Degeneration of species-rich *Calthion palustris* hay meadows; some considerations on the community concept

Grootjans, A.P.¹, Fresco, L.F.M.¹, de Leeuw, C.C.¹ & Schipper, P.C.²

¹Laboratory of Plant Ecology, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands; Tel. +31 50 3632229; Fax +31 50 3632273;
²State Forestry Commission, P.O. Box 1300, 3970 BH Driebergen, The Netherlands

Abstract. An overview of the vegetation history of *Calthion palustris* meadows is presented with special emphasis on the natural habitats of the character species. The response of meadow species under the influence of drainage was calculated using species-environment response curve techniques. The changes were monitored in permanent plots situated on sites with various intensities of drainage. The similarity with an undisturbed local reference type of the hay meadow community was calculated for all plots and years. On this basis a half-life time of the *Calthion palustris* stands could be assessed. The half-life time was small in the plots which are most affected by drainage. The response to drainage of character species of the *Calthion palustris* was very different. This imposes problems for some definitions of the community concept.

Keywords: Drainage; Half-life; Heterogeneity; Permanent plot; Species response curve; Water table.


Introduction

The Braun-Blanquet and similar phytosociological approaches regard a plant community as a vegetation type characterized by its floristic composition. Some of the species - so called character species or faithful species - are, within a relatively large area, restricted to certain vegetation types and do not, or hardly, occur in other types (Pott 1992). Character species are often considered to be very sensitive expressions of biotic and environmental relationships (Westhoff & van der Maarel 1973). Such species are used to arrange communities in a hierarchical classification of vegetation units. This community concept has been used by generations of ecologists mainly to distinguish and map plant communities (Westhoff 1979). The co-occurrence of species becomes interesting from a synsystematic point of view if the environmental constellation is encountered regularly in the landscape and if it endures for a sufficiently long period. The question then arises how suitable this community concept is when we are analyzing temporal changes, for instance using permanent plots. No regular observations of plant communities during the course of several centuries exist from which we can judge whether the character species are indeed characterizing certain plant communities or that they are only co-occurring temporarily in a way that each generation of ecologists recognizes as its own set of plant communities. Important questions would be: have the character species, in the course of time, become adapted to one homogeneous environment or do they co-occur in time in a specific changing environment? Would they react similarly or differently after changes in the environment?

In this paper we will present a brief overview of palynological research on the vegetation history of a relatively common wet meadow community assigned to the *Calthion palustris*. The question is whether the species which are now considered character species originate from similar or different natural habitats. With this information in mind we shall analyze the decline of such a meadow community due to various degrees of drainage, studied over 16 yr using permanent plots. We will try to establish whether the character species respond differently or similarly to such environmental disturbances. Furthermore we shall formulate criteria for deciding when an established stand subjected to change can no longer be considered as belonging to a certain plant community type.

The development of *Calthion palustris* communities

The *Calthion palustris* is characterized by the character species *Caltha palustris*, *Dactylorhiza majalis* *Lotus uliginosus*, *Lychnis flos-cuculi*, *Myosotis palustris* and *Senecio aquaticus* (Westhoff & Den Held 1969; Ellenberg 1978). These species are accompanied by many others that are common in moist meadows, reeds and even alder woods. Many regional associations have been distinguished, corresponding to a large range of...
edaphic, climatic and hydrological conditions (Ellenberg 1978). The meadows are all relatively well buffered against acidification (Kayl 1965; Kotanska 1993; Schrautzer & Wiebe 1993) with a relatively high nutrient status (Klapp 1965; Ellenberg 1978).

These species-rich meadows were widespread in central Europe until 30–40 yr ago, but have now become rare due to drainage and intensive fertilization. Moreover, many of the remaining meadows have decreased in species richness due to cessation of mowing after which some of the component species reached dominance within one or two years (Müller et al. 1992). The remaining fields, which are usually mown, are now highly appreciated in nature conservation because they are species-rich and contain many endangered species (Bakker 1989).

