

THE STATE OF CHANGE OF *ERICA SCOPARIA* L. HEATHLAND THROUGH CATTLE GRAZING AND OAK COLONIZATION

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RÉSUMÉ. — *L'état de changement de la lande à Erica scoparia L. sous l'effet du pâturage et de la colonisation par le chêne.* — Le but de notre étude est de mettre en évidence les modifications de la richesse spécifique et d'autres caractères de la végétation qui surviennent sous l'influence du pâturage et de la colonisation par le chêne dans les landes dominées par *Erica scoparia* L. (brande). L'étude a été menée dans le Parc Naturel Régional de la Brenne (France, Région Centre) où cette Éricacée est aujourd'hui considérée comme patrimoniale et protégée au niveau régional et européen. Dix sites ont été choisis au sein d'une propriété privée, couvrant un large éventail de conditions écologiques (sols superficiels et profonds, brande pâturée et non pâturée, pure et envahie par le chêne). La végétation (pourcentage d'occupation de l'espace par les différentes espèces végétales) a été échantillonnée en mai et juin 2006 (105 relevés de 1 m²) et l'impact de la végétation arbustive et arborée sur la biodiversité végétale a été mis en évidence à l'aide de l'analyse des correspondances (AFC) et de tests de Mantel totaux et partiels (méthode de Monte-Carlo). Un gradient décroissant d'incidence de la lumière a été mis en évidence depuis la brande pâturée jusqu'à la brande âgée puis la chênaie, en rapport avec la variation de nombreux traits écologiques, morphologiques et physiologiques (types phytionomiques, indices d'Ellenberg, stratégies de Grime, indice de tolérance de la communauté). La richesse spécifique décroît à mesure de l'extension des Éricacées ou, dans une moindre mesure, de celle du chêne et s'accroît sous pâturage faible à modéré. Les conséquences pour la gestion durable de la brande sont discutées.

SUMMARY. — Our aim was to ascertain whether changes in plant species richness and other vegetation features occur in heathland dominated by *Erica scoparia* L. (besom heath) through the impact of cattle grazing and oak colonization. Our study took place in the Brenne Regional Natural Park (center of France) where this ericaceous species, locally called 'brande', is now considered of patrimonial interest and protected at regional and European level. We selected 10 sites in a private property, covering a wide range of ecological conditions (shallow and deep soils, grazed and non-grazed besom heath, pure and oak-colonized besom heath). Vegetation (percent occupancy of plant species) was sampled in May-June 2006 (105 samples, 1m² each) and the impact of shrub and tree vegetation on plant biodiversity was assessed by correspondence analysis (CA) and total and partial Mantel tests (Monte-Carlo procedure). An environmental gradient of decreasing light incidence from grazed heath to old heath to oak-wood was depicted, along which a number of ecological, morphological and physiological plant traits (growth habits, Ellenberg values, Grime strategies, Tolerance Index of the plant community) were observed to vary. Species richness decreases when ericaceous or, although to a lesser extent, oak cover increases and it increases under low to moderate cattle grazing. Consequences for the sustainable management of 'brande' are discussed.

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Erica scoparia L. (besom heath) is a tall shrub species which dominates mesic heathlands of South-western France and North-western Spain (Bartolomé *et al.*, 2005). On poorly fertile soils, it establishes spontaneously by seed in grassland after agricultural abandonment and before oak colonization (Perrinet, 1995). Once established, this tall ericaceous shrub (2-3m height) grows vegetatively and resprouts after cutting. It forms dense clumps in the shade of which a 'forest' environment is created. Given the poor pastoral value of ericaceous heath and its richness in allelochemicals (Ballester *et al.*, 1982), fire was used to suppress it at least temporarily for the sake of sheep or cattle grazing (Gimingham *et al.*, 1979; Bartolomé *et al.*, 2005). However, *E. scoparia* was also and is still cultivated for traditional purposes (broom, fencing manufacture or roof making), thereby contributing to its widespread occurrence in the temperate Atlantic region, especially on former agricultural land (Perrinet, 1995; Bartolomé *et al.*, 2005).

In the Brenne Regional Natural Park (Indre, Centre, France), heathland dominated by *E. scoparia*, locally called 'brande' (the name indicate both the plant and the community), covers wide areas of land not managed for agriculture (Rallet, 1935). It is now protected, according to European policies for the conservation of heathland habitats (European Council Directive 92/43). However, the conservation value of 'brande' imposes to preserve it from spontaneous colonization by several oak species [*Quercus robur* L., *Q. petraea* (Matt.) Liebl., *Q. pubescens* Willd. and their hybrids] could occur. Cutting, moderate grazing or prescribed burning are used for the management of *E. scoparia* heathland, which is considered of a higher patrimonial interest, when at an early successional stage, than the succeeding old heath and oak-wood stages (Gaudillat, 1997). In the particular landscape of 'Grande Brenne' (60 000 ha, included in the Brenne Natural Park) hard sandstone outcrops of poor agricultural value, locally called 'buttons', are often covered with a dry variant of *E. scoparia* heath, with Common Heather (*Calluna vulgaris* L.) and Bell Heather (*Erica cinerea* L.) as companion species (Rallet, 1935). Colonization by oak is more difficult on 'buttons', due to shallow soil conditions, and some of these outcrops appear devoid of any shrub vegetation, with an abundant and diversified herb, moss and lichen vegetation (Gaudillat, 1997). 'Buttons' are surrounded by more mesic environments, most often used for pasture, with stagnant water during winter and spring months (Rallet, 1935). Other important components of the Grande Brenne landscape are numerous ponds, traditionally created from the Middle Age for the need of carp breeding.

Our aim was to ascertain whether changes in plant species richness and other vegetation features occur in *E. scoparia* heath through the impact of cattle grazing and oak colonization. The negative impact of dense ericaceous heath on plant species richness has been often recorded (Barclay-Estrup & Gimingham, 1969; Gimingham *et al.*, 1979; Miles, 1979) and we hypothesized that this detrimental effect could be alleviated under either moderate grazing by cattle or colonization by oak.

METHODS

STUDY SITES

The present study was done in a private property (Les Vigneaux, Mézières-en-Brenne, Indre), where the traditional land use of Grande Brenne has been maintained to a large extent, displaying a variety of typical environments: 'buttons' with shallow soils are let covered with spontaneous scrub and forest vegetation while the surrounding land (meadows and ponds) is devoted to extensive cattle pasture and to fishing. Such practices have been widely maintained in Grande Brenne for several centuries (Trotignon & Trotignon, 2007). The landscape includes two 'buttons' covered with grazed or non-grazed ericaceous heath and woodlots of natural oak and planted pine and poplar. Ponds and meadows are also present but they were not included in our study. We selected ten sites (Fig. 1) covering the range of variation of non-agricultural land, from grazed heath to oak woodland, thus expressing a gradient of decreasing opening of the environment and increased vertical stratification (Tab. I). They were chosen on the base of a previous map of vegetation done by F. Pinet (personal communication) and our own observations on plant communities. Soils were classified as shallow or deep whether they were less or more than 20 cm deep. Two intensities of grazing could be ascertained from the morphology of besom heath: in BP1 bushes kept more or less their natural erected form, while in BP2 they exhibited a typical conical shape resulting from the selection of twigs of the year by cattle. BNP did not exhibit any sign of cattle pressure, being located on Button 2, from which cattle was excluded. BA1, BA2 and BA3 were old besom heath sites, hardly accessible and not used by cattle.

