Acta Bot. Neerl. 45(4), December 1996, p. 443–459

REVIEW

Recent developments in phytosociology*

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Key-words: phytosociology, multivariate computer techniques, ecological diagrams, classification, vegetation strategies.

INTRODUCTION

During the last decade, a renewed interest in phytosociology can be observed, not only in The Netherlands but also abroad. In Rinteln, the traditional meetings on phytosociology have been organized since 1987, after an interruption of more than a decade. From 1992 onwards, each spring, vegetation researchers of more than 20 countries come together in Rome to encourage phytosociological study. These meetings are organized as part of the *European Vegetation Survey*, a network of scientists aiming at (1) the promotion of national projects on classification of vegetation, (2) a standardized European Data base for Phytosociology, (3) the publication of a book on the vegetation of Europe, and (4) in the long term, a comprehensive and well-documented overview on European plant communities (Pignatti 1990; Dierschke 1992; Mucina *et al.* 1993e; Rodwell *et al.* 1995; Schaminée 1995; Rodwell 1995).

Long-term projects on national vegetation classification have been started in several European countries; the first results have been published already or will be published shortly. In Germany, the series *Süddeutsche Pflanzengesellschaften* has been completed by the publication of the fourth volume, on woodlands and scrub (Oberdorfer 1992). In the former Soviet Union, Korotkov *et al.* (1991) published the first prodromus of vegetation syntaxa according to the method of Braun–Blanquet. Julve (1993) presented

Nomenclature following Van der Meijden (1990) for plant species, and Westhoff & Den Held (1969) and Schaminée *et al.* 1995b for syntaxa.

*This paper is based on a lecture at the 150th meeting of the Section for Vegetation Research of the Royal Botanical Society of The Netherlands held on 23 November 1995.

a synopsis of plant communities of France, Pott (1992) of Germany. In Austria, the research resulted in the publication of a standard work in three volumes, managed by Mucina and Grabherr (Grabherr & Mucina 1993; Mucina *et al.* 1993a,b). The national vegetation classification of Great Britain will be summarized in five volumes; until now, four of these have been published (Rodwell 1990, 1991, 1992, 1995). In Slovakia, a start of a series of syntaxonomic overviews was made by the publication of the first volume, on pioneer communities (Valachovic 1995). Finally, in The Netherlands, the first two volumes of the national vegetation classification have been launched (Schaminée *et al.* 1995a, 1995b).

This renaissance of phytosociology has various origins. Of course, recent socio-political changes in Europe have played a part. The fall of the Iron Curtain not only deeply influenced economy and culture, but also provided new opportunities for science. During the first half of this century, an intensive cooperation existed between phytosociologists in western and eastern Europe but after the Second World War, exchange of knowledge and mutual field visits became difficult. It is remarkable that simultaneously with the disappearance of the Iron Curtain between east and west, the 'brown blanket' between Britain and the Continent vanished, as the National Vegetation Classification in Great Britain is more or less according to the Braun–Blanquet approach. Furthermore, there is a growing concern in applying phytosociological knowledge not only in nature conservation and nature management, but also in land-use planning. The new interest is based on the increasing awareness that careful analyses of plant communities, documented by recent and historical vegetation relevés, constitute a proper basis for evaluating the consequences of environmental changes, both on local-regional and on (inter)national scale. For the greatest part, however, the revival of phytosociology results from the recent boom in adequate multivariate computer techniques, which allow the handling of large amounts of phytosociological data. In this respect, we may refer to Westhoff (1979), who stated in his review article on 'history, present state and future' of phytosociology in The Netherlands, that 'The further development of vegetation research is hardly thinkable without a major impact of numerical data processing'.

MULTIVARIATE COMPUTER TECHNIQUES

Although the use of multivariate methods (classification and ordination) in the description and ecological interpretation of plant communities has a long tradition (Van der Maarel 1979), the common availability of fast computers, user-friendly software and computerized databases expanded the range of applications enormously. In The Netherlands, the software package TURBOVEG (Hennekens 1994, 1995) was designed for input, processing and presentation of phytosociological data. In Rome 1994, at the meeting of the *European Vegetation Survey*, it was decided to adopt TURBOVEG as a standard for Europe. In the meantime, it has been installed in some 20 countries (Schaminée & Hennekens 1996).

At present, more than 140 000 relevés have been computerized in The Netherlands, at the DLO-Institute for Forestry and Nature Management. From the spatial and temporal distribution pattern of these data, it can be concluded that Dutch vegetation sampling has been rather representative. With regard to geographical distribution (Fig. 1), only some clay polder areas (in the former Zuiderzee, northern Friesland and northern Groningen) are poorly studied. Intensive agricultural land use is dominant in these

Fig. 1. Geographical origin of relevés in The Netherlands (DLO-Institute for Forestry and Nature Research).

polders; wetlands, for instance, are completely lacking. A relatively large percentage of the relevés was made in coastal areas (dunes and salt marshes), in the fluviatile district (including the freshwater tidal delta); furthermore, in those parts of Holland and Overijssel where brackish and fresh water wetland areas occur, in the pleistocene part of the country where well-developed oligotrophic communities are found, and in the chalk district of South Limburg. The major part of the relevés has been made during the last two decades (Fig. 2). Thousands of relevés were made by (provincial) government institutions in order to apply the information in environmental planning. The first relevé was made by W.C. de Leeuw and dates from 1929.

