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Evaluating the impacts of mowing: a case study comparing managed and abandoned meadow patches

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Two abandoned and two mown adjacently situated semi-natural meadow patches were compared for species richness, evenness and soil nutrient values. The differences in flora and vegetation cover between the sites were examined using canonical correspondence analysis (CCA). The physical conditions between the habitats were compared by categorizing the species with two competitive theories for plant strategies: the MacArthur-Fretwell scheme and Grime's CSR model. Both calculated richness indices and direct species counts indicate that diversity is higher in the abandoned meadow patches than in the corresponding managed meadows. The evenness values imply that the species dominance pattern is similar under both types of management. According to the CCA ordination, the differences in nutrient concentration between the sites significantly influenced the occurrence of species. The method of evaluating the succession stage of a habitat by combining diversity measures and counting plant strategy shares, especially with regard to competitive species, may help the manager to decide on the urgency of restoration. As the MacArthur-Fretwell scheme showed the prevailing physical conditions using species life history strategies more illustratively, it can be recommended for studies in which it is important to define the succession stage that might be fatal to high species diversity. This will facilitate the decision-making on management practices.

Key words: canonical correspondence analysis, semi-natural meadows, species life history strategies, vegetation management

INTRODUCTION

Traditional management, e.g. grazing by cattle, sheep or horses, is commonly recommended for maintaining and restoring semi-natural meadows, i.e. grassland habitats originating from the days of early agriculture practices before the use of chemical fertilizers and sowing of fodder plants using commercial seed (Ekstam *et al.* 1988). Appropriate timing and intensity of grazing and/or mowing enriches the species composition by creating diverse microhabitats and thus increasing the total species richness (During & Willems 1984, Rodriquez *et al.* 1995). Intermediate levels of disturbance have been suggested to maintain the highest species diversity (*see*, e.g. Vinther 1983, During & Willems 1984, Kull & Zobel 1991). In addition, it has been postulated that regularly occurring or fluctuating disturbances can be beneficial for weak competitors and species dependent on regenerative propagation in different habitats (Egler 1952, Horn 1974, Connell & Slatyer 1977).

Cessation of management of a semi-traditional meadow results in a series of changes, through which the number of tall herbs and grasses increases at the expense of grazing-tolerant, often small- or medium-sized species. Eventually, bushes and trees may occupy the area. Similar successional patterns have been reported in numerous studies of abandoned pastures, meadows, and formerly cultivated fields (Vinther 1983, Thalen *et al.* 1987, Ward & Jennigs 1990, Schaminée & Meertens 1992, Myster & Pickett 1994). Initially, the process may be slow and therefore difficult to observe. Moreover, it is even harder to determine the stage where the changes have reached an irreversible state. Usually that means a state where one or more organisms dependent on grazing or mowing disappear. The outcome of reintroduced management does not necessarily lead to a community exactly like the original, whether it is evaluated by physiognomical criteria or by comparing species composition (van Andel & van der Bergh 1987, Jonsson *et al.* 1991).

The recent survey type projects on semi-natural habitats in Finland have led to fairly straightforward management practices (*see* Anonymous 1993). In many cases this seems justified; after all, we are dealing with human-influenced habitats that are disappearing quickly through succession (Eriksson *et al.* 1995). It may, therefore, be safer to follow the traditional management practices than to do nothing, to halt the degradation process, even though the general and undefined practices might not be the best suitable solution in all cases. For example, if options are lacking, it is better in the long run to mow a formerly grazed meadow than to do nothing. However, uniformly and inflexibly executed management practices may have drawbacks. For example, some rare species may show notably different responses to different management regimes (T. Lennartsson & J. B. G. Oostemeijer unpubl.).

One way of evaluating management success is to observe the responses of selected species or species groups to grazing and/or cutting and to free succession. The most interesting group with respect to the success of management of semi-natural meadows consists of "archeophytes" (Sukopp & Hejný 1990). These species were introduced to Finland mainly by humans from more southern latitudes before the early 17th century (Suominen & Hämet-Ahti 1993). Their arrival was mainly due to what is called "traditional management", i.e. grazing and cutting. The threatened species of Finnish cultural habitats are almost without exception archeophytes (Rassi *et al.* 1991). The conservation of these species should be considered as equally important as the protection of rare native species: a large number of archeophytes often indicates high species richness and conservation value (Lennartsson & Svensson 1995), they compose coherent and functional ecosystems together with natives, and, last but not least, they are representatives of marginal populations adapted to the northern conditions. In Finland, the native species are usually ones that invade semi-natural habitats as succession proceeds to overgrown stages, i.e. when vegetation is dominated by tall herbs and grasses and, above all, bushes and tree saplings. On the other hand, a high proportion of alien (= neophytic) species, i.e. species introduced in Finland after the 17th century (Suominen & Hämet-Ahti 1993), in a habitat may indicate secondary stages of open-field cultivation or other extremely disturbed habitats (Huhta 1997). The proportional share of archeophytes, which reflects the state of the habitat, may therefore serve as a valuable indicator for a manager.

This long-term study was originally designed to illustrate the impacts of reintroduced management on abandoned dry meadows. Since the managed grasslands near the abandoned meadows also turned out to be former pastures, we decided to directly compare the phytosociology of abandoned and heavily managed meadows. In this study, we compared species diversity, evenness, and the number of species of different origin and life-forms between two continuously mown and two abandoned semi-natural dry meadow patches. A further purpose of this study was to find out how the plant strategy interpretations by Grime (1977, 1979), and the "MacArthur-Fretwell scheme" as defined by Oksanen and Ranta (1992) differ in describing the conditions of mown and abandoned semi-natural grasslands. Grime states that viable plant strategies can be arranged into a triangle, where the corners represent adaptations to selective pressures: competitive (C), stress tolerators (S) and ruderals (R). Furthermore, combinations, i.e. secondary strategies, are formed of these primary strategies (C–S, C–R, S–R and C–S–R). Oksanen and Ranta (1992) define plant strategies in a different way. They acknowledge classical r-strategists, species that colonize habitats exposed to high-intensity low-frequency disturbance, and K-strategists, i.e. competitive plants that are adapted to undisturbed conditions. Although Oksanen and Ranta (1992) emphasize the definitions of the above-mentioned strategies slightly differently from Grime (1977, 1979), the main contradiction is in defining Grime's S-strategy as adaptations to high natural-grazing pressure (grazing-tolerant strategies with graminoid [gg], ericoid [ge] and *Dryas* variants [gd]). For further details, *see* Oksanen and Ranta (1992).

STUDY SITES

The study area is located in the middle boreal vegetation zone (Ahti *et al.* 1968), in the rural community of Keminmaa on the northern coast of the Gulf of Bothnia. The study sites, two managed short-grass meadows and two unmanaged meadows lie at the two churches of Keminmaa. The churches, one built in the 16th century and the other in the 19th century, stand on the western bank of the river Kemijoki, two kilometers from the sea (Fig. 1).

The climate is slightly continental, although the vicinity of the sea moderates the yearly temperatures, especially during the autumn and spring. The duration of the growing season is about 140 days (threshold value + 5°C), and the mean temperature of the growing season lies within + 11.5–12°C. The effective temperature sum during the growing season is ca. 950°C. The annual precipitation is 600 mm, of which approx. 200 mm is received during the growing season (Alalammi 1987).

A summary of the site characteristics is presented in Table 1. The managed short-grass meadows will be referred to as "lawns", on account of their type of utilization (old church lawn [OL] and new church lawn [NL]). The mowings were done once per season by cutting the hay with a lawnmower with rotating blades. Management took place annually in late June. No fertilizers or herbicides were used. Because of the thin organic layer, the lawns are well drained from late July till August. The situation is similar to the conditions prevailing on natural unmanaged dry meadows on rock surfaces, etc. Tall, broad-leaved and moisture-dependent herbs survive poorly under such conditions. In the unmanaged old church meadow [OM] and new church meadow [NM] slight indications of overgrowing by taller species were visible.

