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PLANT COMMUNITY REGENERATION AND SPECIES DIVERSITY IN DRY CALCAREOUS GRASSLANDS

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following articles, which are referred to in the text by their Roman numerals.

I Otsus, M. and Zobel, M. 2002. Small-scale turnover in a calcareous grassland, its pattern and components. — Journal of Vegetation Science 13: 199–206.

II Zobel, M., Otsus, M., Liira, J., Moora, M. and Möls, T. 2000. Is small-scale species richness limited by seed availability or microsite availability? — Ecology 81 (12): 3274–3282.

III Zobel, M., Otsus, M., Rünk, K. and Liira, J. Can limited dispersal shape the regional species pool? (accepted in Folia Geobotanica).

IV Otsus, M. and Zobel, M. 2004. Moisture conditions and the presence of bryophytes determine fescue species abundance in a dry calcareous grassland. — Oecologia 138: 293–299.

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INTRODUCTION

Both large- and small-scale processes determine the patterns of species diversity. However, for a long period, the theory and studies of community ecology have been mainly focused on the processes of the local scale when explaining the variation of species diversity in space. The hump-backed model of species diversity, describing the variation of species richness along the productivity gradient, has remained one of the most generally accepted descriptive models of the pattern of species richness. The universality and possible scale dependency of the relationship are still hotly debated (see Oksanen 1996, Zobel and Liira 1997, Gross *et al.* 2000, Liira and Zobel 2000, Mittelbach *et al.* 2001, Whittaker and Heegaard 2003). In explanations of such variation of species richness along the productivity gradient, the role of two type of driving forces has mainly been stressed: abiotic conditions and biotic interactions, mostly emphasizing the role of competition. There is, however, still no general agreement about the relative importance of competition in determining species diversity: does it increase along the productivity gradient or remain stable at the both ends of the gradient (Grime 1977, Tilman 1988, Goldberg *et al.* 1999).

Not only productivity, but also disturbances — phenomena causing partial or total destruction of the plant biomass (Brooker and Callaghan 1998) — may play a significant role in determining the local level of species richness (Huston 1999, Crawley *et al.* 1999, Naeem *et al.* 2000). The regular or irregular occurrences of disturbances are independent of the productivity gradient. The concept called the non-equilibrium model, or, in a more recent version, the dynamic equilibrium model (Huston 1994, 1999), explains the co-existence of a high number of species by emphasizing disturbances as important forces that balance the negative effect of competition and therefore create possibilities for regeneration of those species, which are otherwise suppressed by competition.

There is increasing evidence that plant species diversity at a local scale is dependent on the presence of species on larger spatial scales, as well as on historical or evolutionary events. This has resulted in a change in the paradigm and in the significant broadening of the understanding of the formation and maintenance of species richness (Cornell and Lawton 1992, Zobel 1992, 1997, Eriksson 1993, Bengtsson *et al.* 1994, Taylor *et al.* 1990, Pärtel *et al.* 1996, Tilman 1993, 1997, Huston 1999, Grace 2001). The so-called species pool concept argues that not only competition and disturbance but also the species pool — locally available assembly of species — plays a significant role in the formation of local species richness. Accordingly, the species pool concept, instead of looking for mechanisms preventing the competition to result in species co-existence, emphesizes the processes that have made it possible for a set of coexisting species to get together in a community. At the same time, the importance of the local processes on the local abundance relations of species is not denied either (Pärtel *et al.* 1996). The size and composition of the species pool is a general outcome of evolutionary and historical processes as well as dispersal events within the particular region.

According to the species pool concept, the size of the regional species pool, species' ability to disperse within the region and between communities, and species' ability to establish in the target community, are the key factors that set the primary level of the local species richness. The numerous studies where the experimental addition of diaspores has resulted in increased species richness at a small-scale, support the species pool theory and also the idea that the presence of a high number of species in a community does not necessarily limit the immigration of new species (Houle and Phillips 1989, Primack and Miao 1992, Eriksson and Ehrlen 1992, Eriksson 1997a, Eriksson and Jakobsson 1998, Burke and Grime 1996, Tilman 1997, Tofts and Silvertown 2002). Also, the examples of large-scale spatial dynamics of plant populations and different regional population structures provide good indication about the existence of significant links between regional and local species pools (Eriksson and Ehrlen 2001, Freckleton and Watkinson 2002). In theory, the effect of the species pool is expected to appear most clearly at moderately low levels of productivity (Huston 1999). In the plant communities of moderate standing biomass, the presence (or immigration) of propagules of species belonging to (or entering) the species pool should be a relatively more important factor from the diversity pattern point of view than the presence of free microsites.