The high quantity of relevés is not only vital for the construction of reliable classification systems on a national scale; it also opens new possibilities in applying phytosociological knowledge. Some examples may illustrate this.

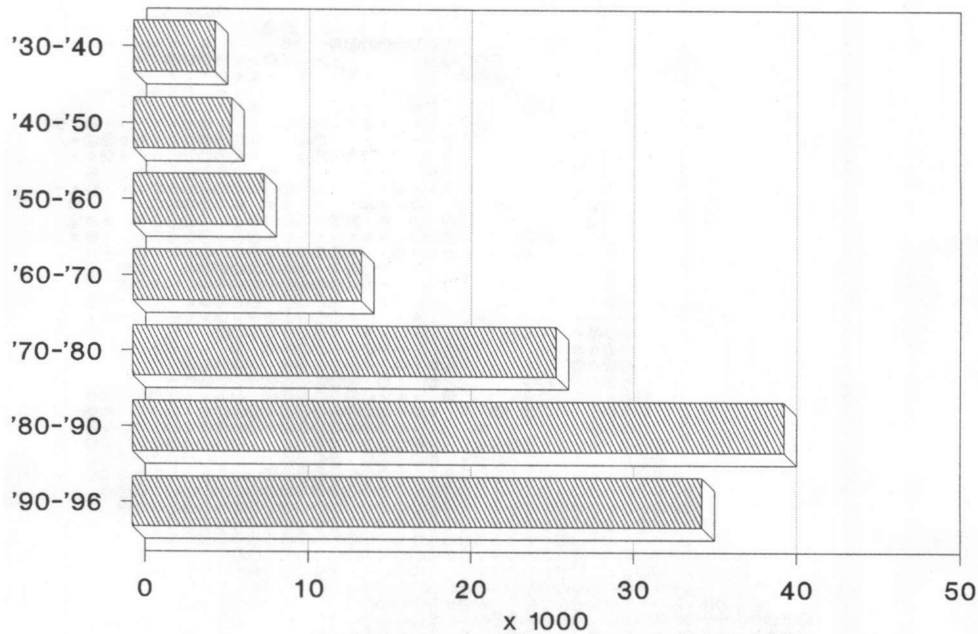

Fig. 2. Temporal distribution of relevés in The Netherlands (DLO-Institute for Forestry and Nature Research).

Changes in the distribution patterns of plant communities

In The Netherlands a long tradition of species mapping, especially in botany, has been established. During the 1980s, the distribution of all Dutch plant species, based on a 5 × 5 km grid, was published in a three-volume atlas (Mennema *et al.* 1980, 1985; Van der Meijden *et al.* 1989). The set of phytosociological data now enables us to present distribution maps of plant communities. First examples were given by Horsthuis & Schaminée (1993). In the near future, the distribution of all Dutch plant communities will be published in an atlas of four volumes (see Van Duuren & Schaminée 1992).

Figure 3 shows the distribution of the *Eleocharitetum multicaulis*, an Atlantic plant community restricted to oligotrophic moorland pools and other terrain depressions on sandy soils; it grows in shallow soft waters with changing water tables. *Deschampsia setacea* and *Eleocharis multicaulis* are character species, whereas species such as *Littorella uniflora*, *Juncus bulbosus*, *Echinodorus ranunculoides* and *Hypericum elodes* occur with high constancy. Due to habitat destruction, eutrophication, and acidification of surface waters, this type of vegetation has become rare in The Netherlands (e.g. Schuurkes 1987; Arts 1990). In the first half of this century and still during the first decades after the Second World War, the *Eleocharitetum multicaulis* was widespread in the pleistocene part of the country, especially in eastern Brabant and Twente (cf. Schoof-Van Pelt 1973). Furthermore, it occurred on the West-Frisian islands, namely Vlieland and Terschelling. From more than 50 localities vegetation relevés have been recorded, but probably not every site has been sampled (Fig. 3a). Nowadays, the community is restricted to some 20 localities (Fig. 3b).

