

Habitat and management preference of *Bromus racemosus* L., a rare species in mesic meadows of Northwest Europe

Habitat- und Managementpräferenz von *Bromus racemosus* L., einer
seltenen Art in mäßig nährstoffreichen Feuchtwiesen Nordwesteuropas

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Abstract

Bromus racemosus L. is a rather rare grass species of moist meadows. It has strongly decreased in the course of the 20th century due to intensification of agricultural grassland management, and is therefore included in Red Lists of several European countries. Its winter annual life-cycle is remarkable for a species of permanent grasslands.

The aim of this study is to determine the habitat preference and optimal management of *B. racemosus* in the Netherlands and surrounding countries. Vegetation, soil and hydrological data from 28 sites in the Netherlands have been compared with *B. racemosus* cover, and with vegetation data from surrounding countries. The results indicate that *B. racemosus* is characteristic of *Molinio-Arrhenatheretea* meadows with good mineralisation and aftermath grazing. The optimum lies in grasslands of the alliance *Alopecurion pratensis* (*Deschampsion cespitosae*), but the species ranges from wetter *Calthion palustris* meadows to drier *Arrhenatherion elatioris* and *Cynosurion cristati* grasslands. It prefers intermediate nutrient levels and hydrological conditions (mesic sites), but within this range the highest cover is found in relatively nutrient rich and dry sites. Because of the absence of a seedbank and a low dispersal capability, *B. racemosus* is vulnerable to changes in grassland management. A management of mowing after 15 June and aftermath grazing is most suitable, since it enables fruit ripening and the maintenance of an open sward, needed for germination and development. The risk of extinction is likely to be higher in flat polders than in floodplain sites with natural relief, where the species may shift between belts in different years.

Keywords: aftermath grazing, alluvial landscape, *Alopecurion pratensis*, grassland management, hydrology, meadows, *Molinio-Arrhenatheretea*, soil nutrients, winter annual

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Bromus racemosus L. is a grass species of moist meadows that has become rather rare in recent times in Northwest Europe. Its winter annual life-cycle is remarkable for a species of moist, permanent grasslands; it flowers in May and June, and the seed germinate in summer and autumn (WEEDA 1994).

According to the Dutch Flora, the species can be divided into two subspecies: *Bromus racemosus* subsp. *racemosus* and *Bromus racemosus* subsp. *commutatus* (VAN DER MEIJDEN 2005). In the Netherlands, the latter is much rarer than the former (WEEDA 1994). In neighbouring countries these taxa are considered separate species: *B. racemosus* and *B. commutatus* (SPALTON 2002, SCHOLZ 2008). In this article we distinguish these latter species, and use the name *Bromus racemosus* s.l. in case data include both taxa, or there is uncertainty or possible confusion between the two taxa. Flora Europaea (TUTIN et al. 2001) is followed with regard to all other vascular plants, SIEBEL et al. (2006) for mosses and SCHAMINÉE et al. (1996) for plant communities.

According to HULTÉN & FRIES (1986) both species are native in large parts of Europe, but the distribution range of *B. commutatus* reaches further eastward than that of *B. racemosus*. BÖHLING et al. (1998) suppose that *B. commutatus* was introduced into Central Europe in Roman times, due to transport of crops from Southern Europe. For *B. racemosus* no Central European records from pre-Roman times are known either. HULTÉN & FRIES (1986) state that both taxa spread towards Central and Northern Europe by man.

In the course of the 20th century, *B. racemosus* is declining in several European countries because of agricultural intensification, including drainage, manuring, a high mowing frequency and ploughing of grasslands (WEEDA 1994, PRESTON et al. 2002). The abandonment of mowing of wet meadows in other regions further contributes to its decline (LUTZ 1996, BÖHLING et al. 1998, ROSENTHAL 2003). Within the Netherlands, *B. racemosus* was present before 1950 in most lowland areas and in some brook valleys in higher parts of the country. During the second half of the 20th century, it showed a strong decline (>50%) in distribution (WEEDA 1985, SPARRIUS et al. 2014). Nowadays it is largely restricted to small nature reserves and only in the Central riverine area still fairly common. In the Dutch Red List *B. racemosus* s.l. is assessed as Vulnerable (SPARRIUS et al. 2014). In the German Red List *B. racemosus* is assessed as Endangered, whereas *B. commutatus* is not considered Endangered (LUDWIG & SCHNITTLER 1996), even though the latter has a smaller distribution range (BFN 2013). Germany has a high international responsibility for the conservation of *B. racemosus*, since this country contains a high proportion of the world population (ca. 10–33%) and is situated in the centre of its distribution range (LUDWIG et al. 2007).

Bromus racemosus is one of the few annuals in moist, permanent grasslands. Therefore different grassland management methods may be needed compared to other grassland species. The aim of this study is to gain insight into the habitat and management preferences of *B. racemosus* s.l. in the Netherlands and surrounding lowlands, by studying in which plant communities and under which site conditions the species occurs and has the highest abundance. Describing the phytosociological position of the species helps to demonstrate the intermediate environmental position of the species. This study should lead to a better understanding of the factors that have contributed to the species decline and of management measures that may contribute to its conservation.

The research was conducted for the MSc thesis of the first author. The thesis report (SIMMELINK 2014) provides an extended overview of the research.

2. Study area

The study deals with 28 nature reserves in the Netherlands where *Bromus racemosus* s.l. has been observed recently (Fig. 1, Supplement E2). All sites contain grasslands owned by nature conservation organisations. Most sites are situated in the Central Dutch riverine area, in floodplains and polders (former floodplains) along the rivers Nederrijn, Lek, Waal, Gelderse IJssel (Rhine branches), Zwarte Water and Meuse. A concentration of locations is situated in the polder Vijfheerenlanden. An additional location is the brook valley Het Merkske near the border with Belgium. Finally, three sites in the polders of the Wadden island of Texel have been studied.

In these study sites, the average temperature ranges from about 3.0 °C in January to ca. 17.5 °C in July; the mean annual temperature is 10.0 °C. The precipitation is on average 800–850 mm per year, with a precipitation surplus of 200–300 mm (KNMI 2011).

In all 28 reserves the soil is dominated by mineral materials deposited during the Holocene by rivers, brooks, tidal rivers or the sea. Some sites have slightly peaty soils. The floodplain sites are located in between the low summer dike and the higher winter dike, a landscape that may be flooded in winter. Most sites in the floodplains still have their origi-

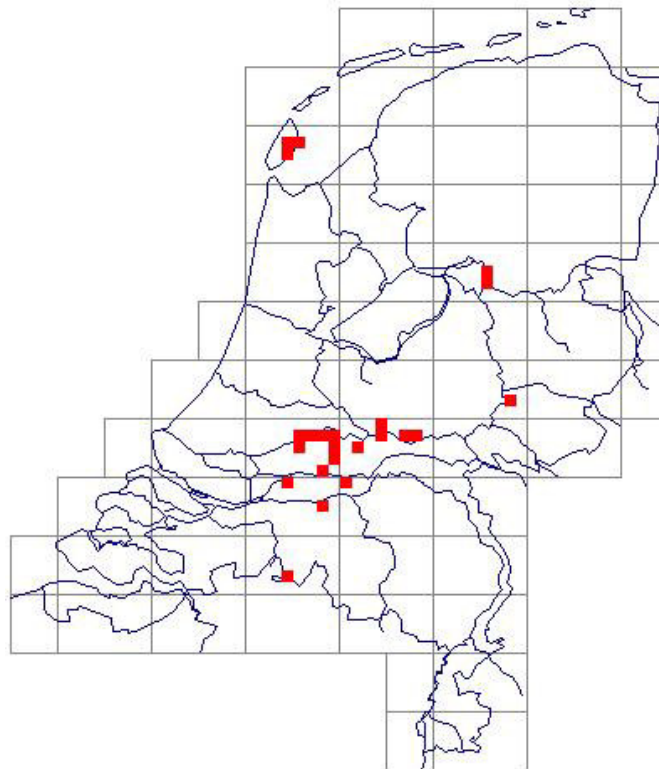


Fig. 1. The studied sites in the Netherlands. See also Supplement E2.

Abb. 1. Die untersuchten Standorte in den Niederlanden. Siehe auch Anhang E2.

nal relief. Ditches were created in all of the polder grasslands. The polder sites have a loamy or clayey top layer, sometimes with a layer of peat underneath. In many polder reserves, a semi-natural water regime is maintained, with a higher water level in winter and a lower level in summer. Because of drainage, the peaty layer oxidised and subsidence occurred. The wetter edges of the lots along the ditches subsided less than the centre of the parcels, resulting in a bathtub shape of parcels. The sites on the Wadden sea island of Texel are flat polders from marine origin (KOOMEN & MAAS 2004) and still have slightly brackish groundwater (VAN GOETHEM & VAN ROOIJEN 2011).

Data from surrounding countries relate to sites with *B. racemosus* s.l. from lowland areas, in the vicinity of a river or a stream (Fig. 2, Supplement S1):

- the Bremen region in Germany, along rivers like the Weser and smaller streams (LUTZ 1996);
- three areas in Flanders (Belgium): Snoekengracht, an area in a brook valley to the east of Leuven; the valley of the river Dijle near Leuven; Bourgoyen, an area in the valley of the river Leie near Gent (VLAVEDAT - Flemish Vegetation Databank: VANDEN-BUSSCHE & HOFFMANN (2001); CALLEBAUT et al. (2007));
- in southern Wallonia (Belgium): valleys along streams and rivers, including the Meuse, in the regions Famenne and Fagne (SOUGNEZ & LIMBOURG 1963);
- four areas in northern France: the valley of the river Sambre, a tributary of the Meuse (GÉHU 1961); stream valleys in the Bocage Virois in Basse-Normandie (DE FOUCAULT 1980); stream valleys in the Boulonnais in the département du Pas-de-Calais (DE FOUCAULT 1986); areas along the river Seine-maritime downstream of Rouen (FRILEUX et al. 1988);
- two areas in the valley of the English river Thames: the North Meadow near Cricklade and the surroundings of Oxford (unpublished data).



Fig. 2. The studied sites in the Netherlands (see also Fig. 1) and surrounding countries. See also the footnotes of Supplement S1 for the names of the locations.

Abb. 2. Die untersuchten Standorte in den Niederlanden (siehe auch Abb. 1) und den umliegenden Ländern. Siehe auch die Fußnoten der Beilage S1 für die Namen der Standorte.

3. Material and methods

3.1 Data gathering

In the 28 Dutch nature reserves in total 144 vegetation relevés were made in representative, homogenous plots in which *Bromus racemosus* s.l. occurred, in the period 19 May – 5 July 2013. Vegetation relevés were made according to the Braun-Blanquet method (BRAUN-BLANQUET 1964, SCHAMINÉE et al. 1995) in plot sizes of 9 m², using the cover-abundance scale of BARKMAN et al. (1964), and environmental and soil data were sampled and recorded. An additional 18 recent relevés with *B. racemosus* were added from the Dutch National Vegetation Database (DNVD; SCHAMINÉE et al. 2012). The locations of these relevés were visited to obtain additional environmental and soil data.

Additionally, 958 relevés containing *B. racemosus* s.l. from the DNVD were selected, in order to look for other plant communities than to those covered by the field sampling.

Further, vegetation samples made by the Instituut voor Biologisch en Scheikundig Onderzoek van Landbouwgewassen, Wageningen (IBS) were analysed on relations between the abundance of *B. racemosus* s.l. and abiotic conditions and grassland management. These samples have been collected in the period 1934–1958, using a sampling method with around 100 subsamples of 25 cm² per sampled parcel, and additional collection of environmental and management data (KRUIJNE et al. 1967). From these set 414 samples made in May and June were selected, of which 87 contained *B. racemosus* s.l. Outside that period *B. racemosus* s.l. may have been overlooked in the samples.

Finally, 250 relevés with *B. racemosus* s.l. were digitised from lowland areas near Bremen in northern Germany (LUTZ 1996), the mentioned nature areas in Belgium (SOUGNEZ & LIMBOURG 1963, CALLEBAUT et al. 2007), northern France (GÉHU 1961, DE FOUCAULT 1980, 1986, FRILEUX et al. 1988) and from southern England (unpublished relevés by A. Corporaal and by M. Raman). Part of the Belgian relevés were obtained in a digitised form from VLAVEDAT (Flemish Vegetation Databank; VANDENBUSSCHE & HOFFMANN 2001).

