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High species richness in an Estonian wooded meadow

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Abstract. A wooded meadow at Laelatu in western Estonia was found to be very rich in vascular plants. The maximum number of species found was 25 in a 10 cm × 10 cm plot, 42 in a 20 cm × 20 cm plot and 63 in a 1 m^2 plot.

Species richness is related to the management history of the site. The highest richness was found in sites with the most regular long-term mowing. Species density was lower in the case of fertilization or temporary cessation of mowing.

The richest community had an LAI of 2.8 and an above-ground dry biomass of 175 g/m^2. With increasing height of the herb layer the number of species decreases. Small disturbances cause a remarkable decrease in species density.

Keywords: Calcicolous grassland; Coexistence; Community structure; Management; Management history.

Nomenclature: Flora of the Estonian S.S.R. I-XI. 1959-1984.

Introduction

Wooded calcicolous meadows with a sparse tree layer and many herbs, are typical for the region around the Baltic Sea and for some mountainous regions in central Europe (Haeggström 1983). All European calcicolous grasslands are rich in species, with local variations related to the vertical structure of vegetation (Zobel 1984; Willems 1985; Rejmánek & Rosén 1988; van der Maarel & Titlyanova 1988).

The existing mechanistic models of plant communities (Rozenberg 1984; Tilman 1988; Wilson 1990) do not allow the prediction of possible maximum numbers of coexisting species. Consequently, the following description of an unusually species-rich calcicolous grassland, probably one of the richest in temperate Europe, is mainly of anecdotal value.

Study site

The study site is a wooded meadow at Laelatu on the coast of western Estonia. The mean temperature for July is ca. 17.0 °C, and for January ca. – 5.0 °C. The mean annual precipitation is 500 mm. The soil is mainly a rendzic leptosol with a pH around 7. The soil profile contains only two horizons: A (humus, 17-20 cm), and C (parent material of limestone shingle mixed with various coastal sediments). The A horizon contains on average 9.2 % humus, 7400 ppm Ca and 0.61 % total nitrogen. The total area of the Laelatu wooded meadow is 153 ha, but most of it became overgrown by woodland in the 1950s. Only ca. 20 ha is still mown regularly.

The wooded meadow proper which can be assigned to the *Sesleria coerulea - Filipendula hexapetala* association (Krall & Pork 1970) has scattered trees (*Quercus robur*, *Fraxinus excelsior*, *Betula* spp., *Populus tremula*).

Laelatu wooded meadow has probably been cut for hay for more than 200 yr. Thus, the present mowing regime should not be considered a disturbance, but rather as a 'normal' component of the environment. There is no record of grazing on the meadow.

Material and Methods

Numbers of vascular plant species were determined in seven sites on 10 cm × 10 cm and 20 cm × 20 cm plots; % cover was determined on 1 m × 1 m plots. *Taraxacum officinale*, *Euphrasia officinalis*, *Anthyllis vulneraria* were treated as collective species, and among *Hieracium* spp. only *H. pilosella* was distinguished. The number of plots of each size was 30, except in disturbed sites. All plots were chosen randomly unless otherwise noted.

To measure light penetration coefficients fish-eye photographs were used (Anderson 1964). For the measurement of light profiles inside the herb community a tube pyranometer of 1.6 cm diameter and 35 cm length was used. All light measurements were made at the end of June, before mowing.

A fertilization experiment was started in 1961 in 10 m × 30 m plots and proceeded until 1981. 35 kg N, 60 kg P_2O_5, and 60 kg K_2O per hectare were added annually.

A short description of the sites is included in Table 1.

Table 1. General characteristics and species richness at sites A - E on the Laelatu wooded meadow; 'd' = disturbed plot. Figures are means + SD (not given for *n* < 5) and range. PL = penetration of light (%) through upper layers.

