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PLANT COMMUNITIES AND SPECIES RICHNESS OF THE CALCAREOUS GRASSLANDS IN SOUTHEAST BELGIUM

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ABSTRACT. — Calcareous grasslands are biodiversity hotspots in Western Europe. In Belgium, a number of phytosociological surveys have been realized in these habitats, but none covers the whole range of calcareous grasslands at the regional scale. The aim of this study was (i) to provide a synthesis of the floristic variation of calcareous grasslands of the Calestienne natural region using a uniform methodology; (ii) to relate floristic variation to environmental variables, and (iii) to characterize the specific diversity of the different grassland communities that occur in the study region. Seven different communities were identified with the TWINSPAN method. The originality of the grasslands on calcareous and calcareo-siliceous rocks was statistically confirmed. Significant differences for environmental variables were identified among the seven communities by a MANOVA. Main differences between communities were related to xericity and pH, although a north-south gradient was also identified. More xeric grasslands were located in the southern part of the study region while northern part was occupied by more mesophilous grasslands. Multiple regressions were used to describe the influence of the environmental conditions on plant species richness. The most mesophilous grasslands appeared to be the most species-rich while soil acidity negatively affected species richness.

KEY WORDS. — Belgium, calcareous grasslands, environmental variables, MANOVA, phytosociology, species richness, TWINSPAN.

INTRODUCTION

Calcareous grasslands of the *Festuco-Brometea* extend from southern Scandinavia to northern Spain, with their main distribution in the Atlantic, central-European and sub-Mediterranean regions (ROYER 1991). Calcareous grasslands are among the most species-rich habitats in Western Europe, both at local and regional scales (WILLEMS 2001, POSCHLOD & WALLISDEVRIES 2002). Belgium coincides with the northwestern boundary of the distribution of many grassland plant species, especially thermophilous ones such as *Teucrium montanum* and *Aster linosyris*, and of plant communities such as *Xerobromion* grasslands (WOLKINGER & PLANK 1981, ROYER 1991). Belgian calcareous grasslands are located at the border between the Atlantic and the Central European floristic regions (BUTAYE *et al.* 2005).

Since World War II, the extent of calcareous grasslands has dramatically decreased in Western Europe (DZWONKO & LOSTER 1998). Many surveys have been made during the last decades in order to determine the most suitable management and restoration measures (e.g., Bobbink *et al.* 1987, Delescaille *et al.* 1995, Köhler *et al.* 2005). In Belgium, ca. 100 hectares of calcareous grasslands have been restored since 1990. Many are still occupied by clear cuttings managed with the aim to restore typical grassland communities. The remaining grasslands are frequently dominated by *Brachypodium pinnatum* or *Bromus erectus* as a result of the absence of grazing or mowing. The total currently managed area is ca. 300 hectares (André & Vandendorpel 2004, Graux 2004). However, managing and restoring plant communities at a regional scale both require a good knowledge of the floristic composition and diversity variation in order to adapt management objectives to the local situation.

Despite numerous local descriptive studies of calcareous grasslands in Belgium (e.g., Duvigneaud 1982, Noirfalise & Dethioux 1982, Duvigneaud 1989), no large-scale general phytosociological synthesis, based on a large number of relevés and consistent statistical analyses, has been realized yet. Van Speybrouck *et al.* (1989) performed a classification of calcareous grasslands in Belgium, only using a limited number of relevés and focusing on the *Xerobrometum* types in its northern locations. Recently, Butaye *et al.* (2005) proposed a detailed study of the floristic variation of calcareous grasslands in Belgium, based on a large number of relevés. The geographic scale of this study, however, was limited to the Viroin valley (western part of the Calestienne natural region).

This paper presents a regional scale study of the floristic variation and diversity of calcareous grasslands across the Calestienne region, with the exception of the Viroin valley already studied by Butaye *et al.* (2005). It differs from previous studies because: (i) we covered the whole geological range of calcareous grasslands; (ii) the large scale considered allowed to take into account biogeographical variability; (iii) we based our analysis on a large number of relevés with an undirected relevé selection.

Our aims were (i) to provide a synthesis of the floristic variation of calcareous grasslands of the Calestienne using a uniform methodology in order to classify grasslands into different communities; (ii) to relate this synthesis to environmental variables and (iii) to characterize the species diversity of the different grassland communities identified.

METHODS

Study region

The studied grasslands were mainly located in the Calestienne region (Belgium), which is characterized by Devonian geological formations consisting of limestone or calcareo-siliceous rocks, the latter supporting soils with higher acidity. The study region also included locally occurring Cretaceous chalk formations near Visé (50°45'N – 5°40'E), and one small Carboniferous calcareous area near Theux (50°32'N – 5°49'E). These two localities were included because of the expected specific floristic composition of their grasslands. The study region is characterized by a hilly landscape, with isolated calcareous grasslands in a matrix of forest and arable land.

Data collection

All existing calcareous grassland patches were first localized through literature and recent ortho-rectified vertical aerial photographs. In the region near Rochefort, grassland locations were obtained from a previous survey (Bottin *et al.* 2005). A representative subset of patches was selected by stratified sampling, using geographical sub-regions as strata. This subset was representative of the different geological formations present and of the different patch sizes. Within the selected patches, transects were established on a slope gradient. Along these transects, one-meter square plots were located every 20 meters, with a minimum of three plots and a maximum of ten plots per patch. When patch configuration (shape or size) did not allow to establish a transect, plots were randomly located. Plots falling in non-grassland vegetation were moved to the grassland zone nearest from their initial location. A total of 477 plots were established (see Appendix 1).

During the 2004 vegetation period, the cover of all higher plant species in the one-meter square plots was recorded using the Braun-Blanquet (1932) scale. A total of 245 plant species were found. Nomenclature followed Lambinon *et al.* (2004). Species were classified following their preference for phytosociological alliances (see Bisteau & Mahy 2005 for details). Environmental variables were derived directly from field observations for each plot. They included (i) biogeographical variables: Belgian Lambert coordinates and altitude; (ii) topographic and soil variables: slope (degrees), mean soil depth (three measurements) and mean soil pH estimated with a Hellige pH-indicator (two measurements); (iii) community structure variables: maximum height of vegetation, bare soil percentage, moss cover, herbaceous vascular species cover and shrub cover (%). Because nutrient status is an important factor explaining grassland floristic composition (AL-MUFTI *et al.* 1977, CRITCHLEY *et al.* 2002), we derived it indirectly from ELLENBERG *et al*. (1992) as the mean indicator value for soil nitrogen richness (mN), computed over all inventoried species in the plot. Soil moisture status was derived in the same way, using the mean Ellenberg value for humidity (mF).

DATA ANALYSES

Prior to the analyses, Braun-Blanquet coefficients were transformed into ordinal coefficients, using the van der Maarel scale (JONGMAN *et al.* 1995). To fulfil our first objective, vegetation data were analyzed using TWINSPAN (HILL & ŠMILAUER 2005). This method was chosen to make our results comparable with those obtained by BUTAYE *et al.* (2005) in the Viroin valley. Pseudospecies were defined using van der Maarel coefficients 3 and 5 as cut-off levels (corresponding to 5% and 25% cover, respectively). A synoptic table was created depicting the constancy of the different species in the groups resulting from the classification. These groups were compared with the communities described in the EUNIS typology (EUROPEAN ENVIRONMENT AGENCY 2005) based on their indicator species. The distribution of the different communities derived from TWINSPAN was analyzed on the basis of the frequency of plots belonging to each community in 10 × 10 km squares.