For 81 of the sampled relevés an earth auger was used to study humus and soil profile until a depth of around 95 cm. Additionally, for 152 relevés a bread knife was used to inspect the upper 20 cm of the humus profile without destroying the structure. The humus characteristics were described according to VAN DELFT et al. (2006).

For every relevé one composite soil sample was taken. With a gouge ten subsamples of 20 cm depth were taken in a systematic pattern within the relevé, and mixed in a bag. Soil chemistry of the composite samples was analysed according to the guidelines as described in HOUBA et al. (1995). The following measurements were carried out: Organic Matter percentage (OM%) with the loss of ignition method; pH-H₂O and pH-KCl; Nitrogen total and Phosphorus total (N-total and P-total respectively; both in mmol/kg, by destruction); Phosphate status (Pw in mg/kg, by water extraction); Potassium and Calcium (K and Ca respectively; both in mg/kg, by water extraction, using the Pw extraction). K and Ca were measured in a spectrometer. N-total, P-total and Pw were measured in an auto analyser. Nitrate (NO₃) and Ammonium (NH₄) were not recorded, because the soil samples became too warm during fieldwork to measure these values in a reliable way.

Measurements of the groundwater table of some sites were derived from www.dinoloket.nl (GDN 2013), and indications for the annual groundwater table fluctuations from www.bodemdata.nl (ALTERRA 2013). These data included measurements of the mean highest and mean lowest groundwater table, calculated over a period of eight years.

Inundation frequencies of some floodplains were estimated using AGGENBACH et al. (2007), www.live.waterbase.nl (RIKSWATERSTAAT 2013) and altitudinal data from www.ahn.nl (HET WATER-SCHAPSHUIS 2013). Together with information from site managers and hydromorphic properties in the soil profiles, these data were used to describe the hydrology in a qualitative way.

3.2 Data analysis

All vegetation relevés were entered in Turboveg (HENNEKENS & SCHAMINÉE 2001). Mean Ellenberg indicator values (ELLENBERG et al. 2001) were calculated for all relevés, based on ordinal cover and on absence/presence.

The vegetation relevés were imported into Juice (TICHÝ 2002) and clustered with help of a modified version of the programme Twinspan (ROLEČEK et al. 2009). The following settings were used: 2 cut levels: 0–25; number of clusters: 19; measure of cluster heterogeneity: total inertia; min. group size: 2. The resulting classification was improved by hand, by dividing, merging and translocating some clusters, and moving some relevés. Species were assigned to clusters according to fidelity, measured by the phi coefficient (CHYTRÝ et al. 2002). The resulting clusters from the field data set were assigned to plant communities as described by ZUIDHOFF et al. (1996) and SCHAMINÉE et al. (2015) using expert knowledge. Indirect ordination in Canoco 5 (TER BRAAK & ŠMILAUER 2012) was used to analyse the relation between plant communities and environmental gradients for the field work data. Because of a short length of gradient (2.9), the linear method Principal Component Analysis (PCA) was applied. Some environmental variables were log-transformed before analysis.

Besides, a representative subset of 237 of all available relevés from the Netherlands and surrounding countries were selected for ordination to analyse the habitat diversity. The unimodal method Detrended Correspondence Analysis (DCA) was chosen, since the length of gradient was 3.24, with the option detrending by 26 segments.

IBM SPSS Statistics 22.0 (IBM CORP. 2013) was used for univariate statistics, which have been applied to the dataset from field work. Because many variables could not be transformed to a normal distribution, non-parametric tests were used. The cover of *B. racemosus* s.l. was correlated to environmental variables with Spearman's rank correlation coefficient test. The Kruskal Wallis test with stepwise stepdown multiple comparisons was used to test the differences of environmental values between plant communities. The Mann-Whitney U test was used in case two groups of relevés (often groups with and without *B. racemosus* s.l.) were compared. This test has also been used to analyse the IBS dataset.

4. Results

4.1 Plant communities

The classification of the Dutch relevés resulted in eleven clusters of relevés (Table 1). The relevé table and a synoptic table are included in Supplement S2 and E1, with the original Twinspan classification given in the header data. In Table 1 for each cluster the species composition and distribution are described, and it is mentioned whether, besides *Bromus racemosus*, also *B. commutatus* was observed in the community. In Table 2 environmental values and significant differences are presented for all clusters.

All clusters are placed within the class *Molinio-Arrhenatheretea* Tüxen 1937, based on the large number of class character species in all relevés, including *Cerastium fontanum* subsp. *vulgare*, *Ranunculus acris*, *Rumex acetosa*, *Trifolium pratense*, *Cardamine pratensis* and *Holcus lanatus*. Within this class, *B. racemosus* has been found in four of the five alliances that have been distinguished in the Netherlands: *Calthion palustris* Tüxen 1937, *Alopecurion pratensis* Passarge 1964, *Arrhenatherion elatioris* Koch 1926 and *Cynosurion cristati* Tüxen 1947.

The same clusters are indicated in the PCA diagram, of which the first three axes are represented (Fig. 3a, b). The first axis can be interpreted as a moisture gradient, the second as a pH gradient and the third as a nutrient gradient. *Bromus racemosus* s.l. cover is mainly correlated to axis 1 ($r = -0.3114$) and 3 ($r = -0.3262$).

Table 1. Description of eleven vegetation clusters resulting from analysis of 162 Dutch relevés with *Bromus racemosus* s.l., completed with three additional clusters from DNVD data. See Supplement E1 for the complete relevé table of the 11 clusters.

Tabelle 1. Beschreibung von elf Gruppen von Vegetationsaufnahmen, die sich aus der Analyse von 162 niederländischen Vegetationsaufnahmen mit *Bromus racemosus* s.l. ergeben, ergänzt mit drei zusätzlichen Gruppen aus DNVD Daten. Siehe Anhang E1 für die komplette Vegetationstabelle der 11 Gruppen.

Cluster	Plant community (after ZUIDHOFF et al. 1995, SCHAMINÉE et al. 2015)	Environmental factors
Cluster 1	<i>Rhinantho-Orchietum morionis</i> (<i>Calthion palustris</i>)	Like cluster 2, but fragmentary developed, without character species <i>Anacamptis morio</i> , and on slightly more productive soils. <i>Bromus racemosus</i> has a medium high cover in most relevés.
Cluster 2	<i>Rhinantho-Orchietum morionis</i> (<i>Calthion palustris</i>)	Restricted to polders on the island of Texel, on low productive soils, with a low cover of the herb layer and a high cover of the moss layer. <i>Bromus racemosus</i> has a low cover in most relevés.
Cluster 3	<i>Lolio-Cynosuretum</i> (<i>Cynosurion cristati</i>)	Restricted to the island of Texel. Sites with management of mowing with aftermath grazing, on slightly higher productive soils than cluster 1 and 2. <i>Bromus racemosus</i> has a relatively high cover in most relevés.
Cluster 4	<i>Arrhenatheretum elatioris typicum</i> (<i>Arrhenatherion elatioris</i>)	Community on relatively drier, but productive sites, often on higher ridges in floodplains. <i>Bromus racemosus</i> s.l. reaches a relatively high cover in most relevés, but lacks in the higher zonation belts, especially when the loam content is lower than 40%. <i>B. commutatus</i> was present in six of 28 relevés.
Cluster 5	Basal Community <i>Bromus racemosus</i> - [<i>Alopecurion pratensis</i>]	Most species-poor of all communities, found both in polders and floodplains. Stands belonging to this community have in general been fertilised heavily until 5 to 40 years ago, and have since then been mown twice a year without fertilisation, to decrease the nutrient availability. In this community <i>B. racemosus</i> reaches its highest cover.
Cluster 6	<i>Fritillario-Alopecuretum pratensis</i> (<i>Alopecurion pratensis</i>)	On two sites in floodplains along the Zwarte Water, close to a former estuary, on relatively acid soils (compared to the Rhine branches). Sites are inundated by river water for a limited period, but water table fluctuations are reduced due to the vicinity to the estuary. <i>Bromus racemosus</i> has a low or medium high cover.
Cluster 7	<i>Sanguisorbo-Silaetum</i> (<i>Alopecurion pratensis</i>)	Rare, species-rich community, found in two floodplains in the western river area, along the Meuse and Nieuwe Merwede (Hengstpolder). <i>Bromus racemosus</i> s.l. has a low cover on relatively low situated parts and a moderate cover on higher parts. Inundation occurs usually in winter, but the soil desiccates superficially in summer. From even higher parts of the Hengstpolder also <i>B. commutatus</i> is known (WEEDA 1991).

Cluster	Plant community (after ZUIDHOFF et al. 1995, SCHAMINÉE et al. 2015)	Environmental factors
Cluster 8	Transition between <i>Sanguisorbo-Silaetum</i> & <i>Calthion palustris</i>	Moderately species-rich community from floodplains along the Nederrijn and Lek. The groundwater table is relatively high during summer, because of respectively tidal influence and the presence of a weir. The soil is relatively nutrient rich. <i>Bromus racemosus</i> has a relatively high cover, on average.
Cluster 9	Basal Community <i>Rhinanthus angustifolius-Lysimachia vulgaris</i> [<i>Calthion palustris</i>]	This community was found in a clay pit along the Lek, on relatively nutrient rich soils with a high amount of tall herb species. All three relevés contain <i>B. commutatus</i> , in low cover.
Cluster 10	<i>Angelico-Cirsietum oleracei</i> (<i>Calthion palustris</i>)	On a gentle slope of the stream valley of Het Merkske (Kempen region), where seepage of calcareous groundwater causes a neutral pH and a constant high groundwater table, but flooding does not occur. <i>Bromus racemosus</i> occurs with low cover and was more common in the past.
Cluster 11	<i>Ranunculo-Senecionetum aquatici</i> , subassociation <i>juncetosum articulati</i> * (<i>Calthion palustris</i>)	Stands on parcels that were bought by nature organisations around 25–50 years ago, and had never been heavily fertilised. Mainly situated in polders on overbank deposits in flood basins and on transitions to natural levees. In winter the groundwater table is high, and in some sites inundation by a mixture of rain and river water occurs for a short period. <i>B. racemosus</i> occurs on average with low cover and is usually rare or absent in lower situated, longer inundated parts of these meadows. <i>B. commutatus</i> was present in one relevé.
Additional cluster DNVD1	<i>Trifolio fragiferi-Agrostietum stoloniferae</i> Sýkora 1982 (<i>Loliotentillion anserinae</i> Tüxen 1947)	Cluster with relevés from around 1940, characterised by species indicating salty or desalinating conditions, like <i>Alopecurus bulbosus</i> , <i>Juncus gerardii</i> and <i>Glaux maritima</i> . This community developed on the former coast of the Zuiderzee in desalinated former salt marshes, after this sea had been dammed to create the IJsselmeer in 1932 (Boer 1955). <i>B. racemosus</i> was abundant in a succession stage between saline communities and fresh water, mesic grasslands.
Additional cluster DNVD2	<i>Carici curtae-Agrostietum caninae</i> Tüxen 1937 (<i>Caricion nigrae</i> Koch 1926 em. Nordhagen 1936)	A cluster indicating very wet, nutrient poor, slightly alkaline conditions in peat areas. Accompanying species are amongst others <i>Pedicularis palustris</i> , <i>Carex diandra</i> and <i>Eriophorum angustifolium</i> . The cover of <i>B. racemosus</i> is low. The relevés are from the period 1936–1999 from several areas in the Netherlands, mainly in the west.
Additional cluster DNVD3	<i>Ranunculo-Senecionetum aquatici</i> , subassociation <i>caricetosum paniceae</i> * (<i>Calthion palustris</i>)	A cluster of wetter, more nutrient poor and more acid conditions than in community 11. All relevés are from the period 1936–1978, mainly in the northeast of the Netherlands; they resemble former vegetation in the Bremen region in Germany.

*Synonym to *Bromo-Senecionetum aquatici* according to POTT (1992).

Table 2. Median values of several environmental variables per community, the names and descriptions of the communities can be found in Table 1. The communities 9 and 10 are omitted, since they were only observed in one site and few relevés have been made. The similar communities 1 and 2 are combined to increase the sample size. Total $n = 153$, d.f. = 7; Kruskal Wallis test with stepwise stepdown multiple comparisons. The letters indicate significant differences. The asymptotic significance (2 sided test) is < 0.001 for all shown variables. E: Ellenberg value, OM: organic matter, Pw: Phosphate status (water extraction).

