Classifying clonal growth forms based on vegetative mobility and ramet longevity: a whole community analysis

ANNELI TAMM[1]*, KALEVI KULL[1] and MAREK SAMMUL[1,2]
[1] *Department of Botany, Institute of Zoology and Botany, Estonian Agricultural University, Riia 181, 51014 Tartu, Estonia;* [2] *Institute of Botany and Ecology, University of Tartu, Lai 40, 51005 Tartu, Estonia*
(*author for correspondence, tel.: +372-7-428619; fax: +372-7-383013; e-mail: a.tamm@zbi.ee)
Present address: Department of Short Rotation Forestry, SLU, Box 7016, 750 07 Uppsala, Sweden

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Abstract. We measured rhizome branching, clonal mobility, and ramet longevity of 98 meadow plant species. A cluster analysis applied to this dataset revealed nine clonal growth types that differ mainly by the ramet lifespan and vegetative mobility. Then we compared the abundance of these groups of clonal species between the three following plant communities: (1) open, (2) restored and (3) overgrown wooded meadows in the Laelatu-Nehatu-Puhtu Nature Reserve, Estonia. This is the first study where the quantitative values of belowground clonal traits have been measured for all species of a species-rich community. We show that species with annual ramets and with a low vegetative mobility were most abundant in open grasslands. The relative abundance of perennial species with annual ramets was positively correlated with shoot density and species diversity, indicating that high ramet turnover rates combined with a high genet longevity can positively affect species coexistence in meadow communities. Hence, this study provides evidence for the fact that the average values of clonal life-history parameters differ between these communities. Herb communities under forest canopy consist, in average, of species with ramets that live longer and are clonally more mobile than in the communities of open sites.

Key words: branching intensity, growth form, life span, plant community dynamics, ramet, ramet turnover rate, species coexistence, vegetative mobility

Introduction

Extensive clonal plant research conducted over the past decades has yielded a good description and ecological understanding of many stoloniferous and rhizomatous species (e.g., Callaghan *et al.*, 1986; Klimeš, 1992; Kull, 1995a, b; Groenendael *et al.*, 1996). Considerable progress has been made in explaining the mechanisms and benefits of plasticity in clonal growth and architecture (e.g., Hutchings and de Kroon, 1994; Huber and Stuefer, 1997; Skalova *et al.*, 1997). However, approaches to the study of clonal plant morphology and life history from a community perspective have been very rare (Eckert, 1999).

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Both meadow and forest floor communities, including semi-natural grasslands, are dominated by clonal perennial plant species (Klimeš *et al.*, 1997). Ramet longevity and the spatio-temporal extent of vegetative spread have been considered to be significant factors both for characterizing and understanding life-history types of clonal plants (e.g., Pokarzhevskaya, 1995; Altesor *et al.*, 1999) and the study of processes affecting community dynamics in herbaceous vegetation (Grubb *et al.*, 1982; Mitchley and Grubb, 1986; Grubb 1990). These two clonal growth traits are major determinants of replacement and dynamics of ramets and of species in plant communities and they form the basis for a phenomenon referred to as 'Carousel model' (Maarel and Sykes, 1993, 1997; Maarel, 1996; Klimeš, 1999), which suggests that in a homogeneous community many (if not all) species can reach virtually all microsites. Ramet lifespan has been used to classify clonal life histories and clonal integration patterns (Jonsdottir and Watson, 1997).

Several clonal growth forms have been distinguished on the basis of combinations of clonal growth traits. These classifications have either aimed at classifying the whole variety of clonal growth characteristics (Klimeš *et al.*, 1997) or they have concentrated on the spatial pattern of clonal growth (*guerilla-* and *phalanx*-type growth; Lovett Doust, 1981; Harper, 1985). Several attempts have been made to distinguish clonal life-history types based on ramet lifespan, longevity of the connecting stem structures (Jonsdottir and Watson, 1997), and on the regeneration strategies (Eriksson, 1997) of clonal plants. A general classification, however, will require detailed and time-consuming measurements of belowground traits (cf. Weiher *et al.*, 1999).

A classification of species on the basis of a few ecologically and functionally significant traits may be useful in order to analyse the specific role of clonal growth in community dynamics and species co-existence. A task for the evolutionary functional ecology of clonal plants is to discover the community-level regularities in the distribution of different clonal life-history types.

In the present study we developed a clonal growth form classification, which is based on measured values of morphological parameters associated with clonal growth. These traits are ramet longevity (i.e. the lifespan of an individual ramet), vegetative mobility (i.e. the distance between a parent and its offspring ramet), and branching intensity (Kull, 1995a, b; Kull *et al.*, 2000). In more detail, ramet lifespan describes how long a ramet occupies a particular microsite in the vegetation. Ramet branching intensity determines the rate of vegetative propagation of a ramet.

In relatively stable communities such as open grasslands, shoots of most species are likely to be short-lived (Maarel, 1996) and species turnover rates are high (Pärtel and Zobel, 1995; Maarel and Sykes, 1997). Plant mobility seems particularly high in open grasslands (Maarel, 1996). Plant mobility is an estimate of the time frame between the appearance and disappearance of above-

ground plant parts in a community. It does not distinguish between vegetative mobility (i.e. mobility by means of vegetative spacers) and mobility through seed dispersal. Plant mobility may alleviate or delay competitive exclusion (Bell, 1984; Herben *et al.*, 1997), which might be particularly relevant for competitively inferior species. Herben *et al.* (1994) have found a negative relationship between the mean aboveground biomass of ramets and plant mobility, suggesting that small plants (i.e. inferior competitors) are more mobile than large plants. These, somewhat contradictory statements, lead us to compare the values of clonal mobility and ramet longevity for the whole sets of species between the communities of different species richness. The communities of wooded meadows serve as a good object for this kind of study, due to the existence of sites of different openness, but otherwise similar in many other respects, close to each other.

Material and methods

Study site

This study has been carried out in the Laelatu wooded meadow at the coast of western Estonia (58°35′ N; 23°33′ E) in 1995. The wooded meadow area, recently 35–40 ha in size (Kukk and Kull, 1997), is a part of the Laelatu-Nehatu-Puhtu Nature Reserve. During the last decades an area of 10–15 ha has been mown once a year. The soil is mesotrophic, lying on Silurian limestone bedrock covered with calcareous moraine. The soil layer is up to 30 cm deep with neutral reaction (pH 6.7–7.0). The content of mobile nutrients in the soil is low to medium (2.5–10.5 mg P_2O_5, 3–16 mg K_2O per 100 g of soil), which is characteristic for natural meadow communities in the boreo-nemoral zone (Krall and Pork, 1970). The mean annual temperature from 1987 to 1997 was 6.3 °C (air) and 7.1 °C (ground); the mean annual precipitation was 600 mm. The rainiest seasons are late summer and autumn with a mean monthly precipitation of 66 mm from July to November and of 38 mm from February to June (Estonian Institute of Meteorology and Hydrobiology; more details in Kukk and Kull, 1997).