Site	PL	Species number 10 × 10cm	20 × 20cm	Management history or type of disturbance
A1	75	15.4 ±1.9 (12 - 18)	28.2 ± 2.0 (24 - 31)	mown permanently during at least 200 yr; with scattered trees
A1d		14.0	15.5	dug by wild boar
A2	82	17.7 ± 2.7 (14 - 25)	33.9 ± 3.1 (28 - 42)	same as A1; without trees
A2d		11.0 ± 1.2	21.8 ± 1.3	mole mounds
B	79	14.1 ± 2.1 (10 - 18)	23.0 ± 2.4 (16 - 27)	mown permanently, fertilized 1961-1981.
C	85	15.6 ± 1.7 (12 - 18)	26.2 ± 2.2 (23 - 30)	mowing ceased some years during the 1970s
Cd		10.5 ± 1.0	18.2 ± 1.3	mole mounds
D1	65	10.9 ± 2.1 (7 - 16)	18.9 ± 3.3 (16 - 26)	overgrown in 1970s, mown again since 1979; scattered trees
D1d		8.7 ± 1.8 6.6 ± 1.3 8.1 ± 1.4 6.7 ± 1.7	17.1 ± 2.9 11.2 ± 1.2 16.2 ± 1.2 10.7 ± 1.7	haycock, 1 month haycock, 2 yr mole mound burned
D2	80	12.2 ± 2.4 (10 - 15)	21.2 ± 2.2 (17 - 27)	same as D2; without trees
E1	77	7.0 ± 1.6 (5 - 11)	11.0 ± 2.2 (8 - 15)	overgrown, cleared 1984, mown since 1989
E2		5.4 ± 1.0 (5 - 8)	9.0 ± 1.5 (6 - 11)	patch of *Calama-grostis epigeios*
F	56	9.2 ± 1.9 (6 - 13)	16.5 ± 2.3 (12 - 21)	overgrown, mowing ceased 10 yr ago
G	30	4.0 ± 1.2 (2 - 6)	6.4 ± 1.9 (4 - 12)	overgrown, not managed

In sites A and B the vertical distribution of biomass was measured in two 0.5 m × 3 m plots. The leaf area index was calculated by taking the leaf biomass for each species from 20 randomly located 7.5cm × 20 cm samples, and specific leaf weight (leaf dry weight divided by leaf area) measured for each species. The same plots were used for counting ramets. The species biomass distribution was calculated using above-ground biomass data for each species from 80 randomly located 7.5 cm × 20 cm samples. Biomass was collected at the end of June, before mowing, and dried before weighing at 85 °C.

Results

Characteristics of the richest community, compared to neighbouring communities

General community characteristics of sites with different management history are presented in Table 1. Species composition of the community with maximum richness (site A2) is given in Table 2.

All sites represented in Table 1 are characterized by similar soil conditions. Differences in species richness and community structure are related to management, which has not been uniform in all parts of the wooded meadow. A gradient of management, from most to least intensive, begins with the community which has been mown permanently over a long period (A), progresses to the community which is overgrown by trees (G). This yields the sequence of sites A-C-D-E-F-G.

Species richness at all sites (except sites A1 and D1 with more trees) was compared using one-way ANOVA with Student' s multiple range test. All sites were different from each other (F-ratio = 671, p = 0.0001) when species richness was compared. Consequently, when the intensity and/or regularity of mowing decreases, species density also decreases.

Within sites A and D the presence of trees is variable. In parts where tree canopy cover is lower, a statistically significantly (p = 0.01) higher species richness was found. Also, when some taller grasses were present (cf. E1 and E2), the richness was higher if the herb foliage was lower. Thus, higher species richness is related to less diverse vertical structure.

Disturbance and species richness

In sites A1, A2, D1 and C, species richness in places dug by wild boar was significantly lower (p = 0.01) than in the undisturbed community (Table 1). In places where haycocks stood for a month, species richness did not differ from that of the undisturbed community. Disturbed places were inhabited by the same species as found in the undisturbed community. More abundant species, such as *Sesleria coerulea* and *Brachypodium pinnatum* were also more common in disturbed sites.