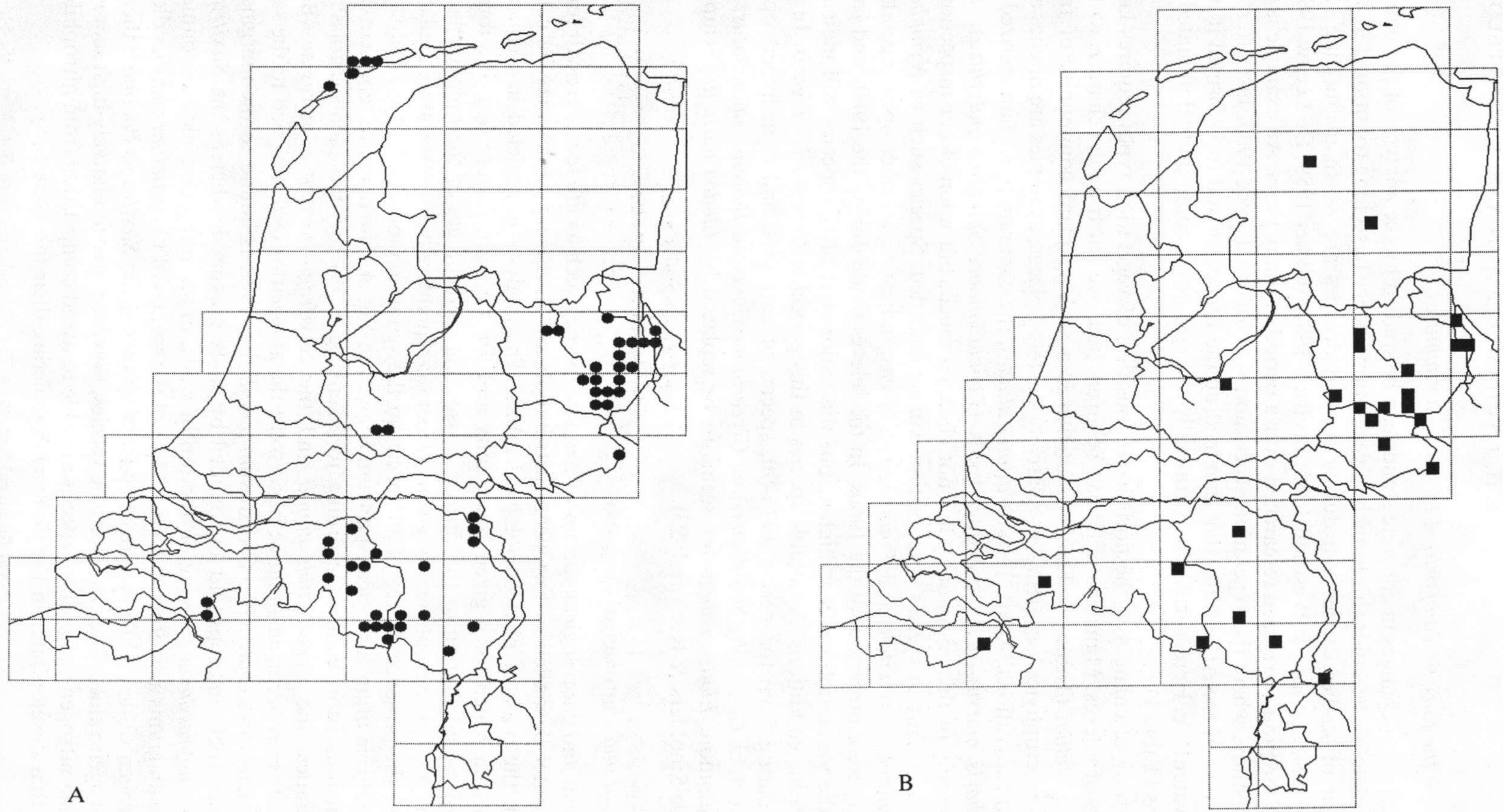

Fig. 3. Distribution of the *Eleocharitetum multicaulis* in the Netherlands, based on the distribution of phytosociological relevés. **A** presents the distribution before 1980; the recent distribution (since 1980) is given in **B**.

Changes in the floristic composition of plant communities

Information on changes in concrete stands can be studied by the analysis of permanent plots. In The Netherlands this branch of vegetation science has a long tradition, but also a number of studies carried out during the last decades are worth mentioning (e.g. Willems 1980; Roozen & Westhoff 1985; Beeftink 1987; Bakker 1989; De Leeuw 1992). Some of the plots have been researched over a period of many years. An example is the IJdoorn study, where the vegetation succession was followed since 1933, just after the construction of the Afsluitdijk, that dammed up the Zuiderzee and transformed it into a freshwater lake. Here, a salt marsh gradually changed into a community dominated by tall forbs (Table 1).

The study of changes in the floristic composition of vegetation types requires large numbers of relevés. Many examples can be given; here, we illustrate the changes within the *Stratiotetum* (Table 2). The *Stratiotetum* is a striking plant community of free-floating macrophytes, occurring on relatively sheltered places; examples are ditches and peatland excavations. Apart from *Stratiotes aloides*, the community is characterized by *Hydrocharis morsus-ranae* and duckweeds (*Lemna minor*, *Spirodela polyrhiza*). The physiognomy of this community has not changed much, but upon closer inspection a conspicuous shift in species composition can be recorded. Species such as *Nymphaea alba*, *Potamogeton natans* and *Potamogeton lucens*, indicating a rather open vegetation structure, were present until the 1960s. In the relevés made during the 1960s and early 1970s, the vegetation cover is higher, but the major part of the species still indicates mesotrophic conditions. A notable species in this period is *Utricularia vulgaris*. In the relevés dating from the period 1976–90, species of eutrophic and even hypertrophic water, such as *Ceratophyllum demersum*, *Glyceria maxima* and *Butomus umbellatus*, are more common; *Elodea canadensis* seems to be replaced by *Elodea nuttallii* (Schipper 1994; see Smolders & Roelofs 1993).