We studied three vegetation types, which differ in their history of management: (1) a long time (over 25 years) overgrown wooded meadow, (2) a restored wooded meadow, and (3) an open meadow. According to the traditional management cycle of wooded meadows, these three community types can also be interpreted as successional stages of the same vegetation type. Some characteristics of the studied communities are given in Table 1. The list of main dominant plant species indicates that mesic conditions prevail in all studied communities. Open meadow sites have been mown regularly for at least 200 years. In the restored part of the wooded meadow, brushwood was cut in

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Table 1. Characteristics of studied communities

Site	Number of relevés	Number of shoots per m^2	Number of species per m^2	Above–ground phytomass (g m^{-2})	Light penetration coefficient (%)	Main dominant plant species in the community (species with cover ≥10% per m^2)
Open meadow						
1	8	1870	21	664	46	*Rubus caesius, R. saxatilis, Brachypodium pinnatum, Comvallaria majalis, Angelica sylvestris, Filipendula ulmaria, Geum rivale, Fraxinus excelsior*
3	11	6250	23	443	16	*Molinia coerulea, Sesleria coerulea, Scorzonera humilis*
4	8	2630	35	327	71	*B. pinnatum, Melampyrum nemorosum, Leontodon hispidus, Serratula tinctoria, R. saxatilis, Festuca arundinacea, Helictotrichon pratense*
5	8	3520	42	301	63	*Pimpinella major, S. tinctoria, Centaurea jacea, Crepis paludosa, Co. majalis, A. sylvestris, Heracleum sibiricum*
6	8	3190	44	262	46	*Le. hispidus, S. tinctoria, Co. majalis, A. sylvestris, Ce. jacea*
Restored wooded meadow						
1	8	1780	36	172	86	*Aegopodium podagraria, Co. majalis, Hepatica nobilis, Succisa pratensis, Calamagrostis epigeios*
2	8	2350	31	318	73	*Co. majalis, Ae. podagraria, B. pinnatum, M. nemorosum, Sarex tinctoria, Ca. epigeios, C. vaginata, Centaurea jacea*
Overgrown wooded meadow						
1	8	715	10	99	ND	*Co. majalis, F. excelsior, Cr. paludosa, Molinia coerulea, R. caesius, Deschampsia caespitosa, Stachys sylvatica*
2	8	652	15	128	ND	*Co. majalis, F. excelsior, C. vaginata, R. saxatilis*
3	7	588	14	168	95	*Co. majalis, F. excelsior, R. saxatilis, Acer platanoides*
4	6	675	14	167	97	*Co. majalis, F. excelsior, R. saxatilis, Ae. podagraria*
5	8	517	18	93	95	*F. excelsior, Co. majalis, Ae. podagraria, Lathyrus vernus*

ND – not determined.

1984 and 1993. In the overgrown wooded meadow site *Fraxinus excelsior, Acer platanoides* and *Populus tremula* form a dense tree layer and *Corylus avellana* is the most common shrub.

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We carried out a total of 96 vegetation analyses using 1 m^2 plots. Forty-three of them were located in open meadows (from five different open grassland areas), 16 in restored wooded meadows (from two sites), and 37 in overgrown wooded meadows (from five sites; Table 1). For each plot we recorded all species and their relative abundance (%) in the beginning of July (Kukk and Kull, 1997). In addition, the number of shoots was counted in two 0.1 × 0.25 m^2 subplots within each plot. Light availability was measured above the herb layer by using a fish-eye photographic technique. Light availabilities were expressed as the light penetration coefficient above the herb layer (Anderson, 1964).

Measurements of clonal growth parameters

For each of the 98 clonal vascular plant species found in the vegetation analyses, a minimum of 25 clonal fragments (polycormones) was collected during 1988–1997. In our definition a ramet is a shoot with its branches, produced by one single apical meristem. The ramet also includes the stolon or rhizome connecting it with its parent shoot. The ramet lifespan, vegetative mobility (mm per year), and branching intensity (number of rhizome branches per ramet per year) were measured for each ramet on each clonal fragment.

For instance, in *Carex panicea*, a species with horizontal rhizomes, a ramet consists of the entire rhizome branch and aboveground shoot produced by the same apical meristem. The elongation of *C. panicea* rhizomes is completed by the end of the first growing season after which a vegetative aboveground shoot will be formed. For *C. panicea* the degree of vegetative mobility is thus equal to the length of the rhizome. During the subsequent growing season the same ramet may form a generative shoot. By that time the rhizome and its scale leaves have turned darker in colour. Such morphological changes allow for an estimate of ramet life spans. After fruiting all aboveground parts of the ramet die. In many cases, however, ramets die already at the vegetative stage after the first growing season.

For *Primula veris*, a species with vertical rhizomes, clonal growth parameters were estimated as follows. *Primula veris* forms one rhizome segment in each growing season (Tamm, 1948). Each rhizome segment consists of nodes and short, thick internodes, which are formed at the beginning of the growing season. Internodes formed late in the growing season are much thinner. Such morphological differences enabled us to estimate ramet longevity based on the number of rhizome segments. The apical meristem of *P. veris* survives several years. Leaves and flower stalks are formed by lateral buds. After the death of aboveground leaves, the leaf bases remain attached to the rhizome segment. During the subsequent growing season new rhizome segments with new aboveground leaves will be formed. The distance between the current and the previous years' shoot hence reflects the degree of rhizome increment (mm/year)

in this species. As the rhizomes of *P. veris* grow in vertical direction, its vegetative mobility is usually close to 0 even if the increment of the rhizome may reach up to 10 mm per year.

The branching intensity was calculated as the number of rhizome branches per ramet divided by ramet lifespan. For living ramets (ramets with a living aboveground shoot) we did not calculate the branching intensity since we could not estimate ramet lifespans.

Data analysis

Due to a highly skewed distribution of all measured clonal growth parameters, we used the median, maximum and quartile ranges for ramet lifespan, vegetative mobility and ramet branching intensity (Table 2) when classifying clonal growth forms. Our cluster analysis was based on a matrix of presence or absence values of clonal growth characteristics. The Unweighted Pair Group Method using arithmetic means (UPGMA) was applied and the squared Euclidean distance was used as a sample dissimilarity measure.

All statistics were calculated by using SAS (version 6.12, SAS Institute Inc., Cary). Differences in Least Square Means of the relative abundance of clonal growth form groups in different community types were estimated with the GLM procedure using the ESTIMATE statement for comparisons.

