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Research article

Impact of land use on vegetation composition, diversity and potentially invasive, nitrophilous clonal species in a wetland region in Flanders

Benny De Cauwer, Dirk Reheul*

Department of Plant Production, Faculty of Bioscience Engineering, Ghent University, Coupure Links 653, 9000 Ghent, Belgium

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Abstract – In the framework of a nature conservation project in a wetland region of Meetkerke, Belgium, a comprehensive study was conducted to analyse and to compare species composition and diversity among wet grasslands under the six following types of agricultural land use: pastures used at high or low stocking rate, hayfields used at high or low mowing frequency, abandoned hayfields and hay pastures. The focus of the study was on the effects of grassland management on species diversity and on the restriction of occurrence of invasive clonal species. The results show that species importance was strongly related to grassland exploitation parameters and soil hydrological parameters, as shown by the ordination diagram drawn by canonical correspondence analysis (CCA). Species number and importance of non-leguminous dicotyledons were negatively correlated to intensity of use, N supply, water table depth and soil drainage. *Phalaris arundinacea*, an invasive species which might reduce species diversity, was better suppressed in grazed grassland than in mown grassland. *Phalaris arundinacea* and *Cirsium arvense* were most prevalent in abandoned hayfields. Grazing at low stocking rate was the best management technique to maximise plant diversity while restricting invasion by nitrophilous clonal species. Although species-rich and of high complementary value on a landscape scale, haylands mown at low frequency are at higher risk of invasion by clonal species.

species richness / invasive species / grazing / mowing / wetland conservation

1. INTRODUCTION

A large body of research has demonstrated how land drainage and agricultural intensification have led to a loss of wetland habitat and species, over the past 30 years or more (Thompson and Finlayson, 2001). In response, agricultural policy in Europe has sought to adopt land management procedures that integrate the need for a viable agriculture with the need for conservation and enhancement of biodiversity.

The distribution of species and plant communities within a wetland is primarily a function of the depth of the groundwater table (Spence, 1982). Moisture availability has often been shown to affect plant distribution and abundance in developing plant communities (Gosselink and Turner, 1978), thus indicating the impact of soil drainage. However, management largely affects biodiversity as well and may be more important than abiotic factors as a driver of grassland biodiversity (Weyand, 2005). Lowland grasslands in Flanders differ in their type of management (grazing, aftermath grazing, mowing) and their intensity of use (N supply, stocking rate, cutting frequency, timing of cuttings).

Most of the above-mentioned biodiversity drivers have been addressed separately in small-scale studies (see Weyand, 2005) but do not consider the potential threat of invasive species, whether native or not. Invasive species present a major challenge to ecological conservation (Williamson, 1996). These species threaten natural communities directly by competing with and displacing desired native vegetation, decreasing species diversity, and changing the structure and functioning of some habitats. Houlahan and Findlay (2004) concluded that the key to the conservation of wetland biodiversity might be to discourage the spread of diversity-threatening community dominants, regardless of their geographical origin. Therefore, against a background of maximisation of plant diversity in wet grasslands, this study focused on the potentially invasive, nitrophilous clonal species *Phalaris arundinacea*, *Elytrigia repens* and *Cirsium arvense*. These species are able to outcompete less competitive and rare species in wetland communities as shown by, e.g. Galatowitsch et al. (2000) and Schooler et al. (2006) for *P. arundinacea*, Grace et al. (2001) for *E. repens*, and Stachion and Zimdahl (1980) and Nuzzo (1997) for *C. arvense*. The threat of these species results from both their nitrophilous status as well as from their clonal growth. Kolb et al. (2002) found that high nutrient

* Corresponding author: Dirk.Reheul@Ugent.be

availability is strongly correlated with invasion success in grasslands. As wetlands receive a large portion of N additions to the landscape via surface runoff and groundwater, these nitrophilous clonal species are a particular threat in wetland communities (Brinson and Malvarez, 2002). Clonal growth predominates in invasive perennial weeds (Boose and Holt, 1999; Heger and Ludwig, 2003). Advantages associated with the reliance on clonal growth for population expansion are (Lambrecht-McDowell and Radosevich, 2005): (1) increased potential to access unevenly distributed resources, (2) increased capacity to recover from stresses, (3) rapid spread and competitive exclusion of other species, and (4) ability to change the spatial and/or temporal distribution of ramets.

The objectives of this study were (1) to explore the species composition and diversity of 99 wet grasslands, located in the lowland region "Meetkerkse Moeren" in Meetkerke (Belgium) in relation to various environmental conditions and types of grassland use, and (2) to determine the impact of land use on nitrophilous clonal species as potential invaders. The "Meetkerkse Moeren", a former peat-cutting region in the Middle Ages, is a contiguous mosaic of wet pastures, hay pastures and hay meadows which will be rehabilitated by reestablishment of proper hydrology. We studied grassland parcels that were mown, grazed or abandoned. This preliminary analysis may suggest management guidelines for preserving and enhancing biodiversity while preventing the competition of potentially invasive, nitrophilous clonal species.