In a few cases, semi-natural plant communities have been preserved as by-products of other activities aimed at maintaining something other than the species composition, such as areas of prehistoric relics, outdoor museum areas, etc. (Ekeland 1988). The surroundings of the Keminmaa churches have long been well-known for rare archeophytes, e.g. *Gentianella campestris*, *Poa alpina*, *Galium verum* and *Pimpinella saxifraga*. In Finland, *Galium* and *Pimpinella* occur in their northernmost range limits in Keminmaa. They are typical species of dry meadows in southern Finland, and have only a few scattered occurrences north of Keminmaa (Lahti *et al.* 1995). According to Jalas (1980), Hämet-Ahti (1980) and Hämet-Ahti *et al.* (1986), the optimum habitats of these two characteristic species are dry meadows on rock surfaces with a thin organic layer. Species-rich, often human-influenced habitats of this kind will slowly disappear if management is not sustained (Ekstam & Forshed 1992).

METHODS

Field work was started at the beginning of July 1995. First, the overall species composition of each of the four study sites was surveyed separately. Thereafter, sixty quadrats, each 1 m^2 in size, were defined using stratified random sampling. Twenty quadrats were studied in each of the meadows whereas ten quadrats in each of the lawns were regarded as sufficient, due to the seemingly uniform species distribution (*see* Results). A projection cover of each field and ground layer species occurring in each quadrat was recorded using a percentage scale (+, 0.5, 1, 2, 3, 5, 7, 10, 15, 20, 30 … 90, 95, 100). For the calculations of average species numbers, ten quadrats from both meadow sites were allotted randomly, to allow direct comparisons with the lawn sites. When the other properties within the sites were examined, all the 60 quadrats were used. The present species number distribution between the mown and unmown quadrats was tested with the *t*-test.

The thickness of the organic layer was measured from each quadrat. Two soil samples per site were taken for analysis of exchangeable Ca, K and Mg concentrations. The amount of exchangeable Ca, K and Mg and soluble P was measured per volumetric unit. Soil samples were mixed with 1 M ammonium acetate (pH 4.56) at a ratio of 1:8, shaken for two hours and filtered through filter paper. The Ca, K and Mg analyses were performed using an atomic absorption spectrophotometer. The amount of P was determined colorimetrically with ascorbic acid (John 1970). The total N content of the soil samples was determined with the Kjel-

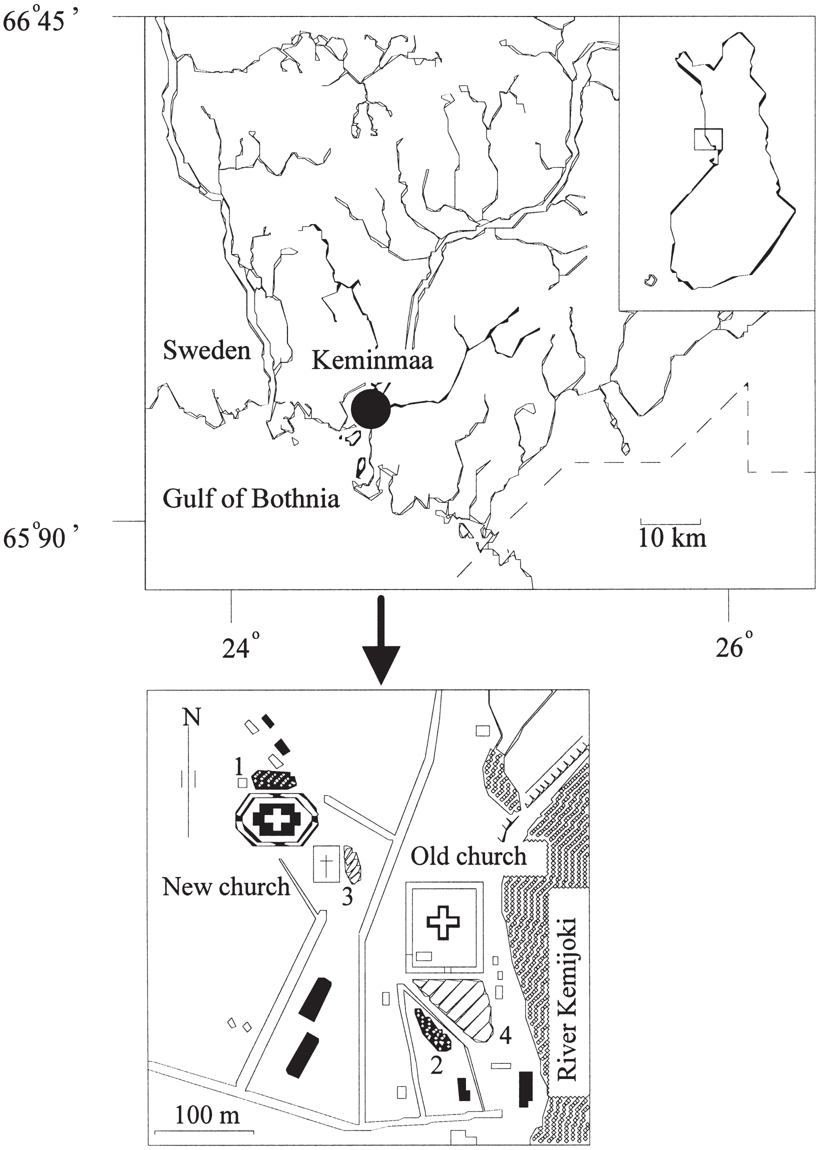

Fig. 1. Location of the study sites. — 1: New Church Meadow (NM). — 2: Old Church Meadow (OM). — 3: New Church Lawn (NL). — 4: Old Church Lawn (OL).

dahl method (Bremner & Mulvaney 1982). An average value from the two measurements was used in further data processing.

Ordination was performed with the CANOCO program (Ter Braak 1987). Compositional gradients of the data set in relation to the measured environmental factors were investigated using canonical correspondence analysis (CCA). Before the analysis, the measured nutrient values were transformed into a logarithmic form and after first computer runs the rare species occurring in less than 5% of the quadrats were omitted to avoid outlier effects (Økland 1990). The management intensity of each quadrat was estimated on a scale of three classes (*see* Table 1). The effect of all environmental variables on species distribution, the significance of the first canonical axis, and finally, the significance of each individual environmental factors were tested using Monte Carlo permutations (Ter Braak 1987).

The nomenclature follows Hämet-Ahti *et al.* (1986) for vascular plants, Koponen (1994) for bryophytes and Ahti (1989) for lichens . The natural, archeophytic and alien species (Suominen & Hämet-Ahti 1993) were counted sitewise, to determine whether there were differences related to the present management practices of the sites (Tonteri & Haila 1990). In the final tabulation, the species were classified into broad categories with their tendency to occur on managed, abandoned or both sites (overall species). For the triangular strategy theory (Grime 1977, 1979), the plant strategy responses were categorized species by species using the responses presented in detail by Grime *et al.* (1988). For the MacArthur-Fretwell (MAF) scheme, Oksanen and

Ranta's (1992) for assignment of plants to different strategies was used (for details *see* Oksanen & Ranta 1992: table 1 on p. 179 and app. 1 on p. 186). The species with uncertain responses were categorized in a separate class "u". The average species number and the average cover values of strategy-categorized species were used to evaluate the differences between the sites.

