLARIO-ALNETUM-SUBCOMPLEX
- 6b TYPICAL SUBCOMPLEX

7 ACERI-FRAXINETUM-COMPLEX
- 7a STELLARIO-ALNETUM-SUBCOMPLEX
- 7b CARPINUS-FRAXINUS-COMM.-SUBKOMPLEX
- 7c TYPICAL SUBCOMPLEX
- 7d ALNUS VIRIDIS-ATHYRIUM F.-F.-COMM.-SUBCOMPLEX

8 ALNUS VIRIDIS-ATHYRIUM FILIX-FEMINA-COMM.-COMPLEX

9 SALICETUM PENTANDRO-CINEREAE-COMPLEX

TO ALNETUM INCANAE-COMPLEX

11 ACER PSEUDOPLATANUS-SORBUS AUCUPARIA-COMM.-COMPLEX

12 SALICETUM FRAGILIS-COMPLEX

13 ABIETI-FAGETUM-COMPLEX

14 LUZULO-ABIETETUM-COMPLEX

15 GALIO-ABIETETUM-COMPLEX

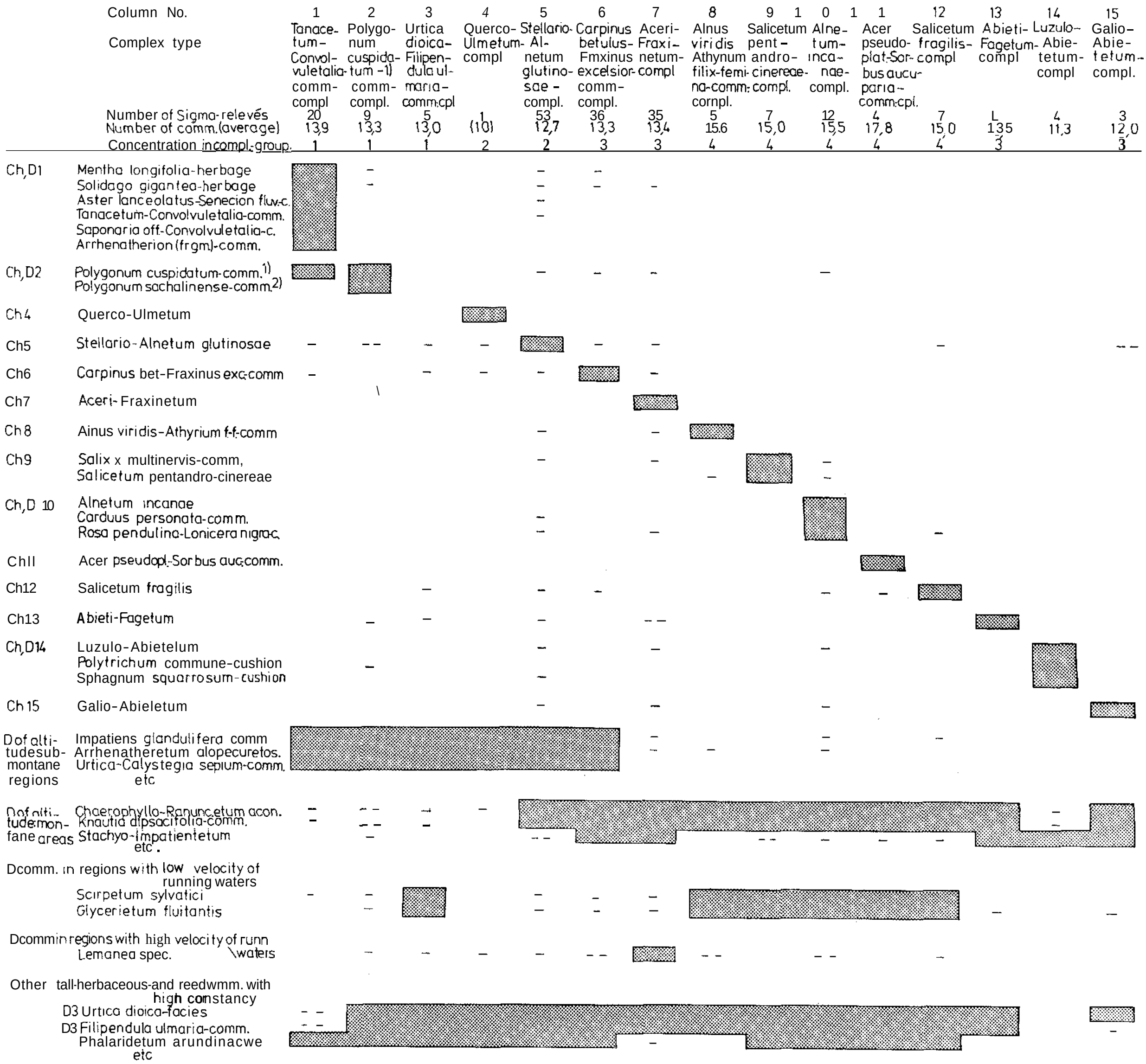

Fig. 2. Scheme developed from the basis of the original table (see Schwabe 1987) in order to characterize and to differentiate vegetation complexes (simplified). Ch = character community; D = differential community; compl., cpl. = complex; frg. = fragment; comm., c = community; (1) syn.: Reynoutria japonica; (2) syn.: Reynoutria sachalinensis.

landscape can be recognized, since only those river areas with a higher run-off pattern and danger of overflow were developed.

The Tanacetum vulgare-Convolvuletalia-community-complex includes many characteristic communities of ruderal habitats; which indicate that there are strongly different ecological conditions at the anthropogenically created sites which do not exist in other parts of the Black Forest.

The Polygonum cuspidatum (syn. Reynoutria japonica)-community-complex grows in riparian areas with layers of set stones. In the Black Forest these plants show much more vitality than in their country of origin, Japan, where frequent disturb-

Fig. 3. Example of a vegetation complex from the complex group of developed and anthropogenically disturbed river sections: Tanacetum vulgare-Convolvuletalia-comm.-complex on river Kinzig (western Black Forest) with Phalaridetum arundinaceae and Artemisietea-communities on a higher level of the embankment.

ances occur caused by typhoon-flooding with large quantities of fluviatile pebbles (Dr. Y. Nakamura, Yokohama, pers. comm.).