In relation to our second objective, a Canonical Correspondence Analysis (CCA) was run with CANOCO 4.5 and CANODRAW for WINDOWS (TER BRAAK & ŠMILAUER 2002). Environmental variables were selected, using 999 Monte Carlo permutations, at a significance level of 0.05. Their values were standard-

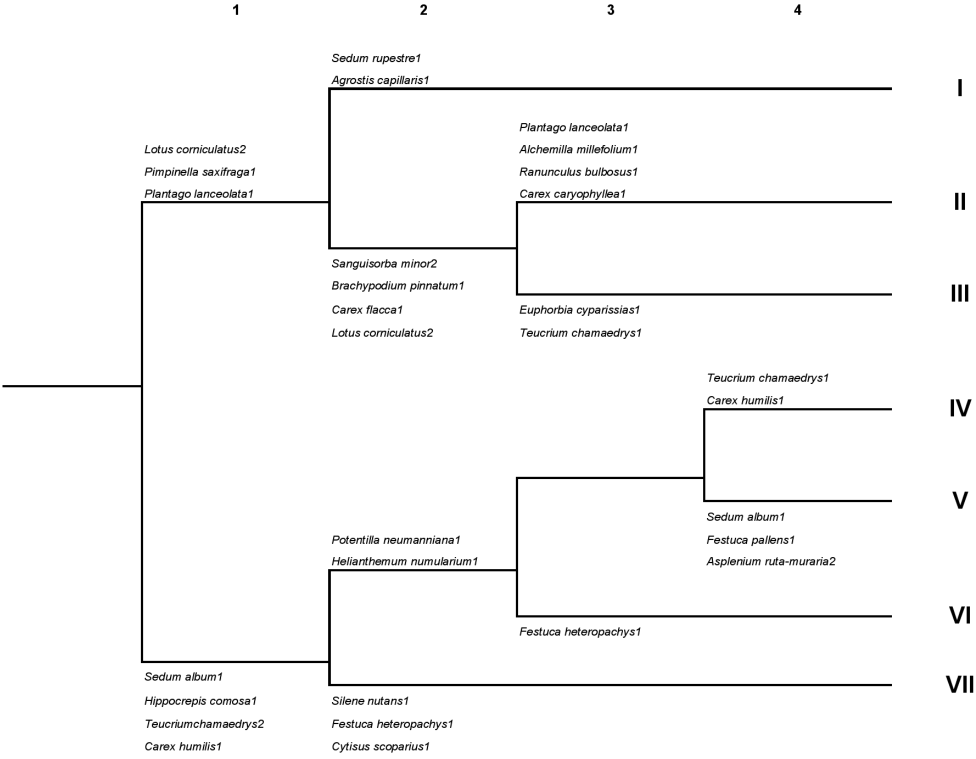

Fig. 1. TWINSPAN classification dendrogram of the calcareous grassland communities of the Calestienne region with their indicator species.

Table 1. Synoptic table of the grassland communities (I–VII) identified on the basis of the TWINSPAN classification. Species frequency of occurrence in the different communities (% of relevés with presence of the species).

	I	II	III	IV	V	VI	VII
Number of relevés	54	155	153	70	28	10	7
Festuco-Brometea							
Potentilla neumanniana	57	50	46	67	79	40	-
Thymus pulegioides	41	42	26	20	7	20	14
Hieracium pilosella	39	22	31	13	32	-	14
Sanguisorba minor	28	88	82	40	68	10	14
Bromus erectus	31	72	57	27	46	-	-
Helianthemum nummularium	24	39	50	67	64	60	14
Festuca gr. *ovina*	67	44	54	27	4	-	14
Campanula rotundifolia	13	12	36	3	14	-	-
Scabiosa columbaria	2	17	31	6	32	-	-
Koeleria macrantha	24	33	17	11	4	-	-
Teucrium chamaedrys	6	6	41	91	21	-	-
Brachypodium pinnatum	4	54	76	39	11	-	-
Euphorbia cyparissias	15	6	47	26	-	-	-
Hippocrepis comosa	2	1	20	69	50	-	-

	I	II	III	IV	V	VI	VII
Number of relevés	54	155	153	70	28	10	7
Mesobromion							
Pimpinella saxifraga	17	60	47	4	7	-	-
Carex flacca	6	44	59	13	-	-	-
Leontodon hispidus	2	26	27	1	-	-	-
Carex caryophyllea	11	38	8	1	4	-	-
Carlina vulgaris	2	6	10	-	4	-	-
Anthyllis vulneraria	2	10	8	4	-	-	-
Ranunculus bulbosus	17	50	15	-	-	-	-
Centaurea scabiosa	6	23	10	1	4	-	-
Genista tinctoria	7	28	15	-	-	-	-
Linum catharticum	2	35	41	-	-	-	-
Medicago lupulina	7	23	22	-	-	-	-
Ononis repens	2	19	6	-	-	-	-
Primula veris	2	11	10	-	-	-	-
Prunella laciniata	2	3	5	-	-	-	-
Genistella sagittalis	4	3	3	-	-	-	-
Polygala comosa	-	2	17	1	-	-	-
Polygala vulgaris	-	18	7	9	-	-	-
Epipactis atrorubens	-	1	7	1	-	-	-
Gymnadenia conopsea	-	1	7	-	-	-	-
Picris hieracioides	-	2	8	-	-	-	-
Plantago media	-	23	12	-	-	-	-
Galium pumilum	-	15	29	1	-	-	-
Cirsium acaule	-	15	18	-	-	-	-
Ononis spinosa	-	2	1	-	-	-	-
Trifolium montanum	-	4	3	-	-	-	-
Platanthera bifolia	-	3	-	-	-	-	-
Platanthera chlorantha	-	2	2	-	-	-	-
Euphrasia nemorosa	-	1	1	-	-	-	-
Carex tomentosa	-	-	3	-	-	-	-
Bunium bulbocastanum	-	1	2	-	-	-	-
Gentianella germanica	-	-	3	-	-	-	-
Gentiana cruciata	-	1	-	-	-	-	-
Ophrys insectifera	-	-	4	-	-	-	-
Calamagrostis epigejos	-	1	-	-	-	-	-
Genista pilosa	-	1	-	-	-	-	-
Anacamptis pyramidalis	-	1	-	-	-	-	-
Gentianella ciliata	-	-	2	-	-	-	-
Onobrychis viciifolia	-	1	-	-	-	-	-
Ophrys apifera	-	3	1	-	-	-	-
Orchis militaris	-	1	1	-	-	-	-

	I	II	III	IV	V	VI	VII
Number of relevés	54	155	153	70	28	10	7
Xerobromion							
Melica ciliata	-	-	-	29	46	50	14
Aster linosyris	-	3	1	30	4	20	14
Cotoneaster integerrimus	-	-	-	3	7	10	-
Sesleria caerulea	2	1	18	50	54	-	-
Allium sphaerocephalon	-	1	1	40	4	-	-
Arabis hirsuta	-	1	1	13	7	-	-
Dianthus carthusianorum	4	-	-	9	4	-	-
Allium oleraceum	-	2	3	10	11	-	-
Carex humilis	-	-	2	63	-	-	-
Stachys recta	-	-	-	17	-	-	-
Thlaspi montanum	2	1	3	14	-	-	-
Globularia bisnagarica	-	-	5	11	-	-	-
Pulsatilla vulgaris	-	-	-	7	-	-	-
Veronica prostrata	-	-	-	3	-	-	-

	I	II	III	IV	V	VI	VII
Number of relevés	54	155	153	70	28	10	7
Molinio-Arrhenatheretea							
Hypericum perforatum	24	19	33	9	4	20	43
Leucanthemum vulgare	11	39	15	-	-	40	14
Lotus corniculatus	26	74	70	7	11	-	-
Taraxacum officinale	4	8	33	4	7	-	-
Centaurea jacea	37	45	19	6	4	30	29
Stachys officinalis	4	3	2	14	-	-	-
Achillea millefolium	24	47	8	-	-	-	-
Dactylis glomerata	19	28	10	3	-	-	-
Succisa pratensis	-	16	2	-	-	-	-
Tragopogon pratensis	-	3	4	1	-	-	-
Trifolium medium	2	8	7	-	-	-	-
Trifolium pratense	2	13	2	-	-	-	-
Trifolium repens	9	5	3	-	-	-	-
Trisetum flavescens	6	23	10	-	-	-	-
Knautia arvensis	2	32	22	3	-	-	-
Vicia cracca	-	5	1	-	-	-	-
Vicia hirsuta	9	13	11	-	-	10	-
Vicia sativa	6	6	1	1	-	-	-
Plantago lanceolata	37	61	22	-	-	-	14
Daucus carota	2	32	12	-	-	-	-
Anthoxanthum odoratum	2	8	-	-	-	-	-
Arrhenatherum elatius	15	15	6	-	-	10	-
Potentilla reptans	11	8	5	-	-	-	-
Prunella vulgaris	2	3	7	-	-	-	-
Geranium molle	4	-	-	1	-	-	-
Senecio jacobaea	4	3	8	-	-	-	-
Avenula pubescens	2	18	5	-	-	-	-
Briza media	4	52	22	-	-	-	-
Crepis biennis	2	3	-	-	-	-	-
Dactylorhiza fuchsii	-	3	1	-	-	-	-
Heracleum sphondylium	-	3	-	-	-	-	-