We calculated average community-wide clonal growth parameters using weighted averages for each sample plot (weighting according to the relative abundance of species in a sample plot).

The effects of vegetation type, light availability, species richness and shoot density on the community-wide parameters of ramet lifespan and vegetative mobility were assessed by using multivariate ANOVA. The median vegetative mobility of ramets was square root transformed, and the maximum ramet lifespan for each plot was $\log_{10}(x + 2)$ transformed prior to data analysis.

We performed regression analyses to estimate how the ramet lifespan and vegetative mobility changed during succession of wooded meadows. Using the CONTRAST statement in the regression analysis the resulting trend lines were compared for the three vegetation types.

Results

Classification of clonal growth forms

Our cluster analysis (Fig. 1) revealed three major groups of species according to ramet longevity: (*a*) species with annual ramets, (*p*) species with perennial ramets, and (*b*) species with mostly biennial ramets. Within each of these three

Table 2. Median, maximum and quartile range values for measured clonal growth parameters

Species	Ramet lifespan (years)			Vegetative mobility (mm/year)			Branching intensity (ramets/ramet year)		
	Median	Max	Range	Median	Max	Range	Median	Max	Range
Achillea millefolium	1	1	0	44	202	67	2	6	1
Ae. podagraria	2.5	5	3	232	645	196	0.33	2	0.71
Agrostis stolonifera	1	1	0	2	135	12.8	1	4	1
Alchemilla glaucescens	1	3	3	11.5	25	11.5	1	2	0.5
An. nemorosa	1	1	0	15	38	10	1	3	0
An. ranunculoides	1	1	0	23	32	10	1	3	0
A. sylvestris	5	13	3	0	0	2	0	0	0
Arrhenatherum elatius	1	1	0	3	16	5	0	7	2
Asperula tinctoria	1	1	0	18	237	31.5	1	3	1
B. pinnatum	1	1	0	4	129	10	1	9	3
Briza media	1	4	1	18	161	26	1	5	1.5
Ca. canescens	1	2	0	6.5	210	109	1	8	4
Ca. epigeios	1	2	0	6	275	81.8	1	5	1.75
Campanula glomerata	1	1	0	10	44	13.2	1	2	0
Cam. persicifolia	1	2	1	16	50	29.5	1	2	0
Cam. rotundifolia	1	1	0	23	50	31.2	1.5	5	2.5
C. flacca	2	2	1	30	300	57.5	1	5	0.5
C. ornithopoda	2	2	0	6	23	14	1.25	1.5	0.63
C. panicea	2	3	0	14	210	39	1	2.5	1
C. pulicaris	2	2	0	4	24	6	1	3	1.13
C. tomentosa	1	2	1	8	190	38	0.5	8	1.5
C. vaginata	2.5	4	0	18.5	205	31	1	1.5	0.5
Ce. jacea	1	3	0	8	70	10	1	5	1
Ce. scabiosa	1	7	2	5	30	12.2	0.78	3	0.97
Cirsium acaule	1	1	0	12	31	9	1	3	0
Clinopodium vulgare	1	1	0	16	67	36.5	1	2	0
Co. majalis	5	10	4	240	418	87	0.2	0.4	0.19
Cr. paludosa	1	1	0	7	33	5	1	3	0
Cr. praemorsa	1	1	0	3.5	6	1.75	1	1	0
Dactylis glomerata	1	3	0	4	19	6.5	0.5	5	1
D. caespitosa	1	1	0	1	34	2	1	5	2
Epipactis helleborine	1	1	0	3	6	1	1	1	0
F. arundinacea	1	3	0	7	90	16	0	8	1
F. ovina	1	2	0	10	70	13	1	3	1
F. pratensis	1	5	0	9	130	10	1	5	1
F. rubra	1	2	1	5	260	21	1	4	2
Fi. ulmaria	1	3	0	18	41	11.2	1	3	0.38
Fi. vulgaris	2	6	3.75	4	19	2	1	1	0.83
Fragaria vesca stolons	1	2	1	252	465	251	0.67	1	0.17
Fr. vesca rhizomes		6		5	15				
Galium boreale	1	1	0	20	260	35.5	1	5	1
G. mollugo	1	1	0	35	263	48	1	6	1
G. verum	1	1	0	25	190	43	1	8	1
Geranium sanguineum	1	1	0	6	22	4	1	10	0
Geum rivale	4.5	8	2	15	25	6.18	0.71	5	0.2
Helianthemum nummularium	1	1	0	10	210	48	0	11	2
H. pratense	2	6	0	8	40	10	0	2.5	1

Table 2. (Continued)

Species	Ramet lifespan (years)			Vegetative mobility (mm/year)			Branching intensity (ramets/ramet year)		
	Median	Max	Range	Median	Max	Range	Median	Max	Range
H. pubescens	1	2	0.25	14	70	11	1	3	0
Hepatica nobilis	1	7	6.5	0.94	10.5	1.43	0.29	2	0.84
Heracleum sibiricum	3	6	2	0	17	8	1	2.5	0.4
Hypericum maculatum	1	1	0	45	152	49	1	8	1
Hypochaeris maculata	4	7	1	4	12	3.95	0.33	2	0.35
Inula salicina	1	1	0	22	330	38	1	4	0
La. pratensis	1	1	0	65	678	90	1	7	2
La. vernus	1	1	0	6	31	6	1	2	0
Le. hispidus	2	9	2	5.63	30	4.5	0.5	3	0.75
Leucanthemum vulgare	1	3	0	16	83	18	1	4	1
Listera ovata	1	1	0	3	10	1	1	2	0
L. corniculatus	1	2	0	4	70	10	1	6	1
Luzula multiflora	1	2	1	3	20	5.75	0	3	1
Lu. pilosa	1	1	0	4	18	1.5	0	4	1
Maianthemum bifolium	1	4	0	50.5	370	131	1	5	1
Medicago lupulina	1	2	0	6.5	30	6	1.25	6	1
Melica nutans	1	1	0	3	136	12	1	6	2.25
Mo. caerulea	1	1	0	3	13	2	1	2	0
Ophioglossum vulgatum	5	14	3	47	127	28			
Origanum vulgare	1	1	0	20	98	37	1	6	1
Paris quadrifolia	1	1	0	53	90	24.8	1	2	0
Pilosella officinarum stolons		2	2	125	234				
Pi. officinarum rhizomes	1	2		0	22	8	0.5	2	0.9
Pim. major	1	7	1	4	27	6.5	1	3	1.25
Pim. saxifraga	1	6	1	0.5	13	5	1	1.5	0.5
Pl. lanceolata	2.5	9	1.5	0	4	1	0.63	1	0.38
Pl. media	2	3	2.25	0	3	2	0.33	1	0
Poa angustifolia	1	2	1	14	190	38.5	0.5	4	1
Polygala amarella	1	1	0	10	75	10	0.5	1	2
Polygonatum odoratum	1	1	0	26	48	12.8	1	2	0
Potentilla erecta	2.5	5	1.75	0	10	3.15	0.4	1.33	0.67
Primula veris	4	7	2	0	6.33	3	0	2	0.21
Prunella vulgaris	1	1	0	24	144	23.2	1	10	3
Pyrola rotundifolia	3	4	1	67.5	350	120	0.79	1.33	0.54
Ranunculus acris	1	2	1	3	10	2	1	2	0
Ra. cassubicus	1	3	1	2	4	1.5	1	1	0.38
Ra. polyanthemus	1	5	2	3	18	2	1	1	0
R. caesius rhizomes	1	2	0	6	40	11	1	6	1.13
R. caesius stolons		2		280	595				
R. saxatilis rhizomes	1	2	0	8	50	15	1	4	2
R. saxatilis stolons		2		77.5	225				
Sc. humilis		6	2	3	20	21	0.33	2.17	0.5
S. tinctoria	1	3	3	0	11	2	0.83	1	0.51
Se. coerulea	1	5	2	13	86.6	11	1	3	1.5
Solidago virgaurea	1.5	8	4	3.75	11.7	2.5	0.29	2	1