b. Complex group No. 2: Alluvial fringing forests of a mild winter climate (see Fig. 2, columns 4, 5; Fig. 4; Fig. 7). This complex group is characteristic for riparian zones in broad flood-plain valleys. A gallery forest formed by Stellario nemorum-Alnetum glutinosae-complex only a few meters wide follows the river and rivulets. This complex group is particularly characteristic for weakly sloping valleys within the lower Triassic areas and in the western Black Forest.

In the submontane form of the typical forest community, Stellario-Alnetum glutinosae, there are thermophilous species such as *Hedera helix* and *Rubus fruticosus* agg. which are sensitive to cold winter climates. Sections with weakly sloping gradients are rich in aquatic vascular plants, such as *Callitriche hamulata* and *Ranunculus peltatus* in less polluted sections, and *Ranunculus fluitans* s.str. in more polluted areas (especially those polluted by ammonium, see Monschau-Dudenhausen 1982).

c. Complex group No. 3: Forest valleys and steep slope sites (see Fig. 2, columns 6, 7, 13–15; Fig. 5; Fig. 7). This complex group occurs in narrow V-shaped valleys and at locations where rivers have undercut solid rocks. These narrow valleys are often deeply embedded in woodland, and the rivulets are not wide. These heavily overshadowed and fast-flowing rivulet sections have no aquatic vascular plants at all; typical cryptogams in this region are *Lemanea* spec. (Rhodophyceae), which is a

Fig. 4. Example of a vegetation complex from the complex group of alluvial fringing forests with a mild winter climate. Stellario nemorum-Alnetum glutinosae-complex with Stellario-Alnetum glutinosae and (left at front) the Salix viminalis-community on river Enz (northern Black Forest).

good indicator of oligosaprobic conditions, and *Scapania undulata* (L.) Dum. (Bryophyta, Hepaticae).

The typical vegetation complex on these steep slope sites is in submontane zones: the Carpinus betulus-Fraxinus excelsior-community-complex, and in montane zones the Aceri pseudoplatani-Fraxinetum-complex.

d. Complex group No. 4: Regions characterized by locally cool or cold winter climate largely subject to long term flooding after the snow melt (see Fig. 2, columns 8–12; Fig. 6; Fig. 7; Fig. 8; Table 5).