Ecological and chorological diagrams

Ecological and chorological spectra of plant properties such as life form, growth form, groundwater dependency, European distribution and Ellenberg values may be calculated on the basis of phytosociological tables. The analysis is depicted in frequency diagrams, in which for a given community and for a certain feature (e.g. life forms) the relative contribution of the various classes (e.g. percentages of therophytes, hemicryptophytes, phanerophytes) is given. Generally, quantitative spectra are calculated, based on the presence degree of all species in the synoptic tables.

An example of an ecological spectrum is given in Fig. 4. The diagram represents the nitrogen indication values (according to Ellenberg 1979) for two pioneer grassland communities, the *Cerastietum pumili* and the *Saxifrago-Poetum compressae*. Both grassland types occur on shallow, basic soils; the associations are assigned to the same alliance (*Alysso-Sedion*). The *Cerastietum pumili*, however, is bound to the margins of calcareous rock outcrops and surrounded by chalk grassland, whereas the *Saxifrago-Poetum compressae* is growing on the top of walls, in an anthropogenic environment. The two diagrams are rather different. Most of the species of *Cerastietum pumili* indicate low nitrogen values, while the greater part of species of the *Saxifrago-Poetum* indicates high nitrogen values. The characteristic species, however, give a relatively high score for the lowest nitrogen class. These species are able to avoid competition from nitrophilous species that develop later in the year, by completing their life cycle early.

Table 1. Vegetation succession in a permanent plot (10 × 10 m) at Ydoorn has been followed since 1933, just after the construction of the Afsluitdijk, to 1960. In gradual stages, a salt marsh changed into a community dominated by tall forbs (after data from Kruseman, Vlieger & Westhoff, unpublished)

Relevé number Year	1 33	2 34	3 35	4 37	5 38	6 39	7 40	8 41	9 42	10 43	11 44	12 46	13 50	14 53	15 56	16 57	17 60
Plantago maritima	2b	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Armeria maritima	2b	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Juncus gerardi	1	+	1	.	.	+	+	.	.	.	.	.	.	.	.	.	.
Triglochin maritima	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alopercurus bulbosus	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aster tripolium	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Apium graveolens	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.
Festuca rubra	5	5	5	4	5	4	4	3	2b	1	.	.	+	+	+	+	1
Agrostis stolonifera	2b	2b	2b	1	2b	2b	2b	+	.	.	.	.	.	.	.	.	+
Phragmites australis	1	1	2b	1	4	3	5	5	5	5	5	4	5	3	3	3	2
Trifolium repens	+	+	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
Poa trivialis	+	.	.	+	.	+	1	2b	1	1	+	1	3	1	5	5	2
Taraxacum sectio *Vulgaria*	.	+	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.
Sonchus arvensis	.	.	+	+	1	1	+	1	1	+	+	.	+	+	.	1	+
Holcus lanatus	.	.	.	+	+	+	+	1	2b	1	+	+	+	.	2a	1	2
Epilobium parviflorum	.	.	.	+	1	1	+	+	+	.	.	.	.	.	+	+	+
Elymus repens	.	.	.	1	.	+	1	1	1	1	.	+	2	+	+	+	1
Cirsium arvense	.	.	.	+	.	+	+	+	1	1	+	+	1	1	2	2	1
Galium aparine	.	.	.	.	.	+	.	1	2b	2b	2b	2b	+	2a	+	.	+
Solanum dulcamara	.	.	.	+	.	+	+	+	+	1	+	.	+	+	+	+	+
Epilobium palustre	.	.	.	.	.	+	+	+	.	+	+	.	.	.	.	.	.
Sonchus palustris	.	.	.	.	.	+	+	.	.	+	+	+	1	1	1	2a	3
Angelica sylvestris	.	.	.	.	.	.	r	+	+	+	.	+	1	+	+	+	1
Rumex crispus	.	.	.	.	.	.	.	+	.	.	.	.	+	+	.	.	+