From the sowing experiments referred to above, it seems to be relevant to conclude that species richness in most plant communities is not saturated against the regional species pool. Therefore, differences in the numbers of coexisting species in plant communities in similar abiotic conditions are mainly due to the different barriers of dispersal in fragmented landscapes, as well as the species-specific spatial scale of dispersal. As long-distance dispersal does not correlate clearly with morphological dispersal syndromes, it is difficult to predict the frequency of immigration attempts of different species (Higgins *et al.* 2003). Still, there is enough evidence that long-distance dispersal takes place quite regularly, which makes it a significant process linking the regional species pool with the target communities (Fischer *et al.* 1996).

The currently observed high species richness of a plant community indicates the high invasibility of this community during its history. Invasion success depends on propagule pressure, the morphological features and resource preferences of invading species, and on the invasibility of the target community. Up to now, studies focused on invasions have given very contradictory answers regarding the relationship of plant community invasibility to productivity, disturbances or species richness *in situ* (Tilman 1997, Stohlgren *et al.* 1999, Davis *et al.* 2000). The classical concept of invasibility argues that species-rich stands are more invasion-resistant because of the high intensity of competition and more completely exploited resources (Elton 1958). The analyses of large-scale distribution patterns of alien plant species have shown that the occurrence of a high number of alien species often coincides with a high number of native species (Lonsdale 1999, Stohlgren *et al.* 1999, Williamson 1999), which indicates that species-rich plant communities are frequently more susceptible to invasions than species-poor communities. This pattern is in general accordance with the species pool theory. However, studies that, in addition to the effect of productivity, disturbances and species richness, also test the dependence of invasibility on the size of the pool of potential invaders are still lacking. The existing overviews show that the rate of competitive exclusion in the community cannot be dealt with as the direct negative correlate of the local species richness, as proposed by the traditional plant community theory (e.g. Elton 1958), although there are some examples of lower invasibility of species-rich experimental plant assemblages (Knops *et al.* 1999). There is more evidence that the number of successful invasion events is well correlated with the rate of disturbances in an ecosystem (Londsdale 1999, Prieur-Richard and Lavorel 2000, but see Stohlgren *et al.* 1999). However, some other studies that emphasize the crucial role of local biotic interactions and external factors like disturbances, without which the high invasibility of a species-rich community would not be possible, do not stress the significance of the availability of propagules (Burke and Grime 1996, Naeem *et al.* 2000). If large-scale spatio-temporal processes play a role in the formation of differences in species richness patterns, as predicted by the species pool concept, one might expect the regeneration patterns of plant communities to explain to a considerable extent the pattern of species diversity.

While large-scale processes determine the availability of diaspores in particular regions and landscapes, small-scale processes are responsible for the fate of a diaspore once it has arrived in a particular community. Keeping the potential competition for space in mind, one may argue that the ability of a species to reach the empty microsites within a community is evidently one of the key processes determining and maintaining species diversity on a small scale (Grubb 1977). According to the theories emphasizing the crucial role of competition and disturbances in species co-existence within a limited space (Huston 1979, Chesson 1986, Tilman 1988), the availability of free microsites rather than the availability of diaspores limits the small-scale species richness. The free microsites in plant communities may arise due to different processes, like the natural or disturbance-induced death of plant individuals, or due to clonal outgrowth of plants from a particular microsite (Grubb 1977). Colonizing of the empty sites can take place either via generative or vegetative regeneration. The resulting rate of small-scale species turnover within the community may be quite high in different types of plant communities, as the so-called ‘carousel model’ suggests (van der Maarel and Sykes 1993, van der Maarel 1996, Sykes *et al.* 1994, Herben *et al.* 1995). The questions about the variation of small-scale turnover in plant communities and its promoting effect on species coexistence along productivity or species richness gradients, or during different successional stages of plant communities, still wait for clear answers. This is partly due to the lack of a uniform approach for measuring plant community turnover, and due to the lack of comparable data (see Rusch and van der Maarel 1992, van der Maarel and Sykes 1993, Herben *et al.*1993, 1995, Klimes 1999, Palmer and Rusch 2001). The hypothesis about the different mobility rate of locally frequent or abundant species (so-called matrix or core species) and subordinate species, as a possible mechanism of species coexistence in species-rich communities, due to mitigated competition (cf. Grubb 1986, Klimeš 1999), has not yet been verified.

However, free microsites (gaps, bare ground) cannot automatically be regarded as safe sites for the germination of the arrived diaspores and the establishment of seedlings, since the real effect of a free microsite depends on the structural and often productivity correlated characteristics of the community (e.g. height and density of established vegetation, presence of tree and bryophyte layer), as well as on the general climatic conditions (e.g. precipitation) (Fowler 1986, 1988, Ryser 1990, 1993, Rusch 1992).