Holcus lanatus	-	4	2	-	-	-	-
Lathyrus pratensis	-	5	1	-	-	-	-
Leontodon autumnalis	-	4	-	-	-	-	-
Molinia caerulea	-	1	-	-	-	-	-
Parnassia palustris	-	1	-	-	-	-	-
Potentilla erecta	-	6	-	-	-	-	-
Rhinanthus alectorolophus	-	5	-	-	-	-	-
Selinum carvifolia	-	1	-	-	-	-	-
Carex panicea	-	4	-	-	-	-	-
Cerastium fontanum	-	5	-	-	-	-	-
Colchicum autumnale	-	1	-	-	-	-	-
Carex tomentosa	-	-	3	-	-	-	-
Silaum silaus	-	-	1	-	-	-	-

	I	II	III	IV	V	VI	VII
Number of relevés	54	155	153	70	28	10	7
Nardo-Callunetea							
Danthonia decumbens	9	13	3	1	-	-	-
Luzula campestris	6	8	3	-	-	-	-
Veronica officinalis	2	1	2	-	-	-	-
Calluna vulgaris	2	1	-	-	-	-	-
Agrostis capillaris	50	9	4	-	-	-	-
Cuscuta epithymum	2	-	-	3	-	-	-
Hieracium maculatum	2	-	1	-	-	-	-
Deschampsia flexuosa	6	-	-	-	-	-	-
Rumex acetosella	22	-	-	-	-	-	-
Teucrium scorodonia	4	1	1	3	-	20	29
Cytisus scoparius	7	2	3	3	-	10	71
Festuca heteropachys	-	-	-	-	-	100	86
Hieracium sabaudum	-	-	-	-	-	-	14
Hieracium lachenalii	-	2	3	-	-	-	-
Melampyrum pratense	-	-	-	-	4	-	-
Genista pilosa	-	1	-	-	-	-	-
Viola canina	-	1	-	-	-	-	-

	I	II	III	IV	V	VI	VII
Number of relevés	54	155	153	70	28	10	7
Sedo-Scleranthetea							
Scleranthus annuus	7	-	-	-	-	-	-
Trifolium arvense	22	1	-	1	-	-	-
Cerastium pumilum	6	2	-	-	-	-	-
Dianthus armeria	7	-	-	-	-	-	-
Trifolium campestre	2	-	-	-	-	-	-
Erophila verna	6	3	-	-	-	-	-
Trifolium dubium	19	5	-	-	-	-	-
Veronica arvensis	9	-	-	3	-	-	-
Echium vulgare	13	1	5	3	11	50	14
Sedum acre	2	-	-	1	7	-	-
Lepidium campestre	4	1	-	-	4	10	-
Sedum album	13	-	-	29	86	90	43
Sedum rupestre	52	1	1	7	-	-	14
Acinos arvensis	2	-	4	16	39	-	-
Arabidopsis thaliana	-	-	-	-	-	40	-
Arenaria serpyllifolia	4	7	5	20	50	40	-
Lactuca perennis	-	-	-	1	-	-	-
Lepidium campestre	4	1	-	-	4	10	-
Poa compressa	9	3	12	4	21	20	-
Teucrium botrys	-	-	1	-	7	-	-
Sedum telephium	-	-	-	-	-	60	-
Sempervivum funckii var. *aqualiense*	-	-	-	-	-	30	-
Thlaspi perfoliatum	-	-	-	1	-	-	-

	I	II	III	IV	V	VI	VII
Number of relevés	54	155	153	70	28	10	7
Festucion pallentis							
Festuca pallens	-	-	-	-	50	-	-
Dianthus gratianopolitanus	-	-	-	-	7	-	-
Asplenium ruta-muraria	-	-	1	3	54	-	14
Cotoneaster integerrimus	-	-	-	3	7	10	-
Sesleria caerulea	2	1	18	50	54	-	-

	I	II	III	IV	V	VI	VII
Number of relevés	54	155	153	70	28	10	7
Trifolion medii							
Galium mollugo	13	1	8	44	14	30	-
Origanum vulgare	-	32	27	34	25	60	-
Agrimonia eupatoria	2	21	4	-	-	-	-
Astragalus glycyphyllos	-	1	1	-	-	-	-
Brachypodium sylvaticum	-	5	4	-	-	-	-
Calamintha clinopodium	-	-	7	-	-	-	-
Centaurium erythraea	6	5	5	-	-	-	-
Festuca rubra	6	20	1	-	-	-	-
Galium verum	20	35	24	6	4	-	-
Inula salicina	-	-	1	-	-	-	-
Poa pratensis	17	27	18	1	-	-	-
Senecio erucifolius	-	1	1	-	-	-	-
Solidago virgaurea	-	1	4	-	-	-	-
Trifolium medium	2	8	7	-	-	-	-
Viola hirta	2	25	52	19	-	-	-

	I	II	III	IV	V	VI	VII
Number of relevés	54	155	153	70	28	10	7
Geranion sanguinei							
Anthericum liliago	-	-	3	29	11	10	14
Seseli libanotis	-	-	-	27	43	-	-
Vincetoxicum hirundinaria	-	-	3	27	14	-	-
Rosa pimpinellifolia	-	-	-	13	4	-	-
Polygonatum odoratum	-	-	-	20	-	-	-
Geranium sanguineum	-	-	-	7	-	-	-
Silene nutans	6	-	-	-	4	40	86
Campanula persicifolia	-	-	-	-	-	10	-
Inula conyzae	-	3	6	7	-	-	-
Bupleurum falcatum	-	1	11	14	-	-	-
Aquilegia vulgaris	-	-	1	1	-	-	-
Digitalis lutea	-	-	-	-	-	-	-
Fragaria viridis	2	5	3	-	-	-	-
Lithospermum officinale	-	-	1	-	-	-	-
Silene vulgaris	-	1	-	-	-	-	-

	I	II	III	IV	V	VI	VII
Number of relevés	54	155	153	70	28	10	7
Koelerio-Phleion phleoidis							
Festuca heteropachys	-	-	-	-	-	100	86
Aster linosyris	-	3	1	30	4	20	14
Artemisia campestris	-	-	-	-	-	30	-
Campanula patula	-	-	-	-	-	10	-

ized to give the same weight to each one of them. We tested whether environmental variables differed significantly between the vegetation types derived from TWINSPAN, through a multivariate analysis of variance (MANOVA) and subsequent ANOVAs, using the SAS CANDISC procedure (SAS INSTITUTE INC. 1999). The considered variables were soil depth, soil pH, slope, height of vegetation, bare soil percentage, shrub cover, herbaceous cover and moss cover. The four latter variables (proportions) were arcsine transformed.

The third objective was first approached through Kruskal-Wallis comparisons of mean species richness per plot among grassland communities (derived from TWINSPAN). Second, the influence of the patch environmental conditions and geographical location on the species richness (one-meter square scale) was examined using best subset multiple regressions. The analysis was carried out both on the whole data set and on the different grassland communities identified. The models were built with the subset of predictor variables for which all *p*-values were significant at the 0.05 minimum level. When necessary, the dependent variables were transformed in order to meet normality and homoscedasticity requirements. Normality of the residuals was tested by Levene's test and their homoscedasticity by Breuch-Pagan's test. Box-Cox transformations on the dependent variable were applied using a MINITAB macro (PALM 2002) in order to improve the results of those tests.

RESULTS

GENERAL CLASSIFICATION

Calcareous grasslands in the study area belong to the *Festuco-Brometea* class, characterized by, among others, *Festuca lemanii*, *Bromus erectus*, *Helianthemum nummularium*, and *Sanguisorba minor* (Table 1). The TWINSPAN classification of relevés revealed seven different groups (Fig. 1, Table 1, Table 2). The number of relevés in each group varied considerably (from 7 to 155 relevés, Table 2). Two groups were represented by a very low number of relevés (groups VI and VII), mainly limited to two sites: "Heid des Gattes" (eight relevés out of ten for group VI) and "Heid de Stinval" (five relevés out of seven for group VII).