In heavily disturbed sites where haycocks stood for two years, and in places which had been burned, species richness in the year after the disturbance was considerably lower. Also some new species (e.g. *Myosotis arvensis* and *Arrhenatherum elatius*) appeared.

The influence of fertilization

The richest community, site A2, and the community in the fertilized variant of A2, site B, were studied in

Table 2. Species composition of the richest site, A2. Columns 1 - 3: species of the richest sample plot of size 10 cm × 10 cm, 20 cm × 20 cm, and 1 m². B = biomass (%), Fr = species frequency (%) in 30 randomly located 1 m × 1 m plots*, Co = mean cover % for plots where species is present.

	1	2	1m²	B	Fr	Co
Aegopodium podagraria			+	.52	43	1.3
Alchemilla glaucescens	+		+	.38	83	.9
Angelica sylvestris			+	.01	53	1.5
Antennaria dioica		+	+	.06	53	.5
Anthoxanthum odoratum	+	+	+	.66	67	. 6
Asperula tinctoria			+	.11	30	.6
Brachypodium pinnatum		+	+	6.14	97	8.6
Briza media		+	+	2.77	70	.7
Campanula glomerata			+	.36	73	.8
Campanula persicifolia		+		.14	53	.7
Carex capillaris			+	.13	33	.7
Carex flacca		+	+	2.55	97	1.0
Carex ornithopoda		+	+	.66	93	.9
Carex panicea		+	+	1.54	53	.S
Carex pulicaris		+		.09	13	.5
Carex tomentosa		+		3.67	37	.7
Centaurea jacea		+	+	3.50	93	4.1
Cirsium acaule		+	+	1.19	67	6.0
Convallaria majalis		+	+	2.53	97	1.7
Crepis praemorsa			+	.16	57	.8
Dactylis glomerata	+	+	+	.10	40	.6
Dactylorhiza fuchsii			+		13	1.6
Euphrasia officinalis			+	.01	53	.5
Festuca arundinacea			+	3.32	77	3.6
Festuca ovina	+	+	+	1.49	3	.5
Festuca pratensis			+	. 62	7	.5
Festuca rubra	+	+	+	2.52	100	1.1
Filipendula hexapetala		+	+	. 63	63	1.1
Frangula alnus			+			
Fraxinus excelsior	+			.04		
Galium boreale			+	.42	90	1.1
Geum rivale		+	+	.18	80	1.0
Helianthemum nummularium	+	+	+	1.08	80	1.1
Helictotrichon pratensis		+	+	4.13	93	3.6
Helictotrichon pubescens	+			.09	3	.5
Hepatica nobilis	+	+	+	.16	97	.9
Hieracium pilosella		+	+	.44	67	.8
Inula salicina			+		27	.8
Lathyrus pratensis		+	+	.93	47	1.4
Lathyrus vernus			+	.32	30	.8
Leontodon hispidus	+		+	3.51	93	4.1
Leucanthemum vulgare	+		+	.51	87	.7
Linum catharticum	+			.02	30	.6
Listera ovata			+	.45	60	1.1
Lotus corniculatus		+		.87	60	1.1
Luzula campestris		+		.08	17	.5
Medicago lupulina	+		+	.34	57	.9
Molinia coerulea	+	+	+	1.07	57	3.2
Ophioglossum vulgatum		+	+	.42	83	1.0
Pimpinella major	+	+	+	.03	53	1.2
Pimpinella saxifraga		+	+	.01	17	.7
Pinguicula vulgaris			+		7	.5
Plantago lanceolata	+	+	+	4.95	97	1.9
Plantago media	+	+	+	1.67	83	5.4
Platanthera bifolia			+		3	.5
Polygala amarella	+			.05	53	.6
Potentilla erecta	+	+	+	3.12	90	3.0
Primula veris			+	.39	83	1.1
Prunella vulgaris		+	+	1.47	97	1.5
Pyrola rotundifolia		+	+	.69	90	.7
Ranunculus acer		+	+	.21	37	.9
Ranunculus polyanthemus	+			1.20	90	.9
Rhinanthus minor			+		7	.5
Rubus saxatilis			+	.13	17	2.3
Salix phylicifolia			+	.01		
Scorzonera humilis	+	+	+	3.85	93	2.1
Serratula tinctoria	+	+	+	4.05	97	4.5
Sesleria coerulea	+	+	+	12.77	97	7.1
Solidago virgaurea	+				30	.8
Succisa pratensis			+	4.50	90	6.6
Thymus serpyllum		+			23	.6
Trifolium pratense		+	+	3.91	90	4.3
Trollius europaeus			+		40	.5
Veronica officinalis		+	+	.10	67	.6
Vicia cracca		+		1.95	87	3.5
Viola arenaria	+		+		30	.5
No. of species	25	42	63			