Given that the availability of diaspores plays a crucial role in the development and maintenance of local species composition and diversity, one has to recognize the significance of the local processes and factors as well. To contribute to the species diversity, the “arrived” diaspore has to germinate and then a viable seedling has to become established. During their first stages of life — germination of seeds and establishment of seedlings — plants are very vulnerable and greatly depend on external factors. First of all, seed germination depends on local environmental factors like moisture and temperature regimes which determine when the seed turns from its dormancy to germination (Baskin and Baskin 1998, Fenner 1987). Seedlings of larger seeds are shown to have advantages in many conditions, e.g. in case of light competition or drought. In unproductive communities the size of seeds may have less importance due to the lack of a thick litter layer, which can be one of the biggest barriers to the establishment of smaller seedlings. Also, the survival of seedlings depends on many external and internal circumstances such as the intensity of negative interactions (pathogens, herbivores, competition), the presence of symbionts (mychorrhizal fungi) or facilitators (established vegetation), the size and desiccation tolerance of seedling, etc. (Schütz 2000). Unsuccessful germination can mask the effect of successful invasion and can give rise to flawed conclusions about the invasibility of the community (Zobel and Kalamees, submitted manuscript).

The main objective of the present study was to describe and test the role of plant community regeneration in relation to the formation and maintenance of the small-scale species diversity in dry calcareous grasslands with low standing crop. In particular, we focused on the role of generative regeneration.

First, we assumed that dry calcareous grasslands are characterized by high small-scale turnover of vegetation, and that high spatio-temporal mobility of plants may be a mechanism enhancing the coexistence of species otherwise outcompeting each other in conditions of limited space and resources. We aimed to describe the changes taking place via the appearances and disappearances of individuals of generative and vegetative origin and by comparing their contributions to the overall yearly turnover rate of a plant community on the small spatial scale.

Second, we assumed that the availability of seeds should have a significant effect on the pattern of small-scale species richness in the oligotrophic dry calcareous grasslands we were studying. In particular, we hypothesized that the plant populations, as well as the local level of species richness, in the grasslands are not so much microsite as seed limited. It was supposed that the experimental introduction of additional diaspores would significantly change the small-scale species diversity, while disturbance events, destroying the established vegetation, would contribute significantly to the number of species coexisting within a limited space only in combination with the experimental addition of diaspores. We used different sets of species in seed addition experiments — species belonging to the community species pool; species belonging to the local species pool, but absent from the community; species absent from the regional species pool.

Third, we aimed to find support for the hypothesis that local species diversity *per se* does not set limits on the establishment of species belonging either to the community, local or regional species pools, but that the establishment of diaspores depends on the local conditions and on the traits of the introduced species. This hypothesis was tested in the seed addition experiments referred to above.

Fourth, we assumed that the rate of germination of arrived diaspores, as well as the success of seedling establishment, in oligotrophic dry calcareous grasslands depends not as much on the competitive effect of established vascular plant vegetation, but mainly on abiotic factors, like ambient rainfall. In particular, we hypothesized that the moisture conditions act as the primary factor ‘screening’ local diaspore rain and regulating seedling establishment. We also hypothesized that the well-formed bryophyte layer, due to its water retaining capacity, acts as an ameliorator of the effect of drought.

MATERIAL AND METHODS

Dry calcareous grasslands of Estonia

Dry calcareous grasslands in Estonia may be classified into two broad type groups: alvar grasslands on thin (0–20 cm) rendzic soils on Ordovician or Silurian limestone plateaus, that are sometimes covered either by calcareous moraine or coastal sediments; and boreo-nemoral grasslands on slightly deeper and thus more fertile rendzic soils (Paal 1997). The current study of calcareous grassland community ecology is focused on dry alvar grasslands (**I, II, IV**) and on a subhumid boreo-nemoral grassland on thin soil (**III**).

The distribution of calcareous grasslands in Estonia is related to the distribution of Ordovician and Silurian limestone: most of them can be found in the coastal areas of North and West Estonia, on the islands of Saaremaa, Hiiumaa, Muhumaa and on western or northern islands. Dry calcareous grasslands are the communities with low or moderate standing crop (usually not more than 300 g/m^2) that exhibit remarkably high species-richness both on a community scale and on a small-scale (van der Maarel 1988, 1996, van der Maarel and Sykes 1993, Kull and Zobel 1991, Pärtel *et al.* 1999a).

Alvar grasslands have a rather specific vegetation physiognomy due to the effects of thin soil and prevailing water stress. Despite the temporal surplus of water in spring or after heavy rainfalls, there may be a deficit of moisture in the soil for most of the vegetation period. These harsh conditions give rise to low and sparse vegetation, which results in increased wind velocity in alvar areas, which further deteriorates moisture conditions due to the increased transpiration of plants. Strong winds also result in the accumulation of snow in certain localities only, while in other areas the snow is blown away. This means that the melting of snow in spring improves moisture conditions very locally.

Some authors have proposed a general ecological classification of alvar areas, using traits like depth, texture and pH of soils, as well as the general physiognomy of the vegetation (Zobel 1984). In particular, alvars on weathered limestone-rich material (ryhk-alvars), alvars on solid limestone material (plate-like alvars), alvars on material where limestone shingle is mixed with limestone-poor sand (alvar heath), and moist alvars with soils of heavy texture have been distinguished. Those ecological types are usually well recognized in nature and they can be characterized by specific species composition (Pärtel *et al.* 1999a).