Characteristics of this complex group is that its vegetation covers areas where *Alnus glutinosa* is absent due to thermal-climatic reasons. Thermophilous plant communities are totally absent within the entire group.

All these areas are situated within reach of the −2°C-January-Isotherm. The vegetation complexes in question grow in valleys formed during the Wuerm glacial period which have thick fluvioglacial deposits (Alnetum incanae-complex), or on swampy soils with a high water level particularly after the snow melt in April. They all share a series of phytogeographically remarkable communities and species (*e.g.*, *Alnus incana*, *Alnus viridis*, *Salix pentandra*).

The concept of vegetation complexes as a key for differentiating landscape units

We are able to differentiate landscape units within a wider region by means of complex groups (Fig. 7). As an example this has been shown for the river

Fig. 5. Example of a vegetation complex from the complex group of the forest valleys and the steep slope sites: Carpinus betulus-Fraxinus excelsior-comm.-complex growing on steep slopes within the submontane belt (Muenstertal, western Black Forest).

and rivulet valleys. This differentiation deviates in the case of regional natural units such as 'Southern Black Forest' and 'Southeastern Black Forest' from the natural spatial differentiation of Germany (Institut für Landeskunde 1959, see Fig. 8). The latter includes the Alnetum incanae-complex in the 'Southern Black Forest'; the vegetation complexes in the river valleys as well as those of the mountain sides refer, however, to the unit 'Southeastern Black Forest'.

An example for complex group No. 4 follows where a differentiation of smaller landscape sections is based upon the typified vegetation complexes (Fig. 8). Such differentiation can also be carried out for complex groups No. 1–3 (see Schwabe 1987).

Five vegetation complexes with cold winter sites belong to the complex group No. 4. The valleys characterized by such complex groups are in accordance with Fig. 8. The boundaries between these vegetation complexes and their spatial extensions were confirmed by inductive research work.

A deductive point of application would differentiate *e.g.*, rivulet and river sections according to altitudinal zones (as it is done by Braukmann 1987, who combined this method with inductive limnological work), according to a west – east differentiation, or to the European watershed Rhine/Danube (as it is partly done by the natural spatial differentiation of Germany, l.c.).

The vegetation complexes show quite clearly that it is not only the present water regime and alti-

Fig. 6. Example of a vegetation complex from the complex group, where a cold winter climate predominates: Salicetum pentandro-cinereae-complex growing on sites with long term overflows during and after snow melt, with Salix × multinervis (= Salix cinera × aurita) and (right in rear) Salicetum pentandro-cinereae (Gutach near Schoenwald, eastern Black Forest).

Table 5. Physical-geographical and anthropo-geographical characteristics of the vegetation complexes of complex group No. 4: Regions of cold winter climate and long term overflows after the snow melt.

VEGETATION COMPLEX	PHYSICALGEOGRAPHICAL AND ANTHROPOGEOGRAPHICAL CHARACTERISTICS
Alnetum incanae-complex	cold winter valleys formed during the wuerm glacial period and with thick fluvioglacial deposits, settlements on terraces or on valley slopes, preferably meadow utilization on fresh sites
Salicetum pentandro--cinereae-complex	cold winter valleys with stagnant gley-habitats settlements on valley slopes, mainly utilized as pasture and wet meadow
Acer pseudoplatanus--Sorbus aucuparia-community-complex	cold winter climate, and sites inclined to stagnant wetness in the valley bottom, under-cut slopes of meandering rivulets covered with same vegetation complex, settlements on valley slopes, mainly utilized as pasture and wet meadow
Alnus viridis-Athyrium filix-femina-community-complex	cold winter sites of higher incline with running waters and better drainage, character of mountain torrents, few solitary farms on the valley slopes, mainly utilized as pasture and wet meadow
Salicetum fragilis-complex	less cold in winter, long period overflow in spring, well drained in summer, settlements on terraces and on valley slopes, meadow utilization on fresh sites