2. MATERIALS AND METHODS

2.1. Study area

The study area consists of 140 hectares of contiguous grassland parcels in the wetland region of Meetkerke, a flat, low-lying area located near Brugge (province of West Flanders, Belgium, 51°15'E, 3°08'N), on a slightly acidic peaty (carbon level between 5 and 25%) sandy soil with a reduction horizon at a maximum depth of 1 m. The elevation of the area varies from 0.73 to 2.45 m above sea level. Ditch water level is maintained around 0.40 m above sea level. Over the last three decades, the mean air temperature was 9.1 °C and the mean annual precipitation was 708 mm (K.M.I. meteorological station in Beitem located near Brugge).

Rectangular grassland parcels are separated by water-filled ditches connected to broader watercourses. Most parcels are structurally homogeneous and exhibit a pattern of 0.2–0.3 m deep parallel drainage trenches (grips) set circa 5–10 m apart with a flat area between them. These small trenches carry only water during winter and early spring. Parcels are partly flooded in winter.

The study area encompassed 99 semi-natural permanent grassland parcels with a diverse grassland use, N supply, vegetation composition, water table depth and drainage class. The studied parcels were not resown for a minimum of ten years. All parcels were at least 0.5 ha. Parcels were relatively homogeneous in terms of vegetation composition, soil drainage class, elevation and water table depth.

2.2. Vegetation data

Botanical data of vascular plants were collected in 2006 during the months of June and July. Each parcel was recorded once. Hayfields with large species were recorded 30 days after mowing. The collected vegetation data comprised species presence, species importance and species number. The botanical composition of the vegetation was recorded following the combined frequency-rank method of De Vries (1948). The combined frequency and rank determination was carried out in the field. For each species, species importance (I, expressed in %) was derived from their presence in sampling quadrats (10 cm × 10 cm). Sampling quadrats were distributed over the rectangular parcels at regular intervals along their diagonals and lines of symmetry. Sampling density was 120 quadrats per hectare. A sampling density of 120 quadrats per hectare was appropriate for an accurate estimation of species number per parcel: potential losses of unrecorded species were small (between 0 and 5% of total species numbers) as shown in a preliminary study on a species-poor and species-rich parcel in the study area. Presence of all species (species presence) within the sampling quadrat was noted. According to their contribution to total biomass, species were ranked as 1st, 2nd or 3rd by visual estimation. The total importance (I_{tot}) of a species in a particular parcel was calculated as a sum of products. Products were the number of times a species ranked first in all sampling quadrats multiplied by a weighting factor 3, the number of times a species ranked second multiplied by a factor 2 and the number of times a species ranked third multiplied by a factor 1. The percentage of importance of an individual species in that particular parcel (I%) was then calculated as the rate of I_{tot} of that species to the sum of I_{tot} of all occurring species. So, the percentage of importance of a species is a measurement of its contribution to the total biomass and is based on the visual ranking of the biomass contributed by the various plant species within each quadrat. Taxonomy follows van der Meijden (2005).

Species were assigned to five plant categories: (i) non-leguminous dicotyledons; (ii) leguminous dicotyledons; (iii) grasses; (iv) rushes; (v) sedges. The I% of a plant category was calculated by adding the I% of all contributing species of that group. The important invasive species *Phalaris arundinacea*, *Elytrigia repens* and *Cirsium arvense* were considered separately.

For each grassland parcel, species number (defined as the number of species per parcel) was calculated as the number of species that were present in at least one sampling quadrat.

2.3. Explanatory variables

Data on nitrogen (N) application were obtained through direct personal interviews with the farmers. N supply was scored on a three-point scale (0 = no N supply; 1 = 0–100 kg N ha^{-1}; 2 = 100–200 kg N ha^{-1}). These N applications correspond with the maximum legally authorised nitrogen dressing of each grassland parcel. N was mostly supplied by slurry injection

Table I. Drainage morphological attributes of drainage classes and corresponding five-point scale.

Drainage class		Depth (in cm) to:	
Drainage symbol	Point scale	rust	reduction layer
f	1	0–20	40–80
e/f	2		
e	3	20–40	> 80
d/e	4		
d	5	40–60	–

in spring or early summer. Within each parcel, N supply had not changed for at least five years.

The soil drainage class of each parcel was derived from the pre-existing soil drainage map (VLM, 2002) based on the visual examination of soil core borings taken at a density of 10 randomly selected auger holes per hectare. Drainage classes were assigned according to the Belgian soil classification system on the basis of the depth and depth-duration of the local water table. This was assessed by examining the type, degree and depth of soil mottling and gleying in the sampled soil. Five classes (d, d/e, e, e/f, f) were used to define soil drainage characteristics. Drainage morphological attributes of drainage classes d, e and f are given in Table I. Drainage classes d/e and e/f are intermediate classes between d and e and between e and f, respectively. The nominal variable drainage class was treated as a semi-quantitative variable by assigning a five-point scale to the drainage symbols, as indicated in Table I. Elevation was measured in centimetres above sea level (a.s.l.) and extracted from a digital elevation model of Flanders, made with the technique of laser altimetry by the Ministry of the Flemish Community (VLM, 2002). Elevation measurements were taken on a semi-regular grid with a mean distance between measurements of 5–10 m.