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Table 2. (Continued)

Species	Ramet lifespan (years)			Vegetative mobility (mm/year)			Branching intensity (ramets/ramet year)		
	Median	Max	Range	Median	Max	Range	Median	Max	Range
S. sylvatica	1	1	0	100	350	131	2	6	1
Su. pratensis		3		0	0	0	0	0	0
Trifolium montanum	4	17	3	0	25	4	0.24	2	0.63
T. pratense	1	3	1.5	2	30	5	1	4.5	2.38
Trollius europaeus	1	3	2	0	9	2	1	2	0.5
Veronica chamaedrys	1	1	0	90	578	98	1	6	2
V. officinalis	1	1	0	18.5	160	34.8	1.5	4	2.5
Vicia cracca	1	1	0	40	300	80	1	6	1
Vi. sepium	1	1	0	70	420	132	1	6	1
Viola mirabilis	1	3	0	13	72	16.8	1	3	1

groups, species were further subdivided according to their vegetative mobility. These subgroups contained species with (*1*) low, (*2*) medium, (*3*) and high mobility (Table 3).

Distribution of clonal growth forms in different sites of wooded meadow

Ramet lifespan
The relative abundance of species with annual ramets (clonal growth types *a1*, *a2*, *a3*) was higher in open meadows (28%) than in restored and overgrown wooded meadows (16 and 15%, respectively; Table 4, Fig. 2). Species with biennial or perennial ramets showed no significant difference in their relative abundance in open, restored and overgrown sites (19, 23 and 18%, respectively for *b* species, 39, 50 and 38% respectively for *p* species).

Vegetative mobility
The relative abundance of species with low vegetative mobility (clonal growth types *a1*, *b1*, *p1*) was higher in open (39%) and in restored wooded meadows (36%) than in overgrown wooded meadows (20%). In contrast, the relative abundance of species with high vegetative mobility of ramets (clonal growth types *a3*, *b3*, *p3*) was higher in restored and in overgrown wooded meadows (39 and 34%, respectively) compared to open meadows (16%). Species with a medium vegetative mobility (clonal growth types *a2*, *b2*, *p2*) had a higher relative abundance in open meadows (31%) than in overgrown (17%) or restored wooded meadows (14%).

Clonal growth forms in three vegetation types
a1-Species (species with annual ramets and low vegetative mobility) were significantly more abundant in open meadows and in restored wooded meadows
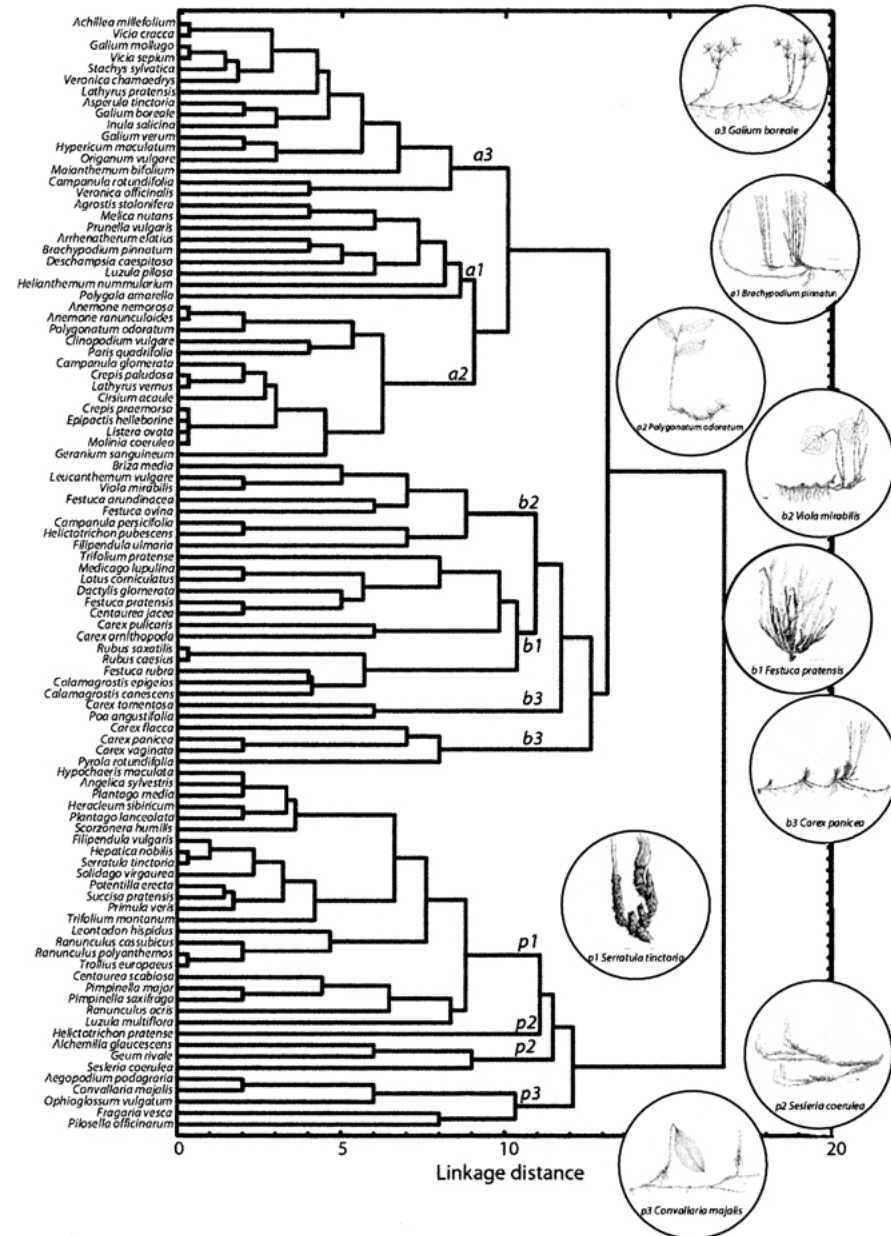
Figure 1. Classification of clonal growth forms according to a cluster analysis. Group: *a* – species with annual ramets, *b* – species with biennial ramets, and *p* – species with perennial ramets. Index: *1* – low, *2* – medium, and *3* – high vegetative mobility.

