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Species richness and distribution in relation to light in wooded meadows and pastures in southern Sweden

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Hay meadows and unfertilised pastures are of great importance for floral and faunal conservation work since a number of rare species are confined to them. Traditional meadows in Scandinavia have shrub and tree layers which have to be managed in order to maintain an appropriate composition and density of shrubs and trees. We examined how light affects the distribution of species in wooded meadows and pastures in southern Sweden. Herbaceous species were recorded in square-metre plots along 60 light gradients. Species composition varied significantly with light availability. Species typical for open areas tended to be confined to them but species characteristic of shaded areas also grew in unshaded plots. Species richness increased with light availability but was not related to grass sward density. The use of the latter as an indicator of management status is therefore questionable, and light availability might be a better tool for evaluating the effectiveness of conservation management and restoration practices involving species-rich meadows or pastures.

Key words: CCA, grassland, light, multivariate analysis, Sweden

INTRODUCTION

In the old agricultural systems in Northern Europe, grassland vegetation was the vegetation type of greatest importance for hay production and grazing. Today, however, there are very few traditionally managed hay meadows left. Most of the previously mown areas have been converted to arable fields, been abandoned, planted with trees or converted to fertilized grass-swards (Hæggström 1983, Losvik 1988, Huhta 1996). Traditionally managed hay meadows and unfertilised pastures are species-rich (Kull & Zobel 1991, Garcia 1992) and contain numerous red-listed species (Aronsson *et al.* 1995), but both meadows and pastures lose much of their conservation values if regular mowing and grazing cease (Persson 1984, Jonsson *et al.* 1991). Therefore, conservation authorities nowadays place high priority on managing the few remaining meadows and unfertilised pastures. Furthermore, there is a growing interest in restoring species-rich grassland in areas that have not been managed for some time (Bakker 1989, Johansson & Hedin 1991, Kotiluoto 1998, Pärtel *et al.* 1998).

Meadows and pastures in Scandinavia and the Baltic, as well as in some other parts of the world, contain trees and shrubs (Hæggström 1998a, 1998b), which constitute an additional management problem. More specifically, resource managers must decide how many trees and shrubs to allow, their size as well as the most preferable species composition but at present, there is no consensus regarding tree and shrub density. Historical sources could provide some guidelines for management, but an alternative approach is to explore how the shadow produced by trees and shrubs affects species typical of grasslands.

In the present study, we investigated how light availability affects species richness and the distribution of species within meadows and pastures. More specifically, we recorded the species composition in transects along a gradient of light intensity from shade to full sunlight, assuming that species richness (m^{-2}) would increase with light intensity (Kull & Zobel 1991) and that species composition would vary along the gradient. In addition, we estimated the grass sward density along the transects, as this is used as tool to evaluate management (Ekstam & Forshed 1996).

MATERIALS AND METHODS

Vegetation analyses

The study was done in three wooded meadows and five wooded pastures in Småland, southern Sweden in 1998. The sites selected had been continuously mown or grazed and had not been fertilised for many decades, nor had they recently been subjected to restoration management. Therefore, we assumed that the species composition in the plots was not in a state of change induced by a recent alteration in management or light conditions. The meadows had been mown with a scythe at the end of July every year, while the pastures had been grazed by cattle (further details in Table 1). Initially, we intended only to include meadows but due to their scarcity and our selection criteria, pastures were included as well. Our sampling, however, was not appropriate for an evaluation of possible differences between meadows and pastures.

One-metre-wide transects were established in random directions, extending from hazel stools (*Corylus avellana*) to open, unshaded areas. The transects ended at the point where the vegetation appeared to become homogeneous, the average length (± SD) of the transects being 6.0 (± 0.98) m. Each transect was divided into square-metre plots. In total, there were 60 transects, and 362 square-metre plots.