Indicator species of groups I to III were *Lotus corniculatus*, *Pimpinella saxifraga*, and *Plantago lanceolata* (Fig. 1). These species are typically mesophilous, so these groups were classified as mesophilous grasslands. Besides the high occurrence of *Mesobromion* species, mesophilous grasslands were characterized by an important proportion of species from the *Molinio-Arrhenatheretea* and the *Trifolion medii* (Table 1). Two mesophilous communities were then identified: the acidic mesophilous grasslands (group I) and the alkaline mesophilous grasslands (groups II and III). On the other hand, indicator species of groups IV to VII were *Sedum album*, *Hippocrepis comosa*, *Teucrium chamaedrys* and *Carex humilis* (Fig. 1), which are typically xerophilous species. In addition to the presence of *Xerobromion* species, these grasslands were characterized by *Sedo-Scleranthetea* and *Geranion sanguinei* species (Table 1). The xerophilous communities were classified into three different plant communities : the very dry grasslands (group IV), the *Festucion pallentis* grasslands (group V) and the *Koelerio-Phleion* grasslands (groups VI and VII).

The MANOVA showed significant differences between groups for environmental variables (Wilks' Lambda, $F = 17.55$, NUM df = 60, DEN df = 2415, $P < 0.0001$). Also ANOVAs on separate environmental variables were significant (excepted for shrub cover). Subsequent pairwise comparisons are detailed in Table 2. Because of their very low number of relevés, groups VI and VII were removed from these analyses, and comparisons were made on a qualitative basis. A strong difference was observed between groups II and III on the one hand and groups IV and V on the other hand. Relevés from groups II and III were characterized by significantly deeper soils, less steep slopes, lower bare soil percentage and higher herbaceous cover, compared to relevés from groups IV and V (Table 2). This typically contrasts mesophilous grasslands (groups II and III) against more xerophilous grasslands (groups IV and V). According to the analysis of the nutrient level (mN), mesophilous grasslands were characterized by a more nitrophilous flora than xerophilous ones. The position of group I was rather difficult to interpret on the basis of environmental variables alone.

ACIDIC MESOPHILOUS GRASSLANDS (GROUP I)

This group is characterized by *Sedum rupestre* and *Agrostis capillaris* (Fig. 1) and

Table 2. Comparisons of mean environmental variables between grassland communities identified on the basis of the TWINSPAN classification. Pairwise comparisons; using Kruskall-Wallis test: different letters indicate significant differences for α = 0.05.

Group		I	II	III	IV	V	VI	VII
	n	54	155	153	70	28	10	7
Altitude		195 [a]	189 [a]	223 [b]	217 [b]	172 [a]	158 [n.t.]	206 [n.t.]
Y		104283 [b]	121816 [c]	95125 [a]	95328 [b]	121174 [c]	131977 [n.t.]	132272 [n.t.]
Soil depth		4.14 [ab]	8.90 [c]	4.67 [b]	2.78 [a]	2.26 [a]	2.90 [n.t.]	3.57 [n.t.]
pH		4.99 [a]	6.27 [b]	6.75 [c]	6.61 [bc]	6.47 [bc]	4.88 [n.t.]	4.68 [n.t.]
Slope		14.9 [a]	13.5 [a]	10.7 [a]	22.8 [b]	33.3 [b]	64.5 [n.t.]	30.0 [n.t.]
MHV		59.9 [a]	81.2 [c]	70.9 [b]	62.4 [ab]	65.9 [ab]	55.9 [n.t.]	55.9 [n.t.]
% Bare soil		16.0 [b]	8.2 [a]	8.7 [a]	15.3 [b]	41.3 [c]	46.0 [n.t.]	45.0 [n.t.]
% Herbaceous		72.0 [b]	88.3 [c]	84.4 [c]	76.4 [b]	47.1 [a]	52.5 [n.t.]	40.0 [n.t.]
% Shrubs		1.96	1.96	2.08	0.69	1.25	2.30 [n.t.]	2.07 [n.t.]
% Mosses		29.3 [c]	12.9 [a]	20.8 [bc]	18.8 [ab]	20.8 [bc]	7.6 [n.t.]	20.7 [n.t.]
Species richness		13.2 [a]	20.7 [b]	18.9 [b]	13.1 [a]	11.2 [a]	13.7 [n.t.]	6.9 [n.t.]
mF		3.58 [c]	3.92 [d]	3.77 [c]	3.09 [b]	2.98 [a]	3.28 [n.t.]	3.12 [n.t.]
mN		2.89 [b]	3.19 [c]	3.08 [b]	2.39 [a]	2.13 [a]	2.86 [n.t.]	2.40 [n.t.]

Notes. n = number of relevés; Y = Y Lambert coordinate; MHV = Maximum Height of Vegetation; % Bare soil = percentage of the relevé covered by bare soil; % Herbaceous = percentage of the relevé covered by herbaceous species; % Shrubs = percentage of the relevé covered by shrub species; % Mosses = percentage of the relevé covered by mosses; mF = pean Ellenberg indicator value for soil moisture; mN = pean Ellenberg indicator values for nutrient status.

contains an important proportion of species from the *Mesobromion* and few species from the *Xerobromion* (Table 1). It is characterized by the important occurrence of species from the *Nardo-Callunetea* and the *Sedo-Scleranthetea* (Table 1) and species richness (ca. 13 species/m^2) was lower than other mesophilous grasslands (Table 2).

Although it was grouped among typical mesophilous grasslands at the first level of the TWINSPAN division (Fig. 1), acidic mesophilous grasslands differed significantly from groups II and III in terms of environmental conditions (maximum vegetation height, bare soil percentage and herbaceous cover). They also differed significantly from xerophilous communities (groups IV and V) for slope and were intermediate for soil depth. Their main characteristic was a significantly lower pH. These communities may be found across the entire Calestienne region except in the more northeastern sites (Fig. 2). Their presence corresponds more to local variations of ecological conditions (embankments on shale with more or less decarbonated soils) than to a biogeographical gradient.

Alkaline mesophilous grasslands (groups II and III)

The two alkaline mesophilous communities (groups II and III) correspond to different levels of xericity. Group II represents the typical mesophilous grassland community, characterized by *Plantago lanceolata, Achillea millefolium, Ranunculus bulbosus* and *Carex caryophyllea* (Fig. 1). It also includes many species of the *Molinio-Arrhenatheretea* (Table 1). Group III corresponds to a mesophilous community typical of more xeric environments and is indicated by *Euphorbia cyparissias* and *Teucrium chamaedrys* (Fig. 1). This community is a transition between the *Mesobromion* and *Xerobromion*, as xeric species such as *Carex humilis*, *Globularia bisnagarica* and *Sesleria caerulea* appear and meadow species become scarce (Table 1). Generally, mesophilous grasslands (groups II and III) are well represented in the study region (308 out of 477 relevés) and are characterized by the high abundance of *Bromus erectus* and *Brachypodium pinnatum*. Many typical species of the *Meso-*

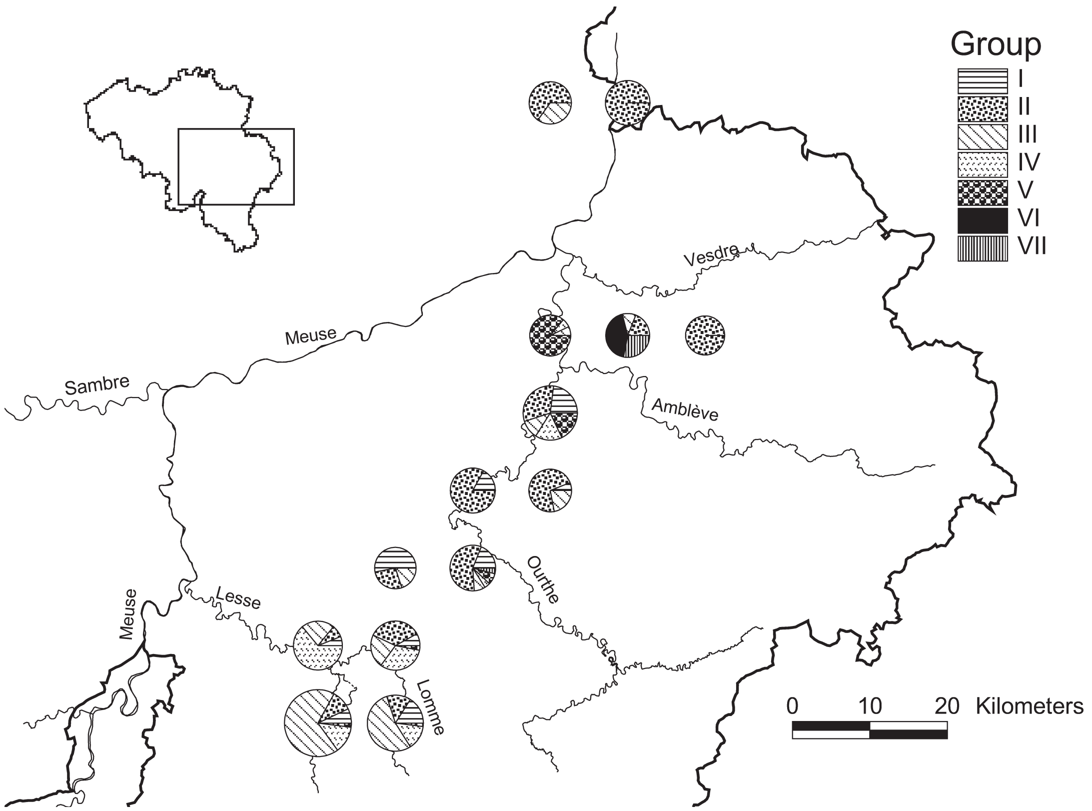

Fig. 2. Study region and proportion of relevés from the different TWINSPAN groups in 10 × 10 km squares. Circle sizes are proportional to the number of relevés in the 10 × 10 km square.