Table 1. *Continued.*

Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Year	33	34	35	37	38	39	40	41	42	43	44	46	50	53	56	57	60
Galium mollugo	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.
Stellaria media	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.
Ranunculus repens	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	1	1
Atriplex prostrata	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.
Epilobium hirsutum	.	.	.	.	.	.	.	.	+	+	+	+	1	3	1	1	1
Calystegia sepium	.	.	.	.	.	.	.	+	.	1	+	2b	3	3	+	+	+
Cirsium palustre	.	.	.	.	.	.	.	.	.	.	+	.	+	+	3	4	2
Urtica dioica	.	.	.	.	.	.	.	.	.	.	+	+	2a	2a	2a	1	2
Eupatorium cannabinum	.	.	.	.	.	.	.	.	.	.	+	.	1	+	+	+	2
Stachys palustris	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	1	2
Lycopus europaeus	.	.	.	.	.	.	.	.	.	.	.	.	1	+	+	+	1
Iris pseudacorus	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	+
Valeriana officinalis	.	.	.	.	.	.	.	.	.	.	.	.	1	1	2a	3	4
Ranunculus acris	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+
Mentha aquatica	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	1
Lychnis flos-cuculi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+
Caltha palustris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
Brachythecium rutabulum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	3	3
Eurhynchium praelongum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.
Rumex conglomeratus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
Glechoma hederacea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
Scutellaria galericulata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+

In only one relevé (+): *Leontodon autumnalis* (3), *Matricaria maritima* (4), *Cerastium fontanum* (4), *Chenopodium album* (8), *Carex cuprina* (8), *Oenanthe lachenalii* (10), *Elymus athericus* (11), *Aegopodium podagraria* (11), *Amblystegium serpens* (15), *Deschampsia cespitosa* (16), *Trifolium pratense* (16), *Galeopsis tetrahit* (17) and *Alopecurus pratensis* (17).

DESCRIPTION AND CLASSIFICATION OF PLANT COMMUNITIES

The first classification system of plant communities in The Netherlands was published in 1937 by Vlieger and followed by more extensive publications in 1942 and 1946 by Westhoff, Dijk and Passchier. In 1969 Westhoff & Den Held published *Plantengemeenschappen in Nederland,* which also contained a critical review of the syntaxonomic literature. Nevertheless, this reference system did not contain any vegetation tables. Mainly for that reason, a project was started, the results of which are being summarized in five volumes. Emphasis is put on complete integration of knowledge on Dutch vegetation, for instance by evaluating ecohydrological and landscape ecological aspects (e.g. Grootjans 1985; Van Wirdum 1991; Everts & De Vries 1991). Compared with the reference system of Westhoff and Den Held, the number of syntaxa in the new classification system do not differ greatly (38 classes versus 40; 294 associations versus approximately 270 now). However, in several cases the syntaxonomic views have changed considerably. Some examples may illustrate this.

On the basis of historical relevés, including ecological data, from the late 1960s and early 1970s, the variation in stonewort communities (*Charetea fragilis*) at that time can now be classified. Eight associations were recognized and their hierarchical position was determined, whereas Westhoff & Den Held (1969) only distinguished one order without any further division. They simply mentioned a couple of communities and noticed that the level of the research was not far enough advanced to evaluate their status. In the following years, most of the associations were seriously threatened (one is almost extinct and five have become very rare) but, due to recently improved water management, some recovery can be observed (e.g. Nat *et al.* 1994).

Increased ecohydrological knowledge (e.g. Bloemendaal & Roelofs 1988; Roelofs 1991) has also enabled phytosociologists to interrelate the revised classification system of aquatic communities (*Potametea*) to ecological factors (Schaminée *et al.* 1990). Until now the syntaxonomy of aquatic vegetation was based strongly on taxonomic differences and variety in growth forms (e.g. Den Hartog & Segal 1964; Westhoff & Den Held 1969). The main division of the *Potametea* in three orders now corresponds with the variation in salinity. The *Zannichellietalia pedicellatae* comprise plant communities of saline, hard and eutrophic water, with characteristic species such as *Zannichellia palustris* subsp. *pedicellata, Ceratophyllum submersum, Ranunculus baudotii* and *Callitriche obtusangula.* On the other hand, communities of soft and mesotrophic water are assigned to the *Callitricho-Potametalia,* differentiated by species such as *Callitriche platycarpa, Callitriche hamulata, Ranunculus peltatus* and *Myriophyllum alterniflorum.* Most communities, however, occur under intermediate ecological conditions; these are summarized in the *Nupharo-Potametalia* and are differentiated by species such as *Potamogeton mucronatus, Ranunculus circinatus, Myriophyllum verticillatum* and *Elodea nuttallii.*

Dry grasslands are widespread in The Netherlands and show a striking geographical and ecological variety. They have been studied from the early days of phytosociology onwards by a great number of authors (e.g. De Leeuw 1938; Diemont & Van de Ven 1953; Boerboom 1957, 1960; Neijenhuijs 1969; Willems 1980; Van Dijk *et al.* 1984; Masselink 1994). In the revised classification these grassland communities are divided into three classes. The chalk grasslands of South Limburg are assigned to the *Festuco-Brometea.* On sandy soils, a distinction is made between vegetation types on deep and on shallow soils; the former are placed in the *Sedo-Scleranthetea,* the latter in the *Koelerio-Corynephoretea.* The *Sedo-Scleranthetea* are widely distributed in

Table 2. Changes in the floristic composition of the *Stratiotetum* in the Netherlands between 1930 and 1990 (from Schipper 1994)