Plants were identified to species level whenever possible and their abundance in plots were recorded on a nine-point scale: 0, < 1, 1–5, 5–10, 10–20, 20–40, 40–60, 60–80, > 80 per cent cover. Grasses, that often dominated in the vegetation, were not identified to species or genus level. Identifying non-flowering grasses is time-consuming and we considered it of less interest since there are few grass species of conservation interest in Swedish grasslands. The nomenclature follows Karlsson (1997).

Table 1. Information about the eight study sites in southern Sweden.

Site	Location	No. of transects	Common trees & shrubs	Area (ha)	Management, history & other information
Bråna	57°38´N, 14°45´E	6	*Betula* spp., *Corylus avellana*	4.0	Meadow; some years grazed by cattle instead of mown
Komstad	57°24´N, 14°37´E	7	*Quercus robur*	0.5 + 0.3	Two mown areas within a pasture (20 ha); one transect was in pasture
Börsebo	57°37´N, 15°20´E	9	*Betula* spp., *C. avellana, Q. robur*	1.5	Meadow
Stockeryd	57°42´N, 15°03´E	4	*C.avellana, Fraxinus excelsior*	0.7	Pasture
Heddarp	57°38´N, 15°01´E	5	*Populus tremula, Betula* spp.	6.0	Pasture
Bållebo	57°43´N, 15°07´E	7	*C. avellana*	5.0	Stony pasture
Kvänsås	57°41´N, 15°00´E	7	*C. avellana*	10.0	Pasture
Brevik	57°39´N, 14°52´E	15	*Q. robur, C. avellana*	10.0	Stony pasture

Light recordings

Light (photosynthetically active radiation) was recorded in the centre of each plot with a Skye instrument (SKP 215/200) with the sensor held about 100 mm above and perpendicular to the ground.

Light influx varies during the day, over the growth season and depends on weather conditions and ideally one would need to integrate numerous light measurements for a full understanding of the light situation in a plot (Canham 1988). We decided to do light measurements at five occasions during a day at the peak of the growth season (July): at noon (i.e. when the sun reached its highest point in the sky), 2 and 4 h before noon, and 2 and 4 h after noon. To get representative light recordings, we only made them in cloudy weather, i.e. when the sun was hidden by thick clouds (cumulus or cumulonimbus). This reduced the impact of sunlight flecks and eliminated the sharp gradients between shaded and unshaded areas within a plot.

Each light measurement was expressed as a proportion of the maximum value recorded in the transect in connection with a specific recording event. The light situation (L) in each plot was described using the following equation

$$L = 100 \times (0.54L_{-4} + 0.75L_{-2} + L_0 + 0.75L_2 + 0.54L_4)/3.58 \quad (1)$$

where L_{-4} is the recording 4 h before noon, L_{-2} 2 h before noon etc. The weighting, i.e. 0.54 and 0.75, was based on light measurements in an unshaded plot on a sunny day. This partly compensates for the fact that the light recordings were made on cloudy days while the photosynthetically most important light is received around noon on sunny days.

Grass sward density

For each plot, we conducted the test of grass sward density suggested by Ekstam & Forshed (1996) to evaluate the success of the management regime. Using a spade, we cut a strip (0.15 m × 1.00 m) in the grass, perpendicular to the transect, to a depth of 100–150 mm. One end was then carefully lifted until the strip broke, and the length of the lifted strip was measured. In cases where the grass sward was thin or absent and we were unable to lift it, we noted its length as 50 mm. A notation of 1.00 m indicated that the strip was pulled out in its entirety. A square root transformation was applied before analysis.

Statistical analyses

We used two ordination methods, Detrended Correspondence Analysis (DCA; Hill & Gauch 1980) and partial Canonical Correspondence Analysis (pCCA; ter Braak 1986, 1988). Partial ordination is an important tool for studying residual variation after "covarying out", or "factoring out", a set of variables (ter Braak 1988, ter Braak & Smilauer 1998). The analyses were conducted with CANOCO 4 (ter Braak & Smilauer 1998). Except for the downweighting of rare species, we employed default options. To test whether species composition was significantly related to light intensity or grass sward density we used permutation tests (999 permutations) in the two pCCA conducted.