The flora of alvar grasslands contains species that originate from arid European steppes (pontosarmatic origin), but also species characteristic of arctic or alpine communities (Laasimer 1965). The size of the species pool for thin-soil alvar grasslands in Estonia has been estimated to be about 270 vascular plant species. The size and composition of the community species pool of alvar grassland stands depends on the local conditions and is rather variable. The greatest difference in species composition among alvar grassland stands is apparent between grasslands in North Estonia and in the rest of Estonia (Pärtel *et al.* 1999a). These differences are related to the geographical variation in ecological conditions, including soil fertility, soil pH and the chemical composition of the parent material. On average, the community species pool of alvar grassland stands remains between 50–75 vascular plant species (Pärtel *et al.* 1999a, Pärtel 2003, Helm 2003). The recorded maximum of species richness per 1 m^2 is 49 vascular plant species (Pärtel 2003).

Slow growth rate (van der Maarel and Sykes 1993) and drought tolerance are characteristics of the plants of dry calcareous grasslands. In conditions of severe water stress, genotypes adapted specifically to the local conditions may become more favored (Prentice *et al.* 1995). Some authors describe the phenomenon of temporal disappearance of aboveground organs (rosette leaves, basal leaves) of ramets of alvar plants as a response to the summer droughts, and consider the ramets of perennials to be short-lived as well (van der Maarel and Sykes 1993, Sykes *et al.* 1994). One might, however, assume that the slow growth rate could correlate with a longer lifetime of established ramets, but there are no field data to support or reject such a hypothesis in regard to alvar plants.

Most of the alvar grasslands are semi-natural communities preserved due to the grazing of sheep or cattle and the cutting of shrubs. Cessation of such activities has caused a significant decrease in the distribution area of alvars. The total area of alvar grasslands in Estonia is currently 16 000 ha, i.e. less than 50% of its area in the 1930s (Aug and Kokk 1983, Pärtel 2003).

The ecological conditions and related features of vegetation of **the dry and mesophyte calcareous boreo-nemoral grasslands** are rather variable, depending on the geographical location of the plant community. The soil in boreo-nemoral grasslands is usually either rendzic leptosol or calcaric gleysol. In comparison with alvars, the soils of calcareous boreo-nemoral grasslands are generally deeper and more humid, the vegetation is higher and more mesophytic. The standing crop of such communities is about 150–300 g/m^2 (Zobel and Liira 1997).

The regional species pool of the boreo-nemoral grasslands contains more than 400 vascular plant species, while the size of the community pool is, on average, 115–130 species; maximum species richness per 1 m^2 is recorded to be 76 species (Pärtel 2003).

The total area of calcareous boreo-nemoral grasslands in Estonia, including also grasslands on deeper soils, was estimated to be around 165 000 ha in the 1950s but is much smaller nowadays and does not exceed 20 000 ha (Laasimer 1965, Aug and Kokk 1983, Pärtel 2003). Boreo-nemoral grasslands represent seminatural ecosystems, thus their formation and persistence is connected with the agricultural activities of man like grazing of domestic animals, and the collecting of hay and firewood. Since the economic situation has not favored the use of low-productivity seminatural grasslands for agriculture, the cessation of mowing and grazing has been a common phenomenon already for decades. Many of the open meadows have in the past been turned into cultivated areas (fertilized; sown with hayplants; areas with deeper soil were also ploughed), therefore the remaining calcareous boreo-nemoral grasslands are often wooded meadows where it was more difficult to carry out such human activities.

Study sites

The study sites were situated in the coastal area in West Estonia. The annual precipitation in the study area is about 500 mm, the mean temperature for July is 17.0°C and for January, –5.0°C. The mean rainfall in the vegetation period (April-October) is 380 mm, but has varied during the last 15 years from as dry as 290 mm up to 480 mm. The amount of precipitation per month also varies considerably between years, e.g. the rainfall in July has varied from 3 mm to 160 mm in different years.

We used an alvar grassland in Hanila (**I, II, IV**) and a calcareous boreo-nemoral grassland near Virtsu **(III)** as study sites. The different mosaic of plant communities around the two study sites makes the conditions of the grasslands different. The boreo-nemoral grassland is surrounded by wooded-meadow and forest. Its abiotic conditions are more favorable for plant growth compared with the alvar site. The Hanila alvar is located in the open landscape: in a mosaic of open alvars, shrubland of pines and junipers (i.e.overgrown alvars), small fragments of young alvar forests. Shelter from tree crowns is missing and the wind velocity is strong. Therefore, the main limiting resource is water in the case of the alvar, while plant growth in the boreo-nemoral grassland is more limited by the shortage of soil nutrients, especially of nitrogen.