Tabelle 2. Medianwerte von mehreren Umweltvariablen pro Pflanzengesellschaft (Namen und Beschreibungen der Pflanzengesellschaften s. Tabelle 1). Die Gesellschaften 9 und 10 sind weggelassen, da sie nur auf einem Standort beobachtet wurden und nur einige Vegetationsaufnahmen vorliegen; die ähnlichen Gemeinschaften 1 und 2 sind kombiniert, um die Probenzahl zu erhöhen. Gesamtes $n = 153$, d.f. = 7; Kruskal Wallis-Test mit schrittweisen multiplen Rückwärtsvergleichen Die Buchstaben zeigen signifikante Unterschiede. Die asymptotische Signifikanz (2-seitiger Test) ist $< 0,001$ für alle gezeigten Variablen. E: Ellenberg-Wert., OM: Organische Substanz, Pw: Phosphat-Status (Wasser-Extraktion).

Predictors	Plant communities from field work data								Test Stat.
	1+2 ($n = 8$)	3 ($n = 15$)	4 ($n = 28$)	5 ($n = 42$)	6 ($n = 10$)	7 ($n = 10$)	8 ($n = 8$)	11 ($n = 33$)	
E_moisture	6.37 ^c	5.93 ^b	5.48 ^a	6.33 ^c	6.83 ^{cd}	7.39 ^d	6.99 ^d	6.96 ^d	100.274
E_nitrogen	4.40 ^a	5.04 ^b	5.78 ^c	5.73 ^c	5.54 ^c	5.31 ^b	5.63 ^c	5.03 ^b	101.210
Pw (mg/kg)	0.8 ^a	2.7 ^b	3.8 ^b	7.4 ^d	4.3 ^{bc}	3.4 ^b	6.2 ^{cd}	5.8 ^{cd}	69.434
P-tot (mmol/kg)	6.2 ^a	10.0 ^b	20.1 ^c	27.4 ^c	22.0 ^{cd}	18.7 ^c	36.65 ^c	24.9 ^d	82.800
K (mg/kg)	15 a	46 ^b	131 ^c	253 ^d	183 ^{cd}	107 ^{bc}	178 ^{cd}	278 ^d	59.305
pH-KCl	5.83 ^{bc}	5.81 ^c	7.05 ^d	5.04 ^b	4.87 ^{ab}	7.11 ^d	7.17 ^d	4.64 ^a	72.309
pH-H ₂ O	6.35 ^{ab}	6.77 ^b	7.59 ^c	6.02 ^a	5.93 ^a	7.66 ^c	7.70 ^c	5.78 ^a	76.867
E_pH	5.48 ^a	5.57 ^{ab}	6.44 ^d	5.96 ^c	6.21 ^c	6.47 ^d	6.44 ^d	5.85 ^{bc}	83.232
Ca (mg/kg)	282 ^{ab}	142 ^a	654 ^c	330 ^b	194 ^a	609 ^{cd}	856 ^d	291 ^b	66.289
OM (%)	9.0 ^b	4.9 ^a	10.1 ^b	14.6 ^{cd}	11.8 ^{bc}	8.5 ^b	12.7 ^{cd}	15.4 ^d	79.119
Clay (%)	13.5 ^{ab}	10 ^a	12 ^{ab}	18 ^c	17.5 ^{bc}	10 ^{ab}	18.5 ^c	20 ^c	59.700
Loam (%)	63 ^{ab}	50 ^a	54 ^a	73 ^{bc}	67.5 ^{abc}	55 ^a	76 ^{bc}	80 ^c	54.155
E_light	7.14 ^c	7.02 ^c	6.86 ^b	6.76 ^a	6.78 ^{ab}	6.88 ^b	6.74 ^a	6.89 ^b	54.382
Herb cover (%)	88.5 ^a	95 ^c	95 ^c	92.5 ^{bc}	90 ^{ab}	95 ^{bc}	94 ^{abc}	90 ^{ab}	26.454
Moss cover (%)	50 ^c	0 ^a	2.5 ^b	3 ^b	10 ^c	3 ^b	2 ^b	10 ^c	43.691
Mean species number	32 ^{bc}	29 ^b	32 ^{bc}	25 ^a	37.5 ^d	41 ^c	31.5 ^{bc}	34 ^{cd}	65.706

Clustering of the 958 older relevés with *B. racemosus* s.l. from the DNVD revealed three additional plant communities in which *B. racemosus* s.l. was found in the past (Table 1). Of these clusters one relates to a *Calthion palustris* community, while two communities are not covered by the class *Molinio-Arrhenatheretea*: one from the alliance *Lolio-Potentillion anserinae* Tüxen 1947 and one from the *Caricion nigrae* Koch 1926.

The clustering of data from foreign countries revealed that most relevés are quite similar to the Dutch relevés and could be assigned to the same alliances. Supplement S1 shows which alliances were covered by the data of the different countries, and which species have a high frequency in the communities. The communities from northern Germany (D), Bel-

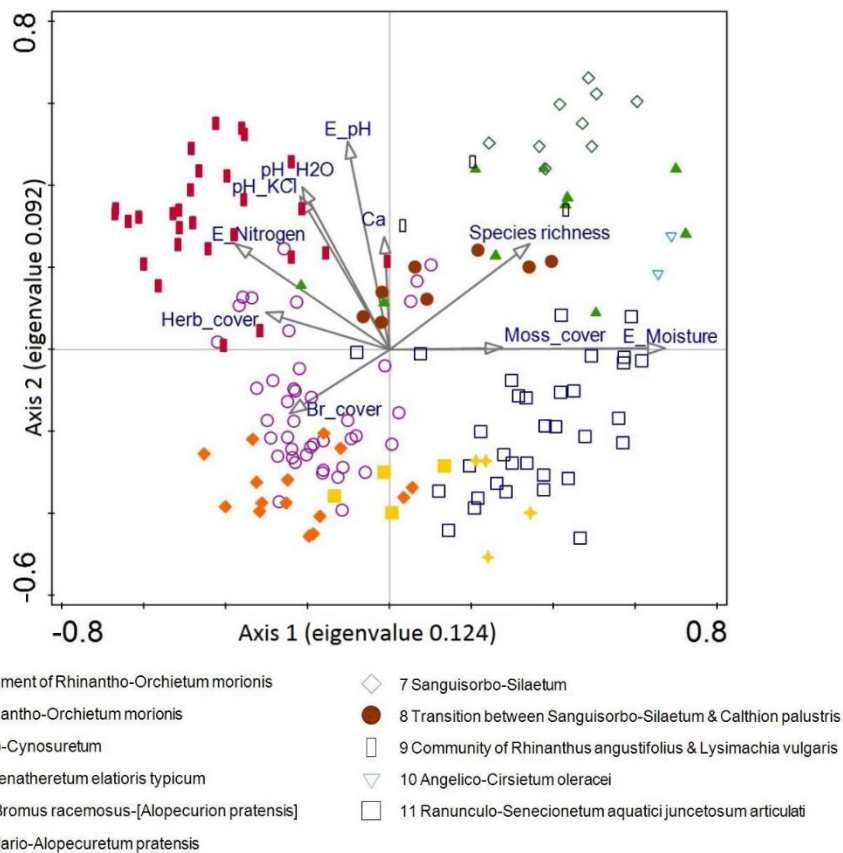


Fig. 3a. Principal Component Analysis (PCA) of 158 relevés from fieldwork, that have been assigned to eleven communities with help of Twinspan, as shown in Table 1 and the relevé table (Supplement E1). The communities are depicted by symbols, as explained in the legend. Axis 1 and 2 are plotted, eigenvalues are 0.124 and 0.092 respectively. Only continuous environmental variables with a correlation of more than 0.30 with one of the plotted axes are shown. E: abbreviation for Ellenberg value. Br_cover: *Bromus racemosus* s.l. cover.

Abb. 3a. PCA von 158 Vegetationsaufnahmen aus Feldarbeit, die mit Hilfe von Twinspan elf Pflanzengesellschaften zugeordnet wurden, wie in Tabelle 1 und der Vegetationstabelle (Anhang E1) gezeigt. Die Gesellschaften werden durch Symbole dargestellt (s. Legende). Achse 1 und 2 sind dargestellt, die Eigenwerte sind jeweils 0,124 und 0,092. Nur kontinuierliche Umgebungsvariablen mit einer Korrelation von mehr als 0,30 mit einer der dargestellten Achsen werden gezeigt. E: Ellenberg-Wert, Br_cover: *Bromus racemosus* s.l. Deckung.

gium (B), northern France (F) and southern England (E) overlap largely with the Dutch relevés and can be assigned to the same four alliances and additional Basal Community of the class *Molinio-Arrhenatheretea*. *Bromus racemosus* can reach a high cover in all of these alliances.

In the DCA plot (Fig. 4) the same clusters from Supplement S1 have been indicated. The Dutch relevés are distributed over a large part of the ordination space. Most relevés from fieldwork are placed on the nutrient-richest half of the ordination space (the lower part),

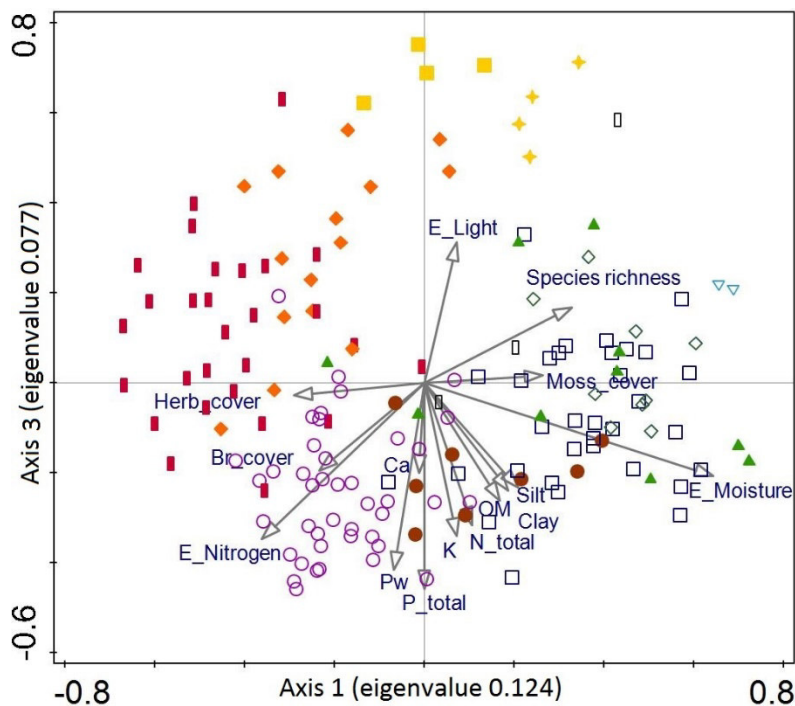


Fig. 3b. Principal Component Analysis (PCA) of 158 relevés from fieldwork, that have been assigned to eleven communities with help of Twinspan (see Fig. 3a for explanation). Here Axis 1 and 3 are plotted, eigenvalues are 0.124 and 0.077 respectively.

Abb. 3b. PCA von 158 Vegetationsaufnahmen aus Feldarbeit, die mit Hilfe von Twinspan elf Pflanzengesellschaften zugeordnet wurden (siehe Abb. 3a für Erläuterung). Hier sind Achse 1 und 3 dargestellt, die Eigenwerte sind jeweils 0,124 und 0,077.

except for the relevés from Texel (Dutch clusters 1 and 2), which do not resemble any foreign relevés. The relevés from Bremen (Germany) and Flanders (Belgium) indicate relatively wet and acid sites. They belong to the *Calthion palustris* and basal communities of nutrient-rich sites. The relevés from Famenne & Fagne (southern Belgium) and the Bassin de la Sambre (northeastern France) are drier and indicate more basic conditions. This *Alopecurion* vegetation is characterised by the presence of *Colchicum autumnale* and a high cover of *Alopecurus pratensis* and *B. racemosus*. The French relevés span a range of all four alliances, like the Dutch. The English relevés overlap with the drier *Alopecurion* and *Arrhenatherion* relevés. Although their average Ellenberg value for moisture is almost the same as for the Dutch relevés, their position in the ordination indicates drier conditions. This may be explained from the more Atlantic (moist) climatic conditions, which enables growing in drier soils.

4.2 Hydrological conditions

The Ellenberg value for moisture of the relevés varied in the range 5–8. *Bromus racemosus* s.l. cover was negatively correlated to the Ellenberg value for moisture ($r = -0.206$, $p = 0.009$, $n = 158$), and reached an optimum around 6.2.