Finally, some commonly used descriptive parameters for each quadrat were calculated along with the Simpson ($\lambda = \sum p_i^2$) and Shannon ($H' = -\Sigma p_i \ln p_i$) species diversity indices, where p_i is the proportion of individuals belonging to the *i*th species. The Simpson index gives the probability that two individuals taken randomly from a population are different species. The value varies from 0 to 1 – 1/s; the nearer the calculated value is to 1, the higher the diversity (s = species in population). The Shannon index, i.e. the average degree of uncertainty, increases as the number of species increases and as the distribution of individuals among the species becomes more even. The evenness index five ($E5 = [(1/\lambda) - 1]/[e^{H'} - 1)]$) also known as modified Hill's ratio (Ludwig & Reynolds 1988), was used to compare the quadrats between the study sites ($e^{H'}$ = exponentiated Shannon index). The value approaches zero, when a single species becomes increasingly dominant in a community (Alatalo 1981, Ludwig & Reynolds 1988).

RESULTS

Species composition

The species composition of the church yard including the four study sites consisted of 82 vascular and 27 bryophyte and lichen taxa. The total taxa number was lower on the managed sites than on the corresponding abandoned sites (Table 2). The taxa found in the quadrats included the total species composition of each study site fairly well, with an average of 72% the species occurring on the study sites were found also in the quadrats. The species occurring on the sites, but not found in the quadrats were found mostly at the meadow edges, ecotones, where the surrounding forest and/ or road verges influenced the species composition.

Continuous management has strong impacts on species composition on OL and NL. The group of species thriving better on managed lawns than on abandoned meadows includes *Agrostis capillaris*, *Botrychium lunaria*, *Campanula rotundifolia*, *Festuca ovina*, *F. rubra*, *Poa alpina*, *Potentilla argentea* subsp. *argentea* and *Rumex acetosella*. The characteristic species of abandoned meadow patches are *Anthoxanthum odoratum*, *Deschampsia flexuosa*, *Elymus repens*, *Fragaria vesca*, *Geranium sylvaticum*, *Melampyrum sylvaticum*, *Ranunculus acris* and *Trifolium pratense*. Tree and bush saplings such as *Picea abies*, *Pinus sylvestris*, *Prunus padus*, *Ribes spicatum* and *Sorbus aucuparia* are also typical.

The species *Galium verum* and *Pimpinella saxifraga* occur abundantly on almost every site. *Galium verum* occurs in every quadrat, most abundantly on the NM and on the intensively managed NL. *Galium verum* occurs only on the OM with a lower abundance compared with the other sites. The most frequent grass species, *Agrostis capillaris*, also occurs frequently on nearly all the

Table 1. Overall characteristics of the studied sites. * 1 = none, 2 = intermediate, 3 = intense.

	New Church Meadow (NM)	Old Church Meadow (OM)	New Church Lawn (NL)	Old Church Lawn (OL)
Total area, ha	0.2	0.4	0.3	0.25
Quadrat numbers	41–60	11–30	31–40	1–10
n	20	20	10	10
Present management status	Unmown quadrats 51, 53–60[a)], Occasional quadrats 41–50, 52[b)]	Unmown	Mowing	Mowing
Management intensity class*	1[a)], 2[b)]	1	3	3
Management history	Mowing stopped 26 yrs ago Last mowing 2 yrs ago	Sheep grazing Stopped > 35 yrs ago	Mown > 30 yrs	Mown > 30 yrs

a) Mowing stopped 26 yrs ago.
b) Last mowing 2 yrs ago.

Table 2. Distribution (frequency of occurrence/% mean cover) of the taxa of the studied sites (*N* = 10). +/+ = species occurrence recorded outside the quadrats, otherwise + = cover values ≤ 0.25%. Supplementary columns indicating individual species characters: 1 = species strategy according to the MAF scheme, 2 = Grime's CSR categorization, 3 = growth form (a = annual, b = biennial, p = perennial, w = woody), 4 = species origin (n = native, ar = archeophyte, al = alien). Field and total species diversity and evenness indices of the study sites are presented at the end of the table. The values have been calculated from ten quadrats per site. The abbreviations for the supplementary columns 1 and 2 are given in Fig. 4.

	Study site							
	NM	OM	NL	OL	1	2	3	4
Field layer								
Management indicators								
Agrostis capillaris	90/11	90/2	100/27	100/16	gg	CSR	p	ar
Botrychium lunaria	–/–	20/+	10/+	10/+	u	u	p	n
Campanula rotundifolia	10/+	–/–	50/1	50/1	gg	S	p	n
Festuca ovina	50/2	40/2	70/1	50/1	gg	S	p	n
Festuca rubra	90/1	20/+	90/3	90/7	gg	CSR	p	n
Poa alpina	10/+	+/+	100/8	10/2	gg	CSR	p	n
Potentilla argentea subsp. *argentea*	10/+	–/–	30/+	40/+	gg	u	p	ar
Rumex acetosella	20/+	+/+	70/1	80/3	gg	CSR/SR	p	n
Abandonment indicators								
Anthoxanthum odoratum	40/3	80/3	–/–	–/–	gg	SR/CSR	p	n
Carex vaginata	+/+	10/+	–/–	–/–	gg	u	p	n
Deschampsia flexuosa	10/+	40/1	–/–	–/–	gg	S/SC	p	n
Dianthus superbus	80/1	50/1	20/+	40/+	u	u	p	n
Elymus repens	20/1	30/3	–/–	–/–	K	C/CR	p	n
Filipendula ulmaria	–/–	10/+	–/–	–/–	K	C/SC	p	n
Fragaria vesca	50/1	+/+	–/–	–/–	u	u	p	n
Galium boreale	–/–	50/12	–/–	+/+	u	u	p	n
Geranium sylvaticum	40/2	100/8	–/–	–/–	K	C	p	n
Juniperus communis	+/+	10/+	–/–	–/–	K	CSR	w	n
Melampyrum sylvaticum	30/1	10/+	–/–	–/–	r	u	a	n
Phleum pratense	30/+	40/1	10/+	+/+	gg	CSR/CR	p	ar
Picea abies	+/+	70/5	–/–	–/–	K	SC	w	n
Pinus sylvestris	+/+	10/+	–/–	–/–	K	SC	w	n
Ranunculus acris	60/4	60/1	–/–	+/+	K	CSR	p	n
Rhinanthus minor	80/2	70/+	–/–	–/–	r	R/SR	a	ar
Rumex acetosa	90/3	10/+	–/–	–/–	K	CSR	p	n
Trifolium pratense	30/2	70/3	–/–	–/–	gg	CSR	p	ar
Vicia cracca	60/+	20/+	–/–	–/–	K	C/CSR	p	n
Viola canina	70/2	100/6	–/–	–/–	u	u	p	n
Ubiquitous species								
Achillea millefolium	100/3	100/5	100/2	100/1	u	CSR/CR	p	ar
Galium verum	100/28	100/6	100/21	100/13	u	CSR/SC	p	ar
Pimpinella saxifraga	100/3	100/4	90/2	90/4	gg	S	p	al
Poa pratensis	100/9	90/2	80/1	50/+	gg	CSR	p	ar
Stellaria graminea	70/+	60/+	30/+	60/+	u	u	p	n
Trifolium repens	50/2	70/+	90/1	10/+	gg	CSR/CR	p	ar
Occasional species								
Alchemilla subcrenata	–/–	30/3	+/+	+/+	K	u	p	ar
Alopecurus pratensis	–/–	10/+	–/–	+/+	gg	CSR/C	p	ar
Angelica sylvestris	–/–	+/+	–/–	+/+	K	C/CR	p	n
Antennaria dioica	30/1	+/+	10/+	+/+	gg	S	p	n
Anthriscus sylvestris	+/+	–/–	–/–	–/–	K	CR	p	ar
Artemisia vulgaris	+/+	–/–	–/–	–/–	K	C/CR	p	ar
Betula pubescens	+/+	+/+	–/–	–/–	K	C/SC	w	n
Calamagrostis purpurea subsp. *phragmitoides*	+/+	–/–	–/–	–/–	K	u	p	n
Carex brunnescens	+/+	–/–	–/–	–/–	gg	u	p	n
Carex nigra	–/–	+/+	–/–	–/–	gg	SC/S	p	n
Carum carvi	+/+	–/–	+/+	–/–	gg	u	b	ar

(Continues …)

Table 2. Continued.