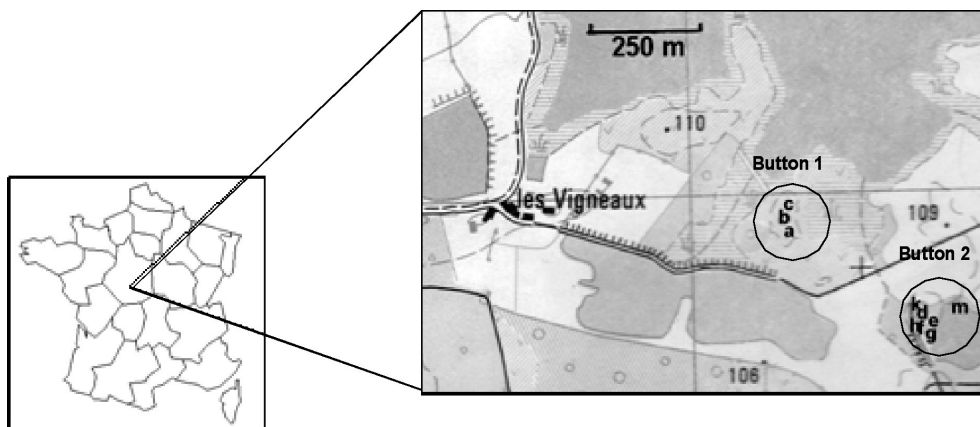


Figure 1. — Map of the study area and location of the 10 sites. a = BP1, b = BA1, c = BP2, d = BNP, e = BA2, f = BA3, g = BSF1, h = BSF2, k = CHM2, m = CHM1.

The elevation is around 120 m a.s.l., with an undulating relief due to an alternation of ‘buttons’ and ponds. The climate is Atlantic, mild oceanic, with a mean annual temperature of 11°C and a mean annual rainfall of 700 mm. Soils are highly heterogeneous, varying from Lithosols (top of ‘Buttons’) to Gleysols (pond shores, not studied here). According to data on BP1, BP2 and BA1 (Benoist, 2006) the topsoil of pastured and old heath is acid ($\text{pH}_{\text{water}} \sim 4.5$) and moderately fertile ($\text{C/N} \sim 18$). These features are quite similar to those of woodlots ($\text{pH}_{\text{water}} \sim 4.4$, $\text{C/N} \sim 19$) but differ from those of pastures ($\text{pH}_{\text{water}} \sim 4.9$, $\text{C/N} \sim 14$). The Humus Index (Ponge & Chevalier, 2006) varies to a great extent, from 1 (Eumull) in BP1 to 5.8 (Eumoder) in average in BP2 (Benoist, 2006).

SAMPLING PROCEDURE

Stratified sampling of vegetation took place in June 2006. The sites CHM1, CHM2, BSF1, BSF2, BA3 and BA2 were sampled as follows: four 1 m² squares were disposed at each angle of a 10 x 10 m square and an additional 1 m² square was placed at the centre. Each unit square was divided into 25 sub-units according to a 20 cm grid, allowing to score plant species by counting the number of sub-units where they were found (ranging from 0 to 25) which was an estimate of their occupancy. When trees were present the projection of their crown was used for the calculation of their score. Only four unit squares could be positioned in BA3, one corner being omitted by lack of space. The choice of a small and constant plot size for our stratified sampling was justified by the need to measure plant species richness at a very local level, and to compare it among different ecosystem types.

BNP was sampled along eight transect lines radiating from a central post. Unit squares were positioned each 4 m. The number of unit squares along a given direction varied from 2 to 5, totalling 29 samples.

BP1, BP2 and BA1 were sampled by positioning unit squares each 6 m along several rows placed 7 m apart, the total number of samples varying according to the site shape.

Differences in sampling design were mainly due to topographic variation and the need to embrace most visible intra-site heterogeneity. However, distances between unit squares within each site remained of the same order of magnitude (4 to 7 m), and allowed to embrace the whole area covered continuously by a given vegetation type.

Mosses and vascular plants were identified at the species level whenever possible (Tab. II).

DATA ANALYSIS

Species richness was calculated as the number of plant species found in each 1 m² unit square (Tab. I). We used species richness at the plot scale (a small-scale community attribute) as a measure of species coexistence (a small-scale community process), considering that the more species co-occurring at a very small-scale (1 m²), the less negative interactions between them (Zobel, 1997; Reitalu *et al.*, 2008). Beta diversity β_w (Whittaker, 1960) was calculated as the total number of plant species found in a given site divided by the mean number of species in unit squares. We used it as an estimate of mosaic heterogeneity of the plant cover.

Plant species were classified into several groups according to their growth habits: mosses, grasses, forbs (non-grassy herbs), legumes (here only Fabaceae), ericaceous shrubs, non-ericaceous shrubs, trees (here only oak) and lianas. The percent occupancy of a given plant group per unit square was estimated by dividing the maximum number of sub-units occupied by a species member of this group by the total number of sub-units (25).

Ellenberg indices (Light, Moisture, Reaction and Nitrogen) were attributed to each species (Tab. II) using data for British vascular species (Hill *et al.*, 1999) completed for moss species by online data (MAVIS 2000, <http://www.ceh.ac.uk/products/software/mavis/download.asp>). Most identified species were present in the British data base (Tab. II). They were taken into account in the calculation of average Ellenberg indicator values (Diekmann & Lawesson, 1999) per unit square. Species were not weighed by percent occupancy, according to Wamelink & Van Dobben (2003) and

TABLE 1

Main site and vegetation features of the 10 investigated plots (mean \pm S.E.). r_M is a Mantel correlation coefficient with Axis 1 values, tested by Monte-Carlo simulation. *** = significant at 0.001 level. NS = not significant at 0.05 level