Period (number of relevés)	1930–1960 (79)	1961–1975 (55)	1976–1991 (42)
Stratiotes aloides	100	100	100
Hydrocharis morsus-ranae	93	67	59
Lemna trisulca	70	56	64
Lemna minor	50	30	57
Spirodela polyrhiza	44	29	54
Elodea canadensis	43	29	16
Nymphaea alba	32	9	—
Nuphar lutea	39	12	11
Potamogeton natans	48	18	23
Potamogeton compressus	16	—	4
Potamogeton lucens	16	10	4
Utricularia vulgaris	21	47	—
Myriophyllum spicatum	8	23	4
Cicuta virosa	7	14	—
Myriophyllum verticillatum	3	12	2
Nitella flexilis	1	12	—
Ceratophyllum demersum	17	23	26
Elodea nuttallii	—	5	52
Lemna gibba	1	5	35
Glyceria maxima	7	1	33
Butomus umbellatus	2	3	21
Agrostis stolonifera	3	—	26

mountainous areas in Central Europe; in The Netherlands, this class is only marginally represented. The *Koelerio-Corynephoretea* have their main distribution in the lowlands of Northwestern Europe. In The Netherlands, they are widespread in the coastal dune area and in the pleistocene part of the country.

By analogy with the fringe communities on base-rich soils (*Trifolio-Geranietea*), the fringe communities on nutrient-poor, sandy soils are classified as a separate vegetation class, namely *Melampyro-Holcetea mollis* (cf. Passarge 1979, 1994; Klauck 1992). The communities are characterized by a more or less dense sward of grasses, with *Holcus mollis*, *Deschampsia flexuosa*, *Anthoxanthum odoratum*, *Festuca rubra* and *Agrostis capillaris*, among others. As well as these grasses, herbs such as *Melampyrum pratense*, *Teucrium scorodonia* and a number of *Hieracium* species occur. Just like the *Trifolio-Geranietea*, the *Melampyro-Holcetea* generally develop in the narrow border between scrub and woodland on the one side and grassland on the other side. Furthermore, they can be found in lanes, rides and avenues (mostly under *Quercus*) and under coppice.

METHODOLOGY: SOME NEW CONCEPTS

Dutch contributions to methods and concepts in phytosociology are various. General considerations on theoretical aspects have been brought forward by,

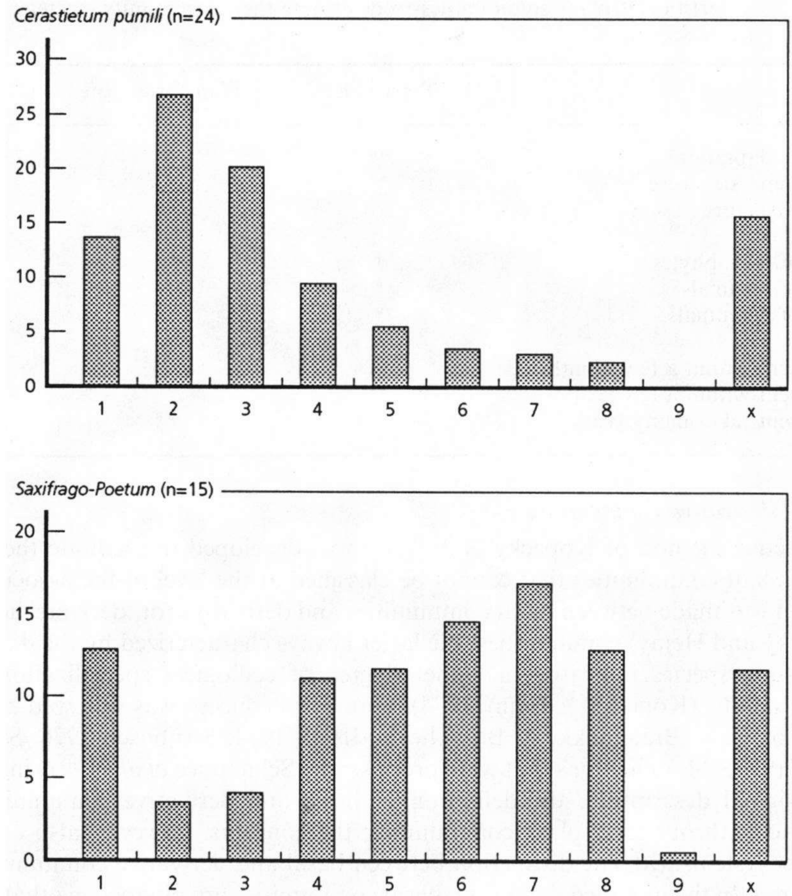

Fig. 4. Nitrogen indication according to Ellenberg (1979) for two pioneer grassland communities, the *Cerastietum pumili* and the *Saxifrago-Poetum compressae*. The nitrogen values range from 1 (low) to 9 (high); x=indifferent.