	Study site NM	OM	NL	OL	1	2	3	4
Chenopodium album agg.	+/+	–/–	–/–	–/–	r	R/CR	a	ar
Deschampsia cespitosa	–/–	10/+	10/+	–/–	gg	CSR/SC	p	n
Epilobium angustifolium	+/+	–/–	–/–	–/–	K	u	p	n
Euphrasia stricta	20/+	30/+	–/–	30/+	r	SR	a	ar
Galium album	+/+	–/–	–/–	–/–	u	u	p	al
Gentianella campestris	–/–	+/+	–/–	–/–	u	u	b	ar
Hieracium umbellatum	10/+	–/–	–/–	–/–	K	S/CSR	p	n
Leontodon autumnalis	+ +	–/–	–/–	+/+	gg	CSR/R	p	n
Leucanthemum vulgare	20/+	–/–	–/–	–/–	K	CSR/CR	p	ar
Luzula multiflora	+/+	–/–	–/–	–/–	gg	u	p	n
Luzula pallescens	–/–	10/+	–/–	–/–	gg	u	p	ar
Moneses uniflora	–/–	–/–	–/–	+/+	u	u	p	n
Plantago major	+/+	–/–	–/–	–/–	gg	R/CSR	p	ar
Poa annua	–/–	–/–	–/–	+/+	gg	R	a	ar
Poa nemoralis	–/–	+/+	–/–	–/–	gg	u	p	n
Polygonum viviparum	–/–	20/3	–/–	–/–	gg	CSR	p	n
Populus tremula	–/–	+/+	–/–	–/–	K	SC	w	n
Prunus padus	–/–	+/+	–/–	–/–	K	SC	w	n
Ranunculus auricomus agg.	–/–	10/+	–/–	–/–	K	u	p	n
Ranunculus repens	+/+	–/–	–/–	–/–	gg	CR	p	n
Rorippa palustris	+/+	–/–	–/–	–/–	r	R	a	n
Rubus saxatilis	+/+	–/–	–/–	–/–	K	u	p	n
Rumex longifolius	+/+	–/–	–/–	–/–	K	u	p	ar
Ribes spicatum	–/–	+/+	–/–	–/–	K	CSR	w	n
Silene dioica	+/+	–/–	–/–	–/–	K	CSR	p	n
Solidago virgaurea	20/+	–/–	–/–	+/+	K	S	p	n
Sorbus aucuparia	–/–	+/+	–/–	+/+	K	CSR	w	n
Tanacetum vulgare	–/–	–/–	–/–	+/+	K	u	p	n
Taraxacum sect. *Taraxacum*	10/+	–/–	20/+	+/+	gg	R/CSR	p	ar
Thalictrum flavum	–/–	+/+	–/–	–/–	K	u	p	n
Thlaspi arvense	–/–	–/–	+/+	–/–	r	R	a	ar
Tripleurospermum maritimum subsp. *subpolare*	+/+	–/–	–/–	–/–	r	R	b	ar
Trollius europaeus	–/–	+/+	–/–	–/–	K	u	p	n
Tussilago farfara	+/+	–/–	–/–	–/–	u	u	p	ar
Urtica dioica	+/+	–/–	–/–	–/–	K	C	p	ar
Vaccinium myrtillus	–/–	+/+	–/–	–/–	gd	SC	w	n
Veronica longifolia	+/+	–/–	–/–	–/–	K	u	p	n
Total number of taxa in quadrats (min., max.)	33 (13, 20)	36 (14, 21)	19 (8, 1)3	16 (7, 11)				
Total number of taxa in sites	58	52	22	30				
Average number of taxa/quadrats (± SD)	16 ± 2.4	17 ± 2.1	11 ± 1.7	9 ± 1.4				
Average field layer cover	87	75	68	46				
Simpson's index	0.78	0.84	0.67	0.66				
Shannon's index *H´*	1.86	2.11	1.44	1.38				
Evenness index 5	0.66	0.75	0.66	0.72				
Ground layer								
Management preferrers								
Abietinella abietina	30/1	40/6	100/17	100/33	ge	SR		
Climacium dendroides	70/4	70/4	80/6	100/19	ge	SR		
Polytrichum juniperinum	30/2	–/–	50/+	90/0	ge	SR		
Sanionia uncinata	–/–	–/–	10/+	50/11	ge	SR		
Cladonia squamosa	–/–	–/–	–/–	30/+	r	S		
Cetraria ericetorum	10/+	–/–	50/+	70/1	ge	S		
Abandonment indicators								
Bryum sp.	60/1	20/+	–/–	10/+	r	SR		
Pleurozium schreberi	10/+	80/9	–/–	–/–	K	SR		

(Continues …)

Table 2. Continued.

	Study site							
	NM	OM	NL	OL	1	2	3	4
Ubiquitous species								
Brachythecium spp.	80/4	20/+	30/1	60/1	K	SR		
Rhytidiadelphus squarrosus	40/+	70/11	–/–	60/1	K	SR		
Peltigera spp.	5/2	20/2	70/4	50/1	K	S		
Occasional species								
Aulacomnium palustre	–/–	10/+	–/–	–/–	ge	SR		
Dicranum fuscescens	–/–	10/+	–/–	–/–	K	SR		
Dicranum scoparium	–/–	10/+	–/–	–/–	K	SR		
Hylocomium splendens	–/–	20/1	–/–	–/–	K	SR		
Plagiomnium spp.	20/+	–/–	–/–	–/–	ge	SR		
Tortula ruralis	20/+	20/+	20/+	–/–	ge	SR		
Barbilophozia quadriloba	–/–	10/+	–/–	–/–	gd	SR		
Cetraria islandica	–/–	–/–	10/+	ge	SR			
Cladonia chlorophaea	–/–	–/–	–/–	10/+	r	S		
Cladonia coniocraea	–/–	–/–	10/+	–/–	r	S		
Cladonia cornuta	–/–	–/–	10/+	–/–	r	S		
Cladonia furcata	5/+	10/+	–/–	–/–	r	S		
Cladonia spp.	5/+	+/+	–/–	10/+	r	S		
Peltigera aphthosa	–/–	5/+	–/–	–/–	K	S		
Peltigera canina	–/–	+/+	–/–	–/–	K	S		
Peltigera rufescens	–/–	+/+	–/–	10/+	K	S		
Total number of taxa in quadrats (min., max.)	13 (1, 8)	15 (1, 8)	11 (2, 7)	13 (4, 9)				
Total number taxa in study sites	13	18	11	13				
Average number of taxa/quadrat (± SD)	3.8 ± 2.0	4.3 ± 2.1	4.3 ± 1.4	6.6 ± 1.6				
Average ground layer cover	1.2	2.9	2.8	6.7				
Simpson's index	0.81	0.84	0.78	0.73				
Shannon's index *H*´	2.07	2.25	1.79	1.55				
Evenness index 5	0.66	0.66	0.72	0.68				

study sites, although it reaches higher abundance on managed sites. The differences in the ground layer species and species coverages between the managed and unmanaged sites are also noteworthy. The bryophytes *Abietinella abietina*, *Climacium dendroides* and *Polytrichum juniperinum* occurred on both, meadows and lawns, although they were more abundant on the managed sites. On the OM and NM, *Abietinella* and *Polytrichum* favour patches of shorter and more open field layer vegetation, unlike *Climacium*, which may also occur under a dense field cover. The moss species *Sanionia uncinata* and the lichen *Cladonia squamosa* occur solely on managed sites, while the lichen *Cetraria islandica* is most abundant on managed lawns, but occurs infrequently on abandoned meadows.