Code	BP2	BP1	BNP	BA3	BA2	BA1	BSF2	BSF1	CHM1	CHM2	r_M
Site (butter)	1	1	2	2	2	1	2	2	2	2	
Vegetation type	Pastured heath	Pastured heath	Non-pastured heath	Old heath	Old heath	Old heath	Oak-heath	Oak-heath	Oakwood	Oakwood	
Soil type	Shallow	Shallow	Shallow	Deep	Deep	Deep	Deep	Deep	Deep	Deep	
Number of samples	20	17	29	4	5	10	5	5	5	5	
Species richness per m ²	14.4 \pm 0.9	12.6 \pm 1	7.9 \pm 0.4	7 \pm 0.7	7.21 \pm 0.9	11.6 \pm 10.9	7.61 \pm 1.2	11 \pm 1.9	7 \pm 0.8	11.6 \pm 1.7	- 0.24***
Beta diversity (Whittaker's β_w)	3.8	3.4	3.7	1.9	2.4	2.8	2.6	2.7	2.1	2.2	
Mosses %	76.8 \pm 3.8	90.6 \pm 2.9	77.5 \pm 5	83 \pm 17	76 \pm 19.4	72.5 \pm 6.7	16.8 \pm 7.2	61.6 \pm 16.7	0.8 \pm 0.8	5.61 \pm 1.6	- 0.60***
Glasses %	53.6 \pm 4.9	46.6 \pm 6	17.2 \pm 4.8	2 \pm 2	17.6 \pm 10.5	24.3 \pm 13.8	40 \pm 17.4	14.4 \pm 6	100 \pm 0	80.8 \pm 19.2	0.08***
Forbs %	43.4 \pm 5.8	41.4 \pm 5.1	15.6 \pm 4.4	5 \pm 3	16.8 \pm 8.2	30.1 \pm 7.6	19.2 \pm 6.4	10.4 \pm 7.1	75.2 \pm 15.3	48.8 \pm 5.6	0.01NS
Legumes %	67.6 \pm 6.5	58.4 \pm 7.6	51.7 \pm 5.5	17 \pm 5	9.6 \pm 5.5	1.7 \pm 0.8	2.4 \pm 1	2.4 \pm 1.6	3.2 \pm 2.3	2.4 \pm 2.4	- 0.39***
Ericaceous shrubs %	56.2 \pm 5.5	62.6 \pm 7.5	85.5 \pm 3.5	95 \pm 5	88 \pm 10.1	87.5 \pm 0	20 \pm 20	45.6 \pm 20	0 \pm 0	0 \pm 0	- 0.38***
Non-ericaceous shrubs %	66.4 \pm 7	67.5 \pm 5.6	58.2 \pm 4.7	75 \pm 25	9.6 \pm 3.5	44.8 \pm 6.7	2.4 \pm 1	8.8 \pm 4.6	0.8 \pm 0.8	15.2 \pm 8.3	- 0.43***
Oak trees %	6.4 \pm 5.1	4.2 \pm 2.6	9.5 \pm 4.9	0 \pm 0	16.8 \pm 15.8	1.7 \pm 0.8	75.2 \pm 16.7	92 \pm 17.8	100 \pm 0	100 \pm 0	0.68***
Lianas %	1.2 \pm 1.2	8.7 \pm 4.9	5 \pm 2.8	5 \pm 3.8	0 \pm 0	6.1 \pm 3.9	14.4 \pm 7.4	22.41 \pm 0.5	75.2 \pm 12.4	41.6 \pm 11.8	0.58***
Light Index	7.3 \pm 0.05	7.27 \pm 0.05	7.31 \pm 0.06	7.17 \pm 0.15	7.1 \pm 0.07	6.71 \pm 0.07	6.58 \pm 0.27	6.51 \pm 0.14	6.13 \pm 0.13	6.31 \pm 0.12	- 0.72***
Moisture Index	5.35 \pm 0.08	5.22 \pm 0.11	5.81 \pm 0.04	6.01 \pm 0.3	5.71 \pm 0.18	5.45 \pm 0.08	5.54 \pm 0.14	5.48 \pm 0.11	5.28 \pm 0.13	5.48 \pm 0.08	0.14***
Reaction Index	3.89 \pm 0.09	4.13 \pm 0.1	3.58 \pm 0.08	4.59 \pm 0.15	4.47 \pm 0.23	4.77 \pm 0.08	4.55 \pm 0.21	4.63 \pm 0.1	4.75 \pm 0.17	4.86 \pm 0.22	0.5***
Nitrogen Index	2.58 \pm 0.1	2.93 \pm 0.08	2.49 \pm 0.09	3.33 \pm 0.16	3.26 \pm 0.13	3.44 \pm 0.08	3.71 \pm 0.27	3.63 \pm 0.19	4.17 \pm 0.21	4.3 \pm 0.19	0.7***
Competitive ability	1.97 \pm 0.04	2.01 \pm 0.06	2.35 \pm 0.8	3.08 \pm 0.08	2.72 \pm 0.12	2.82 \pm 0.08	2.99 \pm 0.14	2.73 \pm 0.14	2.92 \pm 0.05	2.96 \pm 0.04	0.7***
Stress tolerance	3.53 \pm 0.08	3.18 \pm 0.07	3.63 \pm 0.08	2.75 \pm 0.16	3.32 \pm 0.14	3.11 \pm 0.05	3.01 \pm 0.14	3.17 \pm 0.11	2.8 \pm 0.12	2.77 \pm 0.06	- 0.45***
Ruderalness	1.88 \pm 0.11	2.34 \pm 0.11	1.12 \pm 0.04	1.42 \pm 0.25	1.45 \pm 0.14	1.83 \pm 0.1	1.6 \pm 0.21	1.39 \pm 0.06	1.83 \pm 0.09	1.98 \pm 0.14	- 0.11***
Tolerance Index	0.42 \pm 0.02	0.49 \pm 0.02	0.46 \pm 0.02	0.54 \pm 0.04	0.62 \pm 0.05	0.63 \pm 0.02	1.05 \pm 0.09	0.79 \pm 0.1	1.1 \pm 0.03	1.01 \pm 0.01	0.77***
Axis 1 of C/A	0	- 0.62 \pm 0.14	- 0.26 \pm 0.05	0.11 \pm 0.02	0.15 \pm 0.07	0.64 \pm 0.1	0.84 \pm 0.1	1.42 \pm 0.69	1.46 \pm 0.24	2.2 \pm 0.24	

contrary to suggestions made by Diekmann (2003), because we thought that the percent occupancy was too sensitive to growth habits, and may confound habitat preferences. The same method was applied to the three strategies: Competitive ability, Stress tolerance and Ruderalness (Grime, 1987). Grime strategies were also found in the MAVIS data base with the exception of moss species and some vascular species (Tab. II). Ellenberg indices were used to describe habitat preferences and Grime strategies to describe life-history traits.