Water table depth on 15 April, and minimum and maximum water table depth (expressed as cm below soil surface) are average annual values over the three-year period 2002–2004. Measurements were taken every two weeks in 29 observation wells. These observation wells were evenly distributed over the study area, making sure different elevations were sampled. Water table depths of the 99 parcels were estimated by linear interpolation using datasets of bi-weekly recorded water table depths from nearby observation wells.

Agricultural grassland use was considered as a combination of management type (mowing and/or livestock grazing) and intensity (low or high intensity) of grassland use. Intensity was determined by stocking rate for grazing and cutting frequency for mowing. Data on stocking rate and cutting frequency in the years previous to this research were obtained through direct personal interviews with the farmers. The following six classes of grassland use were considered: (1) pastures used at high intensity, continuously grazed by beef and dairy cattle, exceptionally by horses, at a stocking rate of 3–4 livestock units (L.U.) per ha during the grazing season starting in April until the end of October (±190 days); (2) pastures used at low intensity, i.e. used as (1) but grazed at a stocking rate of a maximum of 2 L.U. ha^{-1}; (3) hay pastures, mown in June followed by aftermath grazing in late summer at a stocking rate of a maximum of 2 L.U. ha^{-1}; (4) hayfields used at high intensity, i.e. cut two to four times per year; (5) hayfields used at low intensity, i.e. cut once a year and (6) abandoned hayfields cut less than once per two years. Land use of each parcel had not changed for at least five years.

2.4. Statistical analysis

Differences in species number, species importance, N supply, water table depths (maximum, minimum, depth on 15 April), soil drainage class and elevation between the classes of grassland use were tested using a one-way ANOVA with unequal replications (SPSS11 for Windows); differences were tested for significance using least significant difference (LSD) tests at the 0.05 level. Effects of environmental quantitative variables were further analysed by means of a linear regression followed by t-tests.

Canonical correspondence analysis (CCA) was conducted to explore general patterns in the species composition of the grassland vegetations in the study area and to study the relationship between the species composition and explanatory variables (Jongman et al., 1995). The CCA analyses were performed with CANOCO 4 software. A preliminary analysis of the data by detrended correspondence analysis (DCA) revealed the lengths of gradients for the first and the second DCA axes to be 3.5 and 3.4, respectively. Therefore, an analysis with the unimodal response model (i.e. CCA) was preferred over an analysis with the linear response model (i.e. RDA).

Seven explanatory variables were used in the analysis: the six ordinal environmental variables N supply, soil drainage class, elevation, minimum water table depth, maximum water table depth and water table depth on 15 April, and one nominal variable, agricultural grassland use.

The default options of CANOCO software were applied except that all percentage data of individual species were $\log_{10}(x + 1)$ transformed and rare species were downweighted.

3. RESULTS AND DISCUSSION

The distribution of the different grassland types with their specific abiotic characteristics is given in Table II. Nutrient levels and soil hydrological parameters differed significantly between different types of grassland use (Tab. II). Pastures and hayfields used at high intensity usually received high N supply. So, the more N fertiliser was used, the more often hay meadows were cut and the higher the stocking rate in pastures. Compared with intensively used grasslands, hayfields and pastures used at low intensity showed a significantly lower N supply. Generally, there were no significant differences in water table depths and drainage class between abandoned hayfields and the other classes of grassland use. Classes of grassland use did not differ significantly in maximum water table depth. The water table depth on 15 April, which is mostly used in ecological studies, revealed only a small significant difference

Table II. Classes of grassland use in the studied area: means (±standard deviation) of environmental parameters, number of parcels and total surface area.

	Pasture high intensity	Pasture low intensity	Haypasture	Hayfield high intensity	Hayfield low intensity	Abandoned hayfield
Parameters (mean ± SD):						
Elevation a.s.l. (cm)	113.6 ± 36.0^{ab}	95.0 ± 21.0^{b}	94.3 ± 12.7^{b}	121.8 ± 35.4^{b}	109.4 ± 24.5^{ab}	135.0 ± 31.7^{a}
Water table depth (cm):						
on 15 April	85.1 ± 33.6^{b}	65.8 ± 23.4^{ab}	69.7 ± 14.4^{ab}	79.7 ± 40.6^{ab}	54.3 ± 29.4^{a}	72.8 ± 37.6^{ab}
maximum	109.5 ± 16.6^{a}	101.1 ± 14.2^{a}	102.5 ± 20.4^{a}	102.5 ± 15.3^{a}	100.3 ± 19.1^{a}	104.0 ± 8.8^{a}
minimum	22.8 ± 18.3^{b}	8.3 ± 11.7^{a}	17.9 ± 12.6^{ab}	13.8 ± 12.7^{ab}	13.3 ± 7.1^{ab}	13.3 ± 6.5^{ab}
Drainage class	2.62 ± 1.13^{a}	1.57 ± 1.25^{b}	2.62 ± 1.12^{a}	2.47 ± 1.12^{a}	1.63 ± 1.06^{b}	1.83 ± 1.60^{ab}
N supply	1.74 ± 0.62^{a}	0.95 ± 0.86^{b}	1.23 ± 0.83^{ab}	1.65 ± 0.61^{a}	0.38 ± 0.74^{c}	0.00 ± 0.00^{c}
Number of parcels	34	21	13	17	8	6
Total surface area (ha)	45.5	37.8	22.0	22.0	6.2	6.1

Means within a row followed by the same letter do not differ significantly according to Fisher's LSD test ($P < 0.05$).

between pastures used at high intensity and hayfields used at low intensity.