We know from palynological research that Caltha palustris was already present in England before the Weichselian (Godwin 1975). The species survived the ice ages in Europe and was encountered as macrofossil in iron age settlements in England (Greig 1984) and in Roman-age settlements in Germany (Knörzer 1975). The most likely habitats available after the withdrawal of the glaciers were spring-fed flushes with base-rich water; such habitats can still be found in calcareous mountain areas above the timber line. It is generally accepted that, in lowland areas, the species grew in eutrophic alder woods, reeds and fens (Ellenberg 1978; Janssen 1972; Behre 1979). The most likely habitats available after the withdrawal of the glaciers were spring-fed flushes with base-rich water; such habitats can still be found in calcareous mountain areas above the timber line. It is generally accepted that, in lowland areas, the species grew in eutrophic alder woods, reeds and fens (Ellenberg 1978; Janssen 1972; Behre 1979). Myosotis palustris probably occurred in similar habitats, but whether the present taxon Myosotis palustris is still the same as that in early findings from Flandrian deposits (Godwin 1975), remains doubtful. This reservation could be made for almost every species, but it seems especially relevant for species occurring in man-made habitats, such as hay meadows. Within the species Rhinanthus angustifolius, for instance, several ecotypes have developed a flowering time which is adapted to the time of mowing (ter Borg 1972). Cardamine pratensis is known to be a hybrid between Cardamine amara and Cardamine rivularis that escaped infertility by doubling its chromosome number (Landolt & Grossman 1968). This hybrid probably arose after the felling of woods, and expanded its distribution area to the drained mires, that were exploited as meadows. Other common hay meadow species with a similar history are Juncus articulatus (Zandé 1981) and Dactylis glomerata (Grant 1971).

Lychnis flos-cuculi was never encountered in forests but it probably occurred along banks of large rivers and in open reed communities in fresh to brackish zones in coastal areas, as was demonstrated by Menke (1968) and Behre (1979). When hay making started on a large scale the species was spread into the meadows. Calthion palustris meadows were probably present in NW-European lowlands 2500–2700 yr ago (Janssen 1972; Behre 1979). They were found on relatively open sites in alder woods, along Magnocaricion sedge swamps as fringes in slightly drier places, and also probably in small stream valleys both in flooded areas at stream banks and in spring-fed sites at the valley flanks (Succow 1971). From ca. 1500 BP onwards, the meadow species became more frequent in pollen diagrams (Janssen 1979; van Zeist et al. 1986). We do not know much about the species composition of those meadows, but there is some evidence suggesting that the present species composition deviates from the species composition a century ago (Weber 1892) or even half a century ago (Schrautzer & Wiebe 1993). We may conclude from old vegetation descriptions in the Treene valley in NW-Germany (Weber 1892) that meadows with Calthion palustris were much more mesotrophic and wetter compared to present Calthion palustris communities. Species such as Carex demissa, Carex panicacea and Parnassia palustris were fairly common in these meadows, while species of the moist and highly productive Arrhenatheretum elatioris were lacking. Weber (1892) mentions the new occurrence of Alopecurus pratensis in the Treene valley from 1850, due to the introduction of artificial phosphorus fertilization.

From these palynological observations and the above mentioned vegetation descriptions the picture emerges that the character species of the Calthion palustris originated from different natural habitat types and that the species composition has probably changed considerably during the last century.

Study area

The study area is situated in the catchment of the Drentse Aa in the northern part of the Netherlands at 53°01′N, 6°40′E. The meadow in which the effects of drainage have been studied is ca. 0.7 ha, situated in the middle reaches along a tributary of the Drentse A. A 2.5 m deep drainage channel was dug alongside the meadow in the autumn of 1975, which led to a drop in the phreatic water table of 40–80 cm in the direct vicinity of the channel. This has led to an increased N-mineralization and a drop in soil pH(KCl) from 6 to 4.8 (Grootjans et al. 1985). Consequently, many character species of the Calthion palustris disappeared or decreased in abundance. High water tables were only maintained close to the stream due to the presence of peat with a high resistance to water flow and a strong seepage intensity in the area (4 mm/day; Grootjans et al. 1993). It was estimated that a drop of 10–15 cm in the water level had occurred here. Little change in species composition was observed in the plots close to the
stream during the first five years, but later these parts of
the meadow also lost most of the character species of the
Calthion palustris.

The vegetation of the meadow, classified as Senecio-Brometum racemosii caricetosum nigrae (alliance Calthion palustris) in 1976, was mown annually in June
or July. At the end of the observation period (1990, 1991) the meadow was grazed by sheep for a short time
and not mown.