RESULTS

Species richness

Species richness increased significantly with light intensity ($R^2 = 0.1132$, $P < 0.0001$) but not with the density of the grass sward ($R^2 = 0.00331$, $P > 0.2$; Fig. 1).

DCA and CCA

An initial DCA of the vegetation data indicated that site differences were large (not shown). To eliminate the effect of such differences, we treated the sites as covariables in the subsequent analyses (entered in the analyses as dummy variables).

The first pCCA, with light as the only environmental variable and with sites as covariables, showed that species composition was significantly related to light intensity (eigenvalue = 0.0590, $P < 0.01$). The ordination clearly associated many of the most abundant species with either light or shaded conditions (Fig. 2A) as well as ranked all species according to their affiliation with light (Table 2). *Arnica montana, Helianthemum nummularium, Leontodon hispidus, Polygala vulgaris, Bistorta vivipara* and *Rhinanthus minor* were the species receiving the highest scores in the first pCCA, i.e. they were strongly associated with unshaded plots (Table 2). The distributions of the four most abundant of these species along the light gradient are shown in Fig. 3. The species with the lowest scores, i.e. those characteristically found in shaded plots, were *Convallaria majalis, Geum rivale, Oxalis acetosella, Stellaria media, Thlaspi caerulescens, Vaccinium myrtillus* and *Vicia sepium* (Table 2). The distribution along the light gradient is shown for the three most abundant of these species as well as for the very abundant *Geranium sylvaticum* (Fig. 3).

The second pCCA had grass sward density as

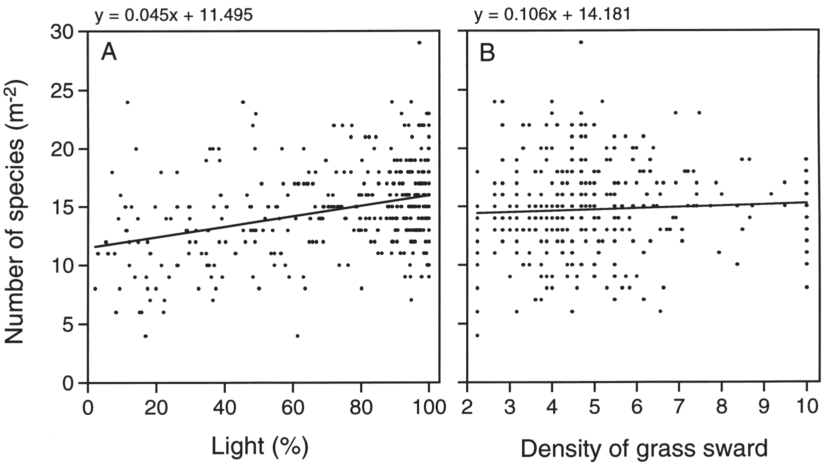

Fig. 1. Relationship between herbaceous species richness and light (A: weighted sum of five recordings made on cloudy days) and grass sward density (B: square root transformation of length of grass strip).