* In addition to the 76 species listed 37 species were found in these plots.

more detail. The community in site B is largely similar to communities D and E with lower species richness.

The main change due to fertilization was the elimination of ca. 30% of the species. These were all subordinates, many of which form the lowest sub-horizon of the herb canopy. Ramet density and LAI values are higher in the fertilized community, while the share of leaves in the biomass is less (Table 3).

The mean above-ground dry weight biomass for unfertilized (A2) and fertilized (B) communities were 175 and 480 g/m², respectively. The vertical canopy structures differ as well (Fig. 1). Due to the increase in biomass and height light penetration decreases. At a height of 20 cm it is three times less in the fertilized community. This is probably the reason for elimination of many low subordinate species from the community.

Discussion

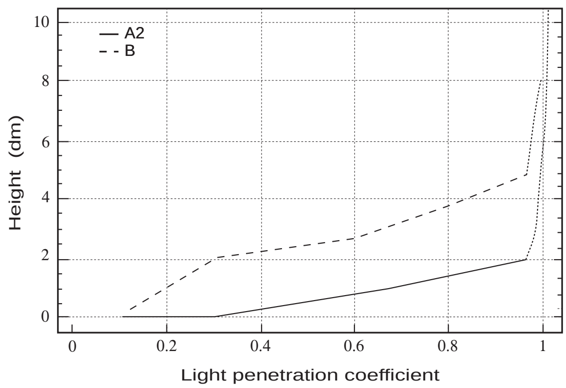
Species richness in the Laelatu wooded meadow is higher than reported in other calcicolous grasslands in Europe (cf. Haeggström 1983; During & Willems 1984). A higher richness is known only to occur in dry steppes (Dohman 1968). Top richness was observed in an edaphically homogeneous part of the meadow, which has long been permanently mown, but not grazed. The herb layer here is lower than elsewhere and trees are mostly absent.

The main difference between the richest and poorer communities on calcareous soil is the degree of light penetration through the vegetation. Temporary cessation of mowing and fertilization increases the height of the herb layer. In abandoned sites less light penetrates into the lowest subhorizon (15-20 cm) and low-growing species will mostly be excluded from the community and the species richness will decrease. Resumption of mowing can increase richness, but at least three decades are needed to restore the previous level of richness.

The presence of a large species pool in all European calcareous grasslands can be related to the widespread occurrence of this habitat type in evolutionary time (Taylor, Aarssen & Loehle 1990). There is room for some further speculation on ecological theory. First, irregular, meso-scale (0.01 - 100 m²) disturbances do not seem to contribute to species richness. If a non-equilibrium state promotes coexistence (Pickett 1980), it appears to operate on other scales. Second, due to the rather low richness of the surrounding communities, seed re-immigration (see Shmida & Ellner 1984) contributes only some forest species, and cannot be the main mechanism of coexistence. Third, the above-ground niche differentiation does not contribute to species richness. Vice versa, the highest richness is correlated with the maximal similarity in plant heights. Consequently,

Table 3. Structural characteristics of the rich community, site A2, and the comparable fertilized community, site B.