Ordination

Thirty-six vascular taxa and 13 bryophytes and lichens were included in the ordination data matrix. The outcome of the species/environment biplot of canonical correspondence analysis is presented in Fig. 2. The meadow quadrats show more variation in species composition. According to the quadrat/environment ordination, the lawn quadrats are the most homogeneous, and they are placed on the right-hand side of the ordination diagram (Fig. 3).

Along with management, the total nitrogen content of the soil explained the differences between the quadrats along the first axis and potassium along the second. The other measured environmental variables had less importance in the CCA ordination. According to Monte Carlo permutations, all the variables were found to be significant ($P < 0.001$, 999 permutations under null model).

Diversity indices

According to both indices, diversity on OM and NM was higher than on corresponding patches of

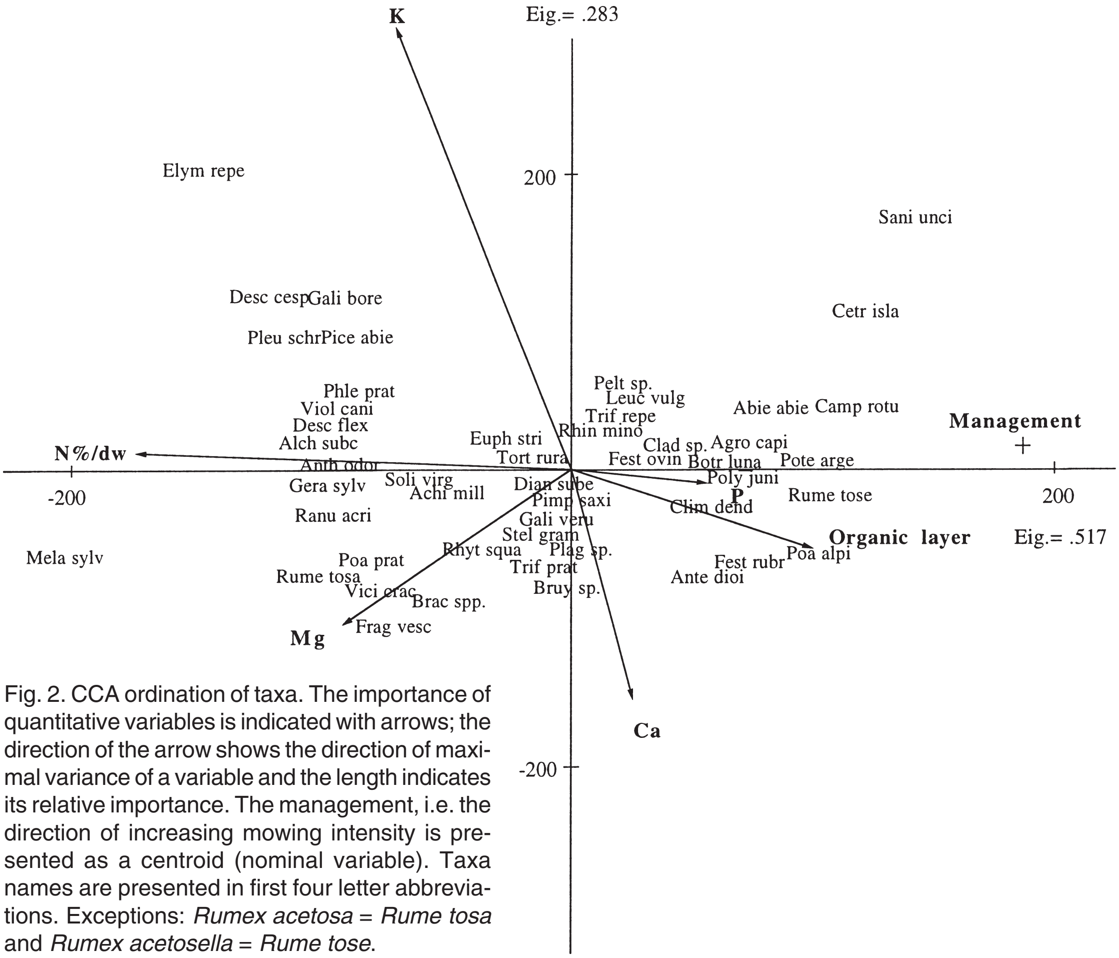

Fig. 2. CCA ordination of taxa. The importance of quantitative variables is indicated with arrows; the direction of the arrow shows the direction of maximal variance of a variable and the length indicates its relative importance. The management, i.e. the direction of increasing mowing intensity is presented as a centroid (nominal variable). Taxa names are presented in first four letter abbreviations. Exceptions: *Rumex acetosa* = *Rume tosa* and *Rumex acetosella* = *Rume tose*.

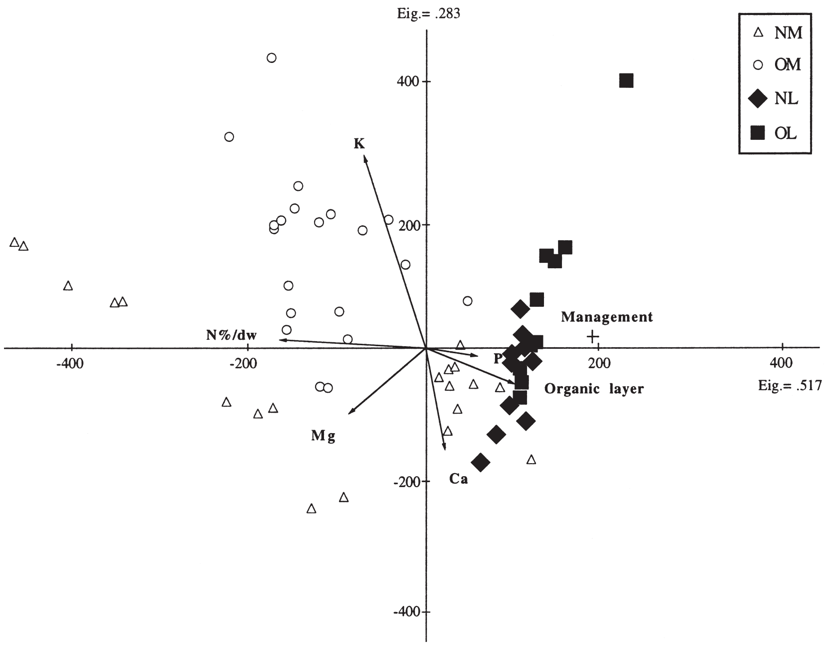

Fig. 3. CCA ordination of the quadrats.

OL and NL (Table 2). The evenness values between the abandoned and managed meadows were about the same, indicating that the species dominance patterns are similar under both management types. At present, the total number of taxa is significantly higher on the abandoned study sites (df = 38, $t = -6.01$, $P < 0.001$).

Comparisons of species strategies between the study sites

There are no major differences in the proportions of native, archeophytic and alien taxa on NM, OL and NL (Fig. 4a). On the OM, the proportion of native species is somewhat greater and the proportion of archeophytes slightly smaller than in other sites. Perennial grasses and herbs comprise the majority of species on all study sites (Fig. 4b). Woody perennials are almost entirely restricted to NM and OM. Fig. 4c–f illustrates the proportions of different plant strategies inhabiting the investigated study sites as defined by the two competing theories, MAF scheme (Oksanen & Ranta 1992) and CSR theory (Grime 1977, 1979). The suggested species responses according to both theories are presented in Table 2. According to the MAF interpretation, the proportion of grazing-tolerant plants (g-strategists, i.e. species adapted to frequent but small losses of aboveground tissues), is larger on OL and NL than on OM and NM (Fig. 4c). Correspondingly, there are more K-strategists, i.e. highly competitive species growing on OM and NM. The trend is even more obvious when examined using the average cover values of the plants with different strategies occupying the quadrats (Fig. 4d). The average cover value of K-strategists on lawns is low and the cover value of r-strategists is extremely low on all sites.