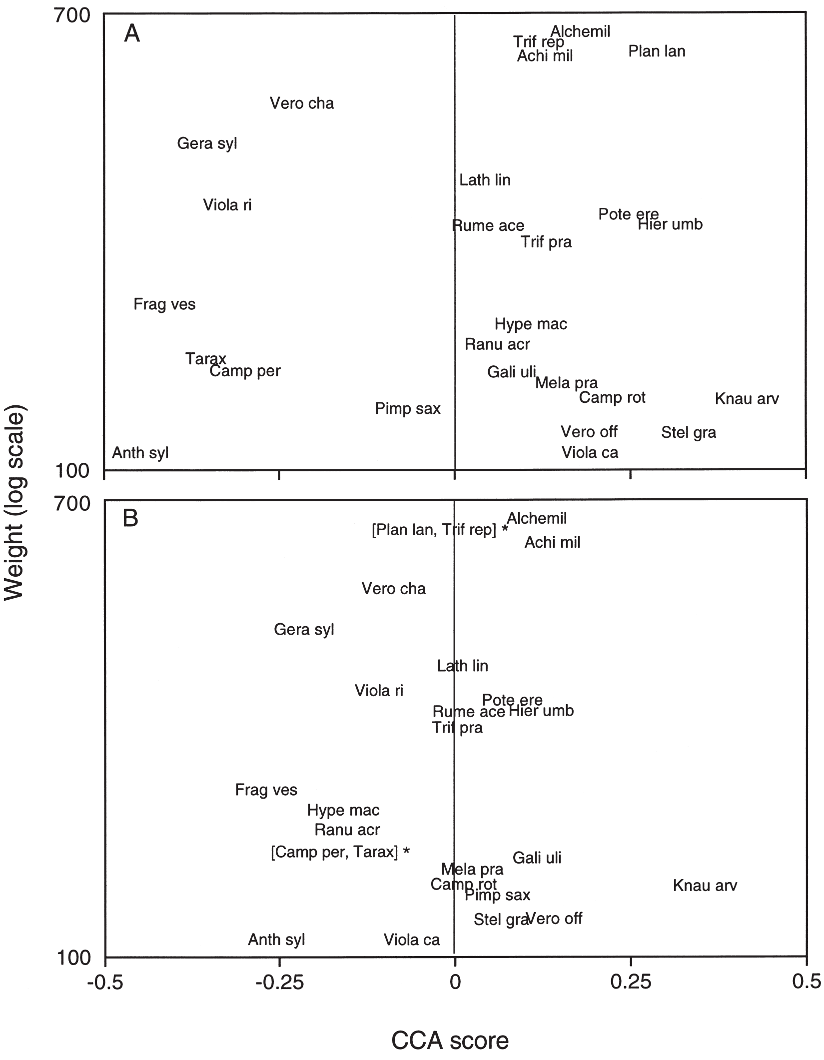

Fig. 2. Ordination of taxa (abbreviations explained in Table 2) in relation to light (A) and grass sward density (B). Only abundant species are shown (weight > 100). The x-axis shows the species scores from a pCCA with light intensity or grass sward density as the only environmental variable and sites as covariables. 'Weight' is the weighted total abundance of species.

Table 2. Ordination scores from pCCA with light or grass sward density as only environmental variable and sites as covariables. 'Weight' is the weighted total abundance of taxa in the data set. There were 23 additional taxa with weight < 1 (not included in the Table). Bold values indicate species deviating > 0.5 SD from the mean score. A large positive value indicates association with high light intensity or high grass sward density.