Methods

Sampling

The vegetation was recorded for the first time in
1976 in 22 permanent plots of 2 m × 2 m, located in
representative sites subjected to different drainage lev-
els. In the course of time three plots were damaged and
had to be discarded. The remaining 19 plots were re-
using a refined Braun-Blanquet cover-abundance scale
(Londo 1976).

The phreatic water table was measured from May to
September 1977, using PVC groundwater wells with
filters at 100 - 120 cm below the surface. The water table
draw down for each quadrat was extrapolated from
water table measurements during the summer in 16 sites,
including a reference site.

Local reference type

To determine the amount and the speed of vegetation
change in the permanent plots, independent of the actual
initial conditions, it was necessary to have a ‘reference
community’ for the local Calthion palustris commu-
nities. This should contain the regionally occurring char-
acter species of the alliance. Furthermore, some local
differentiating species were inserted which, in the study
area, indicate the local differentiation in edaphic factors.
Four character species of the alliance: Caltha palustris, Lychnis flos-cuculi, Myosotis palustris
and Lotus uliginosus and two differentiating species of the sub-
association: Carex nigra and Cynosurus cristatus, oc-
curred in the undisturbed reference community. The relevés
were obtained from Everts & de Vries (1991) who carried out a vegetation survey in hydrologically
undisturbed meadows between 1976 and 1980 in the middle reaches of relatively small river valleys. The
reference community should therefore be regarded as an
average situation in space and time. The species compo-
sition of the local reference type is presented in Table 1.

Data analysis

An ordination of relevés was carried out using
Detrended Correspondence Analysis (DCA) from the
program package CANOCO (ter Braak 1988). The pro-
gram package VEGROW (Fresco 1992) was used for
graphical presentation.

Changes in frequency were calculated in each of the
19 regularly recorded plots, using presence/absence data.

Unimodal optimum curve equations (e.g. Huisman
et al. 1993) cannot express a sudden increase in the
probability of occurrence of a species or its abundance
after a decrease. Third order polynomial were, there-
fore, applied for the purpose of expressing changes in
cover of the plant species during succession:

\[ Y_t = a_0 + a_1 t + a_2 t^2 + a_3 t^3 \]  (1)

where \( Y \) is the estimated abundance and \( t \) is the time in
years since the start of the recording in 1976.
The relationships between the vegetation relevés and the local *Calthion palustris* standard were calculated for each year using Percentage Similarity ($PS$), using character and locally differentiating species only:

$$PS_{ij} = 200 \sum \frac{\min\{y_{ki}, y_{kj}\}}{y_{ki} + \sum_{k} y_{kj}}$$

where $y_{ki}$ is the cover of the $k$-th species at site $i$.

**Half-life**

The half-life is defined here as the number of years needed to reach a $PS$ with the local reference which is less than 50% in vegetation science. This value is used for unstable isotopes and in physics this value is used for unstable isotopes and in vegetation science the 50% similarity ratio is used to distinguish associations (van der Maarel 1979). Because of the fluctuations in time, this value was estimated from the similarity curves using a linear regression analysis:

$$PS_i = a_0 + a_1 t$$

$$HL50_i = t (PS_i = 50)$$

**Results**

**Vegetation types**

The plots described in 1976 were ordinated using DCA. On this basis three groups were distinguished, which all belonged to the *Senecioni-Brometum racemosi caricetosum nigrae* (Fig. 1): (1) a ‘very wet’ group of 2 plots, situated close to the stream, (2) a ‘moist’ group of 5 plots situated close to the drainage channel, and (3) an intermediate ‘wet’ group consisting of the remaining 15 plots.

The very wet plots were characterized by a relatively high cover of *Carex aquatilis* and *Equisetum fluviatile*.
and by the occurrence of *Carex rostrata* (Table 1). Character species of the *Calthion palustris* and species that are common in hay meadows were also present, but only with low cover.

The wet plots had a very high affinity to the local reference type of the *Calthion palustris*. Four character species of the alliance and two differentiating species of the subassociation (*Carex nigra, Cynosurus cristatus*) were present. *Caltha palustris* had the highest abundance in this group.