Table 3. Classification of clonal growth forms, based on ramet lifespan and vegetative mobility parameters

Growth form	Ramet lifespan (years)	Speed of vegetative mobility (mm)	Example species
a1	Annual Med = 1 Max = 1 Range = 0	Low Med < 24 Max 16…144 Range = 1.5…23.2	*Ag. stolonifera, Ar. elatius, B. pinnatum, De. caespitosa, Lu. pilosa, Po. amarella*
a2	Annual Med = 1 Max = 1 Range = 0	Medium Med = 3…53 Max = 6…90 Range = 1…36.5	*An. nemorosa, Cirsium acaule, Ge. sanguineum, La. vernus, Listera ovata, Mo. coerulea, Pol. odoratum*
a3	Annual Med = 1 (1.1) Max = 1 (4) Range = 0	High Med = 18…65 Max = 50…678 Range = 34.8…132	*As. tinctoria, G. boreale, G. mollugo, Hy. maculatum, I. salicina, La. pratensis, Ma. bifolium*
b1	Biennial Med = 1…2 Max = 2 (5) Range = 0…1.5	Low Med = 2…9 (280) Max = 30…275 (595) Range = 5…21(81.8)	*Ca. epigeios, C. ornithopoda, C. pulicaris, Da. glomerata, F. pratensis, F. rubra, Me. lupulina, R. saxatilis*
b2	Biennial Med = 1 Max = 2…4 Range = 0…1	Medium Med = 7…18 Max = 41…161 Range = 11…29.5	*Br. media, F. ovina, Fi. ulmaria, H. pubescens, Le. vulgare, Vio. mirabilis*
b3	Biennial Med = 1…3 Max = 2…4 Range = 0…1	High, mobile in the first year Med = 8…68 Max = 190…350 Range = 11…57.5	*C. tomentosa, C. flacca, C. panicea, C. vaginata, Po. angustifolia, Py. rotundifolia*
p1	Perennial Med = 1…4 Max 17 Range = 0.5…6.5	Low Med = 0…5.6 Max = 0…30 Range = 1…21	*A. sylvestris, Le. hispidus, Pl. lanceolata, P. veris, Sc. humilis, S. tinctoria*
p2	Perennial Med = 1…4.5 Max = 3…8 Range = 0…3	Medium Med = 8…15 Max = 25…86 Range = 6.2…11.5	*Alchemilla vulgaris, Geum rivale, He. pratense, Se. coerulea*
p3	Perennial Med = 1…5 Max = 2…18 Range = 1…4	High, mobile in the first year Med = (0) 47…252 Max = (0) 127…645 Range = 8…251	*Ae. podagraria, Co. majalis, Fr. vesca, Ophioglossum vulgatum, Pilosella officinarum*
g1	Annual	Absent	*M. nemorosum Linum catharticum*
g2	Perennial	Absent	Seedlings of most tree and shrub species

Median (med), maximum (max) and quartile range (range) of species clonal growth parameters from each growth form group are given. Values in brackets denote exceptional species with stolons (e.g. *R. saxatilis*) or species that can occupy the same patch for several years (e.g. *Co. majalis*).

Table 4. Estimated differences in least square means of relative abundance of different clonal growth forms (class names as in Figure 1) between different community types

Contrast	Annual ramets *a1, a2, a3*	Biennial ramets *b1, b2, b3*	Perennial ramets *p1, p2, p3*	Low mobility *a1, b1, p1*	Medium mobility *a2, b2, p2*	High mobility *a3, b3, p3*
Open-overgrown	<0.005	NS	NS	<0.001	<0.005	<0.005
Restored-overgrown	NS	NS	<0.08	< 0.005	NS	NS
Open-restored	<0.05	NS	NS	NS	<0.005	<0.005

NS – not significant.
Significance of differences in relative abundance is shown. Sample sizes were: open meadow (open) – 43 relevés, restored wooded meadow (restored) – 16 relevés, and overgrown wooded meadow (overgrown) – 37 relevés.
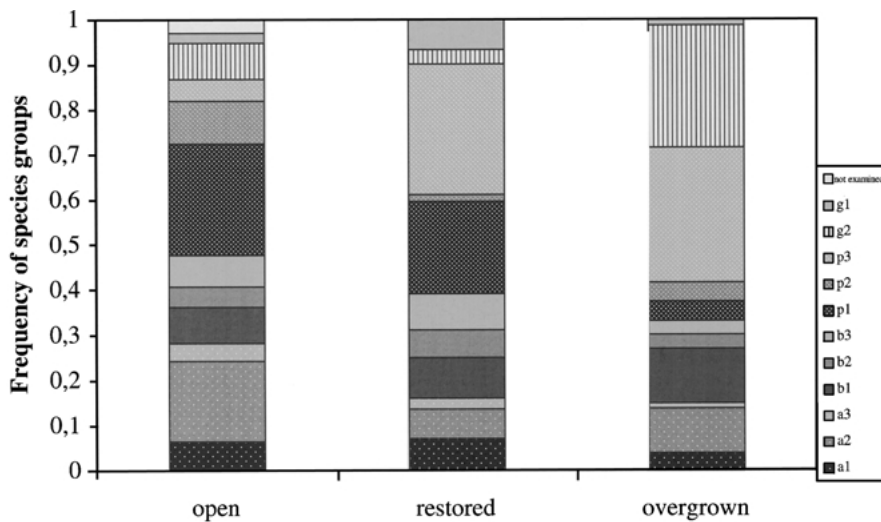
Figure 2. Proportions of clonal growth forms in open meadows, restored wooded meadows, and in overgrown wooded meadows. *g1* Denotes non-clonal annuals and *g2* non-clonal perennials; other symbols correspond to those in Figure 1.

(6 and 7%, respectively) than in overgrown wooded meadows (4%; Table 5, Fig. 2). *a2*-Species (annual ramets with medium vegetative mobility) were more abundant (18%) in open meadows than in restored and overgrown wooded meadows (7 and 10%, respectively).