	Weight	Light intensity	Grass sward density
Poaceae	2 391	–0.083	0.014
Alchemilla spp. (Alchemil)	645	0.18	0.12
Trifolium repens (Trif rep)	618	0.12	0.067
Plantago lanceolata (Plan lan)	593	**0.29**	0.073
Achillea millefolium (Achi mil)	582	0.13	0.14
Veronica chamaedrys (Vero cha)	478	–0.22	–0.089
Geranium sylvaticum (Gera syl)	403	–0.35	–0.22
Lathyrus linifolius (Lath lin)	344	0.043	0.010
Viola riviniana (Viola ri)	310	–0.32	–0.11
Potentilla erecta (Pote ere)	297	**0.25**	0.080
Hieracium umbellatum (Hier umb)	284	**0.30**	0.10
Rumex acetosa (Rume ace)	283	0.046	0.017
Trifolium pratense (Trif pra)	264	0.13	0.001
Fragaria vesca (Frag ves)	203	–0.41	–0.27
Hypericum maculatum (Hype mac)	186	0.11	–0.16
Ranunculus acris (Ranu acr)	171	0.059	–0.16
Taraxacum spp. (Tarax)	159	–0.35	–0.076
Campanula persicifolia (Camp per)	156	–0.30	–0.074
Galium uliginosum (Gali uli)	152	0.081	0.12
Melampyrum pratense (Mela pra)	145	0.16	0.023
Campanula rotundifolia (Camp rot)	136	**0.22**	0.010
Knautia arvensis (Knau arv)	135	**0.42**	**0.35**
Pimpinella saxifraga (Pimp sax)	130	–0.068	0.059
Veronica officinalis (Vero off)	117	**0.19**	0.13
Stellaria graminea (Stel gram)	117	**0.33**	0.075
Anthriscus sylvestris (Anth syl)	108	**–0.45**	–0.25
Viola canina (Viola ca)	107	**0.19**	–0.063
Carex spp.	94	–0.33	**–0.36**
Anemone nemorosa	79	0.048	0.11
Vicia sepium	73	**–0.63**	–0.11
Prunella vulgaris	73	**0.36**	0.085
Primula veris	66	–0.32	–0.079
Geum rivale	65	**–0.60**	**–0.43**
Leontodon autumnalis	62	**0.34**	0.027
Anemone hepatica	61	–0.44	**–0.46**
Bistorta vivipara	59	**0.52**	**0.34**
Trollius europaeus	58	–0.038	–0.15
Lotus corniculatus	57	**0.39**	0.097
Aegopodium podagraria	56	**–0.46**	**–0.31**
Melampyrum sylvaticum	45	–0.31	0.16
Polygala vulgaris	36	**0.47**	–0.019
Hieracium sect. *Vulgata*	36	–0.084	–0.20
Leucanthemum vulgare	28	**0.26**	0.098
Leontodon hispidus	27	**0.58**	**0.38**
Scorzonera humilis	25	–0.41	**–0.46**
Rhinanthus minor	25	**0.66**	**0.27**
Convallaria majalis	24	**–0.75**	–0.21
Vaccinium myrtillus	23	**–0.77**	**–0.50**

Continued

Table 2. Continued.

	Weight	Light intensity	Grass sward density
Ajuga pyramidalis	19	**0.27**	0.061
Vicia cracca	17	**0.40**	0.050
Lathyrus pratensis	15	–0.29	0.089
Plantago major	15	0.093	–0.21
Filipendula ulmaria	14	–0.18	**–0.32**
Viola mirabilis	13	0.067	**0.61**
Equisetum spp.	12	–0.40	–0.16
Galium boreale	10	**–0.59**	–0.13
Helianthemum nummularium	8	**0.51**	–0.098
Succisa pratensis	6.4	0.11	0.046
Galium verum	5.4	**0.31**	**0.30**
Platanthera spp.	4.9	–0.011	0.10
Carduus crispus	4.9	**0.20**	–0.20
Cerastium fontanum	3.9	–0.17	**–0.48**
Pulmonaria obscura	3.8	–0.25	**–0.55**
Stellaria media	3.4	**–0.90**	**–0.54**
Ranunculus auricomus	3.3	0.076	–0.26
Trifolium medium	2.4	–0.24	**–0.60**
Maianthemum bifolium	2.3	**0.40**	–0.20
Filipendula vulgaris	2.2	0.068	**1.10**
Arnica montana	1.7	**0.60**	–0.26
Oxalis acetosella	1.1	**–1.80**	**–0.36**
Thlaspi caerulescens	1.0	**–0.86**	**–0.37**

the only environmental variable and sites as covariables. Although there was a significant relationship ($P < 0.01$), grass sward density explained less of the variation in species composition (eigenvalue = 0.0190) than did light intensity. Species associated with dense swards included *Achillea millefolium* and *Knautia arvensis* while *Fragaria vesca, Geranium sylvaticum, Geum rivale, Anemone hepatica* and *Vaccinium myrtillus* were among the species associated with loose swards (Table 2, Fig. 2B). In the second pCCA (Fig. 2B), species were generally ordinated closer to zero than in the first pCCA (Fig. 2A); the scores deviated > 0.5 SD from the mean for 34 and 54 species in the grass sward and light pCCA, respectively (20 and 33 when excluding species with weight < 1).