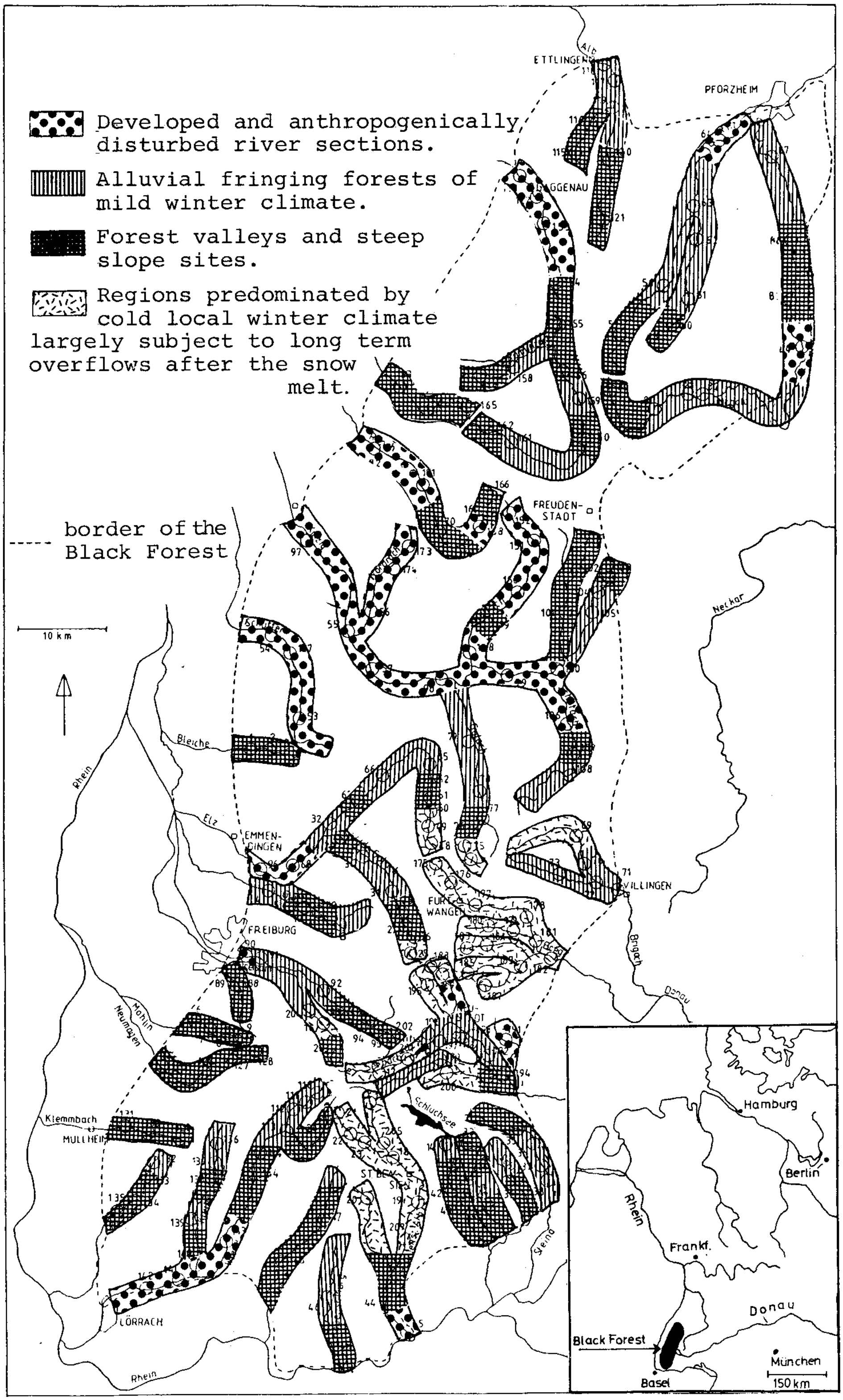

Fig. 7. Distribution of the four groups of vegetation complexes (complex groups) in the Black Forest.