The alvar site (**I, II, IV**) located in Hanila municipality, near to the coast of the Baltic Sea represents the most common vegetation type of Estonian alvars: *Avenetum alvarense* by Pärtel *et al.* (1999). According to the older vegetation classification, it belongs to the *Filipendulo — Trifolietum montani* community type (Laasimer 1965). On the basis of ecological classification of alvar areas, Hanila site may be classified as ryhk alvar (cf. Pärtel *et al.* 1999). The soil is 10–12 cm deep, with underlying weathered limestone material. The mean standing crop in July was 170 g/m^2 and the mean height of vegetation was 11.5 cm (Pilt 1998). Though the vegetation structure is still open and the whole area may be classified as a grassland, invading pines (*Pinus sylvestris*) and junipers (*Juniperus communis*) are rather common at the margins of the study area and the area of open grassland is declining rather quickly.

The community species pool of Hanila alvar grassland contains more than 60 herbaceous vascular species. The mean species richness per 100 cm^2 is 12, the highest richness per 100 cm^2 recorded in the area is 18 species (M.Otsus, unpubl.). The mean species richness per 4 cm^2 was 2 species and the maximum was 7 species. The herb layer is dominated by *Carex tomentosa, Sesleria* *caerulea* and *Helictotrichon pratense*. The moss layer is rather continuous and thick over the all area and is dominated by *Ctenidium molluscum, Hypnum cupressiforme*, *Thuidium abietinum, Homalotecium lutescens*. On average, 30–40 shoots of vascular plants were recorded on 100 cm^2. The ratio of different growth-forms among the rooted plants was quite stable over years: 25% of shoots belonged to sedges, 25% to forbs and 50% to grasses.

Generative regeneration (i.e. established seedlings) has been recorded by us during the four years in the case of more than half of all vascular plant species of the study area. According to data from the descriptive study of the vegetation in the area in 1996, seedlings made up 6% of all rooted plants. By visual impression, the growth and development of plants is slow: a plant may retain the size and morphological characteristics of a seedling for several years (M. Otsus, unpubl.).

The calcareous boreo-nemoral grassland in Virtsu (**III**) is situated ca 10 km away from the alvar site. The vegetation of the site belongs to the *Sesleria caerulea — Filipendula vulgaris* association (Krall and Pork 1970). The most frequent species in the herb layer are *Brachypodium pinnatum, Briza media, Sesleria caereulea*. The moisture conditions are more favorable, compared to the alvar site. The humus layer is about 20–25 cm thick, underlaining by limestone-rich weathered material. The mean standing crop is 200–300 g/m^2 and the height of vegetation is 22.5 cm (Zobel & Liira 1997, Pilt 1998). The size of the community species pool exceeds 200 vascular plant species (Kukk and Kull 1997). There were an average of 15 species and a maximum of 24 species of vascular plants per 100 cm^2, the mean number of shoots per same area was 40–60.

Descriptive study

For description of the small-scale turnover of the alvar vegetation (**I**), 46 metal frames of 10 cm × 10 cm (plots) were fixed on the ground in 1995. Each frame was divided into 25 subplots of 2 cm × 2cm. The presence of all plants of every species (both mature and juvenile plants) rooted within the 2 cm × 2 cm subplots was recorded from June to September 1996–1999. Additionally, the presence of seedlings in the subplots was recorded during the fieldwork. Monthly descriptions were carried out in order to detect more exactly the changes in seedling numbers, so that the potential replacement of seedlings that had died with new ones in the same subplot could be considered. For the analysis of plant community turnover, the data from July were used. This is the time when the peak standing crop and species diversity are observed.

The yearly change of (1) the location of empty and occupied subplots within the plot, referred to as TO_{plot} and of (2) individuals (i.e. ramets in the case of clonal plants) of single species between the subplots of plots, referred to as $TO_{species}$ was described with the help of turnover index, computed as follows:

turnover (TO) = (a+d) / (a+d+pr) $*$ 100; where **a** refers to the appearance of a seedling or ramet in a previously empty subplot, **d** to the disappearance of seedling or ramet from a subplot, **pr** to the persistence of plants or certain species within the subplot.

The small-scale changes in the vegetation pattern take place either due to the appearance and disappearance of individuals of generative origin (seedlings, juveniles, adults), or of individuals of vegetative origin. Because of that, the generative and vegetative component of turnover (GTO, VTO) were distinguished respectively. In the case of GTO, some of the disappearance events were evidently not due to the death of seedlings, but rather due to the development of a seedling into the premature young plant stage. In the case of VTO, we were not able to take into account the events where a disappeared ramet was immediately replaced with a new one in the same cell. Thus, we may have underestimated VTO.