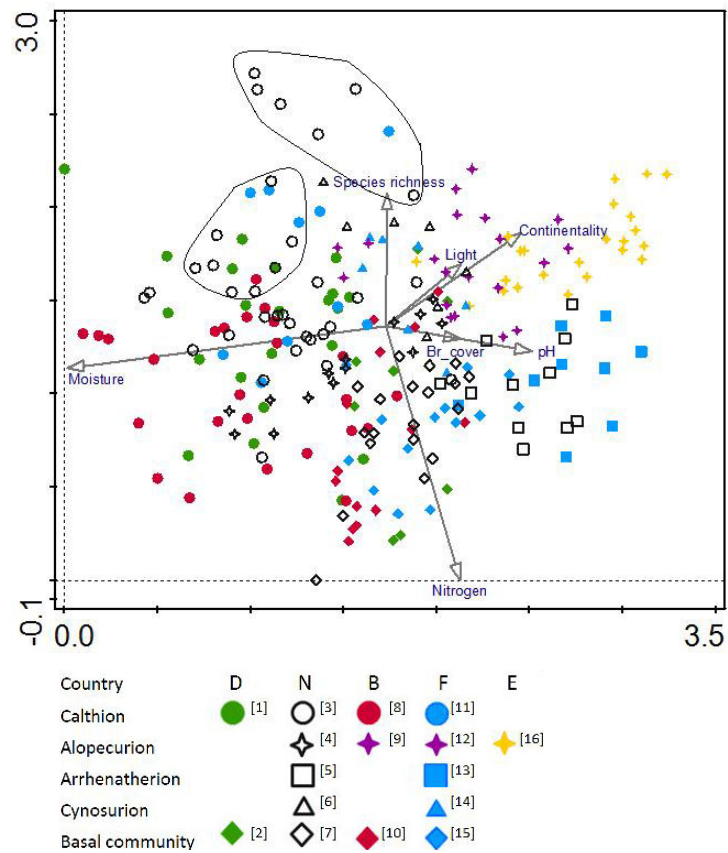


Fig. 4. Detrended Correspondence Analysis (DCA) of a selection of 237 relevés with *Bromus racemosus* s.l. (74 from own fieldwork, 11 from the DNVD, 152 from nearby countries). The communities 8 and 9 are not included. Communities are depicted by the form of the symbols, countries are marked with a colour (Germany (D): green, Belgium (B): red, France (F): blue, border region of Belgium and France (BF): purple, Netherlands (N): transparent). The numbers between [] refer to the footnotes of Supplement S1. Axis 1 and 2 are plotted, eigenvalues are 0.327 and 0.221 respectively. Ellenberg values are plotted as environmental values. Encircled areas indicate relevés from communities 1 and 2 (upper circle) and most relevés from the *Ranunculo-Senecionetum caricetosum paniceae* (made in 1936–1974; lower circle); recent Dutch relevés do not belong to the last group.

Abb. 4. DCA von einer Auswahl von 237 Vegetationsaufnahmen mit *Bromus racemosus* s.l. (74 durch eigene Feldarbeit, 11 aus der DNVD, 152 aus umliegenden Ländern). Die Pflanzengesellschaften 8 und 9 sind nicht enthalten. Gesellschaften werden durch die Form der Symbole dargestellt, Länder mit einer Farbe gekennzeichnet (Deutschland (D): grün, Belgien (B): rot, Frankreich (F): blau, Grenzregion von Belgien und Frankreich (BF): lila, Niederlande (N): transparent). Die Zahlen zwischen [] beziehen sich auf die Fußnoten von Beilage S1. Achse 1 und 2 sind dargestellt, die Eigenwerte sind jeweils 0,327 und 0,221. Ellenberg-Werte sind als Umgebungsvariablen angegeben. Umkreiste Bereiche zeigen Vegetationsaufnahmen der Gesellschaften 1 und 2 (oberer Kreis) und die Mehrheit der Vegetationsaufnahmen aus dem *Ranunculo-Senecionetum caricetosum paniceae* (1936–1974 erstellt; unterer Kreis) an; in der letzten Gruppe befinden sich keine neuen niederländischen Vegetationsaufnahmen.

The hydrological conditions differed between sites in polders and sites in floodplains. In polder grasslands (outside the direct influence of the river), the species was only found in parts with a mean highest groundwater table less than 40 cm below soil surface, in most sites less than 25 cm (ALTERRA 2013, GDN 2013). The species was most abundant on parts of parcels that are never or rarely inundated by rain or groundwater, and was lacking in parts that are inundated for a long period each winter. In areas where the soil consists of clay on top of peat, typically *B. racemosus* had a higher cover on the elevated borders of parcels with a bathtub shape. In the centre, where rain water stagnation occurs during winter, the species had a low cover or was absent. The mean lowest groundwater table was usually between 60 and 110 cm below soil surface. The species was absent or rare in areas with a higher lowest groundwater table.

In floodplains, in sites that are flooded by river water at least once every ten years, the inundation frequency and duration determine the distribution of *B. racemosus*. Also here, the species occurred at relatively dry places with a mean highest groundwater table more than 80 cm below soil surface. In most sites, its upper distribution boundary was the belt that is inundated every few years. On its lower boundaries, *B. racemosus* appeared to be limited by long inundations, but it seemed to tolerate winter inundation with river water for a longer period (probably almost two months) than inundation with rain and groundwater in the polders.

Inundation for a couple of days of flowering *B. racemosus* was observed in Cortenoever (along the Gelderse IJssel) in early June 2013. *Bromus racemosus* died and was not able to produce fruits in zones where the water table had been more than about 80 cm above the surface. The lower the water depth had been, the more individuals survived and produced fruits. Inundation in the flowering period is rare in the Netherlands, but it became more frequent during the 20th century (AGGENBACH et al. 2007).

4.3 Soil conditions

Data from fieldwork ($n = 158$) indicated that *B. racemosus* s.l. is relatively abundant on relatively nutrient-rich, productive sites. Its cover was correlated negatively to the Ellenberg value for light ($r = -0.359$, $p < 0.001$) and positively to the Ellenberg value for nitrogen ($r = 0.252$, $p = 0.001$), N-total ($r = 0.211$, $p = 0.008$), P-total ($r = 0.289$, $p < 0.001$), Pw ($r = 0.250$, $p = 0.002$) and K ($r = 0.162$, $p = 0.041$). *Bromus racemosus* s.l. cover was positively correlated ($n = 162$) to herb cover ($r = 0.358$, $p < 0.001$) and negatively to moss cover ($r = -0.183$, $p = 0.021$). It was also negatively correlated to species richness ($r = -0.288$, $p = 0.001$). From these correlations it may be concluded that *B. racemosus* s.l. cover is higher under more nutrient-rich conditions. However, these conclusions hold only for the mesotrophic range of the study sites. *Bromus racemosus* s.l. was not observed in more nutrient-rich (eutrophic) sites. The Ellenberg value for nitrogen of relevés with *B. racemosus* s.l. varied between 4.36–6.42. Hardly any of the visited sites had been fertilised within the last five years.

In the IBS dataset *B. racemosus* s.l. is negatively correlated to measures for the availability of K ($r = -0.258$, $p < 0.001$, $n = 395$) and P ($r = -0.121$, $p = 0.015$, $n = 406$), and the species was absent from sites with very high values. From the remarks about fertilisation it appears that its cover is somewhat higher in fertilised than in unfertilised sites. This indicates that a moderate gift of fertiliser has a positive effect on the species, whereas heavy fertilisation has a negative effect.

The acidity of the plots varied in the following ranges: pH-H₂O 5.1–7.9, pH-KCl 4.0–7.5, Ellenberg value for reaction lie in the range 4.95–7.13. The pH and the Calcium concentration were not significantly correlated to the cover of *B. racemosus* s.l.

Bromus racemosus occurs normally on soils with a fine texture. In the data from fieldwork, loam percentage (clay + silt) was 20–90% and clay 4–26%, but *B. racemosus* s.l. cover was not significantly correlated to those parameters. If only the communities of drier habitat (cluster 3–5) are selected, the species cover shows a positive correlation to loam percentage ($r = 0.223$, $p = 0.040$, $n = 85$).

In the IBS dataset the species is more often present on sites with a finer texture (Mann-Whitney U: 16402.5, $p = 0.011$, $n = 407$), and it was also found on sites with a clay percentage much higher than 26%. On the other hand, it was found a few times on sites with a coarse texture as well.

In almost all relevés the humus form was a type of mull, a humus form with a thin or absent ectorganic horizon and a good mineralisation. No soils with podzol were found.

4.4 Grassland management

In the IBS dataset *B. racemosus* s.l. was more frequent in meadows with aftermath grazing than in grasslands that are only mown or grazed (Test stat. = 77.741, $p < 0.001$, d.f. = 5, $n = 380$). In the data set, the species was found in 12.5% of the 48 meadows that were only mown, in 48.3% of the 116 meadows with aftermath grazing and in 4.3% of 92 pastures. This makes *B. racemosus* s.l. the species with the strongest preference for meadows with aftermath grazing of around 200 common grassland species studied by the IBS (KRUIJNE et al. 1967).

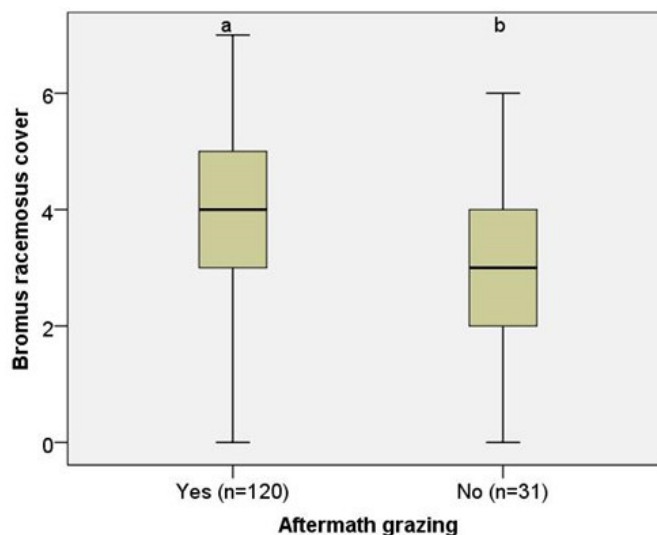


Fig. 5. Cover-abundance of *Bromus racemosus* s.l. on the ordinal scale in meadows with and without aftermath grazing (Mann-Whitney U: 1292.0, $p = 0.007$, $n = 151$).

Abb. 5. Abundanz/Dominanz von *Bromus racemosus* s.l. auf der Ordinalskala in Wiesen mit und ohne Nachbeweidung (Mann-Whitney U: 1292,0; $p = 0,007$; $n = 151$).

With the data from fieldwork, it was tested whether *B. racemosus* s.l. reaches a higher cover on meadows with aftermath grazing, compared to meadows that are only mown. This was indeed the case (Mann-Withney U: 1292.0, $p = 0.007$, $n = 151$, Fig. 5). Within the 120 relevés with aftermath grazing, it was tested whether the yearly number of mowings was related to the cover of *B. racemosus* s.l. (92 relevés were mown once, 28 twice). The cover was higher in sites that were mown twice (Mann-Withney U: 1689.5, $p = 0.010$, $n = 120$).

Most sites visited during fieldwork are mown in the second half of June or later. Only two productive, species-poor sites were mown earlier, around the first of June; here *B. racemosus* was locally abundant.

The species was found quite abundant in two extensively grazed pastures, with mosaics of long and short vegetation. It grew in intermediate grazed sites, but was not found in short-grazed vegetation and very rare in tall vegetation.

5. Discussion

5.1 Plant communities

In the Netherlands *Bromus racemosus* is considered a weak character species of the *Alopecurion pratensis* Passarge 1964 (ZUIDHOFF et al. 1996). In terms of hydrology, this alliance is intermediate between the drier *Arrhenatherion* and the wetter *Calthion palustris*. The phytosociological analysis of the relevés from fieldwork revealed that *B. racemosus* reaches its optimum (highest cover) in the Netherlands in a basal community of the alliance *Alopecurion pratensis*, occurring on relatively nutrient rich, moderately moist soil. Furthermore it occurs in *Alopecurion* associations, relatively dry parts of *Calthion* sites, relatively wet *Arrhenatherion* sites and moist, mown *Cynosurion* sites. Our analyses confirm that the optimum of the species is in the *Alopecurion pratensis*, but also indicates that the range of alliances is wider than suggested in literature.