The moist group had hardly any character species of the *Calthion palustris*. Only *Caltha palustris* was present with low abundances. *Myosotis palustris* was lacking and *Lychnis flos-cuculi* and *Lotus uliginosus* were rare. The cover of grass species such as *Holcus lanatus* and *Festuca pratensis* was relatively high.

*Fig. 3.* Response to drainage of eight meadow species in the three distinguished local vegetation types.
first to become extinct (Fig. 2). Among the character species *Caltha palustris* was most persistent in the meadow. *Myosotis palustris* disappeared from many plots after 10 yr. *Lychnis flos-cuculi* showed a strong decrease slightly before that time, after which some new establishments occurred in a few plots. Many locally rare species such as *Ranunculus lingua*, *Carex ovalis* and *Valeriana dioica* became extinct. Some other species with a low initial frequency such as *Poa pratensis* and *Rhinanthus angustifolius* established themselves after drainage in many plots, but declined again after ca. 10 yr.

The changes described above imply that the species composition has changed considerably in practically all the plots.

**Species response**

The behaviour of frequent species in the three distinguished vegetation types was calculated using third degree polynomial (Fig. 3). A significant decrease of
Degeneration of species-rich Calthion palustris hay meadows

In order to judge whether a specific stand had lost community membership, the percentage similarity of all the relevés with a local reference of undisturbed Calthion palustris meadows (Fig. 4) was calculated. The stands belonging to the ‘very wet’ group showed an increase in the percentage similarity with the local reference type during the first five years (Fig. 4a) due to an increase of character species such as *Lotus uliginosus* and *Lychnis flos-cuculi*. One stand (plot 8) maintained high similarity values until the end of the observation period. The stands belonging to the ‘wet’ group, with a high initial similarity (Fig. 4b), maintained a high similarity with the reference type during at least eight years after which the values dropped. The plots experiencing a large drop in the water table started to show a decrease in similarity with the reference several years earlier. Only one plot (15) maintained a high similarity with the reference during the whole observation period.

Discussion

Species response to drainage

From our results it has become clear that the character species of the meadow reacted differently to drainage. Although we did not study the reasons for this phenomenon it is very likely that both ecophysiological and population dynamic mechanisms are involved.
*Lychnis flos-cuculi*, for instance, has a high population turnover and successful establishment of seedlings requires the occurrence of gaps (Biere 1991). Drainage promotes the development of a closed sward of grasses which reduces the successful establishment of species such as *Lychnis flos-cuculi*. *Caltha palustris* can survive unfavourable conditions for at least 14 yr as an adult, but rejuvenation of the population does no longer occurs (Grootjans & Schipper 1987). Furthermore, it appeared that the lower the initial frequency of several declining species in the meadow the faster they disappeared. Population dynamic processes are, therefore, likely to be responsible for the changes in species composition.

**The community concept**

The above-mentioned results impose some problems on certain definitions of the plant community. Although some authors question the existence of a plant community (Wilson 1991) or suggest that the whole matter is not worth debating (Keddy 1993), we may at least exclude some definitions of a plant community by evaluating the response of established vegetation stands to disturbance over a longer period of time. Our meadow vegetation cannot be considered a community in the sense of McNaughton & Wolf (1973), with “co-occurrence of populations with similar resource demands”. Several other plant community definitions are too vague or too complicated to permit an easy recognition of the community in the field. For instance, many authors define plant communities as assemblages of populations that live in an environment and interact with one another (Whittaker 1975). Westhoff & van der Maarel (1973) defined a phytocoenosis as being “a part of the vegetation consisting of interacting populations growing in a uniform environment and showing a floristic composition and structure that is relatively uniform and distinct from the surrounding vegetation”.

We agree with Palmer & White (1994) that communities should be defined and studied operationally and phenomenologically. We believe that the interactions between plant populations should not be part of the community definition since they are part of the mechanisms of community dynamics. As a descriptive tool, mechanistic definitions including community mechanisms are impractical. The results of any vegetation description include the responses of plant individuals; after the research has been completed, we may hypothesize that some individuals interact. The same remarks can be made with regard to ‘uniform environment’ in the definition of Westhoff & van der Maarel (1973). There is little doubt that the species composition of the vegetation is an expression of its environment, but why should it be uniform and suggestive of some kind of homogeneity?