	Unfertilized (site A2)	Fertilized (site B)
Above-ground biomass (g dry weight/m^2)	175	480
Leaf area index	2.8	6.3
Fraction of leaves in above-ground biomass	0.83	0.58
Mean specific leaf area (cm^2/g)	192	224
No. of ramets per m^2	4200	5300
No. of ramets per species (150 cm^2 plot)	3.3	7.1
No. of vascular species (20 plots of 150 cm^2)	73	43



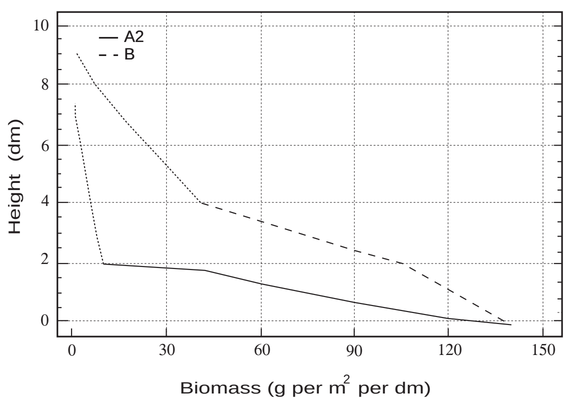


Fig. 1. Light penetration through canopy, and vertical distribution of biomass (volumes 1 $m^2 \times 1$ dm were used for measurements) in communities A2 and B.

niche differentiation can play a role only if below-ground resources are also considered (Tilman 1988). Nevertheless, below-ground niche differentiation probably cannot be the factor distinguishing sites with different management history. The above-ground situation corresponds rather to the state of 'balanced competition' (Aarssen 1989). Since the vertical structure of vegetation is directly dependent on the management conditions, it can be claimed that richness is highest if the external factor (mowing in this case) has led to a balanced competition for light.

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References

Aarssen, L. W. 1989. Competitive ability and species coexistence: a 'plant's -eye' view. *Oikos* 56: 386-401.

Anderson, M. C. 1964. Light relations of terrestrial plant communities and their measurement. *Biol. Rev.* 39: 425-486.

Dohman, G. I. 1968. Forested steppe in the European part of the USSR. Nauka, Moscow (in Russian).

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

Haeggström, C.-A. 1983. Vegetation and soil of the wooded meadows in Natö, Åland. *Acta Bot. Fenn.* 120: 1-66.

Krall, H. & Pork, K. 1970. Laelatu puisniit. In: Kumari, E. (ed.) *Lääne-Eesti rannikualade loodus.* Valgus, Tallinn.

Pickett, S. T. A. 1980. Non-equilibrium coexistence of plants. *Bull. Torr. Bot. Club* 107: 238-248.

Rejmánek, R. & Rosén, E. 1988. The effects of colonizing shrubs (*Juniperus communis* and *Potentilla fruticosa*) on species richness in the grassland of Stora Alvaret, Öland (Sweden) *Acta Phytogeogr. Suec.* 76: 67-72.

Rozenberg, G. S. 1984. *Models in Phytocoenology (Modeli v fitocenologii).* Nauka, Moscow (in Russian).

Shmida, A. & Ellner, S. 1984. Coexistence of plant species with similar niches. *Vegetatio* 58: 29-55.

Taylor, D. R., Aarssen, L. W. & Loehle, C. 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos* 58: 239-250.

Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities.* Princeton University Press, Princeton.

van der Maarel, E. & Titlyanova, A. A. 1989. Above-ground and below-ground biomass relations in steppes under different grazing conditions. *Oikos* 56: 364-370.

Willems, J. H. 1985. Growth form spectra and species diversity in permanent grassland plots with different management. *Munst. Geogr. Arb.* 20: 35-43.

Wilson, J. B. 1990. Mechanisms of species co-existence: twelve explanations for Hutchinson's 'Paradox of the plankton': evidence from New Zealand plant communities. *N. Z. J. Ecol.* 13: 17-42.

Zobel, M. 1984. Ecology of alvar communities in Estonia. *Sovj. J. Ecol.* 4: 15-21 (in Russian).

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