bromion alliance (Wolkinger & Plank 1981) were present in the corresponding relevés, such as *Cirsium acaule*, *Gentianella germanica* and many orchids (*Ophrys insectifera*, *Ophrys apifera*, *Orchis militaris*, *Anacamptis pyramidalis*). Our relevés revealed a species-rich habitat, with a mean species richness of 20 species/m^2 and a maximum of 35 species/m^2. These grasslands develop on gentle slopes or on plateaus with relatively deep soils. They exhibit a high vegetation and little bare soil. Contrary to the previous community, the soil pH was high, varying between 6 and 7 (Table 2). The geographic distribution of these communities over the study zone indicates a tendency towards dominance of the meso-xerophilous community in the southwestern part, which is replaced by the more mesophilous community in the northeastern part (Fig. 2).

Very dry grasslands (group IV)

This community is characterized by *Teucrium chamaedrys* and *Carex humilis* (Fig.1). Many *Xerobromion* species were found, such as *Allium sphaerocephalon*, *Thlaspi montanum* or *Stachys recta*. This community also contains numerous species of the *Sedo-Scleranthetea*, as *Acinos arvensis* or *Sedum album*, owing to a low vegetation cover (76% on average). Its mean species richness was lower than that of the *Mesobromion*, with only 13 species/m^2. It occurred on steep slopes with a very thin alkaline soil (pH ≈ 7). Bare soil percentage was rather important, while maximum height of vegetation was low (Table 2). It was mainly located in the southern part of the study region, in the Lesse and Lomme valleys (Fig. 2).

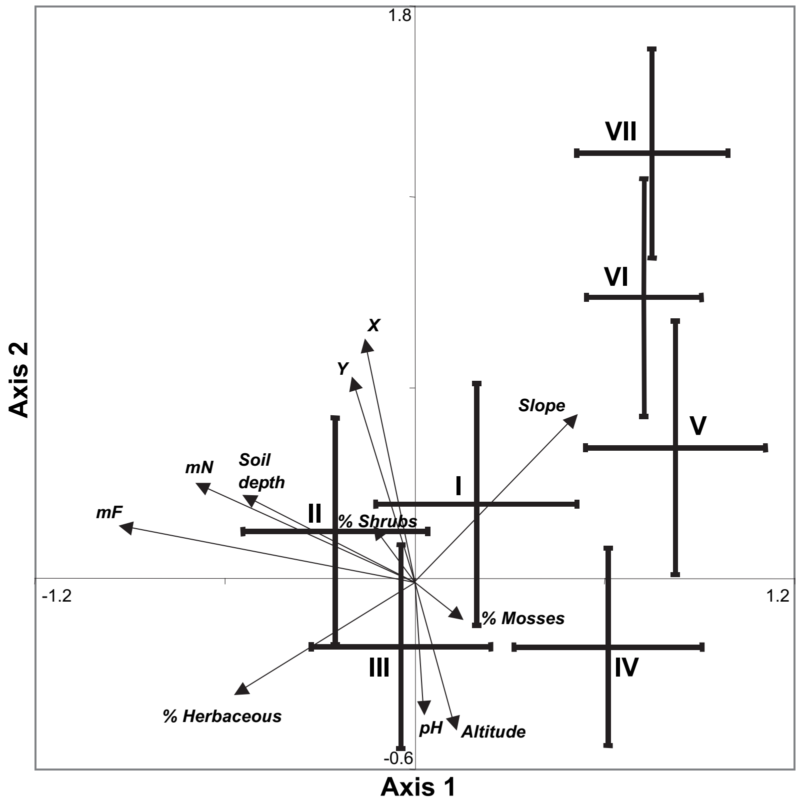

Fig. 3. Position in the CCA ordination graph of communities identified by TWINSPAN. Horizontal and vertical bars represent standard deviation of the positions along the first and second axes of the ordination. Arrows represent environmental variables. X = X Lambert coordinate; Y = Y Lambert coordinate; % Herbaceous = percentage of the relevé covered by herbaceous species; % Shrubs = percentage of the relevé covered by shrub species; % Mosses = percentage of the relevé covered by mosses; mF = mean Ellenberg indicator value for soil moisture; mN = mean Ellenberg indicator values for nutrient status.

Table 3. Correlation between environmental variables and ordination axes from the CCA.

	Axis 1	Axis 2
Altitude	0.1156	-0.4827
X	-0.1478	0.7444
Y	-0.2063	0.6329
Soil depth	-0.5449	0.2376
PH	0.0221	-0.4287
Slope	0.5153	0.5116
% Herbaceous	-0.5794	-0.3585
% Shrubs	-0.1357	0.1607
% Mosses	0.1397	-0.1263
mF	-0.9237	0.1463
mN	-0.7065	0.2953

Notes. X = X Lambert coordinate; Y = Y Lambert coordinate; % Herbaceous = percentage of the relevé covered by herbaceous species; % Shrubs = percentage of the relevé covered by shrub species; % Mosses = percentage of the relevé covered by mosses; mF = mean Ellenberg indicator value for soil moisture; mN = mean Ellenberg indicator values for nutrient status.

Festucion pallentis grasslands (group V)

This relatively species-poor community (11.2 species/m^2 on average) is characterized by *Festuca pallens*, *Sesleria caerulea, Cotoneaster integerrimus*, and by the very rare *Dianthus gratianopolitanus*. These grasslands occupied calcareous rock cliffs and cracks on very steep slopes. The *Festucion pallentis* community is very rare in Belgium and has mainly been found in the Ourthe valley (Fig.2).

Koelerio-Phleion grasslands (groups VI and VII)

Both groups are positively differentiated from the others by the indicator species *Festuca heteropachys* (Fig. 1) and by a higher occurrence of indicator species from the *Koelerio-Phleion* alliance (Table 1). Their species richness was poor to very poor (Table 2).

Mean environmental conditions for these two groups (Table 2) were characteristic of xerophilous communities with superficial soils on steep slopes, supporting open vegetation. These communities, however, differed from the other observed xerophilous communities (groups IV and V) by more acidic conditions (pH ≈ 4.5). They correspond best to the *Koelerio-Phleion phleoidis* alliance. This community is extremely rare in Belgium and mainly occurred in the Amblève valley (Fig. 2).

Ordination of relevés and environmental data

The two first axes explained respectively 27.1% and 15.5% of the species-environment relation. The ordination analysis confirmed the interpretation based on the TWINSPAN classification (Fig. 3). The first axis was highly correlated to herbaceous species cover, soil depth, soil moisture (mF), soil trophic level (mN), slope and bare soil percentage (Table 3). The gradient from negative to positive values on axis 1 corresponded to more superficial soils with lower water content and lower nutrient status,

Table 4. Between-class correlations of environmental variables. Values in italics refer to the associated probabilities.