The effects of fixed factors, such as growth form, mobility category and frequency category, on $\mathrm{VTO}_{\mathrm{species}}$ were studied. As frequency of the species was positively correlated with abundance (Figure 1.a., Spearman R=0.93, p<0.0001), frequency data were used in the analysis. The species were grouped according to their frequency as follows: species occurring in more than 60% of plots (*Achillea millefolium, Antennaria dioica, Asperula tinctoria, Carex flacca, C. tomentosa, Filipendula vulgaris, Galium verum, Helictotrichon pratense, Leontodon hispidus, Sesleria caerulea*) and species occurring in 10–60% of plots (*Anemone sylvestris, Briza media, Campanula rotundifolia, Centaurea jacea, Festuca rubra, F. ovina, Galium boreale, Hieracium pilosella, Carex ornithopoda, Pimpinella saxifraga, Prunella vulgaris, Thymus serpyllum, Viola arenaria*). The type of clonal growth, indicating the potential vegetative mobility of plant species, was determined by using the classification of Klimeš *et al.* (1997). In order to simplify the system, we merged the types defined by Klimeš *et al.* into three broad categories: (1) slow species with vegetative spreading of <10 cm year^{-1}, (2) fast species, with vegetative spreading of >10 cm year^{-1}, (3) intermediate species, the mobility of which varies and which may belong to both the fast or the slow group.

For description of the abundance of the seedling bank and comparison of $\mathrm{VTO}_{\mathrm{species}}$ between forbs with and without an abundant bank of seedlings, the additional data from the previous descriptive study about the establishment of seedlings in the alvar area in the summer of 1995 were taken into account (Otsus 1996).

For analysing the effect of species and year on $\mathrm{GTO}_{\mathrm{species}}$ not the all species having seedlings could be included in the analyses because those with a small number and frequency of seedlings in the plots would have given unbalanced data that does not allow comparisons to be made. 8 forb species that had an abundant and frequent seedling bank were considered: *Anthyllis vulneraria, Campanula rotundifolia, Galium boreale, Hieracium pilosella, Hypericum perforatum, Leontodon hispidus, Linum catharticum, Viola arenaria.*

Field experiments

Seed addition experiments were conducted in alvar grassland (**II**) and in boreo-nemoral grassland (**III**). Respectively, 60 and 40, 10 cm × 10 cm permanent plots divided into 25, 2 cm × 2cm subplots were fixed to the ground in both sites.

In study **II**, two factorial treatments were applied: disturbance and sowing of extra seeds of 15 species randomly taken from the community species pool. The number of replicates per treatment was 15. For the disturbance treatment, both vascular plants and bryophytes were removed from all cells along two main diagonals in plots, altogether from 36% of the total plot area. The germination of seeds and establishment of seedlings were recorded in the period 1996–1998.

In study **III**, seeds of 25 species were sown into the intact vegetation of the boreo-nemoral grassland. The number of replicates per sowing treatment was 20. In addition, 20 control plots (without sowing treatment) were established to estimate the establishment of sown species in the experimental plots against the background of the natural regeneration of the target community. The germination and establishment of seedlings were recorded during 1998–2000. In both experiments all plant individuals within the subplots were recorded and identified according to species.

The regeneration from seed of three species was studied in a microcosm experiment (**IV**). 90, 22cm × 33 cm monoliths with intact plant vegetation were taken from the Hanila alvar grassland, transported to Tartu botanical garden, and placed in an open area under a plastic roof to avoid ambient precipitation. In the central part of each microcosm, a quadrate plot of 10 cm × 10 cm was established. The following experimental treatments were applied: removal of bryophytes, differential irrigation and sowing of 70 seeds of either *Festuca pratensis*, *F. ovina* or *F. rubra*. From half of the randomly selected plots, bryophytes were removed from the 10 cm × 10 cm central plot but the layer of vascular plants was left intact. Meteorological data from the observatory in the region of the target community were used to select the irrigation regimes. The average monthly precipitation during the vegetation period according to the data from a 10-year period was 54.6 mm. The average of all monthly precipitation rates from April to October that were higher than 55 mm was 76.2, and the average of all monthly precipitation rates from April to October that were lower than 55 mm was 27.3 mm. On this basis, it was decided that a precipitation rate of 80 mm per month corresponded to a “rainy summer”, 55 mm to an “intermediate summer” and 25 mm to a “droughty summer”. The regular irrigation regime was used — each microcosm received water every fifth day, i.e. six days per month. Establishment of seedlings was observed in grids 25, 2 cm × 2 cm subplots in 2000 (i.e. in the year of the sowing treatment) and in 2001.

Testing of seed germination

In order to get background information about the germinability of seeds and to obtain samples of seedlings for recognition in the field, 100 seeds of each of the species that were added in the sowing experiments were germinated in the laboratory (**II, III**). Seeds were germinated in Petri dishes on filter paper moistened with distilled water at 22°C. Germination was observed for 30 days.

In experiment **IV**, the general pattern of germination of fescue seeds in conditions of increasing drought was studied with the help of the polyethylenglycol (PEG, 20 000 M) solutions. Seven solutions with different concentrations of PEG were prepared, corresponding to the following osmotic potentials: 0 MPa (distilled water), –0.005 MPa, –0.016 MPa, –0.030 MPa, –0.049 MPa, –0.091 MPa., –0.273 MPa. Number of germinated seeds was recorded every 2 days for 60 days.