Corresponding trends are evident, but weaker in bar graphs presenting Grime's CSR strategy classification. However, meadows have more species representing the R, C and SC strategies than lawns (Fig. 4e). The number of species with uncertain or indefinable strategy responses seems to be quite constant in both classifications. Stress-tolerant ruderals (SR) thrive slightly better under continuously managed conditions (Fig. 4f), whereas competitive species occupy distinctly larger areas on the OM and NM quadrats. Regarding the observed species within the sites, the inconsistency between the MAF and CSR classifications was clear. Only 34% of the species classified as K-strategists in the MAF classifications were C- or CS-strategists in the CSR classification. In the case of grazing strategists (gg, ge and gd compared with S, SR and SC) and r-strategists (r compared with R) within the study sites, compatibility with the CSR classification was over 50%.

DISCUSSION

Ordinations reveal the same species occurrence pattern as do plain species frequency/abundance values. The plant communities under a continuous management regime consist of species able to tolerate regular disturbances, in this case mowing. The more diverse species composition of the abandoned sites indicates more diverse growth strategies and succession preferences. There are, for example, casuals, which owe their existence to microscale disturbances and, on the other hand, persistent survivors as relics of the earlier succession stages.

The lower species diversity on the two lawn study sites reflects the intense management. Mowing in the middle of the growing season decreases the total number of species markedly by eliminating the broad-leaved, tall-growing species. The fairly uniform sward on the lawn study sites is a result of selection, pressured by regularly repeated disturbance. It might be claimed then that the management serves as "a normal component", on which a plant community of this kind is dependent (van Andel & van der Bergh 1987, Kull & Zobel 1991).

The higher species richness on the abandoned sites was a result of ongoing succession. Without management, the abandoned sites are likely to succeed towards a later successional stage within a few years. Tall, broad-leaved, tussocky species as well as bushes and tree saplings, which are commonly present on abandoned sites, are more competitive (Grime *et al.* 1988, Oksanen & Ranta 1992). Therefore, they are expected to increase in cover in the future (Jukola-Sulonen 1983). At the same time, the number of dry meadow species is expected to decline. In fact, this has already hap-

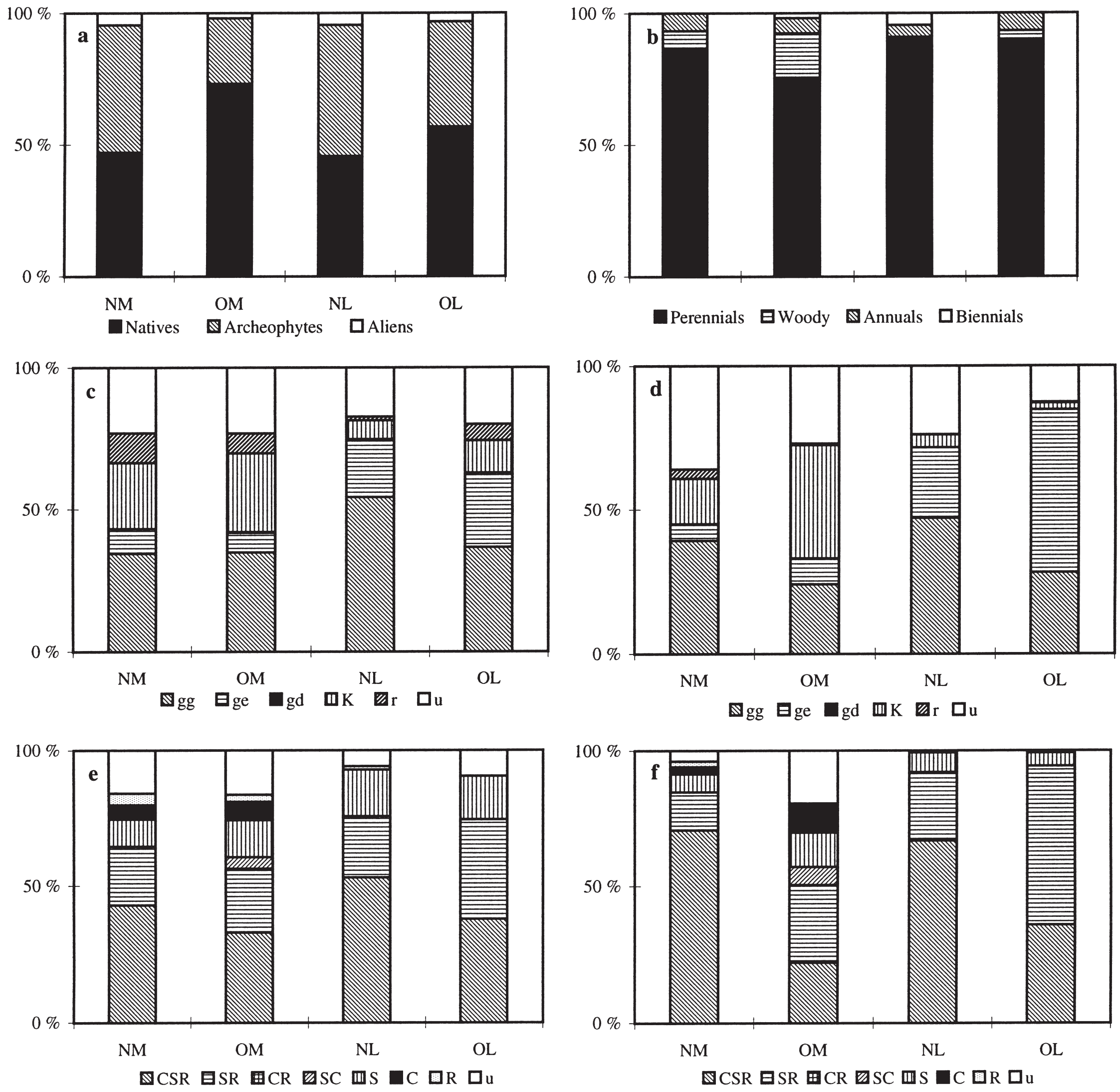

Fig. 4. Percentages of different types of taxa occurring on the study sites/quadrats. — a: Vascular taxa origin. — b: Growth strategies of vascular taxa (woody perennials separated from perennials). — c: Moss, lichen and vascular taxa strategy responses according to the MacArthur-Fretwell scheme (MAF), proportion of taxa within a site. — d: MAF scheme; average cover of taxa in quadrats. Explanations for legend characters: u = unclassified, r = r-strategist, K = K-strategist, gd = *Dryas* variant of the grazing-tolerant strategy, ge = ericoid variant of the grazing-tolerant strategy, gg = graminoid variant of the grazing-tolerant strategy. — e: Strategy responses according to Grime's CSR strategy model, proportion of species within a site. — f: CSR strategy model; average cover of species in quadrats. Legend characters: u = unclassified, R = ruderal, C = competitive, S = stress-tolerant, SC = stress-tolerant competitor, CR = competitive ruderal, SR = stress-tolerant ruderal, CSR = CSR-strategist.

pened: the western side of the OM is changing towards a moister and more homogeneous meadow type dominated by *Geranium sylvaticum*. On the other hand, re-introduced management may not necessarily result in a total disappearance of all late successional indicators. The suppression of tall broad-leaved species would not only favour smaller herbs, but also grasses with a grazing-tolerant strategy.