The studied area was species-rich, with 107 species recorded at least once in the studied area (Tab. III). The abbreviations in Table III correspond with the abbreviations used in the ordination diagram in Figure 1b. The first CCA axis (x-axis) in Figures 1a and 1b captured

7.1% of the variation in the species composition and 35.8% of the variation in the species-environment relation; the second CCA axis (y-axis) captured a minor portion of the variations (3.1% and 19.1%, respectively). The arrow for an explanatory variable depicted in the ordination diagram points in the direction of maximum change of that explanatory variable, and its length is proportional to the rate of change in this direction. N supply and drainage class are the environmental variables that were most strongly correlated with the first axis (Fig. 1a, b and Tab. IV). There was also a good positive correlation with hayfields used at low intensity. Agricultural land use played a key role in determining the species composition in the study area, both strong positive (pastures used at low grazing intensity) and strong negative (hayfields used at high intensity) correlations with axis 2 being observed. So, we can infer that the first axis is a N supply and drainage gradient and that the second axis is separating pastures used at low intensity from hayfields, hay pastures and pastures used at high intensity.

Figure 1a shows that species-poor plant communities were predominantly found in grasslands used at high intensity, irrespective of whether they were used as pastures or as hayfields. The species-richest communities were mainly found in hayfields used at a low cutting frequency followed by hay pastures. In general, species number was lowest in hayfields used at high intensity. Species–poor communities generally belonged to grasslands which received a high N supply. The highest species number was found in grasslands with no N supply.

Each arrow in Figure 1b determines an axis in the diagram and the species points must be projected onto this axis; the projection point of a species indicates the position of a species curve along an environmental variable. So, it can be deduced that *Bellis perennis*, *C. cristatus*, *Oenanthe fistulosa*, *Potentilla anserina*, *Cerastium fontanum, Ranunculus flammula and Hydrocotyle vulgaris* benefit from grazing at low grazing intensity, whereas *Poa annua*, *Lolium perenne*, *Taraxacum officinalis and Poa trivialis* mainly occur in pastures with high grazing intensity. *P. arundinacea*, *Phragmites australis*, *Arrhenatherum elatius*, *Anthoxanthum odoratum and Rumex acetosa* mainly occur in hayfields and not in pastures. *Carex disticha*, *Plantago lanceolata*, *Juncus conglomeratus*, *Cirsium palustris*, *Polygonum amphibium*, *R. acetosa* and *Achillea ptarmica* mainly occur in hayfields used at low cutting frequency. *L. multiflorum*, *Stellaria media* and *R. obtusifolius* are more abundant in hayfields used at high intensity. Tall forbs, e.g. *Cirsium palustris*, *Rumex crispus* and *P. amphibium*, and tall clonal grasses such as *Phalaris arundinacea* and *Phragmites australis* are typically found in abandoned hayfields.

The species *R. flammula, O. fistulosa, Cardamine pratensis*, *Ranunculus acris*, *Glyceria fluitans*, *Senecio aquaticus*, the moisture-loving *Juncaceae*, *e.g. Juncus articulatus and Cyperaceae*, *e.g. Carex nigra* and *Eleocharis multicaulis* prefer very moist grasslands on badly drained soils with low water table depth. Indicators of nutrient-poor habitats such as *Juncus* spp., *Hydrocotyle vulgaris*, *Oenanthe fistulosa*, *Ranunculus flammula*, *Anthoxanthum odoratum* and *Agrostis canina* were more abundant in grasslands without N supply. As expected, the nitrophilous species *Lolium* spp., *Poa annua*, *Taraxacum officinalis* and *R. obtusifolius* and the nitrophilous rhizomatous weeds *E. repens*, *C. arvense* and *U. dioica* were more abundant in grasslands under high N supply, whereas *Alopecurus geniculatus*, *Trifolium* spp. and *Holcus lanatus* were more abundant under moderate N supply.

The sward of the wetlands in Meetkerke was a mosaic of mesotrophic grassland communities typical of old and wet hay meadows and pastures. The biplot ordination diagram shows that haylands used at high intensity were predominantly *Lolium multiforum* grasslands whilst pastures used at high intensity were mostly *Lolium perenne* leys. As can be derived from the biplot ordination diagram, most haylands used at low intensity were the so-called sedge meadows. Pastures used at low intensity were mostly *Cynosurus cristatus* grasslands and *Potentilla anserina – Agrostis stolonifera* grasslands. The development of species-rich *Cynosurus cristatus* grassland

Table III. Present species ranked within plant categories: acronyms or numbers are added per species.