Data analysis

The effects of different factors on species diversity and the number of seedlings were analysed with the mixed model of ANOVA (I, II, III) and GLM (IV). The applied experimental factors were included in the models as the fixed factors. The effect of study plot was accounted for as a random factor and the temporal trend of sampling was taken into account with the help of the repeated measures factor (I, II, III, IV). For the analyses of numbers and species richness of seedlings log-transformation was used.

RESULTS

Small-scale turnover of the calcareous grassland community (I)

At any given time, nearly 20% of the subplots (defined as 2 cm × 2 cm subplots in the current study) within the 100 cm^2 plots were empty of rooted vascular plants. The location of such unvegetated subplots changed year by year. A change in status — either filled with plants or left empty — of the microsites took place in 20–40% of all those subplots within the 100 cm^2 plot in which plants had occurred during a period of two consecutive years. The amount of rainfall contributed to the rate of TO_{plot}: both the processes of colonisation of the previously empty subplots and of the disappearance from previously occupied subplots were more intense when a moist vegetation period followed to a dry one (Table 1). The two successive humid vegetation periods resulted in modest rates of disappearances and appearances within the plots.

Table 1. The characteristics describing turnover of vegetation on the 100 cm^2 plots (consisting of 25 subplots of 2 cm × 2 cm), components of turnover and the other related parameters (**I**); the means and standard error in parentheses are given. Turnover on the level of all individuals on the plot level (incl. both changes in presence of ramets and seedlings) is indicated by TO_{plot}, turnover of ramets by $VTO_{species}$ and turnover of seedlings by $GTO_{species}$

YEAR	1996	1997	1998	1999
Prevailing weather conditions during summer	dry	rainy	rainy	dry
Number of shoots in the plot	42 (2)	40 (2)	37 (1)	33 (1)
Percentage of subplots with living shoots	84 (1)	79 (2)	79 (1)	73 (2)
Percentage of previously empty subplots colonized via generative or vegetative propagation during the year of observation		79 (3)	42 (4)	45 (6)
Percentage of relieved subplots (being colonized in the previous year)		21 (2)	12 (1)	16 (1)
TO_{plot}		42 (2)	21 (2)	23 (2)
$VTO_{species}$		52 (3)	45 (3)	61 (3)
$GTO_{species}$		82 (2)	91 (2)	92 (2)
Number of previously empty subplots colonized by **ramets** during the year of observation		5.9 (0.2)	2.0 (0.2)	1.7 (0.2)
Number of subplots, where only seedlings occurred in the previous year, but which were colonized by **ramets** during the year of observation		7.1 (0.3)	2.2 (0.2)	1.8 (0.2)
Number of empty subplots colonized by **seedlings** during the year of observation		0.7 (0.1)	0.5 (0.1)	0.1 (0.1)
Number of subplots, where only ramets occurred in the previous year, but which were colonized by **seedlings** during the year of observation		1.4 (0.2)	2.0 (0.2)	0.7 (0.1)

In the empty subplots, more appearances of young ramets took place than appearances of seedlings. The establishment of seedlings in the previously vegetated subplots was more than two times as numerous as in the non-vegetated subplots, and was rather similar to the establishment of new ramets (Table 1).

The intensity of colonization of previously empty subplots was related to the weather conditions. During the two successive rainy years, relatively more appearances of seedlings in previously empty subplots were recorded, but it was not the period of the most intense spreading of new ramets to the empty subplots. New subplots were actively settled by ramets in the first rainy year after the severe drought.