Studying some other definitions we can observe an outspoken view on what a community really is and how it has evolved. Tallis (1991) wrote: “a community is a chance assemblage of species in space and time, each species having unique requirements and behaviour”. This definition is in fact a nice redefinition of the community concept of Gleason (1917). Chance in this respect seems to be related to opportunity rather than to probability, as Tallis states that “plant communities have arisen fortuitously at meeting points in time and space of a series of different migration pathways”. Here, the word chance assembly expresses a theory on how a plant community may have arisen, but his view on plant communities does not lead to a practical definition.

We favour a more practical definition of a plant community: largely spontaneously growing plant individuals which are present within a distinguishable space-time unit (cf. Palmer & White 1994).

**Studying vegetation dynamics**

Now we have omitted some controversial aspects of community definitions, we can concentrate on some interesting aspects of vegetation dynamics: is the species composition of our hay meadow a chance assemblage or the result of co-evolution, and was the original environment of the meadow homogeneous or heterogeneous?

Palynological research of *Calthion palustris* meadows seems to support the view of Tallis. Our character species originated from different natural habitats. Their response to drainage is also different during our 16-yr observation period. This may be due to differences in life form or population dynamics of the species leading to different rates of extinction. Whatever the mechanisms involved, these results do not support the idea that the long-term co-existence of the character species is the result of co-adaptation to one and the same homogeneous environment. A plant community studied on the scale of a meadow seems to be a co-occurrence of species with distinctly different ecological characteristics in a relatively constant heterogeneous environment enabling the survival of several populations. Drainage affects the characteristic heterogeneity of the site and creates a new environment, which may, or may no longer sustain the characteristic combination of species that have been found together all over Europe during at least half a century. It may also lead to new combinations of species (syntaxa), as was shown by Succow (1986), who studied the long term effects of deep drainage on fen meadows in eastern Germany.

To answer the question as to whether the classification system of the Braun-Blanquet approach is a useful
tool in analyzing temporal changes; it is not possible in any simple way. It all depends on the scale of observation, both the temporal and the spatial scale. On the scale of a meadow our plant community still exists. It has only retreated to a small area within the meadow. In sites heavily influenced by drainage all the character species have disappeared, almost at the same rate within a few years and the community no longer exists. Over a longer time span (several decades) all stands can probably no longer be considered the same community. The use of local reference types in combination with the half life of a stand may be useful in describing the degeneration process in the intermediate time scale. Other solutions of the problem are possible. For instance, we may adopt the concept of ‘frame community’ (Kopecký & Hejnø 1974), a type of plant community impoverished in character species. Eventually, the study of mechanisms responsible for the decline will require studies on individual plants within the framework of populations, both inside and outside the community studied.

Acknowledgements. The authors would like to thank Jelte van Andel, Jan Bakker, Rudy van Diggelen and J.B. Wilson for commenting on the manuscript. Eddy van der Maarel and Rick Looyen contributed much to the discussion on community definitions. We also thank many students who assisted with the data collection, and acknowledge Johan de Jong and Dick Visser for preparing the illustrations.

References

Behre, K.E. 1979. Zur Rekonstruktion ehemaliger Pflanzen- 
gesellschaften an der Deutschen Nordseeküste. In: Will-
Godwin, H. 1975. History of the British flora; a factual basis for phytogeography. Cambridge University Press, Cam-
bidge.
Grootjans, A.P., van Diggelen, R., Everts, F.H., Schipper, P.C., 


Janssen, C.R. 1979. Pollenassoziation als Ausdruck der Veg-
Kayl, R. 1965. Verbreitung, Entwicklungsgeschichte und standörtliche Bewertung von Kulturrasen-Und Ödland-

Knörzer, K.H. 1975. Entstehung und Entwicklung der Grün-
tatio 29: 17-20.
Kotanska, M. 1993. Dynamics of the wet meadow community (Calthion alliance) in the Wierzbanówka valley in 1976-

tationsveränderungen und Ökologie nordwestdeutscher Feuchtgrünlandbrachen. Tyxenia 12: 223-244.

Received 21 November 1994; Revision received 18 October 1995; Accepted 20 October 1995.