	Soil Depth	pH	Slope	MHV	% Bare Soil	% Herb	% Shrubs	% Mosses	mF
pH	0.001 *0.998*								
Slope	-0.460 *0.299*	-0.302 *0.511*							
MHV	0.913 *0.004*	0.382 *0.397*	-0.519 *0.232*						
% Bare Soil	-0.492 *0.262*	-0.452 *0.309*	0.914 *0.004*	-0.569 *0.183*					
% Herb	0.682 *0.092*	0.449 *0.312*	-0.819 *0.024*	0.741 *0.057*	-0.957 *0.001*				
% Shrubs	0.655 *0.110*	-0.058 *0.901*	-0.212 *0.648*	0.594 *0.159*	-0.269 *0.560*	0.394 *0.382*			
% Mosses	-0.654 *0.111*	-0.398 *0.376*	-0.028 *0.953*	-0.709 *0.075*	0.254 *0.583*	-0.501 *0.253*	-0.485 *0.270*		
mF	0.819 *0.024*	0.065 *0.889*	-0.726 *0.065*	0.777 *0.040*	-0.734 *0.060*	0.799 *0.031*	0.773 *0.042*	-0.362 *0.425*	
mN	0.767 *0.044*	0.028 *0.952*	-0.676 *0.095*	0.701 *0.080*	-0.729 *0.063*	0.790 *0.035*	0.801 *0.030*	-0.369 *0.415*	0.986 *<.0001*

Notes. MHV = Maximum Height of Vegetation; % Bare soil = Percentage of the relevé covered by bare soil; % Herb = percentage of the relevé covered by herbaceous species; % Shrubs = percentage of the relevé covered by shrub species; % Mosses = percentage of the relevé covered by mosses; mF = pean Ellenberg indicator value for soil moisture; mN = pean Ellenberg indicator values for nutrient status.

Table 5. Optimal multivariate models for the local species richness, considering the whole grassland set and the different TWINSPAN grassland types. Positive relationships are indicated by + and negative by -.

	Transformation on independant variable	Altitude	X	Y	Soil depth	pH	Slope	Maximum height of vegetation	% Bare soil	% Herbaceous	% Shrubs	% Mosses	mF	mN	R^2
All grasslands	4thRT Y			-**		+***				+***	+*	-*	+***	-***	18.1%
Mesophilous acidic grasslands (Group I)	SQRT Y											-*	+***		38.4%
Mesophilous grasslands (Groups II, III)	4thRT Y							-***	-***		+**	-***	+***	-**	39.8%
Xerophilous grasslands (Group IV)	$LOG_{10}Y$			-***									+***	-***	58.5%
Calcareous rocks grasslands (Group V)	Y^2							+**			+*				33.1%

Notes. Significance is indicated as follows: * $0.01 < P \leq 0.05$; ** $0.001 < P \leq 0.01$; *** $P \leq 0.001$. 4thRT Y = fourth root transformation; SQRT Y = square root transformation; LOG_{10} Y = logarithmic transformation; Y^2 = square transformation. X = X Lambert coordinate; Y = Y Lambert coordinate; % Bare soil = percentage of the relevé covered by bare soil; % Herbaceous = percentage of the relevé covered by herbaceous species; % Shrubs = percentage of the relevé covered by shrub species; % Mosses = percentage of the relevé covered by mosses; mF = mean Ellenberg indicator value for soil moisture; mN = mean Ellenberg indicator values for nutrient status.

steeper slopes and lower herbaceous cover, reflecting the transition from mesophilous to xerophilous grasslands. For the second axis, high correlations were found with most environmental variables although pH exhibited a particularly high correlation. As no significant correlation was found between soil pH and any other environmental factor (Table 4), it can be considered as an independent factor affecting the floristic composition of the studied communities. The biogeographical parameter Y Lambert coordinate, however, exhibited the highest correlation with the second axis, confirming the influence of a south-north biogeographic influence on floristic composition.

Species diversity

Multiple regression analyses of local species richness on environmental variables yielded significant results for all grassland sets considered, explaining between 18.1% and 58.5% of the species richness variation (Table 5). Groups II and III were considered together given that they were just variations of the same community (mesophilous grasslands). Variables included in the models differed from one community to another. Considering all grasslands together, local species richness increased with soil moisture (mF) and decreased with soil nutrient status (mN). Species richness in mesophilous grasslands was also negatively influenced by maximum vegetation height, bare soil percentage, moss cover and positively influenced by shrub cover. Soil pH was a significant factor only for the whole data set. In acidic mesophilous grasslands, species richness was negatively influenced by the moss cover and positively by mF. These two variables explained 38.4% of the variation. Local species richness in xerophilous grasslands was significantly influenced by geographic location (Y Lambert coordinate). Grasslands with a more southern location showed higher species richness. *Festucion pallentis* grasslands richness was positively influenced by structure variables (maximum height of vegetation and shrub cover).

DISCUSSION

Acidic mesophilous grasslands

A similar grassland type has been described in the Viroin valley by Butaye *et al.* (2005) (*Agrostis capillaris-Cytisus scoparius* community). Butaye *et al.* (2005) were nevertheless unable to provide a complete description of this community because of the low number of relevés. From our more general survey, we suggest that these grasslands belong to the *Chamaespartio-Agrostidenion* alliance. Such grasslands were often spatially related with *Sedo-Scleranthetea* open grasslands, which could explain the presence of species from this phytosociological class. Despite some affinities with xerophilous grasslands regarding environmental variables, their floristic composition is typically mesophilous. Acidic grasslands have a unique composition because of the simultaneous occurrence of acidic and calcareous species at a 1 m^2 scale. This floristic originality provides a high conservation value to this community.

Alkaline mesophilous grasslands (groups II and III)

These grasslands belong to the *Mesobromion* alliance. Their very high species richness gives them a high conservation value and they are the principal habitat for orchid species. The presence of orchid species is the condition to consider calcareous grasslands as a priority habitat, following the European Directive 92/43/CEE (Habitat Directive). Of the 93 sites that were investigated, about one third contained at least one orchid species. Moreover, some orchids may have been present in the remaining sites but did not occur in the relevés. The division between meso-xerophilous and typical mesophilous grasslands was not reported by Butaye *et al*. (2005) in the Viroin valley. This was maybe due to the absence of a north-south gradient in their survey. Van Speybrouck *et al.* (1989) reported a similar influence of the north-south gradient in a comparison of calcareous grasslands between the Belgian Meuse and the Lorraine districts.

VERY DRY GRASSLANDS (GROUP IV)

The *Xerobromion* reaches its northern boundary in Belgium, which was confirmed by its southern distribution within the study zone (Fig. 2). Nevertheless, the classification of these very dry grasslands in this phytosociological alliance is debatable. Following ROYER (1991), some of them should be classified in the *Teucrio-Mesobromenion* sub-alliance. This sub-alliance is characterized by *Teucrium chamaedrys*, *Globularia bisnagarica* and *Pulsatilla vulgaris,* among others. Nonetheless, following NOIRFALISE & DETHIOUX (1982), those species are some *Xerobromion* differential species. Although the communities we studied may well belong to the *Xerobromion*, they are very impoverished as compared to its optimal range in central France (ROYER 1982), which does not prevent it from having an indisputable conservation value. Many species from this community are of particular interest for conservation in Belgium. These xerophilous grasslands are not as species-rich as the mesophilous ones and therefore the management objectives should be different, in terms of plant species richness.

FESTUCION PALLENTIS GRASSLANDS (GROUP V)

Sites where this community occurred were previously described by DUVIGNEAUD (1982) and by DUVIGNEAUD & SAINTENOY-SIMON (1997). Nevertheless, this survey is the first to characterize its originality. We demonstrated that the floristic composition of this community has specific characteristics compared to the other grassland communities. Most of its typical species such as *Dianthus gratianopolitanus* and *Festuca pallens* are rare and of conservation interest. *Festuca pallens* has its western limit of distribution in the Meuse valley.

KOELERIO-PHLEION GRASSLANDS (GROUPS VI AND VII)

The *Koelerio-Phleion phleoidis* alliance was described as a rare vegetation in Belgium, and, therefore, provides a high conservation value to the sites where it occurs (DUVIGNEAUD & SAINTENOY-SIMON 1988, DUVIGNEAUD & SAINTENOY-SIMON 1989). A distinction between groups VI and VII could be made as *Xerobromion* species were more represented in group VI (Heid des Gattes; Table 1). This has traditionally been interpreted as an impoverishment of the flora in the 'Heid de Stinval' as compared to 'Heid des Gattes' (DUVIGNEAUD & SAINTENOY-SIMON 1988, DUVIGNEAUD & SAINTENOY-SIMON 1989), and this was confirmed in our study by the lower local plant species richness recorded at the former site (Table 2). To our knowledge, this is the first time that these grassland communities are characterized through direct comparisons at the regional scale and that their particularity is confirmed by statistical analysis.