Correspondence analysis (CA) was used to discern trends in the distribution of plant species across the 10 investigated sites (Greenacre, 1984). This indirect gradient method was chosen because of its ease to discern trends in matrices of count numbers (Benzécri, 1969; Kenkel, 2006). However, it was slightly improved, as explained below. Species present in less than two samples were omitted from the analysis, because they were not judged very informative. Species were coded as in Tab. II and their percent occupancy in the different samples was used to build a data matrix crossing 79 species as rows (active variables) and 105 samples as columns. Passive variables were added as additional lines: soil (shallow or deep, each coded as 1 or 0), sites (10 sites, each coded as 1 or 0), species richness per sample (number of species), growth habit occupancy (eight types, each in percent), average Ellenberg indices (4) and Grime strategies (3) per sample (each in percent). All variables (active and passive) were reweighted and refocused (variance equal to 1 and mean equal to 20), in order to (i) avoid advantaging rare species, (ii) interpret factorial coordinates of variables in terms of their contribution to the axes and (iii) allow mixing data of varying type (Fédoroff *et al.*, 2005). Additional variables with floating values were doubled ($X' = 40 - X$, X being the original value, X' the new, conjugate value), each variable being represented by two points, one for its higher values (original values), the other for its lower values (conjugate values), symmetrical around the origin of the axes, with a gradient between them (Fédoroff *et al.*, 2005). The choice of 40 was justified by the need to avoid negative values, but it has no effect on the calculation of eigen values.

The first axis of CA was used to measure the tolerance of the different plant species to overall environmental influences, or niche width (McNaughton & Wolf, 1970). For each plant species the variance of CA coordinates along Axis 1 was averaged over all samples, each sample being weighted by the percent occupancy of the species. The higher was the variance the higher was the tolerance of the species to the environmental variation depicted by Axis 1 of CA. The average tolerance of the plant community or Tolerance Index (Dolédéc *et al.*, 2000) was calculated by averaging the unweighted tolerance value of the different plant species found in each sample.

Given that our data could be thought at first sight to be autocorrelated (samples taken in the same site are not independent), correlation was tested by Signed Mantel tests (Legendre & Legendre, 1998; Oberrath & Böhning-Gaese, 2001). For that purpose geographical and ecological distance matrices were built. The ecological distance between two samples was measured by the signed (algebraic) difference in the value of a parameter (for instance the percent occupancy of a given species or group of species or Axis 1 of CA). The correlation between two distance matrices was calculated as the product-moment correlation coefficient, which was then tested by Monte-Carlo simulation. Partial Mantel tests were used to discern possible causal relationships within a set of self-correlated variables (Legendre & Fortin, 1989).

All statistical treatments were performed with XLStat Pro[®] version 2007.5 (Addinsoft[®]).

RESULTS AND DISCUSSION

WITHIN-SITE SPATIAL AUTOCORRELATION

Species richness of unit squares and percent occupancy of ericaceous vegetation were used to test for the existence of within-site spatial autocorrelation (between-site autocorrelation being considered trivial in our study). Only sites with a higher number of unit squares (BP1 with 17 samples, BP2 with 20 samples and BNP with 29 samples) were considered. Signed Mantel correlation coefficients r_M between geographic distance and species richness showed a negative spatial autocorrelation of species richness in the more pastured heath BP2 ($r_M = -0.21$, $P < 0.01$): nearby unit squares differed more than null expectation, i.e. there was a mosaic of species-rich and species-poor zones at a scale $\sim 6-7$ m. A positive spatial autocorrelation was detected in the non-pastured heath BNP ($r_M = 0.12$, $P < 0.05$), showing the existence of patches of species-rich and species-poor vegetation at a scale in excess of 6-7 m (nearby samples differed less than remote samples). No spatial autocorrelation was detected in the slightly pastured heath BP1 ($r_M = 2.10 \cdot 10^{-17}$, $P = 0.98$), showing the absence of species-rich and species-poor vegetation patches at least at the scale of the sampling grid ($\geq 6-7$ m).

Contrary to species richness, the percent occupancy of ericaceous vegetation, as well as that of *E. scoparia* alone, did not show any spatial autocorrelation at the scale of the sampling grid.

THE GRADIENT OF FLORISTIC COMPOSITION DEPICTED BY CORRESPONDENCE ANALYSIS

Most significant variation in the floristic composition was depicted by Axis 1 (10% of the total variation), along which all plant species were regularly distributed. Axis 2 (7.6%

TABLE II

Code and latin name of plant species recorded in the study area in at least two samples, together with their tolerance values, Ellenberg values and CSR strategies when known. Codes in bold type for vascular species (lower case for herbs and shrubs, upper case for trees and shrubs), in italic lower case type for mosses and lichens, underlined for legumes

Code	Latin name	Light	Moisture	Reaction	Nitrogen	Competitive ability	Stress-tolerance	Ruderalness	Tolerance value
amo	<i>Arenaria montana</i> L.								0.37
aod	<i>Anthoxanthum odoratum</i> L.	7	6	4	3	2	3	3	0.90
apr	<i>Aira praecox</i> L.	8	2	4	2	1	3	3	0.41
ate	<i>Agrostis tenuis</i> Sibth.	6	5	4	4	3	3	3	0.95
<i>aun</i>	<i>Atrichum undulatum</i> (Hedw.) P. Beauv.	7	6	3	4				1.02
<i>bca</i>	<i>Bryum caespitium</i> Hedw.								0.00
<i>bru</i>	<i>Brachyhectium rutabulum</i> (Hedw.) B., S. & G.	6	5	6	5				0.35
<i>bsp</i>	<i>Bryum</i> sp.	7	5	7	7				0.14
<i>bsu</i>	<i>Bryum subapiculatum</i> Hampe								0.12
cgl	<i>Cerastium glomeratum</i> Thuji.	7	5	6	5	1	2	4	0.20
CMO	<i>Crataegus monogyna</i> Jacq.	6	5	7	6	3	3	1	1.37
cpi	<i>Carex pilulifera</i> L.	7	5	3	2	1	5	1	0.27
<i>cpu</i>	<i>Ceratodon purpureus</i> (Hedw.) Brid.	5	5	4	5				0.21
CSC	<i>Cytisus scoparius</i> (L.) Link	8	5	4	4	3	3	1	1.50
cs1	<i>Carex</i> sp.								0.00
cs2	<i>Cerastium</i> sp.	8	3	7	4				0.31
CVU	<i>Calluna vulgaris</i> (L.) Hull	7	6	2	2	3	3	1	0.18
dde	<i>Danthonia decumbens</i> (L.) DC.	7	6	4	2	1	5	1	0.01
<i>dhe</i>	<i>Dicranella heteromalla</i> (Hedw.) Schimp.	9	3	4	1				0.73
<i>dsc</i>	<i>Dicranum scoparium</i> Hew.	9	3	4	1				0.21
ECl	<i>Erica cinerea</i> L.	7	5	2	2	2	4	1	0.31
ESC	<i>Erica scoparia</i> L.								0.55
<i>est</i>	<i>Eurtynchium striatum</i> (Hew.) Schimp.	7	5	4	3				0.12
FAL	<i>Frangula alnus</i> Mill.	6	8	5	S				0.00
<i>fbr</i>	<i>Fissidens bryoides</i> Hedw.								0.22