e.g. Barkman, Schaminée and Stortelder, and have been summarized in Schaminée *et al.* (1995a). Barkman discussed the association concept in the Braun–Blanquet approach (1988a) and gave a critical evaluation of the concepts of fidelity and character-species (1989a) as well as of minimum-area concepts (1989b). Furthermore, he presented new systems of plant growth forms and phenological plant types (1988, 1990). Also, Dutch scientists have contributed to the development of new concepts in high level syntaxonomy (Pignatti *et al.* 1995). The rapid deterioration and impoverishment of European vegetation enforced syntaxonomists to extend the tradional classification system. Kopecký and Hejný therefore introduced the so-called deductive method (e.g. Kopecký & Hejný 1974, 1978; Kopecký 1992), which was adapted to the Dutch situation by Schaminée *et al.* (1991). Stortelder (1992) proposed the concept of vegetation strategies, inspired by the plant strategies concept of Grime (1979). In the following, the two last-mentioned ideas will be discussed in more detail.

Table 3. Characteristics of plant communities to determine their community strategy (**=high score; *=moderate score)

	Persistence	Transformation	Escape
Particular adaptations	**	*	
Simple comm. structure	**		**
Complex structure		**	
Number of therophytes	*		**
Number of biennials	*		*
Number of perennials	*	**	*
Development within a few months			**
Development within a few years	**		
Development takes many years	*	**	

Basal and derivative communities

The deductive method of Kopecký and Hejný was developed to facilitate the classification of plant communities that cannot be classified at the level of the association. A distinction was made between basal communities and derivative (or 'derivate' according to Kopecký and Hejný) communities, the latter always characterized by the dominance of a 'leading species indicating a higher degree of ecological specialization of the pertinent stands' (Kopecký & Hejný 1974). Soon, this concept was followed by Dutch phytosociologists (Braakhekke & Braakhekke-Ilsink 1974; Strijbosch 1976; Sýkora & Westhoff 1979). Modifications that were proposed by Schaminée *et al.* (1991) include: (i) In the original description, the definition of basal and derivative communities was confined to anthropogenic plant communities; the concepts, however, also applies to natural ecosystems. (ii) The distinction between basal and derivative communities was reconsidered. In the modified definition, basal communities are phytocoena that contain character and differential species of syntaxa above the level of association as well as accompanying species. Dominant species, if present, are 'normal' to the syntaxon the basal community is assigned to, as can be deduced from the classification system that is referred to. Also derivative communities contain character and differential species of syntaxa above the level of association as well as accompanying species; dominant species, however, are always present and do not occur in the well-developed syntaxon the derivative community is assigned to. According to the original concept, the name of a basal or derivative community is formed by the initial abbreviation, followed by the name of one or two characteristic species, and the superior syntaxonomic unit to which the community has been assigned to (in square brackets). Meanwhile, the deductive method has proved to be of great help in describing the variety of Dutch plant communities, for instance of road verge vegetation (Sýkora *et al.* 1993). Most important basal and derivative communities of each class are listed and elucidated in the new classification system.

Vegetation strategies

Grime (1979) based the processes which control the structure and composition of vegetation on adaptive strategies which have evolved in individual plant species. These strategies may be defined as groupings of similar genetic characteristics, which recur

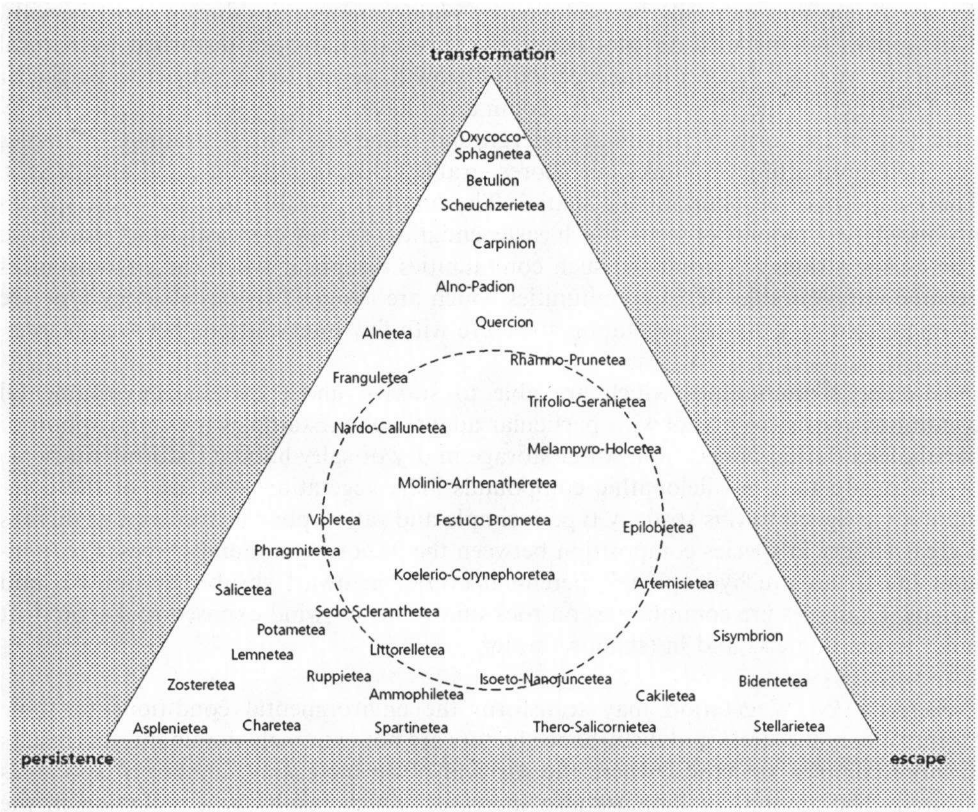

Fig. 5. Indication of the position of plant communities in the triangle of strategies (after Stortelder 1992).