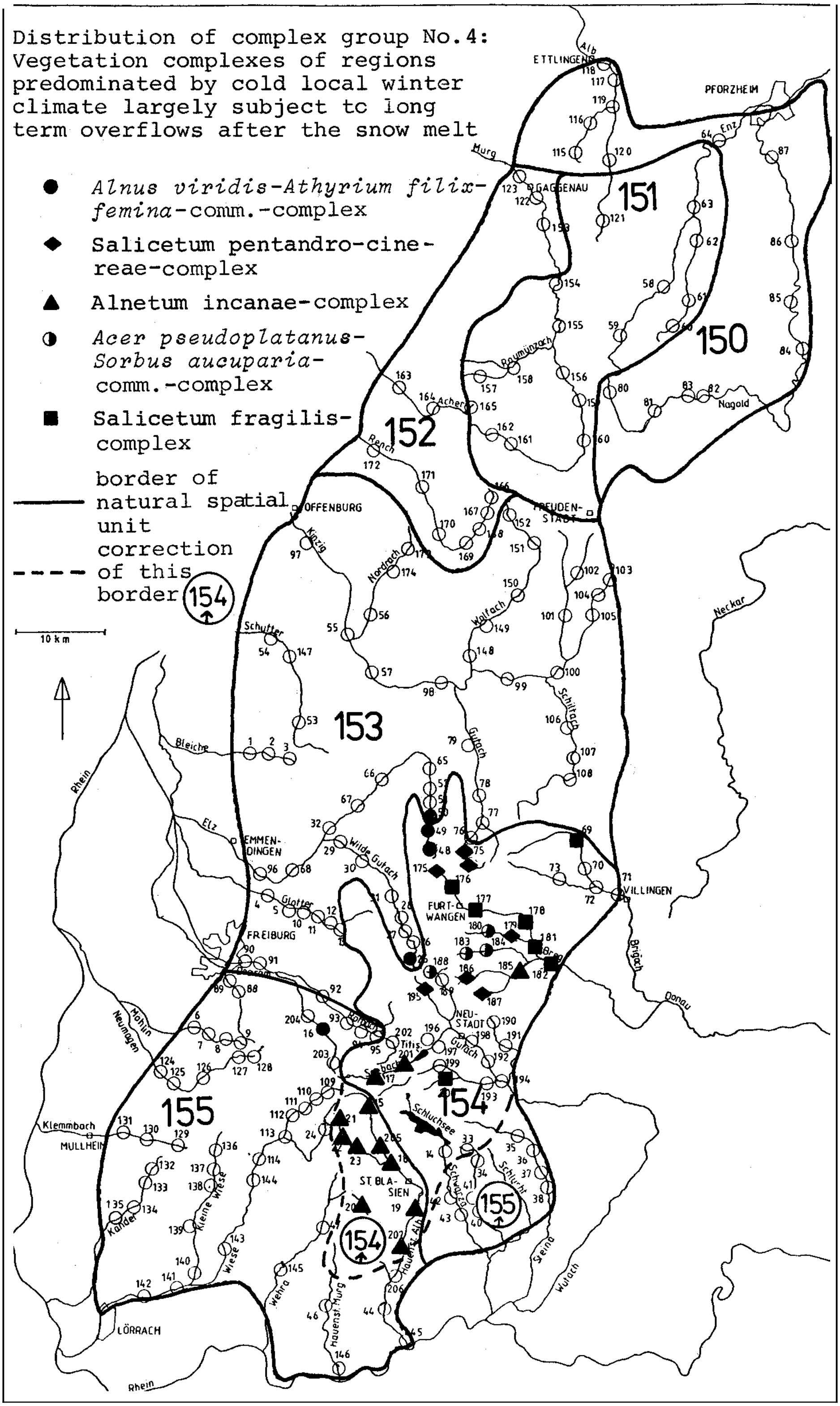

Fig. 8. **Distribution of the vegetation complexes of complex group** No. **4 and natural spatial borders** of **the Black Forest (150–155).**

tude which is important for the character of a special landscape unit but historical processes, such as during or after the last glacial period when the geomorphology had been formed by glacial and periglacial processes. Thus the vegetation complexes of a wuerm glacial formed valley flowing today to the Rhine (*e.g.*, the 'Hauensteiner Alb, see Fig. **8)** are quite similar to those of the typical Danubian valleys of the eastern Black Forest with low velocity, and the vegetation complexes differ from those growing in valleys with postglacial retrogressive erosion from the Rhine. These points led to the proposed differentiation of unit 153/154 in Fig. 8.