Although species with biennial ramets (*b*) were equally abundant in the three vegetation types, there was a difference in the relative abundance of *b*-species with low and high vegetative mobility. The relative abundance of *b1*, *b2* and *b3* species in open and in restored wooded meadows were equally low (4–9%). In

Table 5. Estimated differences in least square means of relative abundance of clonal growth forms (class names as in Figure 1) between different community types

	a1	a2	a3	b1	b2	b3	p1	p2	p3
Open-overgrown	<0.05	NS	<0.01	NS	NS	<0.01	<0.01	<0.01	<0.01
Restored-overgrown	<0.05	NS	<0.09	NS	NS	<0.01	<0.01	NS	NS
Open-restored	NS	<0.05	<0.06	NS	NS	NS	<0.05	<0.01	<0.01

Significance of differences in relative abundance is shown. Sample sizes are as in Table 4.

overgrown wooded meadows the relative abundance of *b3*-species was significantly lower (3%) compared to the other two sites (Table 5, Fig. 2).

p1-Species (perennial ramets with low vegetative mobility) decreased in relative abundance in the sequence of open meadows, restored wooded meadows, overgrown wooded meadows (25, 20 and 4%, respectively; Table 5, Fig. 2). The relative abundance of *p3*-species was significantly lower in open meadows (5%) than in restored wooded meadows (29%) or overgrown wooded meadows (30%; Table 5). *p2*-Species (perennial ramets with medium vegetative mobility) were significantly more abundant in open meadow communities (9%) than in restored (1%) or overgrown (4%) wooded meadow communities.

None of the effects described above did change significantly when absolute abundances were used instead of relative ones.

Relationships between density of ramets and number of species

The vegetation type and the number of species did not have any statistically significant relation with maximum ramet longevity (Table 6). The number of shoots per m^2 had the strongest negative effect on this trait (Table 6, Fig. 3A). All multiple regressions of median vegetative mobility (on number of species, ramet density, and light availability) were statistically significant (Table 6, Fig. 3B). Shoot density showed a strong negative relationship with vegetative mobility.

The slopes of trend lines describing the relationship between community-wide clonal growth parameters were significantly different for open and overgrown wooded meadows as well as for restored and overgrown wooded meadows (Fig. 4, Table 7). No such difference was found between open and restored wooded meadow communities.

Discussion

A cluster analysis revealed large differences between two major groups of clonal herbaceous species present in our study system. The first group con-

Table 6. Results of multivariate ANOVA

Factor	Sums of squares	d.f.	F	P	r²
Median of vegetative mobility of ramet					
Model	8.75	11	31.08	<0.0001	0.83
Error	1.74	68			
Stage	0.27	2	5.36	<0.01	
Number of species	0.31	1	12.08	<0.001	
Shoot density	0.34	1	13.35	<0.0005	
Light	0.11	1	4.45	<0.05	
Number of species × stage	0.23	2	4.41	<0.05	
Number of shoots × stage	0.56	2	11.02	<0.0001	
Light × stage	0.17	2	3.31	<0.05	
Maximum ramet lifespan					
Model	0.02	11	10.86	<0.0001	0.64
Error	0.01	68			
Stage	0.001	2	2.23	NS	
Number of species	0.0001	1	0.13	NS	
Number of shoots	0.003	1	23.94	0.0001	
Light	0.001	1	9.24	<0.05	
Number of species × stage	0.001	2	13.82	<0.05	
Number of shoots × stage	0.004	2	3.56	0.0001	
Light × stage	0.002	2	7.62	<0.001	

The effects of vegetation type (stage), number of species (per 1 m^2), shoot density (per m^2) and light penetration coefficient to herb layer (light) on maximum ramet lifespan and median of vegetative mobility of community.

tained species with annual and biennial ramets, while the second one was composed of species with perennial ramets (Fig. 1).

Vascular plant species grown in calcareous grassland have been classified in terms of mobility types by Maarel (1996). His five mobility types (constant, local, circulating, pulsating, and occasional species) were based on above-ground estimates of cumulative species frequency in a series of small subplots. Vegetative mobility (i.e., mobility by clonal propagation) and mobility by means of seed dispersal were not separated from each other in that study, thereby confounding different processes underlying the spatio-temporal dynamics of ramets and genets in communities. In the classification mentioned above, species with a low vegetative mobility, such as *Plantago lanceolata* and *Lotus corniculatus*, shared the same group (*circulating species*) as species with long rhizomes (e.g., *Achillea millefolium*, *Galium verum*). The high turnover rate of *Pl. lanceolata* and *L. corniculatus* in calcareous grasslands, however, is a likely result of frequent regeneration from seeds (cf. Pärtel *et al.*, 1998).

According to our study, the relative abundance of species with a short ramet lifespan (group *a*) and low vegetative mobility increased with shoot density. Another relationship between different community-wide parameters of clonal
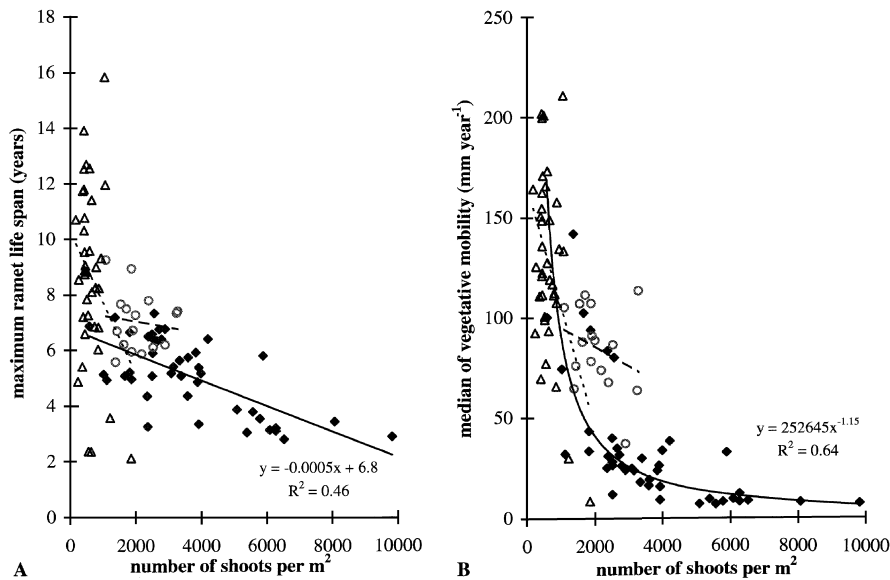
Figure 3. Weighted average of (A) ramet lifespan and (B) vegetative mobility in relation to shoot density in our sample plot communities. Diamonds, circles and triangles represent open meadows, restored wooded meadows, and overgrown wooded meadows, respectively. The R^2 value of the regression line and the equation are shown for open meadow plots only.

growth shows that in overgrown wooded meadows, maximum ramet longevity increases with increasing vegetative mobility (Fig. 4). The latter trend can be attributed to the relatively higher frequency of species from growth form *p3* in overgrown wooded meadow sites. Good examples are *Convallaria majalis* and *Aegopodium podagraria* with ramets developing aboveground shoots after rhizome formation, and which can persist in the same patch for a long time (Kivenheimo, 1947; Rysin and Rysina, 1987). In shade, where the overall number of ramets per unit area is lower than in open sites, this persistence will lead to a dominance of such species.