Plant species	Acronym/ number	Plant species	Acronym/ number	Plant species	Acronym/ number
Grasses:		**Leguminous**			
Agrostis stolonifera	2	**dicotyledons:**		*Lysimachia vulgaris*	*Lys vul*
Agrostis tenuis	*Agr ten*	*Trifolium pratense*	*Tri pra*	*Matricaria chamomilla*	*Mat cha*
Agrostis canina	*Agr can*	*Trifolium repens*	*Tri rep*	*Mentha aquatica*	6
Alopecurus geniculatus	*Alo gen*	*Lotus uliginosus*	*Lot uli*	*Myosotis palustris*	*Myo pal*
Alopecurus pratensis	*Alo pra*	*Medicago lupulina*	4	*Lythrum salicaria*	*Lyt sal*
Anthoxanthum odoratum	*Ant odo*	*Vicia cracca*	*Vic cra*	*Oenanthe fistulosa*	*Oen fis*
Arrhenatherum elatius	*Arr ela*	*Vicia hirsuta*	*Vic hir*	*Plantago lanceolata*	*Pla lan*
Bromus racemosus	1			*Plantago major*	*Pla maj*
Cynosurus cristatus	*Cyn cri*	**Non-leguminous**		*Polygonum lapathifolium*	*Pol lap*
Deschampsia cespitosa	*Des ces*	***dicotyledons:***		*Polygonum amphibium*	*Pol amp*
Dactylis glomerata	*Dac glo*	*Achillea ptarmica*	*Ach pta*	*Polygonum aviculare*	*Pol avi*
Elytrigia repens	*Ely rep*	*Angelica archangelica*	*Ang arc*	*Polygonum persicaria*	*Pol per*
Festuca arundinacea	*Fes aru*	*Anthriscus sylvestris*	*Ant syl*	*Potentilla anserina*	*Pot ans*
Festuca rubra	*Fes rub*	*Artemisia vulgaris*	*Art vulg*	*Prunella vulgaris*	*Pru vul*
Glyceria maxima	*Gly max*	*Bellis perennis*	*Bel per*	*Ranunculus acris*	*Ran acr*
Glyceria fluitans	*Gly flu*	*Calystegia sepium*	*Cal sep*	*Ranunculus flammula*	*Ran fla*
Holcus lanatus	*Hol lan*	*Capsella bursa-pastoris*	*Cap bur*	*Ranunculus repens*	*Ran rep*
Hordeum secalinum	*Hor sec*	*Cardamine pratensis*	*Car pra*	*Ranunculus sardous*	*Ran sar*
Lolium multiflorum	*Lol mul*	*Centaurea jacea*	*Cen jac*	*Ranunculus sceleratus*	*Ran sce*
Lolium perenne	*Lol per*	*Cerastium fontanum*		*Rorippa sylvestris*	*Ror syl*
Phalaris arundinacea	*Pha aru*	subsp. *vulgare*	*Cer fon*	*Rubus fruticosus*	*Rub fru*
Phleum pratense	5	*Chenopodium album*	*Che alb*	*Rumex acetosa*	*Rum ace*
Phragmites australis	*Phr aus*	*Cirsium arvense*	*Cir arv*	*Rumex crispus*	*Rum cri*
Poa annua	*Poa ann*	*Cirsium palustre*	*Cir pal*	*Rumex obtusifolius*	*Rum obt*
Poa pratensis	*Poa pra*	*Coronopus didymus*	*Cor did*	*Sagina procumbens*	*Sag pro*
Poa trivialis	*Poa tri*	*Epilobium hirsutum*	*Epi hir*	*Samolus valerandi*	*Sam val*
		Epilobium montanum	*Epi mon*	*Senecio aquaticus*	*Sen vul*
Sedges:		*Eupatorium cannabinum*	*Eup can*	*Sonchus arvensis*	*Son arv*
Carex acuta	*Car acu*	*Galeopsis tetrahit*	*Gal tet*	*Stachys palustris*	*Sta pal*
Carex disticha	*Car dis*	*Galinsoga parviflora*	*Gal par*	*Stellaria graminea*	*Ste gra*
Carex hirta	*Car hir*	*Galium aparine*	*Gal apa*	*Stellaria media*	*Ste med*
Carex nigra	*Car nig*	*Galium palustre*	*Gal pal*	*Symphytum officinale*	*Sym off*
Carex riparia	*Car rip*	*Geranium dissectum*	*Ger dis*	*Tanacetum vulgare*	*Tan vul*
Eleocharis multicaulis	*Ele mul*	*Glechoma hederacea*	*Gle hed*	*Taraxacum officinale*	*Tar off*
		Hydrocotyle vulgaris	*Hyd vul*	*Torilis japonica*	*Tor jap*
Rushes:		*Iris pseudacoris*	*Iri pse*	*Urtica dioica*	*Urt dio*
Juncus articulatus	*Jun art*	*Lamium purpureum*		*Veronica persica*	*Ver per*
Juncus bufonius	3	var. *purpureum*	*Lam pur*		
Juncus conglomeratus	*Jun con*	*Leontodon autumnalis*	*Leo aut*		
Juncus effusus	*Jun eff*	*Lychnis flos-cuculi*	*Lyc flo*		

communities is often targeted by nature conservationists during the restoration of botanically-rich grazed wetlands. *Cynosurus* grasslands were found in parcels receiving low N supply; they grew mostly on moderately to poorly drained wet soils and were grazed at low stocking rate.