SPECIES RICHNESS

The different results concerning species richness were generally in accordance with previous surveys. Biogeographic influences have been described by different authors (e.g., VAN SPEYBROEK *et al.* 1989, BRUUN 2000). These influences are often not easy to explain. In the current study, there was a species decline towards northern locations. This trend was particularly strong for the *Xerobromion* grasslands (group IV), confirming that these grasslands reach their northern boundary in Belgium (WOLKINGER & PLANK 1981, MAUBERT & DUTOIT 1995). The pH influence was due to the fact that acidic grasslands exhibited, on average, lower species richness as compared to other grasslands (Table 2). Higher species richness in alkaline grasslands has also been found by CRITCHLEY *et al.* (2002). Increased vegetation height and shrub cover generally negatively affected local species richness in calcareous grasslands (BOBBINK & WILLEMS 1987). Nevertheless, at a larger scale, variation in vegetation structure may provide a higher diversity of microhabitats and promote species richness (LINDBORG & ERIKSSON 2004). The results found in this study are in accordance with the fact that higher soil fertility induces a decrease in species richness (e.g., AL-MUFTI *et al.* 1977, MARRS 1993, CRITCHLEY *et al.* 2002).

REFERENCES

AL-MUFTI M.M., SYDES C.L., FURNESS S.B., GRIME J.P. & BAND S.R., 1977. — A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *J. Ecol.* **65**: 759-791.

ANDRÉ B. & VANDENDORPEL A., 2004. — Le projet LIFE Nature de restauration et de gestion des milieux calcaires en Lesse et Lhomme (PROJET LIFE2000NATURE/B/7168) : une tradition pastorale séculaire en dernier recours. *Parcs & Réserves* **59**: 22-37.

BISTEAU E. & MAHY G., 2005. — Vegetation and seed bank in a calcareous grassland restored from a *Pinus* forest. *Appl. Veg. Sci.* **8**: 167-174.

BOBBINK R. & WILLEMS J.H., 1987. — Increasing dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grasslands : a threat to a species-rich ecosystem. *Biol. Conserv.* **40**: 301-314.

BOBBINK R., HEINJO J.D., SCHREURS J., WILLEMS J.H. & ZIELMAN R., 1987. — Effects of selective clipping and mowing time on species diversity in chalk grassland. *Folia Geobot. Phytotax.* **22**: 363-376.

BOTTIN G., ETIENNE M., VERTÉ P. & MAHY G., 2005. — Methodology for the elaboration of Natura 2000 sites designation acts in the Walloon Region (Belgium) : calcareous grasslands in the Lesse-and-Lhomme area. *Biotechnologie, Agronomie, Société, Environnement* **9**: 101-110.

BRAUN-BLANQUET J., 1932. — *Plant sociology : the study of plant communities*. McGraw-Hill, New York.

BRUUN H.H., 2000. — Patterns of species richness in dry grassland patches in an agricultural landscape. *Ecography* **23**: 641-650.

BUTAYE J., HONNAY O., ADRIAENS D., DELESCAILLE L.M. & HERMY M., 2005. — Phytosociology and phytogeography of the calcareous grasslands on devonian limestone in southwest Belgium. *Belg. J. Bot.* **138**: 24-38.

CRITCHLEY C.N.R., CHAMBERS B.J., FOWBERT J.A., BHOGAL A., ROSE S.C. & SANDERSON R.A., 2002. — Plant species richness, functional type and soil properties of grasslands and allied vegetation in English environmentally sensitive areas. *Grass Forage Sci.* **57**: 82-92.

DELESCAILLE L.M., DEWITTE T. & HOFMANS K., 1995. — La gestion mécanisée des pelouses sèches. *Parcs Nationaux* **50**: 13-19.

DUVIGNEAUD J., 1982. — Les pelouses xériques colonisant les falaises calcaires des vallées de l'Ourthe et de l'Amblève (province de Liège, Belgique) : leur importance floristique et phytogéographique. *In*: *Colloques phytosociologiques : la végétation des pelouses calcaires*, pp. 297-309. Strasbourg.

DUVIGNEAUD J., 1989. — La petite Tinaimont à Han-sur-Lesse (province de Namur). *Parcs Nationaux* **44**: 113-121.

DUVIGNEAUD J. & SAINTENOY-SIMON J., 1988. — La Heid des Gattes à Sougné-Remouchamps (Aywaille). *Parcs Nationaux* **43**: 108-126.

DUVIGNEAUD J. & SAINTENOY-SIMON J., 1989. — Flore et végétation de la Heid de Stinval (Louveigné, province de Liège). *Les Naturalistes Belges* **70**: 129-138.

DUVIGNEAUD J. & SAINTENOY-SIMON J., 1997. — Les "Tartines" de Comblain-au-Pont (province de Liège, Belgique). *Les Naturalistes Belges* **78**: 11-16.

DZWONKO Z. & LOSTER S., 1998. — Dynamics of species richness and composition in a limestone grassland restored after tree cutting. *J. Veg. Sci.* **9**: 387-394.

ELLENBERG H., WEBER H.E., DÜLL R., WIRTH V., WERNER W. & PAULISSEN D., 1992. — Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobot.* **18**: 3-258. Accessed online at http://www.boku.ac.at/statedv/edvbotanik/zeigerwerte/, November 2005.

EUROPEAN ENVIRONMENT AGENCY, 2005. — *EUNIS database version 2.0*. Accessed online at http://eunis.eea.europa.eu/index.jsp, March 2006.

GRAUX G., 2004. — Le projet LIFE "restauration et gestion durable des pelouses sèches en Haute Meuse". *Parcs & Réserves* **59**: 38-48.

HILL M.O. & ŠMILAUER P., 2005. — *TWINSPAN for Windows version 2.3*. Centre for Ecology and Hydrology & University of South Bohemia, Huntingdon & České Budějovice.

JONGMAN R.H.G., TER BRAAK C.F.J. & VAN TONGEREN O.F.R., 1995. — *Data analysis in community and landscape ecology*: 299 p. Cambridge university press, Cambridge.

KÖHLER B., GIGON A., EDWARDS P.J., KRÜSI B., LANGENAUER R., LÜSCHER A. *et al.*, 2005. — Changes in species composition and conservation value of limestone grasslands in Northern Switzerland after 22 years of contrasting managements. *Perspect. Plant Ecol. Evol. Syst.* **7**: 51-67.

LAMBINON J., DELVOSALLE L. & DUVIGNEAUD J., 2004. — *Nouvelle flore de Belgique, du Grand-Duché de Luxembourg, du Nord de la France et des régions voisines*. 5ème édn. Jardin botanique national de Belgique, Meise.

LINDBORG R. & ERIKSSON O., 2004. — Effects of restoration on plant species richness and composition in Scandinavian semi-natural grasslands. *Restor. Ecol.* **12**: 318-326.

MARRS R.H., 1993. — Soil fertility and nature conservation in Europe: theoretical considerations and practical management solutions. *Adv. Ecol. Res.* **24**: 241-300.

MAUBERT P. & DUTOIT T., 1995. — *Connaître et gérer les pelouses calcicoles*: 65 p. Ministère de l'environnement, Cahier ATEN, Montpellier, France.

NOIRFALISE A. & DETHIOUX M., 1982. — Les pelouses calcaires de la Belgique et leur protection. *In*: *Colloques phytosociologiques : la végétation des pelouses calcaires*, pp. 201-218. Strasbourg.

PALM R., 2002. — *Macros Minitab pour la régression linéaire*: 16 p. Available at http://www.fsagx.ac.be/si/reglin/accueil.htm

POSCHLOD P. & WALLISDEVRIES M.F., 2002. — The historical and socioeconomic perspective of calcareous grasslands: lessons from the distant and recent past. *Biol. Conserv.* **104**: 361-376.

ROYER J.M., 1982. — Caractérisation, répartition et origine du Xerobromion. *In*: *Colloques phytosociologiques : la végétation des pelouses calcaires*, pp. 243-267. Strasbourg.

ROYER J.M., 1991. — *Synthèse eurosibérienne, phytosociologique et phytogéographique de la classe des Festuco-Brometea.* Dissertationes Botanicae, vol. 178: 296 p. J.Cramer, Berlin-Stuttgart.

SAS INSTITUTE INC., 1999. — *SAS/STAT® User's Guide, version 8*. SAS Institute Inc., Cary, NC, USA.

TER BRAAK C.F.J. & ŠMILAUER P., 2002. — *CANOCO reference manual and CanoDraw for Windows user's Guide : software for canonical community ordination*, version 4.5: 500 p. Microcomputer Power, Ithaca, NY, USA.