The same range of alliances of the class *Molinio-Arrhenatheretea* was found in our analysis of relevés from England, Germany, Belgium and France.

In Germany, *B. racemosus* is considered a character species of the *Calthion palustris*, an alliance of wet, mesotrophic meadows (LUTZ 1996, BÖHLING 1998, BURKART et al. 2004, PÄZOLT & JANSEN 2004). OBERDORFER (1957) describes four types of *B. racemosus* meadows typical for base-rich soils with a low lime content along streams and rivers in the lowlands, which besides typical *Calthion* species, also contain species that are characteristic of the *Alopecurion pratensis*. In the sites near Bremen, at the end of the 20th century, *B. racemosus* had disappeared from many *Calthion palustris* grasslands and was mainly found in species poor basal communities (LUTZ 1996), that are similar to the Dutch basal community from cluster 5. It is remarkable that relevés from the *Senecioni-Brometum racemosi* (*Calthion palustris*) near Bremen are quite similar to the relevés of the *Ranunculo-Senecionetum aquatici caricetosum paniceae* from the DNVD, made in the period 1936–1978 in the north-east of the Netherlands, as currently *B. racemosus* seems to be absent from sites in this latter region.

In Austria WILLNER et al. (2013) found *B. racemosus* with a low cover in an association belonging to the *Calthion*.

BOTTA-DUKÁT et al. (2005) studied lowland wet meadows in a large part of Central Europe. They conclude that the *Alopecurion pratensis* cannot be floristically separated from the alliances *Agrostion albae* Soó 1941, *Cnidion venosi* Balátová-Tuláčková 1966, *Deschamps-*

ion cespitosae Horvatić 1930 and *Veronico longifoliae-Lysimachion vulgaris* Balátová-Tuláčková 1981. Therefore they propose to use the name *Deschampsion cespitosae* for all these alliances. They mention *B. commutatus* as a diagnostic species for mesic, continental *Deschampsion cespitosae* meadows in Hungary and southern Slovakia.

In England, GOWING et al. (2002) state that *B. racemosus* occurs in the community *MG4 Alopecurus pratensis - Sanguisorba officinalis* grassland (RODWELL 1992), a floodplain meadow comparable to the Dutch *Alopecurion pratensis*. This is confirmed by the analysed British relevés. Also French authors describing floodplain communities (SOUGNEZ & LIMBOURG 1963, DE FOUCAULT 1986, FRILEUX et al. 1988), indicate that *B. racemosus* is absent or rare in the wettest flood meadows (like the *Ranunculo-Alopecuretum geniculati*) and the driest sites (*Arrhenatherion* sites), having its optimum in between. In France and Wallonia communities with *B. racemosus* are often placed in the alliance *Bromion racemosi* (GEHU 1961, SOUGNEZ & LIMBOURG 1963, DE FOUCAULT 1986), which corresponds to the *Calthion palustris*. However, in some case the species composition is closer to the *Alopecurion pratensis*. Besides, the species has been observed in the *Arrhenatherion elatioris* (DE FOUCAULT 1988, FRILEUX et al. 1988), and also in our data the French data covered the relatively driest alliances *Arrhenatherion* and *Cynosurion*.

Overall, although *B. racemosus* occurs regularly in communities of the *Calthion palustris*, our data demonstrate that its optimum in Northwestern Europe lies in communities of somewhat drier habitats, where the species reaches the highest covers. *Bromus racemosus* can be considered as a character species of the *Molinio-Arrhenatheretea*, with a preference for moderately moist, mesotrophic *Alopecurion pratensis* meadows. This is in accordance with the situation described by BOTTA-DUKÁT et al. (2005) for Central Europe.

Outside these alliances of semi-natural, mesic grasslands, *B. racemosus* occurs sometimes in desalinating sites, as described for the Netherlands (BOER 1955), and reported from Belgium (ZWAENEPOEL 2006) and Germany (LUTZ 1996). This is however a rare situation, and the only example of more 'natural' plant communities.

It is noteworthy that the genus *Bromus* (s.str., comprising only annual species) is a group of species confined to anthropogenic habitats (anecophytes), and many *Bromus* taxa having probably evolved in Holocene times in the context of agriculture (SCHOLZ 2008). Some of them are weeds in arable land and mimic crops in their floral characters, like *B. secalinus* (*Secale cereale*, *Hordeum vulgare*), *B. bromoides* (*Triticum spelta*), and *B. interruptus* (*Onobrychis viciifolia*, *Trifolium* spp.). The latter two had a very restricted area (East Belgium and England respectively) and are extinct in the wild nowadays (SMITH 1980). Other *Bromus* species are adapted to grassland management, like *B. racemosus*, whose ecology suggests an origin as a hay-field specialist.

5.2 Hydrology

Since moisture could not be measured in the field during our study, mean Ellenberg values were used. This method has been criticised (ZELENÝ & SCHAFFERS 2012), but in practice it works well for comparing vegetation plot data (DIEKMANN 2003).

Bromus racemosus has a quite narrow hydrological amplitude. It grows only on sites with moist conditions in winter or limited periods of inundation. The species cannot survive long inundation (GALL 1995, cited in LUTZ 1996), probably because the wintering plants need oxygen. In floodplains, spring flooding may be disastrous for *B. racemosus*, as was observed along the river IJssel in Cortenoever and confirmed by GREVILLIOT (1996). Also flooding in summer may cause a decline (LUTZ 1996). Many floodplain plants are more

tolerant to (regular) winter flooding than occasional summer floods (VAN ECK et al. 2006). The species seems to tolerate inundation with river water better than inundation with rain and ground water, which may be explained by the higher nutrient content and alkalinity of river water.

In floodplains, the species was found under drier circumstances than in polders, provided the soil was sufficiently loamy (> 40%) and inundation occurred at least every 5–10 years. The cover of *B. racemosus* was higher in the relatively drier sites, which is confirmed by LUTZ (1996) and KALUSOVÁ et al. (2009). Probably *B. racemosus* benefits from summer desiccation, in competition with other species, since it can survive as a fruit until moist conditions occur. GOWING et al. (2002) suggest that the winter annual life cycle of *B. racemosus* could be an adaptation to avoid summer drought and/or to fruit before the first hay-cut. In even more dry sites the species may lack because of sensibility to desiccation in spring, or because of a weaker competitive ability. The hydrologic range of the species is smaller in polders than in floodplains. But in polders, the species reached more often high covers (> 12,5%). Here a more stable water table enables the species to build up a large population with a high cover. However, the risk of extinction with changing hydrology is higher in flat polders than in floodplains, as in the latter the population may shift between higher and lower places within the natural gradient.

5.3 Soil conditions

The cover of *B. racemosus* s.l. was higher in relatively nutrient-rich plots, but the species is absent from even more nutrient-rich (eutrophic) sites. It's likely that other grass species outcompete *B. racemosus* under eutrophic soil conditions. Besides, in heavily manured parcels the first hay cut is usually already in April or May, before ripening of fruits of *B. racemosus* (GREVILLIOT et al. 1998).

When nutrient richness of former agricultural grasslands is decreased by mowing without fertilisation, *B. racemosus* can be among the first species that recolonise the grasslands, provided fruits are present in the vicinity, as was demonstrated in the Drentsche Aa region by VAN DUUREN et al. (1981). Under moderate nutrient-rich conditions it can compete well with perennial, nitrophilous grasses, and here the species has its optimum (KALUSOVÁ et al. 2009). A further reduction of soil fertility may lead to a decline of *B. racemosus*. Nowadays in the Drentsche Aa region the species has completely vanished, possibly due to continued lowering of nutrient availability and/or rising of the water table.

Bromus racemosus is probably not dependent on soil texture, but on correlated factors like moisture and nutrient availability. Heavy clay for example seems unsuitable for *B. racemosus*, because its low permeability may lead to long stagnation of water. A relatively open substrate is important for germination of *B. racemosus*. During fieldwork the species was only observed on sites with mull humus, characterised by a good mineralisation, few litter and without a well-developed root mat. Moss cover was negatively correlated to *B. racemosus* s.l. cover.

5.4 Grassland management

Bromus racemosus flowers in May and early June and fruits in June, before the traditional mowing dates. It is monocarpic, dying soon after ripening (or failure) of the seeds. In this way it is not sensitive to superficial drying of the soil in summer (WEEDA 1994). After shedding, the seeds germinate as soon as they become moist. Light does not influence germina-

tion. In moist meadows all seeds usually will germinate, and therefore no seedbank is formed (LUTZ 1996, JENSEN 2004). In this respect, *B. racemosus* behaves like a cereal, like the closely related *B. secalinus*. The seeds have a good germination ability: 86% respectively 93% germinated in experiments of LUTZ (1996) and JENSEN (2004).

Bromus racemosus responds rapidly to changes in environmental conditions. The species disappeared from some sites where it had been abundant one or a few years before, and on the other hand it was able to establish and increase remarkably on a parcel within a few years (VAN DUUREN et al. 1981, LUTZ 1996). An appropriate and stable management is necessary to assure that the population survives the two most important bottlenecks of the species life-cycle each year. The first bottleneck is that it should not be mown or grazed before the seeds have ripened. Mowing after 15 June is advisable (see also LUTZ 1996). Since the fruits are relatively heavy (LUTZ 1996, JENSEN 2004), they may be unable to travel large distances by wind transport, and dispersal by mowing machines may be important.

The second bottleneck is the establishment of the seedlings in summer and autumn. The vegetation should not be too dense and tall, which can be guaranteed by aftermath grazing and/or mowing twice a year. Aftermath grazing generates open spots in the sward through trampling, which are a good substrate for germination and development of seedlings. MEISEL (1969) also states that *B. racemosus* has the highest frequency in meadows with aftermath grazing. OBERDORFER (1994) mentions that *B. racemosus* is more frequent in meadows that are only mown than in meadows with aftermath grazing.

The advantage of mowing twice a year is questionable. Since this management practice is mostly applied on nutrient rich parcels, *B. racemosus* may reach a higher cover partly because of the high nutrient availability. Continuation of mowing with the same frequency will decrease nutrient availability faster and may lead to a lower *B. racemosus* cover on the longer term, without any change in management.

6. Conclusion

Bromus racemosus has its optimum in moderately moist, moderately nutrient-rich *Molinio-Arrhenatheretea* meadows with good soil mineralisation. In the Netherlands its highest cover is in a basal community of the *Alopecurion pratensis* (= *Deschampsion cespitosae*). Further it occurs in other *Alopecurion* communities, relatively dry parts of wet meadows (*Calthion palustris*), and relatively moist parts of drier meadows and pastures (*Arrhenatherion* and *Cynosurion*). In the lowlands of surrounding countries the species occurs in a similar range of vegetation types, with the same optimum.

Since it is a winter annual species without a seedbank, fruit ripening, germination and seedling development should be successful every year to maintain a population. Mowing (once or twice) after 15 June is essential, while a relatively open sward in summer and autumn is critical for establishment, which can be guaranteed by aftermath grazing.

Bromus racemosus requires a high groundwater table and/or river flooding during winter for a limited period at least every few years. Under these conditions the species competes successfully with nitrophilous grasses. Within its optimum, its cover is highest under relatively dry, nutrient-rich conditions. The species can establish in restored grasslands within a few years, but dispersal over larger distances is probably very limited.

Erweiterte deutsche Zusammenfassung

Einleitung – *Bromus racemosus* L. ist eine ziemlich seltene Grasart der Feuchtwiesen. In den Niederlanden wird sie in zwei Unterarten unterteilt, subsp. *racemosus* und subsp. *commutatus*, die in anderen Ländern meist als separate Arten aufgefasst werden (SPALTON 2002). Die vorliegende Arbeit befasst sich hauptsächlich mit *B. racemosus* s.str. (= *B. racemosus* subsp. *racemosus*). *Bromus racemosus* gehört innerhalb der Gattung zu *Bromus* s.str., mit einjährigen, auf anthropogene Standorte beschränkte Arten (Anökophyten). Das Areal von *B. racemosus* umfasst weite Teile Europas. In vielen Ländern steht sie auf der Roten Liste, weil sie aufgrund der Intensivierung der Landwirtschaft in den letzten Jahrzehnten in starkem Rückgang begriffen ist. Ihr winterannueller Lebenszyklus ist bemerkenswert für eine Sippe des Dauergrünlands. Die Samen keimen sofort nach der Reifung, sobald sie feucht werden. Dies verhindert die Bildung einer Samenbank (LUTZ 1996, JENSEN 2004). Die vorliegende Studie soll das Wissen über die Habitat- und Managementpräferenz von *B. racemosus* in den Niederlanden und den benachbarten Gebieten vergrößern. Dazu wurden der Einfluss von abiotischen Bedingungen und der Grünlandbewirtschaftung auf ihre Abundanz und ihre syntaxonomische Position untersucht.