Code	Latin name	Light	Moisture	Reaction	Nitrogen	Competitive ability	Stress-tolerance	Ruderalness	Tolerance value
fov	<i>Festuca ovina</i> L.	7	5	4	2	1	5	1	0.23
<u>GAN</u>	<i>Genista anglica</i> L.	8	5	3	2				0.00
gap	<i>Galium aparine</i> L.	6	6	7	8	3	1	3	0.12
gmo	<i>Geranium molle</i> L.	7	5	6	5	1	2	4	0.36
<i>hcu</i>	<i>Hypnum cupressiforme</i> Hedw.	8	8	4	2				1.01
HHE	<i>Hedera helix</i> L.	4	5	7	6	3	3	1	1.00
hhu	<i>Hypericum humifusum</i> L.	7	6	4	3	2	4	2	0.89
him	<i>Hieracium umbellatum</i> L.								0.05
<i>hju</i>	<i>Hypnum jutlandicum</i> Balcerk. et Brzeg	8	8	4	2				0.41
hla	<i>Holcus lanatus</i> L.	7	6	6	5	3	3	3	0.11
<i>him</i>	<i>Hypnum lacunosum</i> (Brid.) Hoffm. ex Brid.								0.32
hmo	<i>Holcus mollis</i> L.	6	6	3	3	4	2	2	1.05
hpi	<i>Hieracium pilosella</i> L.	8	4	7	2				0.38
hra	<i>Hypochoeris radicata</i> L.	8	4	5	3	3	3	3	0.34
hum	<i>Halimium umbellatum</i> (L.) Spach.								0.26
jsp	<i>Juncus</i> sp.	7	8	4	3				0.28
<i>kpr</i>	<i>Kindbergia praelonga</i> (Hedw.) Ochyra	7	5	4	3				0.56
lea	<i>Luzula campestris</i> (L.) DC.	7	4	5	2	2	4	2	0.50
LPE	<i>Lonicera periclymenum</i> L.	5	6	5	5				1.10
<i>isp</i>	Unidentified iichen species								0.34
lvu	<i>Linaria vulgaris</i> Mill.	7	4	8	6	3	1	3	0.45
<u>mmi</u>	<i>Medicago minima</i> L.	9	3	7	2				1.36
mmr	<i>Montia minor</i> C. C. Gmel.	7	8	5	3	1	2	4	0.31
pan	<i>Poa annua</i> L.	7	5	6	7	1	1	5	0.32
<i>pfo</i>	<i>Polytrichum formosum</i> Hew.	4	5	6	6				0.33
<i>pju</i>	<i>Polytrichum juniperinum</i> Hew.	4	5	6	6				1.04
pla	<i>Plantago lanceolata</i> L.	7	5	6	4	3	3	3	0.57
ppr	<i>Poa pratensis</i> L.	7	5	6	6	3	3	3	0.03

Code	Latin name	Light	Moisture	Reaction	Nitrogen	Competitive ability	Stress-tolerance	Ruderalness	Tolerance value
pre	<i>Potentilla reptans</i> L.	7	5	7	5	3	2	3	0.00
pse	<i>Polygala serpyllifolia</i> Hose	8	7	2	2				0.02
PSP	<i>Prunus spinosa</i> L.	e	5	7	6	3	3	1	1.15
QHY	<i>Quercus</i> (hybrid)								0.79
QPE	<i>Quercus petraea</i> (Mattuschka) Lieblein	6	6	3	4	3	3	1	1.61
QPU	<i>Quercus pubescens</i> Willd.								0.64
QRO	<i>Quercus robur</i> L.	7	5	5	4	3	3	1	1.37
QSE	<i>Quercus</i> (seedling)								0.89
rac	<i>Rumex acetosella</i> L.	7	5	4	3	2	3	3	0.93
RAR	<i>Rosa arvensis</i> Huds.	6	4	7	5				0.00
rbu	<i>Ranunculus bulbosus</i> L.	7	4	7	4	1	3	3	0.21
RCA	<i>Rosa canina</i> L.	6	5	7	6				0.03
RFR	<i>Rubus fruticosus</i> L.	6	6	6	6	3	3	1	0.93
<i>rla</i>	<i>Racomitrium lanuginosum</i> J. H. Tallisl.	7	5	5	4				0.35
RSA	<i>Rubus</i> sp. A								0.31
RSB	<i>Rubus</i> sp. B								0.05
RSC	<i>Rubus</i> sp. C								0.09
<i>spu</i>	<i>Scleropodium purum</i> (Hedw.) Limpr.	8	5	6	2				0.63
sti	<i>Serratula tinctoria</i> L.	7	6	6	2				0.00
STO	<i>Sorbus torminalis</i> (L.) Crantz	4	5	6	5				0.21
tnu	<i>Teesdalia nudicaulis</i> (L.) R.	8	3	2	2				0.58
tsc	<i>Teucrium scorodonia</i> L.	6	4	4	3	2	4	2	1.30
<u>UNA</u>	<i>Ulex nanus</i> T. F. Forster ex Symons	8	6	1	2				0.24
vca	<i>Viola canina</i> L.	8	4	5	2				0.30
vch	<i>Veronica chamaedrys</i> L.	6	5	6	5	3	3	3	0.29
vsp	Unidentified vascular species								

of the total variation) corresponded to only one sample taken in BP2, and thus was not considered. Axis 1 correlated well with all vegetation parameters measured at the community level (Tab. I). Highest correlation values were with Tolerance Index and Light Index, 60% and 52% of the total variation of which being depicted by Axis 1, respectively (Fig. 2). The Light Index decreased while Moisture, Reaction and Nitrogen Ellenberg indices increased when Axis 1 values increased. Grime strategies ‘Stress tolerance’ and ‘Ruderalness’ decreased while ‘Competitive’ ability increased when Axis 1 values increased. Local species richness and beta diversity decreased when Axis 1 values increased. The percent occupancy of mosses, legumes,