The advantage of the inductive approach of landscape differentiation using vegetation complexes and complex groups is as follows: Vegetation complexes reflect very complicated ecosystem functions with biocoenotic connexions, and their limits represent differences of important ecological factors such as air moisture, inclination, sedimentation or erosion conditions, light intensity, occurrence of anthropogenic influences, long or short term flooding etc. It is possible to map these complicated connexions using vegetation complexes as exponents of certain, usually definable combinations of ecological factors. For example, the community combination in the Aceri-Fraxinetum-complex (see Table 4, column **7)** proves, that there is high air moisture, shown by the combination of Stachyo-lmpatientetum, Athyrium filix-femina-community, Chaerophyllo-Ranunculetum aconitifolii and others. Furthermore, there is no direct solar irradiation (shown by *Petasites albus* colonies and *Lemanea*-thalli), seepage water on the slopes (shown by *Chrysosplenietum oppositifolii*) and mostly oxygen-rich conditions in the rivulet (shown by *Lemanea* spec.). For each vegetation complex this specific combination of plant communities reflects a definable mosaic with groups of plant communities, which have diagnostic ecological value. More examples are given in Schwabe **(1988).** This gives a new synthetical view, including hydrological and other geographical data. Thus the defined vegetation complex can be a synthetic agent for geographical and biological characteristics.

The attempt of a synthesis of phytosociology and physical-geographical data was already introduced by Grootjans (1980) in the Netherlands, with detail maps of vegetation units in brook areas (source area, upper, middle, lower course). The approach of Grootjans (1980) needs mapping of all plant communities at a large scale (not only an estimation of cover-abundance ratings, as the sigma sociology). Therefore the proposed study of vegetation complexes is a quicker method, and it is possible to study more river sections within the same time frame. But mapping of ecologically important river sections as 'case studies' is very useful in vegetation complex studies.

The concept of vegetation complexes and its importance for application

Each vegetation complex corresponds to a specific inventory of woody species, empirically drawn from approximately 200 sample stands. The inventory of woody species can then be compiled with separate lists for wet and moist/fresh sites. From the point of view of water economy such inventory is desirable today because many efforts are again being made to plant woody species in accordance with natural conditions along river and rivulet embankments. Precisely in cold winter areas many incorrect and costly estimates for replanting projects have been made in the past.

From the distribution maps of certain woody species conclusions can be made on the mutual occurrences of other woody species and about regions where certain woody species grow for the river and rivulet valleys of the Black Forest. These maps show thermophilous woody species growing in the V-shaped valleys of the western Black Forest; these species follow the rivulets to rather high altitude. Nonetheless, cold resistant woody species, which are typical for the cold winter glacial-formed valleys of the southern Black Forest (*e.g.*, *Alnus incana)*, grow on riparian stands downwards to lower altitudes.

Further applied aspects are briefly mentioned which, however, are not dealt with further in this paper (see Schwabe **1987)**, and for which the differentiated vegetation complexes are important standardized units:

- Questions of values for nature conservation.
- Model character for 'renaturalisation project'.
- Management of alluvial forests according to the criteria of biological landscaping ecology.

Concluding remarks

It 'was possible to prove that two fundamental problems of landscape ecology can be dealt with using the concept of vegetation complexes and using inductive methods.

These problems were named by Neef **(1982)** as follows:

1. 'connexion of natural and social systems in the landscape';
2. 'relation between individuals and types or other forms of abstraction and the problem of integration'.

The aims of future investigation should include social systems to a greater degree than presently, *e.g.*, 'releves' of house forms (H. and Ch. Ellenberg, in press). Including soil communities as well would be important, however, such research might not be worth while in the case of scarcely developed soils along the embankments. Finally vegetation complexes are important as standardized units first for experimental ecological research projects and second for biocoenological investigations, especially regarding animal species of great mobility (for the second point see Kratochwil **1987;** Seitz **1988).**

The method of investigating vegetation complexes can only be applied when there is an exact knowledge of the occurring plant communities; work on the latter has to be reinforced. This method could at present be usefully applied to large areas of Europe, Canada, Japan and in some regions of the USA, Australia, South America and the western parts of Asia, since in these parts of the world sufficient knowledge of plant communities does exist.

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