The species number differed clearly in the six classes of grassland use (Tab. V). Grasslands used at high intensity were species-poorer than grassland used at low intensity, irrespective of whether they were grazed or mown. The grasslands with the highest species number were hayfields used at low intensity, followed by abandoned hayfields and pastures used at low intensity. The species number of hay pastures was intermediate between species numbers of pastures and hayfields. The species-poorest communities were found in hayfields used

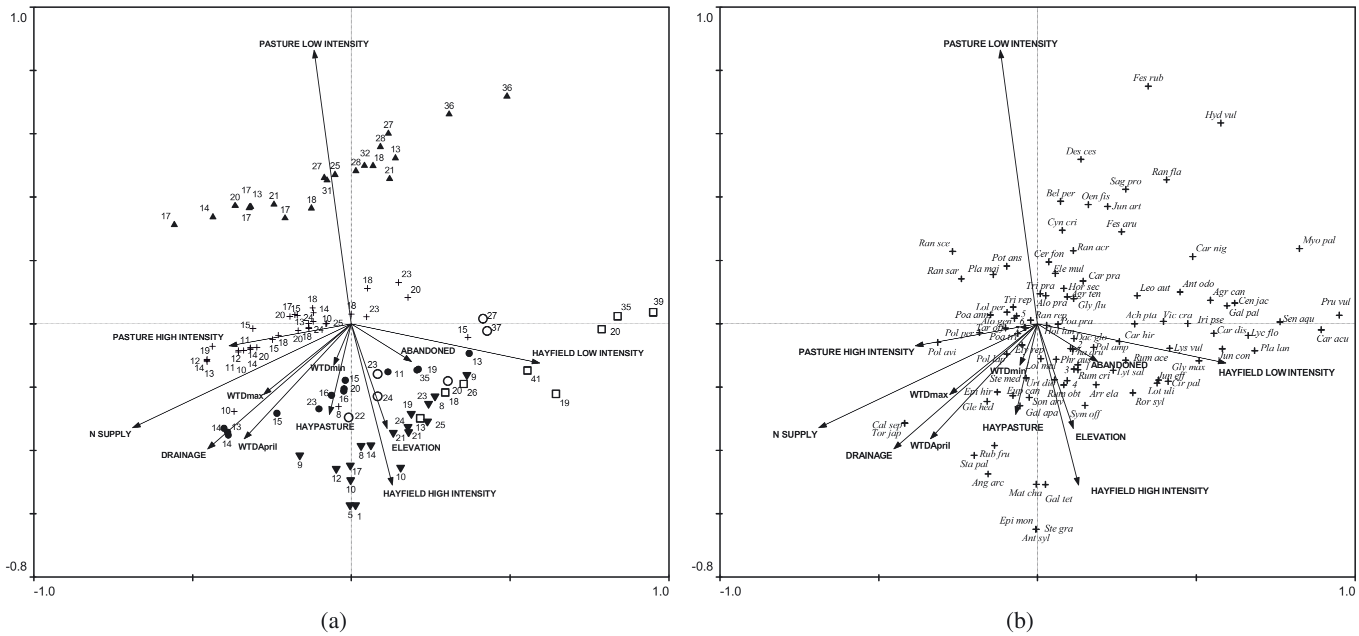

Figure 1. Canonical correspondence analysis: ordination diagram based on species composition of 99 parcels. Explanatory variables are represented by arrows. Symbols represent parcels and species number is plotted for each parcel. Parcels are classified by land use: pastures used at high intensity (+), pastures used at low intensity (▲), hay pastures (●), hayfields used at high intensity (▼), hayfields used at low intensity (□), abandoned hayfields (○). WTDmax: maximum water table depth; WTDmin: minimum water table depth; WTDApril: water table depth on 15 April. (b) Canonical correspondence analysis: ordination diagram based on species composition of 99 parcels. Explanatory variables are represented by arrows, species by points. Species names are shown by acronyms or by numbers (see Tab. III). WTDmax: maximum water table depth; WTDmin: minimum water table depth; WTDApril: water table depth on 15 April.

Table IV. Canonical correspondence analysis: correlation coefficients of explanatory variables with the first two axes of CCA.

Environmental variables	Correlations	
	Axis 1	Axis 2
Elevation	0.1129	–0.3303
N supply	–0.6887	–0.3291
Drainage class	–0.4524	–0.3948
WTDmax	–0.2764	–0.2229
WTD April	–0.3370	–0.3638
WTDmin	–0.0552	–0.1308
Pasture high intensity	–0.3845	–0.0695
Pasture low intensity	–0.1173	0.8636
Haypasture	–0.0686	–0.2862
Hayfield high intensity	0.1288	–0.5096
Hayfield low intensity	0.5929	–0.1237
Abandoned hayfield	0.1889	–0.1191

at high intensity followed by pastures used at high intensity. Although grazing wetlands at high stocking rates reduced species number compared with mowing at low intensity, no loss of biodiversity was found in the case of grazing at low stocking rates. According to Esselink et al. (2000), livestock grazing with low to moderate stocking rates allows for selective grazing, which may induce a vegetation of enhanced botanical and structural diversity. The heterogeneity brought about by cow prints and heterogeneously distributed urine and dung patches, and uneven seed dispersal by animals, offers a higher diversity of available ecological niches (Duelli and Obrist, 2003). This may promote species richness provided the pastures are not intensively grazed, offering plants with limited capacity the opportunity for regrowth and survival.