Untersuchungsgebiet – Die Studie berücksichtigt 28 Naturschutzgebiete mit *Bromus racemosus* in den Niederlanden (Abb. 1 und Anhang E2). Die meisten Fundorte befinden sich in den Auen und Poldern der niederländischen Flusslandschaft. Der Boden wird dominiert von Mineralschichten, die während des Holozäns von Flüssen (einschließlich Tide-Flüssen) oder vom Meer abgelagert wurden. An einigen Stellen wächst *B. racemosus* auf torfigen Böden.

Daten aus den umliegenden Ländern wurden analysiert und mit den Daten aus den Niederlanden verglichen. Es handelt sich um Aufnahmestellen im Bremer Raum, vier Naturschutzgebieten in Belgien, vier in Nordfrankreich und zwei in Südengland (Abb. 2). Sie liegen ausnahmslos im Tiefland, in der Nähe eines Flusses oder Baches.

Material und Methoden – Es wurde die Braun-Blanquet-Methode angewendet. An Wuchsstellen von *Bromus racemosus* wurden Vegetationsaufnahmen von 9 m² gemacht. Der Aufbau der Boden- und Humusprofile wurde mit einem Erdbohrer und einem Brotmesser sichtbar gemacht. Für eine bodenchemische Analyse wurde für jede Vegetationsaufnahme eine integrierte Bodenprobe aus zehn Teilproben bis 20 cm Tiefe entnommen.

Die Daten wurden in Juice mit Twinspan klassifiziert, und mit verschiedenen Ordinationsmethoden in Canoco sowie mit univariaten Statistiken analysiert. Vegetationsaufnahmen aus der niederländischen Vegetationsdatenbank (SCHAMINÉE et al. 2012) und aus den umliegenden Ländern wurden mit Vegetationsaufnahmen aus der eigenen Feldarbeit verglichen. Die Hydrologie wurde anhand hydromorpher Bodeneigenschaften und Online-Daten über Grundwasserschwankungen und Überschwemmungen beschrieben.

Ergebnisse – Die Klassifizierung ergab elf Gruppen von Vegetationsaufnahmen (Tabelle 1, 2), die auch in der PCA sichtbar werden (Abb. 3a, b). Die erste Achse kann als Feuchtigkeitsgradient interpretiert werden, die zweite als pH-Gradient und die dritte als Nährstoffgradient. Alle Vegetationsaufnahmen sind in die Klasse *Molinio-Arrhenatheretea* einzuordnen. Sie verteilen sich über Gesellschaften des *Alopecurion pratensis* (synonym: *Deschampsion cespitosae*), *Calthion palustris*, *Arrhenatherion elatioris* und *Cynosurion cristati*, wobei die Art innerhalb des *Calthion* relativ trockenere, im *Arrhenatherion* und *Cynosurion* die feuchteren Ausbildungen bevorzugt. Die meisten Vegetationsaufnahmen aus benachbarten Ländern ähneln den niederländischen Aufnahmen und können den gleichen Verbänden zugeordnet werden (Beilage S1, Abb. 4). In den meisten Gesellschaften kann *Bromus racemosus* eine hohe Deckung erreichen, aber gerade im *Calthion* erscheint die Deckung in allen untersuchten Gebieten relativ gering. Das Optimum der Art liegt eher im *Alopecurion*, insbesondere in mäßig nährstoffreichen Basalgesellschaften.

In Wiesen ohne Flussüberflutungen wurde *B. racemosus* an Standorten mit einem mittleren höchsten Grundwasserspiegel von weniger als 40 cm unter der Bodenoberfläche gefunden. Die Art fehlt an Standorten, die jeden Winter über einen längeren Zeitraum überflutet werden und erreicht die höchste

Deckung an relativ trockenen Standorten. An Standorten, die mindestens einmal in zehn Jahren von Flusswasser überflutet werden, wächst die Art auch auf trockeneren Böden mit einem mittleren höchsten Grundwasserspiegel von mehr als 80 cm unter der Bodenoberfläche.

Während *B. racemosus* die höchste Deckung an relativ nährstoffreichen Standorten erreicht, kommt dieses Gras jedoch nicht an sehr nährstoffreichen Böden vor. Es wächst vor allem auf Böden mit Mull als Humusform, gekennzeichnet durch eine gute Mineralisierung. *Bromus racemosus* hat auf Wiesen mit Nachweide höhere Deckungen als auf ausschließlich gemähten Wiesen (Abb. 5). Die meisten Wiesen mit *B. racemosus* werden ab der zweiten Junihälfte gemäht. Nur selten tritt die Art in Weiden auf.

Diskussion – *Bromus racemosus* wächst nur an Standorten mit feuchten Bedingungen im Winter oder kurzzeitiger Überflutung, die Lücken in der Vegetation schafft. Wahrscheinlich wird *B. racemosus* von leichter Sommeraustrocknung in der Konkurrenz mit anderen Arten begünstigt, weil die Samen im Ruhezustand überleben, bis feuchte Bedingungen auftreten. Die aktuelle hydrologische Amplitude ist geringer innerhalb als außerhalb der Deiche. Die Deckung innerhalb der Deiche ist aber durchschnittlich höher als außerhalb. Ein konstanter Wasserhaushalt ermöglicht der Art, eine große Population mit hohem Deckungsgrad aufzubauen. Wenn die Hydrologie sich ändert, ist das Risiko des Verschwindens im flachen Polder höher als in Auen mit reichem Relief, wo die Population im Höhengradient pendeln kann. In den Auen besteht aber die Gefahr der Überflutung in der Blütezeit, wodurch die Samenproduktion verhindert wird.

Das Fehlen von *B. racemosus* in sehr nährstoffreichen Wiesen ist wahrscheinlich der starken Konkurrenz zuzuschreiben; darüber hinaus werden diese durchweg zu früh gemäht für ausreichenden Fruchtansatz der Art. Wird der Nährstoffreichtum von ehemaligem Wirtschaftsgrünland durch Mahd ohne Düngung verringert, so kann *B. racemosus* die Wiesen innerhalb weniger Jahre wiederbesiedeln. Auf längere Sicht erscheint eine niedrige Düngergabe alle paar Jahre wohl vorteilhaft für *B. racemosus*. Das Fehlen einer Samenbank und eine geringe Ausbreitungsfähigkeit gefährden die Art. Voraussetzung für die Erhaltung der Populationen ist erfolgreiche Samenreife und Etablierung der Keimlinge in jedem Jahr. Eine Bewirtschaftung mit Mahd nach dem 15. Juni und Nachweide eignet sich am besten, da diese Nutzungsweise die Samenreife zulässt und anschließend eine ausreichend lückige Krautschicht erhält.

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Supplements

Supplement S1. Shortened synoptic table of all studied vegetation, grouped by country and syntaxa.

Beilage S1. Gekürzte Stetigkeitstabelle aller untersuchten Vegetation, gruppiert pro Land und Syntaxa.

Supplement S2. Complete synoptic table of relevés from own field work.

Beilage S2. Komplette Stetigkeitstabelle der Vegetationsaufnahmen von eigener Feldarbeit.

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Table of relevés from own field work.

Anhang E1. Tabelle der Vegetationsaufnahmen von eigener Feldarbeit.

Supplement E2. Overview table with header data of relevés from own field work.

Anhang E2. Übersichtstabelle mit Kopfdaten der Vegetationsaufnahmen von eigener Feldarbeit.

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Supplement S1. Shortened synoptic table of all studied vegetation, grouped by country as columns (D = Germany, N = Netherlands, B = Belgium, F = France, E = England) and syntaxa as rows (sensu Schaminée et al. 1996). Per combination of a country and a syntaxon, a unique subset of relevés was used, shown in a framed section of the column. The number of relevés per group is given above in italics (in total 412 relevés are included). In the footnotes, given between [], the locations, the original names of the syntaxa and references are given; only the Dutch relevés are mainly from own field work. The table contains percentage frequency values and average non-zero cover in % (as superscript).

Beilage S1. Gekürzte Stetigkeitstabelle aller untersuchten Vegetation, gruppiert pro Land als Spalten (D = Deutschland, N = Niederlande, B = Belgien, F = Frankreich, E = England) und Syntaxa als Reihen. Pro Kombination aus einem Land und einem Syntaxon wurde eine Selektion von Vegetationsaufnahmen verwendet; diese wird in einem gerahmten Abschnitt der Spalte gezeigt. Die Zahl der Vegetationsaufnahmen pro Kombination ist oben in kursiv angezeigt (insgesamt sind 412 Aufnahmen enthalten). In den Fußnoten, angegeben zwischen [], werden die Standorte, die ursprünglichen Namen der Syntaxa und die Referenzen beschrieben; nur die niederländischen Vegetationsaufnahmen sind hauptsächlich von eigener Feldarbeit. Die Tabelle enthält prozentuale Frequenzwerte und mittlere nicht-null Deckungswerte in % (hochgestellt).

Country	D	N	B	F	E			
Calthion palustris	22 ^[1]		53 ^[3]		34 ^[8]		16 ^[11]	
Bromus racemosus	100	12	100	4	100	3	100	5
Caltha palustris	82	10	26	4	62	7	44	3
Lychnis flos-cuculi	91	4	75	3	91	3	63	4
Lotus pedunculatus	41	8	58	6	47	9	50	3
Dactylorhiza majalis	23	5	8	2	12	1	0	
Cirsium palustre	5	1	64	3	15	3	25	2
Alopecurion pratensis	19 ^[4]		21 ^[9]		13 ^[12]		23 ^[16]	
Bromus racemosus	100	4	100	12	100	8	100	2
Sanguisorba officinalis	63	10	0		0		70	10
Fritillaria meleagris	37	3	0		0		65	3
Lathyrus pratensis	84	4	95	5	69	5	65	2
Silaum silaum	5	3	57	5	0		74	3
Alopecurus pratensis	100	5	67	13	100	17	65	4
Arrhenatherion elatioris	25 ^[5]		16 ^[13]					
Bromus racemosus	100	5			100	6		
Arrhenatherum elatius	80	13			94	23		
Dactylis glomerata	92	8			94	6		
Trisetum flavescens	68	7			63	3		
Tragopogon pratensis	36	3			81	2		
Peucedanum carvifolia	20	5			13	3		
Cynosurion cristatus	14 ^[6]		16 ^[14]					
Bromus racemosus	100	9			100	25		
Cynosurus cristatus	93	8			75	13		
Lolium perenne	100	11			88	16		
Bellis perennis	57	2			56	3		
Trifolium dubium	79	6			88	14		
Agrostis capillaris	64	20			38	16		
Basal communities Molinio-Arrhenatheretea	8 ^[2]	42 ^[7]	41 ^[10]	40 ^[15]				
Bromus racemosus	100	17	100	8	100	4	100	8
Alopecurus pratensis	63	4	95	7	66	14	18	5
Ranunculus repens	75	15	98	10	98	30	98	13
Alopecurus geniculatus	50	7	33	13	37	6	23	3
Lolium perenne	50	11	93	9	80	16	98	12
Bromus hordeaceus	88	8	62	4	49	5	15	2

Origin of relevés:

- 1 *Senecioni-Brometum racemosi* (*Calthion palustris*), near Bremen, Lutz 1996 (relevés from several authors, 1951-1996)
- 2 BC / Basalgesellschaft *Molinio - Arrhenatheretea*, near Bremen, Lutz 1996 (relevés from several authors, 1951-1996, but most from Lutz 1996)
- 3 Communities 1, 2, 10, 11 (own field work) and eleven additional relevés from the DNVD (Schaminée et al. 2006) from 1936-1974, assigned to the *Ranunculo-Senecionetum caricetosum paniceae*
- 4 Communities 6, 7 (own field work)
- 5 Community 4 (own field work)
- 6 Community 3 (own field work)
- 7 Community 5 (own field work)
- 8 Snoekengracht near Leuven, Dijlevallei near Leuven & Bourgoyen near Gent (Flanders), Callebaut et al. (2007) & VLAVEDAT (Flemish Vegetation Databank; Vandenbussche & Hoffmann 2001); assigned to the *Calthion palustris* based on an analysis of the species composition.
- 9 *Colchico-Brometum racemosi* (*Bromion racemosi*, *Molinieta*), Femenne & Fagne (southern Wallonia), Sougnez & Limbourg 1963; assigned to the *Alopecurion pratensis* based on an analysis of the species composition.
- 10 Dijlevallei near Leuven & Bourgoyen near Gent (Flanders), Callebaut et al. (2007) & VLAVEDAT (Flemish Vegetation Databank; Vandenbussche & Hoffmann 2001); classified as basal communities based on the absence of character species on the alliance level.
- 11 *Brometo-Senecietum* (*Bromion racemosi*, *Molinieta*), Bassin de la Sambre, Gehu 1961 & *Cirsio dissecti - Scorzoneretum*, Bocage Virois, Basse-Normandie, De Foucault 1980; assigned to the *Calthion palustris* based on an analysis of the species composition; in the relevés of De Foucault 1980 additionally some *Junco-Molinion* species are present.
- 12 *Arrhenatheretum Colchicetosum* (*Cynosurion cristati*), Bassin de la Sambre, Gehu 1961; assigned to the *Alopecurion pratensis* based on an analysis of the species composition; species from the *Cynosurion* were rare and *Arrhenatherion* species not very frequent; several moisture indicating species were present.
- 13 *Hordeo secalini-Arrhenatheretum elatioris* & *Galio veri-Trifolietum repentis* (both *Arrhenatherion*), Seine-maritime downstream of Rouen, Frileux et al. 1988
- 14 *Oenanthe peucedanifoliae - Brometum racemosi* (*Cynosurion cristati*), Bocage Virois, Basse-Normandie, De Foucault 1980
- 15 *Senecio aquatici-Oenantheum mediae*, Seine-maritime, Frileux et al. 1988 & *Senecio-Brometum racemosi* (*Bromion racemosi*, *Agrostieta-stoloniferae*, *Agrostio-Arrhenatheretea elatioris*), Boulonnais, De Foucault 1986; classified as basal communities based on the absence of character species on the alliance level.
- 16 Unpublished relevés from A. Corporaal, near Cricklade, 1991, all with *Fritillaria meleagris* & from M. Raman, near Oxford, 2010; assigned to the *Alopecurion pratensis* based on an analysis of the species composition.

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Supplement S2. Complete synoptic table of relevés from own field work, with percentage frequency values. All relevés are from the Netherlands and belong to the *Molinio-Arrhenatheretea*. The communities are described in Table 1 in the article. The assignment of species to the communities is according to fidelity, this is explained in supplement E1. Species that are diagnostic for one community are in dark grey, species that are diagnostic for a group of communities are in light grey. Layer: h: herb, m: moss.

Beilage S2. Komplette Stetigkeitstabelle der Vegetationsaufnahmen von eigener Feldarbeit, mit prozentualen Stetigkeitswerten. Alle Vegetationsaufnahmen sind aus den Niederlanden und gehören zu den *Molinio-Arrhenatheretea*. Die Gesellschaften sind in Tabelle 1 im Artikel beschrieben. Zuordnung von Arten zu den Gesellschaften entsprechend der Treue (s. Anhang E1). Für eine Gesellschaft diagnostische Arten sind dunkelgrau, für eine Gruppe von Gesellschaften diagnostische Arten hellgrau hervorgehoben. Schichten: h: Kraut, m: Moos.

Communities / Pflanzengesellschaften:

- 1: Fragment of / Fragment des *Rhinantho-Orchietum morionis*
- 2: *Rhinantho-Orchietum morionis*
- 3: *Lolio-Cynosuretum*
- 4: *Arrhenatheretum elatioris typicum*
- 5: BC / Basalgemeinschaft *Bromus racemosus*-[*Alopecurus pratensis*]
- 6: *Fritillario-Alopecuretum pratensis*
- 7: *Sanguisorbo-Silaetum*
- 8: Transition between /Übergang zwischen *Sanguisorbo-Silaetum* & *Calthion palustris*
- 9: BC / Basalgemeinschaft *Rhinanthus angustifolius-Lysimachia vulgaris*-[*Calthion palustris*]
- 10: *Angelico-Cirsietum oleracei*
- 11: *Ranunculo-Senecionetum aquatici juncetosum articulati*

Community		1	2	3	4	5	6	7	8	9	10	11	
Number of relevés		4	4	15	28	42	10	10	8	3	2	33	
	Bromus racemosus	h	100	50	93	68	100	90	100	88	100	97	
	Bromus commutatus	h				21				100		3	
1	Hydrocotyle vulgaris	h	100	
	Leontodon taraxacoides subsp. taraxacoides	h	100	25	
	Juncus articulatus	h	75	25	7	.	.	20	.	.	.	3	
	Juncus conglomeratus	h	100	50	20	.	5	6	
	Rhytiadelphus squarrosus	m	100	50	13	4	33	9	
2	Danthonia decumbens	h	50	50	7	
	Luzula campestris	h	50	100	20	7	.	10	.	.	.	3	
	Carex ovalis	h	25	50	
	Ophioglossum vulgatum	h	25	75	7	33	.	.	
	Hypochoeris radicata	h	25	100	27	.	.	10	
	Orchis morio	h	.	100	
	Daelylorhiza majalis subsp. praetermissa	h	.	75	7	
	Carex flacca	h	.	50	
1-3	Odontites verna subsp. serotina	h	75	.	47	
	Juncus gerardi	h	50	.	13	
	Lotus tenuis	h	50	25	7	
	Sagina procumbens	h	50	25	7	
	Euphrasia stricta	h	50	25	27	
	Cynosurus cristatus	h	100	75	93	11	31	79	
	Agrostis capillaris	h	75	100	67	11	14	18	
	Rhinanthus minor	h	75	100	80	43	.	.	30	13	.	100	
	Carex nigra	h	25	50	20	.	2	3	
	Triglochin maritima	h	.	25	7	
	Ranunculus bulbosus	h	.	25	20	
	Vulpia bromoides	h	.	50	47	
	Ranunculus sardous	h	25	.	33	
	Potentilla anserina	h	.	.	27	7	7	3	
	Plantago major	h	.	.	27	4	7	.	10	.	.	.	
3-5	Bromus hordeaceus	h	.	50	73	71	62	30	.	25	33	12	
	Lolium perenne	h	75	50	100	96	93	30	20	75	67	79	
	Cirsium arvense	h	.	.	53	61	31	.	40	25	33	.	
	Hordeum secalinum	h	.	.	13	25	10	
	Elymus repens	h	.	.	60	64	5	.	30	13	100	6	
4	Daelylis glomerata	h	.	.	.	93	10	10	.	13	100	9	
	Achillea millefolium	h	.	.	.	57	2	.	10	.	.	.	
	Trisetum flavescens	h	.	.	.	71	7	.	20	13	.	18	
	Tragopogon pratensis subsp. pratensis	h	.	.	7	39	
	Equisetum arvense	h	.	.	.	43	2	.	.	13	.	3	
	Arrhenatherum elatius	h	.	.	.	79	14	30	.	.	100	50	
	Anthriscus sylvestris	h	.	.	7	32	5	
	Senecio jacobaea	h	.	.	.	21	
	Peucedanum carvifolia	h	.	.	.	21	2	
	Galium mollugo	h	.	.	.	29	.	.	20	.	.	.	
	Heracleum sphondylium	h	.	.	.	29	.	20	.	13	.	.	
	Potentilla reptans	h	.	.	.	39	5	.	20	38	33	.	
	Crepis biennis	h	.	.	.	46	17	.	30	63	33	6	
	Pimpinella major	h	.	.	.	14	.	.	10	.	.	.	
	Convolvulus arvensis	h	.	.	.	7	
	Eryngium campestre	h	.	.	.	7	
	Carex spicata	h	.	.	.	7	
	Medicago lupulina	h	.	.	.	7	
	6	Fritillaria meleagris	h	80
		Poa palustris	h	40
Leontodon autumnalis		h	.	100	67	4	2	100	30	.	.	.	
Ranunculus ficaria		h	.	.	.	7	7	80	.	25	.	100	
Eleocharis palustris		h	5	50	30	13	.	6	
Poa pratensis		h	25	25	27	36	2	70	.	.	.	3	
Senecio aquaticus		h	20	
Leontodon hispidus		h	20	
6-7	Festuca pratensis	h	.	.	7	61	26	100	100	25	100	100	
	Sanguisorba officinalis	h	50	70	.	.	.	
	Stellaria palustris	h	40	60	.	.	6	
	Centaurea jacea	h	.	.	.	29	5	50	80	.	33	27	
7	Symphitum officinale	h	.	.	.	14	7	30	80	25	100	6	
	Achillea ptarmica	h	60	.	33	.	
	Mentha aquatica	h	.	.	7	2	20	60	13	.	50	9	
	Silaum silaus	h	10	.	.	.	
6-10	Rumex crispus	h	25	.	27	21	33	20	80	88	33	21	
	Thalictrum flavum	h	2	.	60	25	67	6	
	Filipendula ulmaria	h	.	.	.	4	2	20	90	50	33	18	
	Galium palustre	h	50	.	.	.	7	60	80	38	.	100	
	Myosotis scorpioides	h	2	50	60	.	.	100	
	Carex acutiformis	h	90	.	.	100	
	Valeriana officinalis	h	2	10	30	.	67	100	
6-11	Carex acuta	h	.	.	.	4	.	80	40	100	33	100	
	Carex disticha	h	.	.	.	18	5	90	100	75	100	100	
	Calliergonella cuspidata	m	100	50	13	7	17	80	100	88	100	100	
	Equisetum palustre	h	.	.	.	14	43	50	100	88	100	100	
	Lychmis flos-cuculi	h	75	75	33	4	5	70	80	63	67	100	
	Lysimachia nummularia	h	.	.	.	29	2	70	90	25	67	50	
	Cardamine pratensis	h	50	75	60	68	83	100	100	100	100	100	
	Polygonum amphibium	h	.	.	.	21	52	70	100	63	67	61	
	Lathyrus pratensis	h	.	.	.	46	21	60	100	75	100	100	
	Phalaris arundinacea	h	.	.	.	4	48	50	40	38	67	64	
	Agrostis canina	h	100	25	.	.	2	70	.	.	.	39	
	Vicia cracca	h	50	50	53	39	12	30	80	63	100	100	
	Caltha palustris	h	30	.	38	.	100	
	Phragmites australis	h	100	75	27	7	5	40	60	88	100	100	
	Carex riparia	h	20	13	.	9	
	9	Lysimachia vulgaris	h	100	.	3
	10	Juncus acutiflorus	h	10	.	.	.	100
		Cirsium oleraceum	h	50
Crepis paludosa		h	100	
Primula elatior		h	100	
Stellaria uliginosa		h	100	
Plagiomnium affine		m	100	
11	Equisetum fluviatile	h	.	.	.	4	5	10	.	.	.	100	
	Pedicularis palustris	h	100	
	Lotus pedunculatus	h	.	.	7	14	12	.	40	.	67	100	
	Cirsium palustre	h	100	.	.	.	19	100	
	Glyceria fluitans	h	33	20	.	13	.	50	
	Rhinanthus angustifolius	h	.	75	73	7	26	.	.	13	100	50	
	Myosotis laxa subsp. caespitosa	h	10	.	25	.	42	
	Ranunculus flammula	h	2	10	.	.	.	33	
	Carex hirta	h	.	.	.	18	38	.	.	.	33	55	
	Juncus effusus	h	100	25	27	.	19	.	10	.	.	79	
	Prunella vulgaris	h	.	25	7	.	2	30	30	.	33	55	
	Companions	Poa trivialis	h	100	75	100	96	100	70	100	100	67	100
		Cerastium fontanum subsp. vulgare	h	75	75	87	89	93	80	90	100	100	100
		Rumex acetosa	h	50	100	87	79	76	100	100	88	100	50
		Ranunculus acris	h	100	75	80	93	74	100	90	75	100	100
		Taraxacum officinale s.l.	h	25	75	60	89	95	80	80	100	100	50
		Ranunculus repens	h	75	.	40	68	98	80	100	100	.	100
		Brachythecium rutabulum	m	25	75	60	86	83	90	30	75	100	.
		Trifolium pratense	h	.	100	73	100	69	80	60	100	67	.
		Alopecurus pratensis	h	.	.	.	71	95	100	100	88	100	50
Trifolium repens		h	100	50	87	79	76	80	100	75	.	.	
Plantago lanceolata		h	50	100	93	96	50	90	90	88	6		

Supplement E1. Overview table with header data of relevés from our own field work.