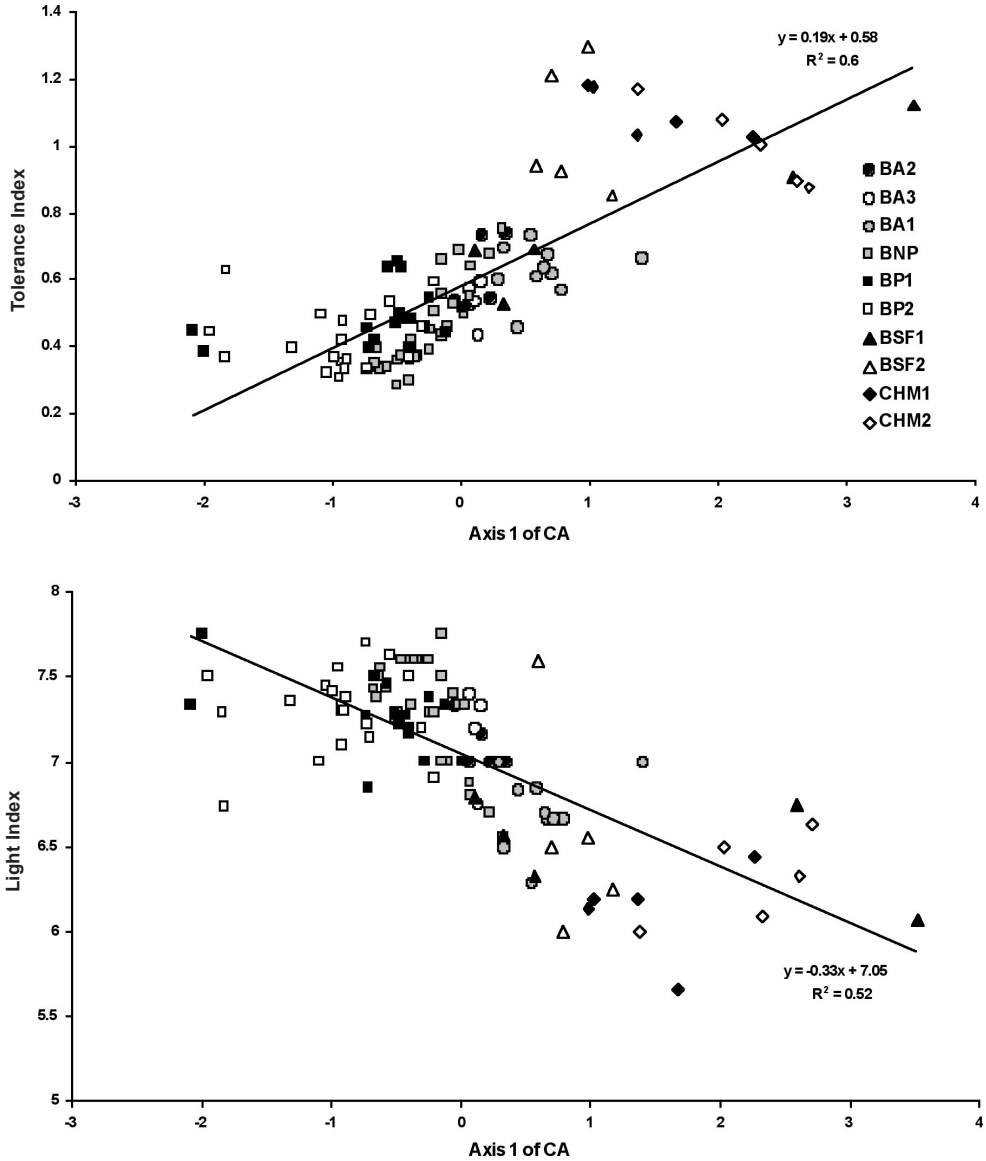


Figure 2. — Relationship between Tolerance Index (Dolédéc *et al.* 2000) and Ellenberg’s Light Index with the first axis of Correspondence Analysis (CA). Equations of regression lines and determination coefficients are indicated. Codes for the 10 study sites as in Tab. I.

ericaceous and non-ericaceous shrubs decreased while that of grasses, oak trees and lianas increased when Axis 1 values increased. This was reflected in the projection of passive variables along Axis 1 (Fig. 3). All vegetation parameters negatively correlated with Axis 1 were projected on the negative (lower) side, while those positively correlated were projected on the positive (upper) side, as expected. In addition, shallow soil was projected far from the origin on the negative side, the contrary for deep soil, and the 10 sites were classified in the following order, from negative to positive values of Axis 1: BP2 < BP1 < BNP < BA3 = BA2 < BA1 = BSF2 < BSF1 = CHM1 < CHM2. We interpreted Axis 1 as a gradient of stability of the ecosystem, from pastured heath to oak-wood, associated with increasing soil thickness and fertility, the latter being indirectly ascertained from (i) Ellenberg indices (less light, more nitrogen, more moisture, less acidity), (ii) Grime plant strategies (less ruderals and stressors, more competitors) and (iii) niche width (increasing Tolerance Index of the community).

More woody species were projected on the positive side of Axis 1 (Fig. 4), while more herb species were projected on the negative side of this axis. The increase in the number of woody species and the decrease in the number of herb species along Axis 1 contrasts with the absence of any significant correlation between Axis 1 and percent occupancy by forbs (Tab. I, Fig. 3), and the weak (although significant) correlation between Axis 1 and percent occupancy by grasses. This means that although more forbs and grasses were present in more open environments (negative side of Axis 1), they occupied more restricted areas than under higher vegetation (positive side of Axis 1), thus giving them low scores of occupancy.

Two species of patrimonial interest were present in our samples: *Arenaria montana* L., which is protected locally, and *Halimium umbellatum* (L.) Spach., which is protected regionally (Pinet, 2005). Both species were projected far from the origin, on the negative side of Axis 1, i.e. they were typically present in pastured heath. No invasive species was found in the investigated sites, which are in a fairly good state of naturalness (Pinet, personal communication).

It may be questioned whether the main gradient depicted by Axis 1 of CA was a potential trajectory of the ecosystem (from pastured heath to oak forest) or the juxtaposition of separate habitats. A nearby wet meadow with grasses and rushes was excluded from our study because it did not exhibit any relationships with the vegetation types used for our study, thereby restricting comparisons to well-drained sites with varying soil depth. In the environmental conditions prevailing in the studied region, lowland is commonly used for pasture and fish breeding, and sandstone outcrops ('buttons') are abandoned to colonization by heath and oak-wood. The colonization of outcrops by oak can be observed whenever soils are at least 20 cm thick, i.e. when soils were not completely destroyed by human activities (pasture, mining) or had time to recover from naked bedrock (Rallet, 1935; Perrinet, 1995; Gaudillat, 1997). The same successional trajectory may thus be arrested at different stages according to the slow, sometimes nil, soil development, like in a primary succession (Miles & Walton, 1993). In that sense Axis 1 describes both a (potential) successional trajectory and a continuum of habitats.