DISCUSSION

Although species richness varied greatly between plots, it generally increased with light availability (Fig. 1A) which confirmed our expectations (e.g., Borgegård & Persson 1990, Kull & Zobel 1991). Furthermore, the pCCA clearly identified species characteristically found in shaded or sunlit areas as well as ranked all species according to their affiliation with light (Table 2). It is important to note that other variables than light, e.g., soil moisture and litter deposition, could also be involved in shaping the detected gradients in species composition. Nevertheless, it is clear that trees and shrubs, directly or indirectly, creates a mosaic of habitats that enable more shade-tolerant species to occur, contributing to high species richness on a larger scale. However, it is interesting to note that species strongly associated with shaded areas (Fig. 2A), e.g., *Geranium sylvaticum* and *Geum rivale*, also occurred in relatively sunlit areas, albeit in lower numbers (Fig. 3). In contrast, the regionally rare species found in the study (e.g., *Rhinanthus minor, Leontodon hispidus* and *Polygala vulgaris*) were restricted to unshaded plots receiving > 50%, and in some cases even > 75%, of full sunlight (Fig. 3). Consequently, since many species favoured by shade also occurred in sunny plots, we conclude that the shaded areas

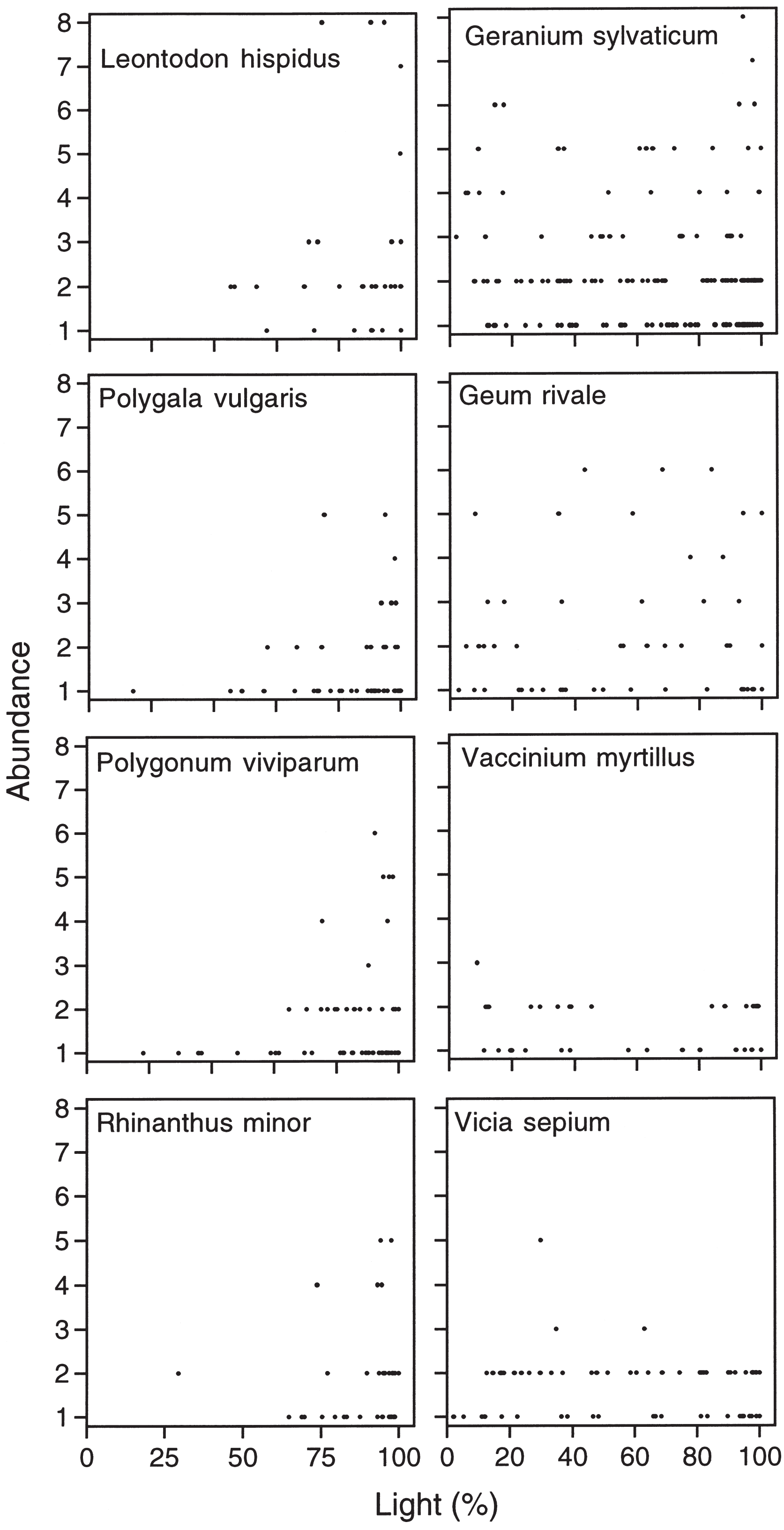

Fig. 3. Abundance of eight species in relation to light intensity. Species in the left and right column were characteristic for sunlit and shaded areas, respectively, in the pCCA (Table 2). Light values are the weighted sum of five recordings made on cloudy days.

needed to maintain them in a grassland can be relatively small. In contrast, large patches lacking a tree cover would be needed to favour light-requiring species, many of which are rare in certain regions, since most of them tolerate only a small amount of shade. For example, in areas where preserving herb species richness is a main priority, shrubs and smaller trees or pollarded trees should be preferred over large trees, which shade large areas. It is also important to consider the spatial distribution of the trees and shrubs since the shade created by patchily distributed trees affects a smaller total area than that created by evenly distributed ones.