The CCA ordination suggests that the overall nutrient concentration is slightly higher on abandoned meadows. The differences in soil nutrient status may have certain effects on species distribution between the study sites. However, it seems that the observed slight difference does not have strong implications for species diversity. This was to be expected on the basis of studies by Bülow-Olsen (1980), Bakker (1987) and Pegtel (1987). Bülow-Olsen (1980) studied a *Deschampsia flexuosa* stand, and found that grazing by sheep did not have any significant effects on the amounts of available Ca, Mg, K and P in the soil. Bakker (1987) detected only 1 to 3% yearly removal of N, P and K from the soil by hay-making and concluded that "the off-take nutrients in hay amount to only a few percentages of the soil nutrient store". The results of ordination analysis compared with richness and evenness indices suggest that, on the abandoned sites, the seemingly enhanced rate of litter accumulation along with accelerated mineralization have not reached the point where the effect of a positive nutrient balance followed by a decrease in species diversity becomes apparent (Oomes 1990).

On dry meadows, even a minor quantity of yearly accumulated litter may have a major effect on the vegetation development. The yearly biomass accumulation on unmanaged meadows is seemingly low, but in the long run even a slight increase in litter accumulation may lead to visible differences in species composition (Facelli & Facelli 1993). The positive nutrient balance due to accumulating litter on OM and NM, however, did not become visible very clearly when compared with the nearby lawns characterized by a negative nutrient balance, i.e. regular removal of the plant biomass. In general, the effect of activities aimed at reducing the amount of extractable nutrients on meadows with a thick organic humus layer only becomes visible after years, or even decades of management (Berendse *et al.* 1993). In the future, it would be worth paying attention to the mineralization rates, along with the nutrient contents of the soil (*see*, e.g. Aber 1987).

Differences in species composition between sites: reflections on plant strategies

Species representing the S and SR strategies (Grime *et al.* 1988) are able to persist well on managed sites. These species reproduce vegetatively or flower early in the season before or after the mowing, even if slightly injured (pers. obs.). The bulk of the plant species on managed lawns have their rosettes pressed tightly against the ground surface, so that the main part of their living tissue is seldom damaged, *Poa alpina* being probably the best example of this kind of growth form. The proportions of ruderals (Grime 1977, 1979) or r-strategists (Oksanen & Ranta 1992) reflect the degree of disturbance prevailing on different sites. According to the MAF scheme, the proportion of r-strategists, i.e. annuals, is evenly scarce on all sites, on NL their number is very low. Using the CSR strategy model, the number of ruderals is fairly even on both meadows. Using the average cover values of species in the quadrats as a measure, it is apparent that there are very few regenerating gaps for ruderal/r-strategists amongst the dense swards on every studied site. Perhaps the most conspicuous difference between the two approaches is in the case of competitive species (Grime 1977, 1979) or K-strategists (Oksanen & Ranta 1992). According to the MAF scheme, K-strategists dominate under abandonment, whereas the trend is slightly weaker when Grime's classification is used. The fact that the number of species reflecting the grazing strategies is at least as equally frequent as the K- and r-strategists on the meadow sites, but dominate on the lawn sites describes the prevailing physical conditions in these habitats quite well. Considering the average values they cover per quadrat, the situation is even clearer. In a way, lawn-mowers act as an unselective and sudden horde of grazers that regularly invade and instantly consume every plant reaching the height of ca. 5–7 cm. As a result, grazing strategists are favoured over K-strategists on the Keminmaa lawn-like meadow sites.

Grime's triangular strategy theory (Grime 1977, 1979) and the MAF scheme defined by Oksanen and Ranta (1992) described the prevailing conditions on meadow and lawn sites quite well. Since both of the two theories were developed in different climate conditions to this study, and the species may have different responses in different climate conditions, the superiority or feasibility of these two approaches will not be considered in detail here. However, since the MAF classification seemed to be more successful in this particular case, it can be recommended for works of a similar kind. It is interesting to notice that, according to the MAF classification, intensive mowing may direct plant communities towards graminoid-dominated vegetation. Using Grime's scheme, particular trends in different strategies are more difficult to identify.

CONCLUDING REMARKS

In spite of the fairly intense management of the lawns around the Keminmaa churches, several rare and typical species have persisted to now. This indicates that the management of these lawn-like meadow patches is not too intense with respect to species richness and, on the other hand, that on the abandoned meadows the ongoing succession has not yet lowered species richness, as is expected to happen if one or a few competitive species invades. However, management intensity in lawn-like meadow patches could easily be abated without any loss in species composition. On the contrary, it is probable that species richness would increase somewhat if the timing and cutting methods were altered by, for instance, delaying the mowing and cutting of the forage with machines which have cutting blades or with scythes. This would allow the late-flowering plants to set seed and prevent excessive drying (Johansson & Hedin 1991). Finally, it must be remembered that, in the long run, abandonment of semi-natural meadows is more harmful for the archeophytes with weak competitive abilities than intense management (Ekstam & Forshed 1992). A preliminary increase in species richness due to a successional change may create the illusion that abandonment is more desirable from the manager's point of view. It is reasonable to claim that after the original management ceases, a dry meadow can be maintained seemingly unchanged for years with even minor management efforts. Later on, after an appropriate species and community analysis, the management practices can be adjusted and specified in a more subtle way.

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REFERENCES

Aber, J. D. 1987: Restored forests and the identification of critical factors in species-site interactions. — In: Jordan, W. R., Gilpin, M. E. & Aber, J. D. (eds.), Restoration ecology. A synthetic approach to ecological research: 241–250. Cambridge Univ. Press.

Ahti, T. 1989: Jäkälien määritysopas. Toinen korjattu painos. — Helsingin yliopiston kasvitieteen laitoksen monisteita 118. Helsinki. 77 pp.

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — Ann. Bot. Fennici 5: 169–211.

Alalammi, P. (ed.) 1987: Climate. — In: Atlas of Finland, Folio 131. Helsinki. 32 pp.

Alatalo, R. V. 1981: Problems in measurement of evenness in ecology. — Oikos 37: 199–204.

Anonymous 1993: Landscape management. Report I of the working group on landscape areas. — Mietintö 6/1992, Helsinki. [In Finnish with English abstract.]

Bakker, J. P. 1987: Restoration of species-rich grassland after a period of fertilizer application. — In: van Andel, J., Bakker J. P. & Snaydon R. W. (eds.), Disturbance in grasslands: 185–200. Dr W. Junk Publ., Dordrecht.

Berendse, F., Aerts, R. & Bobbink, R. 1993: Atmospheric nitrogen deposition and its impact on terrestrial ecosystems. — In: Vos, S. S. & Opdam P. (eds.), Landscape ecology of a stressed environment: 104–121. Chapman & Hall, London.

Bremner, J. M. & Mulvaney, C. S. 1982: Nitrogen – total. — In: Page, A. L., Miller, R. H. & Keeney, D. R. (eds.), Method of soil analysis. Part two – Chemical and micro biological properties: 595–622. Agronomy no. 9. ASA and SSSA, Madison, Wisconsin.

Bülow-Olsen, A. 1980: Nutrient cycling in grassland dominated by Deschampsia flexuosa and grazed by nursing cows. — Agro-Ecosystems 6: 209–220.

Connell, J. H. & Slatyer, R. O. 1977: Mechanisms of succession in natural communities and their role in community stability and organisation. — Am. Nat. 111: 1119–1144.

During, H. J. & Willems, J. H. 1984: Diversity models applied to a chalk grassland. — Vegetatio 57: 103–114.

Egler, F. E. 1952: Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development — Vegetatio 4: 412–417.