THE EFFECT OF ERICACEOUS VEGETATION, GRAZING AND OAK COLONIZATION ON PLANT BIODIVERSITY

Compared with other vegetation features, plant species richness did not display a good relationship with the gradient depicted by Axis 1, despite a negative and highly significant Mantel correlation coefficient (Tab. I). However, on the negative side of Axis 1, BNP, BP1 and BP2 form a sequence of increasing distance to the origin which is related to an increasing level of grazing (nil in BNP, low in BP1, medium in BP2) and an increasing level of species richness (Tab. I). The three sites are on shallow soils, at the top or near the top of Buttons A and B (Tab. I). Species richness near doubled from BNP to BP2, BP1 being intermediate, while the beta diversity β_w did not vary to a great extent (Tab. I). Other pronounced differences between non-pastured and pastured heath were in the percent occupancy of grasses, which tripled from BNP to BP2 (BP1 being intermediate) and ruderalness, which increased from BNP to BP1 then to BP2 (Tab. I). Plotted against the percent occupancy of ericaceous vegetation in treeless sites, plant species richness showed a decreasing trend (Fig. 5), indicating that in the absence of trees any decrease in ericaceous vegetation would increase plant species richness. This is

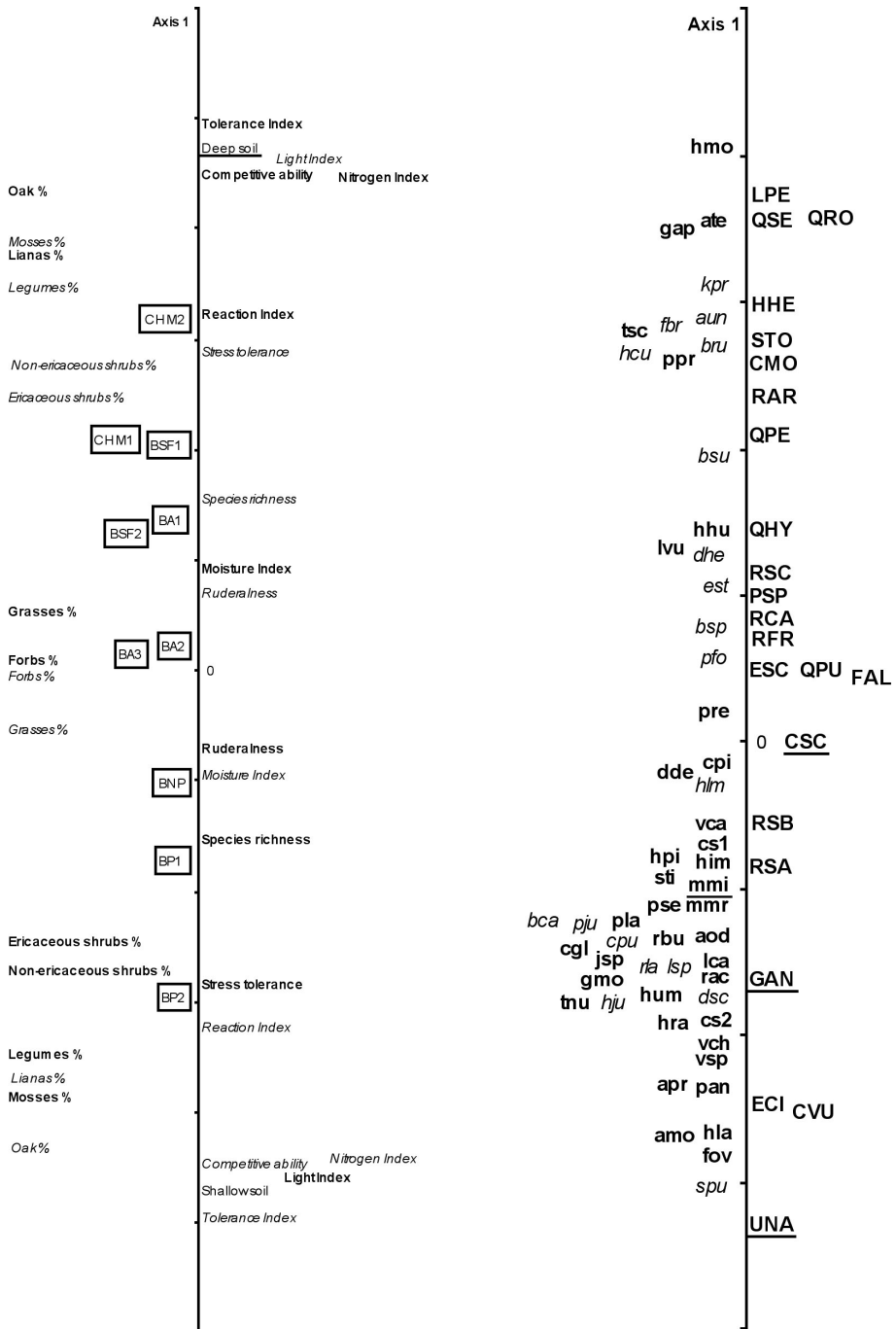


Figure 3 (Left). — Projection of passive variables along Axis 1 of CA: sites (in boxes), soil types (underlined), percent occupancy by species groups, average Ellenberg indices, average Grime strategies and Tolerance Index (higher values in bold, lower values in italics, see text for more details).

Figure 4 (Right). — Projection of the 79 plant species along Axis 1 of CA. Species codes and letter types as in Tab. II.

reflected in a negative and highly significant Mantel correlation coefficient ($r_M = -0.54$, $P < 0.0001$) between species richness and percent occupancy by ericaceous vegetation. The projection of individual samples from the same site (Fig. 5) suggests that the decreasing trend displayed when all treeless sites are plotted together is still depicted at the inside of individual sites, except in BA1, BA2 and BA3 (old heath) where the percent occupancy by ericaceous vegetation is always high. The Mantel correlation coefficient between species richness and percent occupancy by ericaceous vegetation was negative and highly significant ($P < 0.0001$) in BNP ($r_M = -0.32$), BP1 ($r_M = -0.36$) and BP2 ($r_M = -0.43$). When all sites (oak-heath and oak-wood included) were taken into account, the Mantel correlation coefficient between species richness and percent occupancy by ericaceous vegetation was higher ($r_M = -0.25$) but still highly significant ($P < 0.0001$). When corrected for percent occupancy by trees (oak), partial r_M calculated on all sites became as low as -0.42 thus of the same magnitude as when only treeless sites were considered.

Calculated on all sites, there was a very weak (although still highly significant) negative effect of percent occupancy by oak on species richness ($r_M = -0.09$, $P < 0.0001$). When corrected for percent occupancy by ericaceous vegetation the negative oak effect became much more prominent (partial $r_M = -0.36$, $P < 0.0001$) but remained at a lower level than the negative effect of ericaceous vegetation when corrected for oak effect (partial $r_M = -0.42$, $P < 0.0001$).