Contrary to the results of Kahmen and Poschlod (2004), species number in abandoned hayfields was not significantly smaller than in hayfields used at low intensity, despite the thick layer of dead plant material in the abandoned parcels. Most of these abandoned hayfields were only recently abandoned and were still sporadically mown. In the longer term, species number will probably further decrease due to the higher mortality of sub-canopy plants (Jacquemyn et al., 2003).

Since land use categories only slightly differed in the pedohydrological parameters (see Tab. II), these parameters are not expected to interfere substantially with the observed responses of species diversity and community composition to agricultural land use.

Greater percentages of sedges and rushes (Tab. V) were significantly higher in hayfields, used at low or very low intensity, than in pastures and hay pastures. The importance of non-leguminous dicotyledons was significantly lower in grasslands used at high intensity than in grasslands used at low intensity and in abandoned hayfields. The importance of grasses was significantly lower in hayfields used at low or very low intensity than in pastures and hay pastures. Leguminous dicotyledons were significantly more important in pastures than in hayfields, irrespective of the intensity of grassland use.

The importance of *P. arundinacea* (Tab. V), was significantly lower in pastures than in abandoned or mown hayfields.

Table V. Species number, importance (%) of plant categories and importance (%) of three invasive clonal species for different classes of grassland use (standard deviation in brackets).

	Pasture high intensity	Pasture low intensity	Haypasture	Hayfield high intensity	Hayfield low intensity	Abandoned hayfield
Species number	16.21[b]	22.67[a]	17.23[b]	13.88[b]	26.38[a]	25.50[a]
	(4.58)	(7.28)	(6.25)	(7.25)	(10.64)	(6.09)
Importance (%) of plant categories:						
Non-leguminous dicotyledons	0.87[d]	1.16[bc]	1.16[bc]	0.92[cd]	1.41[ab]	1.49[a]
	(0.35)	(0.30)	(0.24)	(0.35)	(0.11)	(0.18)
Leguminous dicotyledons	0.77[a]	0.81[a]	0.30[b]	0.16[b]	0.20[b]	0.14[b]
	(0.36)	(0.26)	(0.28)	(0.22)	(0.28)	(0.15)
Monocotyledons	1.93[ab]	1.88[b]	1.92[ab]	1.95[a]	1.80[c]	1.79[c]
	(0.04)	(0.07)	(0.05)	(0.04)	(0.10)	(0.10)
Rushes (*Juncaceae*)	0.01[b]	0.07[b]	0.03[b]	0.02[b]	0.32[a]	0.34[a]
	(0.03)	(0.12)	(0.10)	(0.06)	(0.42)	(0.23)
Sedges (*Cyperaceae*)	0.04[b]	0.18[b]	0.09[b]	0.04[b]	0.71[a]	0.55[a]
	(0.08)	(0.28)	(0.21)	(0.09)	(0.56)	(0.45)
Importance (%) of clonal species:						
Phalaris arundinacea	0.11[c]	0.30[c]	0.57[b]	0.74[b]	0.79[b]	1.35[a]
	(2.14)	(0.32)	(0.43)	(0.59)	(0.45)	(0.28)
Elytrigia repens	0.43[b]	0.38[b]	0.81[a]	0.72[a]	0.67[ab]	0.47[ab]
	(0.31)	(0.34)	(0.34)	(0.50)	(0.57)	(0.52)
Cirsium arvense	0.10[b]	0.12[b]	0.07[b]	0.04[b]	0.26[a]	0.36[a]
	(0.04)	(0.05)	(0.06)	(0.05)	(0.08)	(0.09)

Means (± SD) within a row followed by the same superscript do not differ significantly according to Fisher's LSD test ($P < 0.05$) Importance percentages of species and plant groups are expressed as $\log_{10}(x + 1)$ transformed data.

Within hayfields the importance of *P. arundinacea* was significantly highest in abandoned hayfields. Paine and Ribic (2002) also found lower abundance of *P. arundinacea* in rotationally or continuously grazed pastures compared with unmown grassy vegetations. Pykälä (2005) showed a positive response of *P. arundinacea* to reduced mowing frequency and abandonment.

E. repens (Tab. V) was significantly less important in pastures than in hay pastures and hayfields used at high intensity. The negative response of *E. repens* to grazing was also reported by Raven (1986). Andresen et al. (1990) and Esselink et al. (2000) reported a positive response of *Elytrigia repens* to reduced grazing.

Hayfields with reduced cutting frequency (hayfields used at low intensity or abandoned) revealed a higher importance of *C. arvense* than pastures, hay pastures and hayfields used at high intensity (Tab. V). Pykälä (2005) also found the highest abundance in abandoned grasslands. Grekul (2003) reported that mowing once a year is ineffective in reducing the abundance of *C. arvense*.