Ekeland, K. 1988: The preservation of ancient monuments and conservation of biological species. — Svensk Bot. Tidskrift 82: 490–498. [In Swedish with English abstract.]

Ekstam, U. & Forshed, N. 1992: If grassland management ceases. Vascular plants as indicator species in mead-

ows and pastures. — Naturvårdsverket. Värnamo. 209 pp. [In Swedish with English summary.]
Ekstam, U., Aronsson, M. & Forshed, N. 1988: Ängar. Om naturliga slåttermarker i odlingslandskapet. — LTs Förlag, Stockholm. 209 pp.
Eriksson, Å., Eriksson, O. & Berglund, H. 1995: Species abundance patterns of plants in Swedish semi-natural pastures. — Ecography 18: 310–317.
Facelli, J. M. & Facelli, E. 1993: Interactions after death: plant litter controls priority effects in a successional plant community. — Oecologia 95: 277–282.
Grime, J. P. 1977: Evidence for three primary strategies in plants and its relevance to ecological and evolutionary theory. — Am. Nat. 111: 1169–1194.
Grime, J. P. 1979: Plant strategies and vegetation processes. — John Wiley & Sons, Chichester. 222 pp.
Grime, J. P., Hodgson, J. G. & Hunt, R. 1988: Comparative plant ecology. A functional approach to common British species. — Hyman, London. 742 pp.
Horn, H. S. 1974: The ecology of secondary succession. — Annual Rev. Ecol. Syst. 5: 25–37.
Huhta, A.-P. 1997: Vegetation changes in semi-natural meadows after abandonment in coastal northern Finland. — Nordic J. Bot. 16: 457–472.
Hämet-Ahti, L. 1980: Pimpinella saxifraga L. — In: Jalas, J. (ed.), Suuri kasvikirja III: 216–217. Otava, Helsinki.
Hämet-Ahti, L., Suominen, J., Ulvinen, T., Uotila, P. & Vuokko, S. (eds.) 1986: Retkeilykasvio. — Suomen Luonnonsuojelun Tuki, Helsinki. 598 pp.
Jalas, J. 1980: Galium verum L. — In: Jalas, J. (ed.), Suuri kasvikirja. III: 620–622. Otava, Helsinki.
Johansson, O. & Hedin, P. 1991: Restaurering av ängs och hagmarker. — Naturvårdsverket. Solna. 146 pp.
John, M. K. 1970: Calorimetric determination of phosphorous in soil and plant materials with ascorbic acid. — Soil Science 100: 214–220.
Jukola-Sulonen, E.-L. 1983: Vegetation succession of abandoned hay field in Central Finland. A quantitative approach. — Comm. Inst. For. Fen. 112: 1–85.
Jonsson, L., Persson, S. & Emanuelsson, U. 1991: Vegetation changes before and after restoration in the wooded meadows of Ire, Blekinge, Sweden. — Svensk Bot. Tidskrift 85: 417–442. [In Swedish with English abstract.]
Koponen, T. 1994: Lehtisammalten määritysopas. Kolmas uusittu painos. — Helsingin yliopiston kasvitieteen laitoksen monisteita 139. Helsinki.119 pp.
Kull, K. & Zobel, M. 1991: High species richness in an Estonian wooded meadow. — J. Veg. Sci. 2: 711–714.
Lahti, T., Lampinen, R. & Kurtto, A. 1995: The database for distribution of vascular plants in Finland. — Univ. Helsinki, Finnish Mus. of Nat. Hist., Bot. Mus., Helsinki. Version 2.0. 23 pp. + 1604 charts as a database.
Lennartsson, T. & Svensson, R. 1995: Patterns in the decline of three species of Gentianella (Gentianaceae) in Sweden, illustrating the deteoriation of semi-natural grasslands. — Symb. Bot. Ups. 31: 170–184.
Ludwig, J. A. & Reynolds, J. F. 1988: Statistical ecology. A primer on methods and computing. — John Wiley & Sons, New York. 337 pp.
Myster, R. W. & Pickett, S. T. A. 1994: A comparison of rate of succession over 18 yr in 10 contrasting old fields. — Ecology 75: 387–392.
Økland, R. H. 1990: Vegetation ecology: theory, methods and applications with reference to Fennoscandia. — Sommerfeltia Suppl. 1: 1–223.
Oksanen, L. & Ranta, E. 1992: Plant strategies along a mountain vegetation gradient: a test of two theories. — J. Veg. Sci. 3: 175–186.
Oksanen, L. & Virtanen, R. 1997: Adaptation to disturbance as a part of the strategy of arctic and alpine plants: perspectives to management and restoration. — In: Crawford, R. M. M. (ed.), Disturbance and recovery in arctic lands: 91–113. Kluwer Acad. Publ., Dordrecht.
Oomes, M. J. M. 1990: Changes in dry matter and nutrient yields during the restoration of species-rich grasslands. — J. Veg. Sci. 1: 333–338.
Påhlsson, L. (ed.) 1995: Öppen brukningsbetingad vegetation. — In: Vegetationstyper i Norden. TemaNord 1994: 665. Nordiska ministerrådet: 381–457.
Pegtel, D. M. 1987: Soil fertility and the composition of the semi-natural grassland. — In: van Andel, J., Bakker J. P. & Snaydon, R. W. (eds.), Disturbance in grasslands: 51–65. Dr W. Junk Publ., Dordrecht.
Rassi, P., Kaipiainen, H., Mannerkoski, I. & Ståhls, G. 1991: Report on the monitoring of threatened animals and plants in Finland. — Committee Report 1991: 30. Min. Env., Helsinki. 328 pp. [In Finnish with English abstract.]
Rodriquez, M. A., Brown, V. K. & Gomez-Sal, A. 1995: The vertical distribution of below-ground biomass in grassland communities in relation to grazing regime and habitat characteristics. — J. Veg. Sci. 6: 63–72.
Schaminée, J. H. J. & Meertens, M. H. 1992: The influence of human activities on the vegetation of the subalpine zone of the Monts du Forez (Massif central, France). — Preslia 64: 327–342.
Sukopp, H. & Hejny, S. 1990: Urban ecology: Plants and plant communities in urban environment. — SPB Acad. Publ., The Netherlands. 282 pp.
Suominen, J. & Hämet-Ahti, L. 1993: Archeophytes in the flora of Finland. — Norrlinia 4: 1–90. [In Finnish with English abstract.]
Ter Braak, C. J. F. 1987: CANOCO – a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (version 2.1). — TNO Institute, Wageningen. 95 pp.
Thalen, D. C. P., Poorter, H., Lotz, L. A. P. & Oosterveld, P. 1987: Modelling the structural changes in vegetation under different grazing regimes. — In: van Andel, J., Bakker, J. P. & Snaydon R. W. (eds.), Disturbance in grasslands: 167–183. Dr W. Junk Publ. Dordrecht.
Tonteri, T. & Haila, Y. 1990: Plants in a boreal city: Ecological characteristics of vegetation in Helsinki and its surroundings, southern Finland. — Ann. Bot. Fennici

27: 337–352.
van Andel, J. & van der Bergh, J. P. 1987: Disturbance in grasslands. Outline of the theme. — In: van Andel, J., Bakker, J. P. & Snaydon R. W. (eds.), Disturbance in grasslands: 51–65. Dr W. Junk Publ., Dordrecht.
Vinther, E. 1983: Invasion of Alnus glutinosa (L.) Gaertn. in a former grazed meadow in relation to different grazing intensities. — Biol. Conserv. 25: 75–89.
Ward, L. K. & Jennigs, R. D. 1990: Succession of disturbed and undisturbed chalk grassland at Aston Rowant national nature reserve: details of changes in species. — J. Appl. Ecol. 27: 913-923.