We showed that the species richness at the unit square (1 m^2) level decreased in parallel with the development of woody (shrub or tree) vegetation. Within the limits of causality inference based on correlation values (Thagard, 1998), we interpret it as a result of the detrimental effect of woody vegetation to the small-scale coexistence of plant species, which has been observed to occur in wooded pastures (Gillet *et al.*, 1999). This effect was more prominent with ericaceous than with oak cover and could be attributed to a combination of factors such as competition for light and nutrients (Aerts *et al.*, 1990) and mycorrhizal interference (Genney

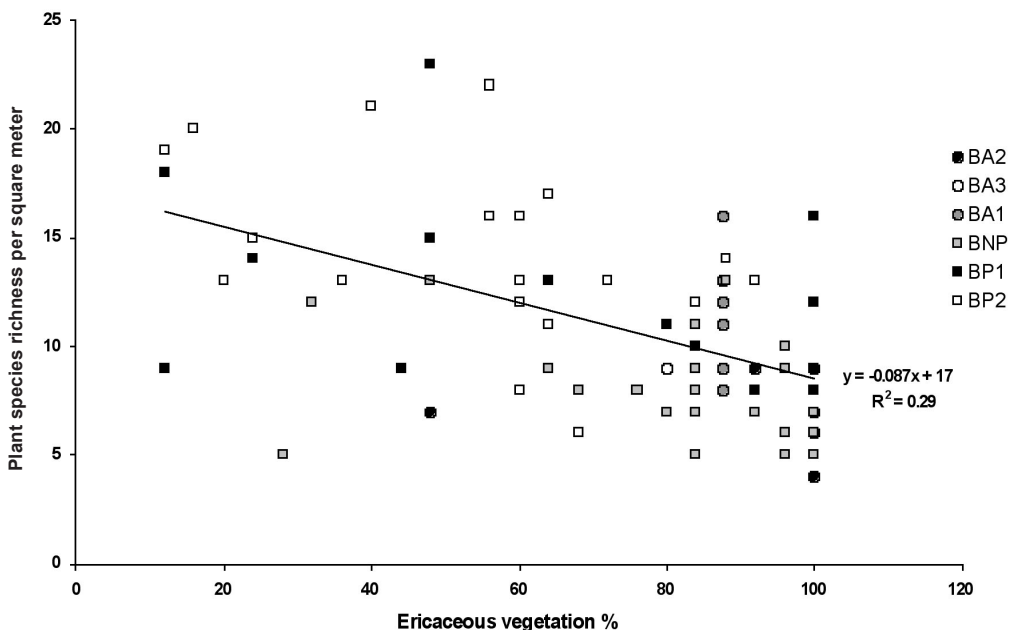


Figure 5. — Relationship between percent occupancy by ericaceous vegetation and plant species richness of unit samples, in 6 oak-free heath sites. Codes for sites as in Fig. 1. Equation of regression line and determination coefficient are indicated.

et al., 2000). The nutrient status of the soil improved along the environmental gradient from heath to oak-wood (Axis 1 of CA), as ascertained from habitat preferences and life-history traits of plant species (Fig. 2, Tab. I). Similar changes have been observed when ericaceous heath becomes colonized by oak (Nielsen *et al.*, 1987, 1999). Thus, the observed decrease in plant species richness under oak cannot be ascribed to scarcity of nutrients and increased acidity (Roem & Berendse, 2000). Given that Grime's Competitive ability and Tolerance Index of the community (mean niche breadth) increased along the environmental gradient depicted by Axis 1 of CA while Stress Tolerance decreased, we interpret the observed decrease in species coexistence level as a result of increased exploitative competition rather than direct interference or environmental stress (Huston, 1979; Grime, 1985; Connell, 1990).

On shallow soils ('buttons'), we observed a favourable effect of grazing on species coexistence level when comparing non-grazed heath (BNP) to slightly grazed (BP1) and to moderately grazed heath (BP2). Grime's Ruderalness increased and Competitive ability decreased from BNP to BP1 and BP2 (Tab. I), thus pointing to an alleviation of competition through herbivory (Bardgett *et al.*, 1998) and associated disturbances known to favour non-ericaceous plant species such as trampling (Gallet & Rozé, 2001; Kohler *et al.*, 2006) and dung deposition (Welch, 1985; Feeley, 2005). Such a small-scale effect of grazing has been registered at a moderate level of cattle pressure (Dupré & Diekmann, 2001), and was verified experimentally (Lavorel *et al.*, 1998). The explanation lies in an increase in spatial and temporal heterogeneity and multi-scaling of the ecosystem at a moderate level of disturbance, known to favour the coexistence of species (Denslow, 1985; Lavorel *et al.*, 1994; Levin, 2000), more especially at the time of seedling establishment (Grubb, 1977). In the case of rocky outcrops ('buttons') which are submitted to harsh climate conditions and poor nutrient availability, most plants are stress tolerant (Tab. I) and exhibit low nutrient loss rates due to their evergreen habits (Aerts, 1995). They devote a prominent part of energy requirements to resistance to environmental and biological hazards (Stowe & Osborn, 1980), this being reinforced in the presence of cattle grazing by the resistance of seedlings and mature plants to herbivory (Coley *et al.*, 1985; Hanley, 1998). It must be noted that species of patrimonial interest were also favoured by cattle grazing on shallow soils.

Temporary but repeated grazing and trampling by cattle may thus be considered as a factor allowing vegetation and soil to remain at a pioneer stage with a richer and patrimonial flora (Partzsch, 2007).

CONCLUSION

Our study, although limited in time and space, allowed us to describe a number of vegetation types which are representative of rocky outcrops of the Brenne Regional Natural Park, as ascertained from the extensive study done by Gaudillat (1997). We showed that a variety of plant strategies and ecological traits could be found within a limited area where natural (soil depth) and man-induced (cattle grazing) conditions interfere to create a mosaic of environments. That such regional hot spots of biodiversity must be protected is now out of dispute at the European level. More problematic are the management rules which should be applied to protect them in the long-term. We showed that the development of shrub (heath) and tree (forest) vegetation induced a change in plant communities, shifting from stress-tolerant to competitive species, and that moderate grazing allowed more species, and especially those of patrimonial interest, to cohabit. Rather than prescribed fire and clear-cut operations, which are known to induce severe environmental stresses to a lot of organisms, thereby impoverishing communities in the long-term (Donegan *et al.*, 2001; Lloret *et al.*, 2005), moderate grazing by cattle or sheep might be the best method for the sustainable management of outcrop vegetation in agricultural landscapes, as this has been successfully experimented in other regions (Pakeman *et al.*, 2003; Agreil & Greff, 2008).

ACKNOWLEDGEMENTS

François Pinet (Parc Naturel Régional de la Brenne) is greatly acknowledged for his precious vegetation maps and help in the identification of vascular plant species. The private owners, Mr and Mrs Lefébure, deserve a special mention for free access to the site and fruitful discussions. Financial support was partially provided by IFR 101.

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