The ordination of species in the two pCCAs, with light or grass sward density as the only environmental variable, agreed relatively well (Table 2, *Rhinanthus minor, Polygala vulgaris, Bistorta vivipara, Leontodon hispidus, Geum rivale* and *Anemone hepatica*) although species scores were generally closer to zero in the grass sward pCCA (Fig. 2, Table 2).

With regard to grass swards, the aim of conservation management is to maintain, or in the case of restoration to increase, the species richness and the abundance of rare grassland species. Species richness generally increased with light intensity (Fig. 1A) whereas grass sward density (Fig. 1B) could not explain the variation in species richness in the present data set. Furthermore, the pCCA demonstrated that light explained more of the variation in species composition than grass sward density did (pCCA eigenvalues). These results cast some doubt on the value of using grass sward density to evaluate a management regime or the success of restoration attempts (Ekstam & Forshed 1996) and suggest that it might be more useful to measure light influx in connection with such assessments. If and when more information becomes available, it should be possible to characterize shade conditions based on the species and size composition of the tree and shrub layer (the filtering capacity is likely to differ between species and to depend on size of the tree/shrub). Such information could be useful when deciding which shrubs and/or trees to remove or to pollard.

In general, the ordination of species in relation to light corresponded well with previous reports (e.g., Ellenberg *et al.* 1992). The only abundant species in the present study that differed substantially was *Scorzonera humilis*. It is typically found in mown areas in Sweden (Carlsson & Gustafsson 1983), and is classified as a "plant generally in well lit place, but also occurring in partial shade" by Ellenberg *et al.* (1992). In this study, however, it occurred in shaded plots with a less dense grass sward. Since *S. humilis* is a long-lived perennial, its distribution in our study might reflect where open areas previously have occurred.

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