Anhang E1. Übersichtstabelle mit Kopfdaten der Vegetationsaufnahmen von eigener Feldarbeit.

Relevé name	Date name (year/month)	X-coordinate (x 1000)	Y-coordinate (x 1000)	Length relevé (m)	Width relevé (m)	Surface relevé (m ²)	SW	Exposition	Inclination (degrees)	Height above NAP (AHN2)	Total cover (%)	Cover herb layer (%)	Cover moss layer (%)	Cover litter layer (%)	Cover bare soil (%)	Average height high herb layer (cm)	Average height low herb layer (cm)	Maximum height herb layer (cm)	Location (with parcel number)	Natura 2000-area	Cover B. racemosus	Phenology B. racemosus	Community	pH-H2O	pH-KCl	OM (%)	K (mg/kg)	K (mg/L)	Ca (mg/kg)	Ca (mg/L)	Pw (mmol/kg)	P205 (mg/L)	P-total (mmol/kg)	N-total (mmol/kg)	CN-ratio	Light (Ellenberg value)	Moisture (Ellenberg value)	Reaction (Ellenberg value)	Nitrogen (Ellenberg value)	GL9 (Wananciels value)	GVG (Wananciels value)	Humus profile (names exist only in Dutch)	Texture (above 20 cm, in Dutch)	Clay %	Silt %	Loam %	Aftermath grazing	Number of mowings	Management	Mowing date (first last date)	Number of plant species	
AB1	20150521	158.600	444.677	3	3	9		N	1	5.3	93	93	2	0	7	50	65	65	Anerongse Bovenpolder p1	66	7	begin flowering	8	7.61	7	13.5	179	2.36	724	9.55	4.5	8.3	26.7	439.3	10.99	6.71	6.82	5.94	5.28	72.15	37.01	Kleiboderm	matig lichte zavel	15	50	65	1	1	G1	25.6	34	
AB2	20150603	157.413	440.915	3	3	9		N	2	6.2	95	95	2	0	11.4	40	146	138	Anerongse Bovenpolder p6	66	4	mid flowering	8	7.55	7.11	10	134	2.37	656	9.3	7.1	11.9	338	28.7	439.3	10.99	6.71	6.82	5.94	5.28	72.15	37.01	Kleiboderm	zeer lichte zavel	14	50	65	1	1	G1	25.6	34
AB3	20150603	157.402	443.820	3	3	9		N	0	5.6	95	95	1	35	2	40	15	80	Anerongse Bovenpolder p1	66	2	mid flowering	4	7.38	6.6	8.2	134	2.43	247	4.55	6.6	16.5	20.7	249.0	10.34	6.87	5.4	6.37	5.82	88.96	52.36	Zure worstmull	matig lichte zavel	12	40	52	1	1	G1	15.6	24	
AB4	20080527	157.816	444.233	4	4	16		N	10	7.38	100	100	0	10	0	80	0	130	Anerongse Bovenpolder p1	66	4	mid flowering	4	7.67	7.2	10.4	190	2.61	872	11.99	3.6	6.9	20.3	260.5	14.26	7	5.36	6.27	6.05	86.4	51.74	Kalkwormmull	matig lichte zavel	14	45	50	1	1	G1	25.6	31	
ABa	20080526	158.996	444.412	4	4	16		N	0	7.03	100	100	1	10	0	70	0	0	Anerongse Bovenpolder p3	66	4	mid flowering	4	7.58	7.21	11.6	177	1.07	844	11.72	1.4	2.8	20.7	339.2	12.32	6.98	5.17	6.33	5.8	89.5	49.12	Kalkwormmull	matig lichte zavel	10	40	50	1	1	G1	25.6	33	
ABb	20080526	158.573	444.412	4	4	16		N	0	7.03	100	100	1	10	0	70	0	0	Anerongse Bovenpolder p3	66	4	begin flowering	4	7.58	7.21	11.6	177	1.07	844	11.72	1.4	2.8	20.7	339.2	12.32	6.98	5.17	6.33	5.8	89.5	49.12	Kalkwormmull	matig lichte zavel	10	40	50	1	1	G1	25.6	33	
ABc	20080526	158.713	444.453	4	4	16		N	0	6.99	100	100	1	0	0	70	0	0	Anerongse Bovenpolder p1	66	4	begin flowering	4	7.77	7.02	10.6	116	1.48	822	10.5	3.1	5.5	23.6	302.8	12.51	6.8	5.5	6.29	5.57	86.05	48.12	Kalkwormmull	zeer lichte zavel	12	40	52	1	1	G1	25.6	30	
ABF	20080526	159.169	444.500	4	4	16		N	0	6.36	100	100	0	10	0	80	0	110	Anerongse Bovenpolder p3	66	4	mid flowering	4	7.73	7.02	12.4	126	1.42	622	7.34	4.4	6.9	23.5	319.5	13.8	7.07	5.28	6.42	5.57	91.43	52.58	Kalkwormmull	matig lichte zavel	15	55	70	1	1	G1	25.6	28	
ABG	20080605	159.461	445.169	4	4	16		N	0	6.01	100	100	5	40	0	60	0	0	Anerongse Bovenpolder p5	66	3	mid flowering	5	5.84	4.83	12.5	272	4.04	214	3.18	6.1	12.4	18.8	326.7	13.63	6.82	6.26	5.82	5.37	78.05	39.58	Schrale zure worstmull	lichte klei	12	50	62	1	1	G1	15.6	31	
AH1	20100427	160.525	445.623	3	3	9		N	0	5.42	95	95	5	40	0	60	0	0	Achterberge Hooldalen p1	no	7	begin flowering	5	6.05	5.67	10.1	161	1.47	641	6.1	5.9	39.7	58.6	16.42	6.51	6.12	75.6	61.6	Zure worstmull	matig lichte zavel	12	50	62	1	1	G2	15.6	31				
AH2	20100427	170.256	444.515	3	3	9		N	0	5.19	98	98	3	40	15	70	30	100	Achterberge Hooldalen p2	no	7	begin flowering	5	5.76	5.1	30.9	95	1.08	380	4.33	35.1	5.5	64.7	84.67	13.04	6.71	6.29	5.81	5.79	79.03	43.08	Moererdood	zeer lichte zavel	12	45	57	1	1	G2	15.6	21	
AH3	20100427	169.827	444.459	6	4	24		N	0	5.29	97	97	5	35	0	70	15	10	Achterberge Hooldalen p4	no	3	end flowering	5	5.56	5.1	33.9	102	1.13	269	2.99	6.3	9.6	40.6	967.9	12.52	7.06	6.68	5.44	5.33	71.41	35.13	Kleiboderm	zeer lichte zavel	12	40	52	1	1	G2	15.6	26	
AH4	20100427	170.082	444.818	5	5	25		N	0	5.18	100	100	1	40	0	70	25	110	Achterberge Hooldalen p5	no	5	end flowering	5	5.37	4.95	36.7	401	4.62	289	3.33	10.4	16.5	52.9	1190.3	11	6.7	6.04	5.92	5.67	86.23	47.84	Schrale moererdood	matig lichte zavel	14	50	64	1	2	G2	15.6	12	
AH5	20100427	170.298	444.507	5	5	25		N	0	5.14	100	100	0	40	0	90	20	120	Achterberge Hooldalen p6	no	6	end flowering	5	5.37	4.64	37.7	284	3.74	284	3.31	7.7	12.4	44.2	115.1	11.43	6.55	6.08	5.83	6.06	80.22	42.51	Moererdood	zware zavel	14	55	69	1	2	G2	15.6	20	
AH6	20100426	170.345	444.757	5	5	25		N	0	5.12	100	100	0	40	0	55	20	90	Achterberge Hooldalen p3	no	6	end flowering	5	5.22	4.64	27.7	141	1.98	114	1.6	4.3	8.3	29.8	655.3	15.09	6.63	6.35	5.38	5.44	81.6	43.36	Moererdood	zware zavel	18	60	78	1	2	G2	15.6	15	
BB1	20130617	132.110	425.131	3	3	9		NW	0	3.19	95	95	1	25	10	70	20	100	Bakelse Benedewaard zuid	71	4	end flowering	4	7.87	7.09	10.1	117	1.83	708	11.11	3.2	6.9	20.8	253	14.24	6.74	5.46	6.52	5.77	89.77	51.1	Nesvaagmull	matig lichte zavel	16	40	56	0	0	G0	15.6	32	
BR2	20130617	132.082	425.139	3	3	9		NW	0	3.19	95	95	1	25	10	70	20	100	Bakelse Benedewaard zuid	71	5	end flowering	4	7.7	7.24	11.1	169	2.61	835	12.87	4.5	9.6	22.6	326.6	11.99	6.75	5.74	6.4	5.64	79.65	45.76	Kalkwormmull	matig lichte zavel	14	50	64	0	0	G0	15.6	32	
BR3	20130617	132.088	425.077	3	3	9		NW	0	3.05	95	95	1	25	10	70	25	100	Bakelse Benedewaard zuid	71	5	end flowering	4	7.7	7.24	11.1	169	2.61	835	12.87	4.5	9.6	22.6	326.6	11.99	6.75	5.74	6.4	5.64	79.65	45.76	Kalkwormmull	matig lichte zavel	14	50	64	0	0	G0	15.6	32	
BB4	20130618	132.170	425.444	4.5	2	9		SSE	28	2.58	90	90	3	5	30	75	25	100	Bakelse Benedewaard noord	71	5	end flowering	4	7.86	7.34	6.3	112	1.49	608	8.1	9.8	17.9	18.9	98.2	23.2	0.9	5.1	7.13	5.34	88.44	49.66	zandige Nesvaagmull	kliegn zavel	8	35	43	0	0	G0	15.6	34	
BB5	20130618	132.165	425.453	3	3	9		N	0	3.01	90	90	4	10	20	60	10	80	Bakelse Benedewaard noord	71	0	-	4	7.61	7.26	6.8	229	2.96	519	6.71	17.8	31.1	27.3	86.7	27.91	7.13	4.88	6.78	5.57	93.51	59.84	zandige Nesvaagmull	kliegn zavel	7	35	42	0	0	G0	15.6	28	
BG1	20130525	136.674	440.903	3	3	9		NW	1	3.11	95	92	30	25	5	40	25	60	Bolgeren oost	no	5	begin flowering	5	5.61	4.58	14.6	587	8.48	325	4.7	7.6	15.1	19.2	40.9	12.93	6.59	6.6	6	6.13	81.01	41.94	Bekvaagmull	zware zavel	24	65	89	1	2	G2	20.5	22	
BG2	20130525	136.693	440.915	3	3	9		NW	0.5	3.09	95	95	30	25	5	40	25	60	Bolgeren oost	no	5	begin flowering	5	5.81	4.84	19.2	415	5.07	278	3.4	7.6	15.1	29.2	40.9	12.93	6.59	6.6	6	6.13	81.01	41.94	Bekvaagmull	zware zavel	24	65	89	1	2	G2	20.5	22	
BG3	20130525	136.157	441.183	3	3	9		SE	0.5	3.18	90	87	20	10	5	60	30	90	Bolgeren perceel 1/6e	no	4	begin flowering	11	6.27	5.81	17.4	473	3.87	1848	6.9	14.8	23.1	419.9	14.75	6.84	6.87	6.3	6.15	63.6	79.93	45.77	Bekvaagmull	lichte klei	18	50	68	1	1	G1	25.6	37	
BG4	20130525	136.553	441.197	3	3	9		SE	0.5	3.11	93	92	3	10	8	50	25	80	Bolgeren perceel 1/6e	no	4	begin flowering	5	5.71	6.55	13.4	466	1.16	509	6.15	10.8	17.9	34.1	171.3	12.85	6.86	6.33	6.03	5.6	73.74	40.32	Versteerde Kalkwormmull	zware zavel	18	50	68	1	1	G1	25.6	31	
BG5	20130526	135.711	441.462	3	3	9		N	0	0.23	85	80	10	20	12	50	12	50	Bolgeren perceel 1/34A	no	5	begin flowering	11	6.12	5.35																											