Species number and importance of plant categories were not always significantly affected by soil hydrological parameters and N supply. Leguminous dicotyledons were negatively affected by drainage class and elevation. N supply, elevation, drainage class and water table depths were negatively related to species number and importance of non-leguminous dicotyledons (Tab. VI). Inversely, grasses were positively affected by these environmental variables. Rushes and sedges were negatively affected by N supply, drainage class and water table depth on 15 April.

The importance of the highly invasive species *P. arundinacea* was significantly reduced by high values of N supply and of soil hydrological parameters (Tab. VII). On the contrary, well-drained soils enhanced the importance of *E. repens*.

4. CONCLUSION

Species number and importance of plant categories were significantly affected by grassland use, N supply, water table depth and drainage class. Grazed or mown grassland used at high intensity was species-poorer than grazed or mown grassland used at low intensity. Non-leguminous dicotyledons, which are important for the biodiversity and aesthetic value of the grasslands, were more abundant in grasslands used at low intensity. Intensively used grasslands were grassier. Higher water levels were beneficial for species number. High N supply corresponded with the species-poorest grassland, irrespective of grassland use.

Nitrophilous clonal species are a particular threat in wetland grasslands for both nature conservationists and farmers.

Table VI. Relationships between environmental parameters, and species number and importance (%) of plant categories.

Parameters	Species number			Importance (%) of plant categories: Grasses			Non-leguminous dicotyledons			Leguminous dicotyledons			Sedges			Rushes		
	–/+	F	*P*	–/+	F	*P*	–/+	F	*P*	–/+	F	*P*	–/+	F	*P*	–/+	F	*P*
Elevation a.s.l. (cm)	–	12.78	**	+	10.38	**	–	5.57	*	–	7.06	**	–	1.39	NS	–	0.03	NS
Water table depth:																		
on 15 April (cm)	–	34.52	***	+	20.40	***	–	15.84	***	–	0.02	NS	–	8.90	**	–	12.10	**
maximum (cm)	–	4.63	*	+	7.95	**	–	5.04	*	–	3.22	NS	–	1.44	NS	–	0.12	NS
minimum (cm)	–	5.64	*	+	3.42	NS	–	2.84	NS	+	0.01	NS	–	1.77	NS	–	5.26	*
Drainage class	–	56.78	***	+	37.27	***	–	18.97	***	–	4.32	*	–	17.84	***	–	11.61	**
N supply	–	30.13	***	+	20.45	***	–	22.51	***	+	3.02	NS	–	17.79	***	–	16.26	***

Significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS non significant –/+: negative/positive relation of linear regression equation.

Table VII. Relationships between environmental factors and importance (%) of some nitrophilous clonal species.

Parameters	*Phalaris arundinacea*			*Elytrigia repens*			*Cirsium arvense*		
	–/+	F	p	–/+	F	p	–/+	F	p
Elevation a.s.l. (cm)	–	0.91	NS	+	0.01	NS	–	0.02	NS
Water table depth:									
on 15 April (cm)	–	9.04	**	+	0.37	NS	+	0.03	NS
maximum (cm)	–	6.48	*	+	0.03	NS	–	3.71	NS
minimum (cm)	–	4.35	*	+	0.04	NS	+	2.48	NS
Drainage class	–	8.64	**	+	10.16	**	+	0.11	NS
N supply	–	11.94	**	+	0.16	NS	–	6.53	NS

NS significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS non significant –/+: negative/positive relationship of linear regression equation.

The importance of *P. arundinacea*, a major invader of wetlands in temperate areas (Galatowitsch et al., 2000), was best reduced by grazing or aftermath grazing. Grazing also substantially restricted *Elytrigia repens*. In low quality grasslands, cattle prefer these species when stems and leaves are young and succulent, but leave these species once stems become old and tough. In abandoned hayfields, the importance of the tall species *Cirsium arvense* and *Phalaris arundinacea* was the highest.

The results suggest that grazing at low stocking rate may reduce the competitiveness of the invasive species *Phalaris arundinacea*, *Elytrigia repens* and *Cirsium arvense* and allow survival of many grasses, rushes, sedges and forbs. The high plant diversity of parcels grazed at low stocking rate was probably the result of the more open canopy created by grazing and the reduction in competitiveness from *Phalaris arundinacea* and other aggressive species by selective grazing. Mowing hayfields once or twice a year is ineffective in controlling these nitrophilous rhizomatous invaders. This is probably due to the stimulation of additional stem production and suppression of the competitiveness of surrounding vegetation lacking big creeping underground rootstocks. Although high frequency mowing (more than 5 cuttings per year) might probably be more effective by continuous depletion of assimilates bound in the root system, weak and irregular accessibility of wet haylands makes this management unfeasible.

Hobbs and Humphries (1995) state that managing ecosystems to reduce their vulnerability to invasions may be a more effective strategy for invasive species control over the long term. Hence, in order to maximise plant diversity while controlling invasive species, wetland grassland is better maintained by grazing at low stocking rate than by mowing at low cutting frequency. Although at the landscape level, extensively mown sedge meadows are certainly complementary to extensively grazed *C. cristatus* pastures, they might entrain a higher risk of getting invaded by aggressive clonal species, which might threaten species richness. As long as wetlands receive large N additions via surface runoff and groundwater, flower-rich sedge meadows might remain threatened because of their vulnerability to invasive clonal species.

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