Mowing of open grasslands results in a disproportional removal of tall plants and hence equalizes size hierarchies and reduces the asymmetry between plants in their competition for light (Lepš, 1999). Inferior competitors are thus more likely to establish in new gaps created by mowing.

Herben *et al.* (1997) have suggested that high turnover rates may promote coexistance of a large number of plant species. Also, in some other studies the high mobility was related to high species richness (Sykes *et al.*, 1994). Contrary to that conclusion, Klimeš (1999) found low plant mobility in species-rich grassland in S. Moravia (Czech Republic). In the latter study plant mobility was very low, which indicates that many species either kept their positions over many years or established in micro sites that had previously been occupied by
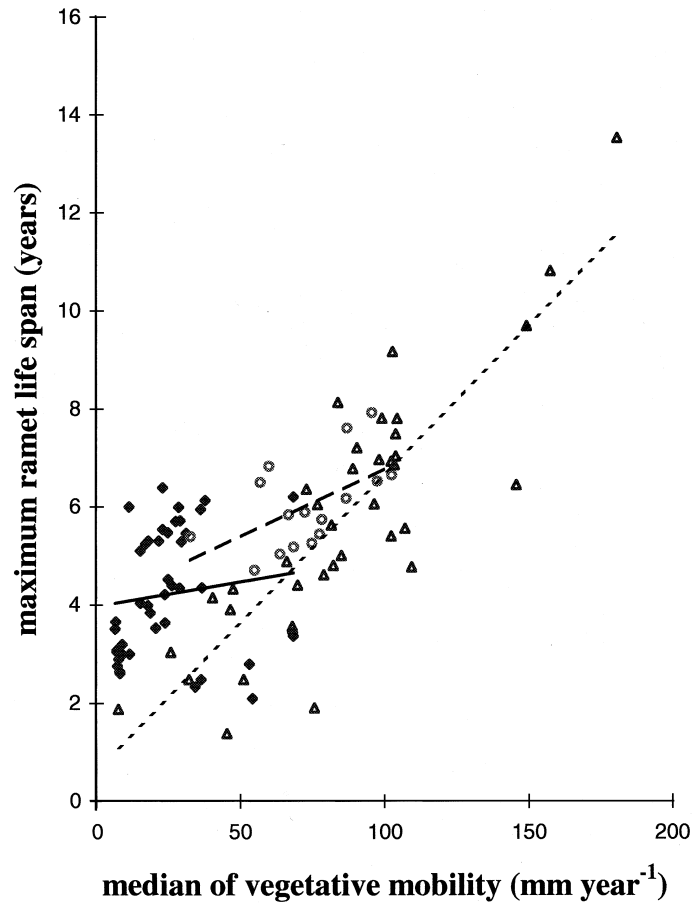
Figure 4. Relationship between weighted averages of maximum ramet life span and median vegetative mobility. Diamonds, circles and triangles represent open meadows (solid regression line), restored wooded meadows (widely dotted regression line), and overgrown wooded meadows (dotted regression line), respectively.

ramets belonging to the same species. At that point we want to emphasize that high plant mobility and high ramet turnover rate are separate things. High ramet turnover rate means that ramets are short-lived and they replace each other within a short period of time, irrespective of their vegetative mobility.

According to our results, which are based on the measurements of the clonal growth characteristics of all species of a community, we can clearly state that, when transforming a temporal forest into a meadow, the clonal mobility of the herb community and the average lifespan of ramets decreases, which, in turn, leads to a higher turnover rate of ramets. This may possibly contribute to the higher potential species richness of the community.

[176]

Table 7. Regression of weighed average of maximum ramet lifespan on weighed average of median of ramet vegetative mobility (mobility) in different community types (stage)

Factor	Sums of squares	d.f.	F	p	r^2
Maximum ramet lifespan					
Model	0.02	5	30.86	<0.0001	0.63
Error	0.01	90			
Stage	0.004	2	13.84	<0.0001	
Mobility (stage)	0.003	3	19.76	<0.0001	
Contrast					
Open vs. overgrown	0.004	2	13.58	<0.0001	
Open vs. restored	0.0006	2	2.01	NS	
Restored vs. overgrown	0.001	2	4.53	<0.05	

The comparison of trend lines (contrast) in different community types was obtained by using the GLM Contrast method.

Acknowledgements

References

Altesor, A., Pezzani, F., Grun, S. and Rodriguez, C. (1999) Relationship between spatial strategies and morphological attributes in a Uruguayan grassland: a functional approach. *J. Veg. Sci.* **10**, 457–462.

Anderson, M.C. (1964) Studies on the woodland light climate. I. The photographic computation of light conditions. *J. Ecol.* **52**, 27–41.

Bazzaz, F.A. (1998) *Plants in Changing Environments*: *Linking Physiological*, *Population*, *and Community Ecology*. Cambridge University Press, Cambridge.

Bell, A.D. (1984) Dynamic morphology: a contribution to plant population ecology. In R. Dirzo and J. Sarukhán (eds) *Perspectives on Plant Population Biology*. Sinauer Assoc., Sunderland, MA, pp. 48–65.

Callaghan, T.V., Headley, A.D., Svensson, B.M., Lixian, L., Lee, J.A. and Lindley, D.K. (1986) Modular growth and function in the vascular cryptogam *Lycopodium annotinum*. *Proc. R. Soc. Lond. B.* **228**, 195–206.

Eckert, C.G. (1999) Clonal plant research: proliferation, integration, but not much evolution. *Am. J. Bot.* **86**, 1649–1654.

Eriksson, O. (1997) Clonal life histories and the evolution of seed recruitment. In *The Ecology and Evolution of Clonal Plants*. Backhuys Publishers, Leiden, H. de Kroon and J. van Groenendael (eds) pp. 211–226.

Groenendael, J.M., van Klimeš, L., Klimešova, J. and Hendriks, R.J.J. (1996) Comparative ecology of clonal plants. *Phil. Trans. R. Soc. Lond. B.* **351**, 1331–1339.

Grubb, P.J. (1990) Demographic studies on the perennials of chalk grasslands. In S.H. Hillier, D.W.H. Walton and D.A. Wells (eds) *Calcareous Grasslands: Ecology and Management.* Bluntisham Books, Bluntisham, pp. 93–97.