widely among species and cause them to exhibit similarities in ecology. Different intensities of two factors (stress and disturbance) brought about three primary strategies or plant types: ruderals, competitors and stress-tolerators. However, the concept of strategies as an unifying approach may be applied also to plant communities.

Properties of plant communities cannot simply be understood by summarizing properties of species of that particular community. Ecological amplitudes of communities, for instance, are in general much narrower than those of the individual constitutive species and the adaptive strategy of plant communities is in general much more specific (Schaminée *et al.* 1995a).

Three main trends in plant community strategies can be recognized, based on the concept that communities exist because of their social structure. Stress and disturbance may be coped with by attenuation of the extremes, leading to the strategy of 'transformation'. Other strategies are 'escape' (during the unfavourable periods) and 'persistence'. These strategies can be arranged at the corners of an equilateral triangle similar to the model of Grime (1979). Various characteristics of plant communities can be used to determine to what strategy type the community shows most similarity. The properties refer to morphological adaptation, physiognomy, life history, and life-form spectrum. The prevailing scores of the properties are given in Table 3 (after Stortelder 1992).

Escape. Some sites can only be exploited by plant communities during short periods. This applies for instance on sites where the substrate has been disturbed by natural factors or by man. After a limited period of growth, vegetation is subject to partial or total destruction and all species of the community have to flee by seed production or by reduction in the form of perennial underground tissue (e.g. bulbs, stolons). Examples are communities of river banks, sea shores, arable fields, trampled ground and deserts. The escape may be temporal or spatial. The latter is possible because most species produce large amounts of seeds which easily emigrate; so they can easily start elsewhere. The escape strategy is nomadic: such communities disappear when the circumstances become unfavourable. Most communities which are assigned to this strategy type are characterized by a simple vegetation structure with few interrelations between plants.

Persistence. Communities which are able to survive under extreme environmental conditions consist of plants with particular adaptations. Examples are interruption of metabolism during desiccation, water storage in dry or salty habitats, storing nutrients or the production of allelopathic compounds. The vegetation structure of the communities assigned to this strategy type is simple and rather poor in species, but there is a great variety in species composition between the various community types. Predominant life forms are hydrophytes, perennial evergreen dwarf shrubs, bryophytes and lichens. Examples are communities on rock and walls, on wind-exposed rocks, on drift sand, in semi-deserts and in (shallow) water.

Transformation. Vegetation may transform the environmental conditions to some extent. Where the stress and disturbance factors are not extremely dominant, this results in more complex structures where the survival of an increasing number of species is ensured. The amount of biomass also increases, which results in a reduction in the environmental fluctuations. A clear example of this strategy type are ombotrophic bog communities. A thick peat cushion of several metres brings about a constant water table and the exclusion of the influence of the underlying mineral soil on plant growth. Under favourable climatic conditions, bogs of the same type may be found on different parent rock and on different slopes. Also the zonal forest type, in The Netherlands beech forest, tends to this strategy type. Small environmental differences in parent material and relief are no longer reflected in plant growth when the climax is finally established. A transformation of the soil has taken place (displayed in thick humus layers) and a specific forest-microclimate with high humidity values is established. The community structure is complex with many interrelations between species. Another example of the transformation strategy is formed by communities with a dense cover of bracken (*Pteridium aquilinum*).

An indication of the position of each plant community (on a high level of classification) in the triangle of strategies is given in Fig. 5. Communities assigned to a clear strategy are placed at the corners of the triangle, while plant communities which are judged to be of an intermediate strategy type are placed towards the centre of the triangle. The determination of the position is done on the basis of the given criteria on best professional judgement.

The corners of the triangle also correspond with different forms of human influence. Intensity of land use decreases going from the escape corner to the other corners. Real 'escape communities' in our country are man-determined (by agriculture and urbanization). Nature management plays a dominant role in the centre of the triangle, keeping up intermediate situations (avoiding plant communities to assign an extreme strategy type). These semi-natural communities contribute to a large extent at the variety in ecosystems. Nature conservation (in the traditional way) is focused on communities in the corner of transformation and persistence. An adequate environmental management is a prerequisite for the conservation of communities assigned to the latter strategy type, whereas the time factor is the most important for the transformation communities; development of these communities takes a long time.

ACKNOWLEDGEMENTS

We are indebted to Dr John Rodwell (University of Lancaster) for correcting the English.

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