VAN SPEYBROEK D., KOEDAM N. & BÜSCHER P., 1989. — On the delimitation of the *Mesobromion* and *Xerobromion* in Belgium and French Lorraine. *Vegetatio* **81**: 137-144.

WILLEMS J.H., 2001. — Problems, approaches, and results in restoration of Dutch calcareous grassland during the last 30 years. *Restor. Ecol.* **9**: 147-154.

WOLKINGER F. & PLANK S., 1981. — *Les pelouses sèches en Europe.* Collection Sauvegarde de la Nature, vol. 21: 57 p. Conseil de l'Europe, Strasbourg.

APPENDIX

Name, number of plots, coordinates and location of the different study sites.

Site name	Number of plots	Site coordinates	Location
Aisne	3	50°21'30" N - 5°33'54" E	Durbuy
Aye	6	50°13'9" N - 5°18'18" E	Marche-en-Famenne
Baillonville	6	50°17'34" N - 5°20'2" E	Somme-Leuze
Bâtis d'Haur	8	50°6'4" N - 5°14'42" E	Tellin
Belvédère	5	50°8'4" N - 5°12'11" E	Rochefort
Biernauchamps	6	50°6'52" N - 5°14'24" E	Rochefort
Bois Niaux	4	50°6'13" N - 5°9'59" E	Rochefort
Bourdon	3	50°14'32" N - 5°23'22" E	Hotton
Brochamps	10	50°5'55" N - 5°8'5" E	Wellin
Brouire	3	50°6'18" N - 5°14'8" E	Tellin
Carrière de Mont	3	50°32'18" N - 5°47'55" E	Theux
Carrière de Resteigne	9	50°5'23" N - 5°10'54" E	Tellin
Carroi-Chenêt	6	50°5'48" N - 5°12'22" E	Tellin
Chafosse	3	50°12'55" N - 5°16'57" E	Marche-en-Famenne
Chéfiri	6	50°5'49" N - 5°10'28" E	Tellin
Chénisse	4	50°23'57" N - 5°30'40" E	Durbuy
Cocrai	2	50°11'54" N - 5°14'29" E	Marche-en-Famenne
Comblain-la-Tour	6	50°27'28" N - 5°34'2" E	Hamoir
Coteau du Tunnel 1	5	50°45'41" N - 5°38'22" E	Bassenge
Coteau du Tunnel 2	7	50°45'34" N - 5°38'32" E	Bassenge
Coteau du Tunnel 3	5	50°45'39" N - 5°38'23" E	Bassenge
Deulin	3	50°18'24" N - 5°23'19" E	Hotton

Falize	6	50°28’58” N - 5°41’29” E	Aywaille
Fond des Vaulx	3	50°13’48” N - 5°21’24” E	Marche-en-Famenne
Fond Saint-Martin	10	50°8’3” N - 5°12’0” E	Rochefort
Fouyeu	6	50°20’56” N - 5°30’6” E	Durbuy
Grand Va	3	50°23’40” N - 5°33’25” E	Ferrières
Grignaux 1	3	50°6’50” N - 5°10’13” E	Rochefort
Grignaux 2	5	50°6’52” N - 5°10’11” E	Rochefort
Grignaux 3	3	50°7’3” N - 5°10’10” E	Rochefort
Grignaux 4	3	50°7’6” N - 5°10’4” E	Rochefort
Gros Tienne de Lavaux	10	50°6’21” N - 5°5’57” E	Rochefort
Hamoir	8	50°25’30” N - 5°31’31” E	Hamoir
Hampteau	3	50°15’45” N - 5°27’33” E	Hotton
Hazalles	7	50°19’50” N - 5°28’54” E	Durbuy
Hé des Gattes	9	50°28’50” N - 5°41’21” E	Aywaille
Heid de Stinval	7	50°32’13” N - 5°41’50” E	Sprimont
Herbet	6	50°23’10” N - 5°31’35” E	Durbuy
Hérimont	4	50°6’54” N - 5°10’20” E	Rochefort
Heyoule 1	3	50°46’60” N - 5°39’59” E	Bassenge
Heyoule 2	8	50°46’47” N - 5°40’3” E	Bassenge
Heyoule 3	3	50°46’54” N - 5°39’58” E	Bassenge
La Soyère	5	50°5’13” N - 5°11’54” E	Tellin
Les Vevis	3	50°6’34” N - 5°15’9” E	Rochefort
Logne	6	50°23’39” N - 5°32’15” E	Ferrières
Lorinchamps	10	50°5’45” N - 5°14’20” E	Tellin
Maupas	10	50°6’37” N - 5°12’30” E	Rochefort
Mignées	5	50°19’10” N - 5°28’28” E	Erezée
Mont	7	50°32’24” N - 5°48’7” E	Theux
Mont des Pins	6	50°22’1” N - 5°31’11” E	Durbuy
Naurdichamps	3	50°6’38” N - 5°15’12” E	Rochefort
Noiseux	5	50°17’48” N - 5°22’29” E	Somme-Leuze
Pairées centre	10	50°5’59” N - 5°11’4” E	Tellin
Pairées est	5	50°5’59” N - 5°11’15” E	Tellin
Pairées sud	5	50°5’53” N - 5°10’53” E	Tellin
Pairées ouest	8	50°6’0” N - 5°10’20” E	Tellin
Palogne	4	50°23’50” N - 5°32’1” E	Ferrières
Parking Han	3	50°7’42” N - 5°11’14” E	Rochefort
Petit Herbet	3	50°23’0” N - 5°31’5” E	Durbuy
Pierreux/Xhoris	8	50°27’7” N - 5°35’25” E	Ferrières
Plome Mohon	5	50°17’20” N - 5°26’42” E	Hotton
Prairie Hazalles	3	50°19’60” N - 5°29’1” E	Durbuy
Rochers Masbourg-Forrières	3	50°7’22” N - 5°17’29” E	Nassogne
Roches Noires	5	50°28’57” N - 5°34’29” E	Comblain-au-Pont
Roké	4	50°7’22” N - 5°9’8” E	Rochefort
Roptai	4	50°7’4” N - 5°8’32” E	Rochefort
Rouge-Croix	10	50°8’8” N - 5°10’28” E	Rochefort
Route Bure-Belvaux 1	4	50°6’33” N - 5°13’8” E	Rochefort
Route Bure-Belvaux 2	6	50°6’32” N - 5°12’43” E	Rochefort
Route Han-Hamerenne	4	50°8’4” N - 5°11’41” E	Rochefort
Route Resteigne-Belvaux 1	1	50°6’1” N - 5°11’18” E	Tellin
Route Resteigne-Belvaux 2	3	50°5’57” N - 5°11’19” E	Tellin
Route Resteigne-Belvaux 3	6	50°5’51” N - 5°11’9” E	Tellin
Route Resteigne-Belvaux 4	1	50°5’49” N - 5°11’19” E	Tellin
Route Resteigne-Belvaux 5	2	50°5’44” N - 5°11’18” E	Tellin
Route Tellin-Wavreille 1	3	50°6’2” N - 5°13’53” E	Tellin
Route Tellin-Wavreille 2	3	50°6’6” N - 5°13’54” E	Tellin
Saint Remy	9	50°10’48” N - 5°13’31” E	Rochefort
Soy-Biron	3	50°19’14” N - 5°29’15” E	Durbuy

Spinets 1	2	50°10’32” N - 5°17’5” E	Marche-en-Famenne
Spinets 2	9	50°10’13” N - 5°16’29” E	Marche-en-Famenne
Sur Tombeux	4	50°25’55” N - 5°32’32” E	Hamoir
Tartines	9	50°28’42” N - 5°35’25” E	Comblain-au-Pont
Terre Telle	7	50°17’12” N - 5°27’11” E	Hotton
Thier Pirard	3	50°28’30” N - 5°34’41” E	Comblain-au-Pont
Tienne Moseray	3	50°5’44” N - 5°10’43” E	Tellin
Tinaimont 1	4	50°7’45” N - 5°13’7” E	Rochefort
Tinaimont 2	2	50°7’48” N - 5°12’55” E	Rochefort
Tinaimont 3	2	50°7’48” N - 5°12’51” E	Rochefort
Tinaimont 4	4	50°7’47” N - 5°12’42” E	Rochefort
Tombe	9	50°47’37” N - 5°40’19” E	Bassenge
Verlaine	4	50°23’55” N - 5°30’57” E	Durbuy
Viaduc E411	4	50°5’59” N - 5°7’33” E	Rochefort
Warre	3	50°21’53” N - 5°28’15” E	Durbuy