Grubb, P.J., Kelly, D. and Mitchley, J. (1982) The control of relative abundance in communities of herbaceous plants. In E.I. Newman (ed.) *The Plant Community as a Working Mechanism.* British Ecological Society, Cambridge, pp. 79–97.

Harper, L. (1977) *Population Biology of Plants.* Academic Press, London.

Harper, L. (1985) Modules, branches, and the capture of resources. In J.B.C. Jackson, L.W. Buss and R.E. Cook (eds), *Population Biology and Evolution of Clonal Organisms.* Yale University Press, New Haven, pp. 1–33.

Herben, T., Krahulec, F., Hadincová, V. and Kovárová, M. (1994) Small-scale spatial dynamics of plant species in a grassland community over six years. *J. Veg. Sci.* **4**, 171–178.

Herben, T., Krahulec, F., Hadincová, V. and Pecháčková, S. (1997) Is a grassland community composed of coexisting species with low and high spatial mobility? *Folia Geobot. Phytotax.* **29**, 459–468.

Huber, H. and Stuefer, J.F. (1997) Shade-induced changes in the branching pattern of a stoloniferous herb: functional response or allometric effect? *Oecologia* **110**, 478–486.

Hutchings, M.J. and de Kroon, H. (1994) Foraging in plants: the role of morphological plasticity in resource acquisition. *Adv. Ecol. Res.* **25**, 159–238.

Jonsdottir, I.S. and Watson, M.A. (1997) Extensive physiological integration: an adaptive trait in resource-poor environments? In H. de Kroon and J. van Groenendael (eds) *The Ecology and Evolution of Clonal Plants.* Backhuys Publishers, Leiden, pp. 109–136.

Kalamees, R. (1999) *Seed Bank, Seed Rain and Community Regeneration in Estonian Calcareous Grasslands.* PhD Thesis. Tartu University Press, Tartu.

Kalamees, R. and Zobel, M. (1998) Soil seed bank composition in different successional stages of a species rich wooded meadow in Laelatu, western Estonia. *Acta Oecol.* **19**, 175–180.

Kivenheimo, V.J. (1947) Untersuchungen über die Wurzelsysteme der Samenpflanzen in der Bodenvegetation der Wälder Finnlands. *Ann. Bot. Soc. Zool. Bot. Fenn. Vanamo* **22(2)**, 1–180.

Klimeš, L. (1992) The clone architecture of *Rumex alpinus* (*Polygonaceae*). *Oikos* **63**, 402–409.

Klimeš, L. (1999) Small-scale plant mobility in a species-rich grassland. *J. Veg. Sci.* **10**, 209–281.

Klimeš, L., Klimešova, J., Hendriks, R. and van Groenendael, J. (1997) Clonal plant architecture: a comparative analyses of form and function. In H. de Kroon and J. van Groenendael (eds) *The Ecology and Evolution of Clonal plants.* Backhuys Publishers, Leiden, pp. 1–29.

Krall, H. and Pork, K. (1970) Laelatu puisniit. In E. Kumari (ed.) *Lääne-Eesti rannikualade loodus.* Valgus, Tallinn, pp. 115–128.

Kukk, T. and Kull, K. (1997) Puisniidud [Wooded Meadows]. *Estonia Maritima* **2**, 1–249.

Kull, K. (1995a) Growth form parameters of clonal herbs. In K. Aaviksoo, K. Kull, J. Paal and H. Trass (eds) *Consortium Masingii.* Tartu University, Tartu, pp. 106–115.

Kull, T. (1995b) Genet and ramet dynamics of *Cypripedium calceolus* in different habitats. *Abstr. Bot.* **19**, 95–104.

Kull, K., Sammul, M. and Tamm, A. (2000) *Comparative Ecomorphology of Clonal Growth: A Little Atlas.* Manuscript Institute of Zoology and Botany, Tartu.

Lepš, J. (1999) Nutrient status, disturbance and competition: an experimental test of relationships in a wet meadow. *J. Veg. Sci.* **10**, 219–230.

Lovett Doust, L. (1981) Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*). 1. The dynamics of ramets in contrasting habitats. *J. Ecol.* **69**, 743–755.

Maarel, E. van der (1996) Pattern and process in the plant community: fifty years after A.S. Watt. *J. Veg. Sci.* **7**, 19–28.

Maarel, E. van der and Sykes, M.T. (1993) Small-scale plant species turnover: the carousel model and a new niche concept. *J. Veg. Sci.* **4**, 179–188.

Maarel, E. van der and Sykes, M.T. (1997) Rates of small-scale species mobility in alvar limestone grassland. *J. Veg. Sci.* **8**, 199–208.

Mitchley, J. and Grubb, P.J. (1986) Control of relative abundance of perennials in chalk grassland in Southern England. 1. Constancy of rank order and results of pot- and field-experiments on the role of interference. *J. Ecol.* **74**, 1139–1166.

Pärtel, M. and Zobel, M. (1995) Small-scale dynamics and species richness in successional alvar plant communities. *Ecography* **18**, 83–90.

Pärtel, M., Kalamees, R., Zobel, M. and Rosén, E. (1998) Restoration of species-rich limestone grassland communities from overgrown land: the importance of propagule availability. *Ecol Engin.* **10**, 275–286.

Pärtel, M., Zobel, M., Zobel, K. and Maarel, E. van der (1996) The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos* **75**, 111–117.

Pokarzhevskaya, G.A. (1995) Morphological analysis of alpine communities of the north-western Caucasus. *Folia Geobot. Phytotax.* **30**, 197–210.

Rysin, L.P. and Rysina, G.P. (1987) *Morfostruktura Podzemnyh Organov Lesnyh Travjanistyh Rastenii.* Nauka, Moskva.

Skálová, H., Pecháčková, S., Suzuki, J.I., Herben, T., Hara, T., Hadincová, V. and Krahulec, F. (1997) Within population genetic differentiation in traits affecting clonal growth: *Festuca rubra* in a mountain grassland. *J. Evol. Biol.* **10**, 383–406.

Sykes, M.T., Maarel, E. van der, Peet, R.K. and Willems, J.H. (1994) High species mobility in species-rich plant communities: an intercontinental comparison. *Folia Geobot. Phytotax.* **29**, 439–448.

Tamm, C.O. (1948) Observations on reproduction and survival of some perennial herbs. *Botaniska Notiser* **3**, 305–321.

Weiher, E., Werf, A. van der, Thompson, K., Roderick, M., Garnier, E. and Eriksson, O. (1999) Challenging Theophrastus: a common core list of plant traits for functional ecology. *J. Veg. Sci.* **10**, 609–620.