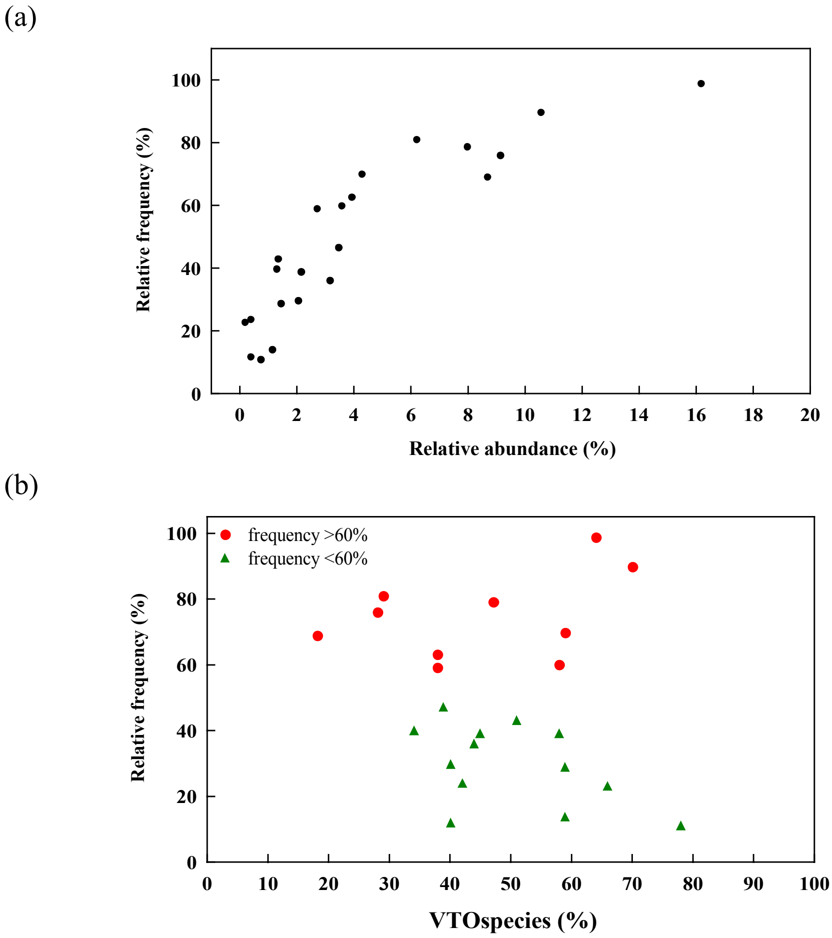


Figure 1. (a) The relative abundance and frequency of species in the study area. For estimation of abundance the data from previous studies of the vegetation of the area with the help of vegetation descriptions of 100 plots of 100 cm^2 (monthly from May to September in 1995) were used. (b) The mean turnover of the ramets of a species (VTO$_{species}$) and the relative frequency of species in the study plots.

The high mean values of $VTO_{species}$ refer to the considerable small-scale turnover at species level within the plots (Figure 1). The $VTO_{species}$ varied remarkably between all species, also within the group of frequent species, but it did not show a statistically significant relationship with species frequency. Those forb species, that frequently established seedlings, had a higher $VTO_{species}$ than the rest of the forb species (the respective means were 52 and 45%), although the difference was marginally non-significant ($F_{1,1120}$=3.68, p = 0.0552).

The turnover rate of species in the alvar grassland was in good accordance with the mobility categories defined according to Klimeš *et al.* (1997). Differences from the categorization were noted in the case of *Campanula rotundifolia, Carex ornithopoda, Leontodon hispidus* and *Pimpinella saxifraga*, which are all considered to have slow vegetative spreading but had rather high turnover rates (respectively 58%, 66%, 59% and 47%).

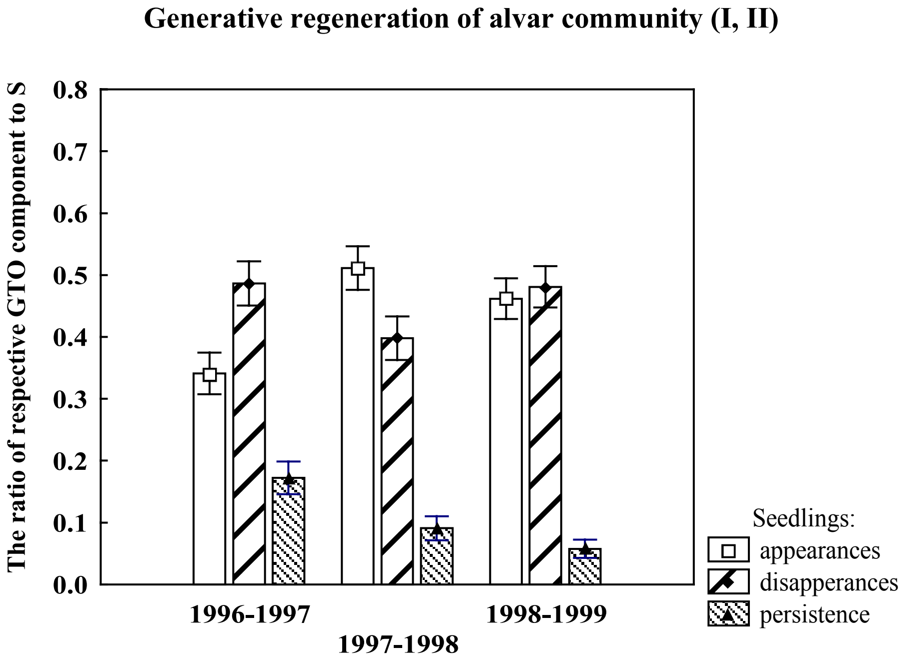


Figure 2. The ratio (mean, standard error) of respective components of the generative turnover of species ($GTO_{species}$) — the number of the 2 cm × 2 cm subplots with either appearance (a), disappearance (d) and persistence (pr) of seedlings — to the summed up number of subplots (S) with either appearance, disppearance or persistence of seedlings during the consecutive years, i.e. S = a + d + pr.

On average, there were three seedlings per 10 cm × 10 cm plot in Hanila alvar grassland. Two short-lived species, *Anthyllis vulneraria* and *Linum catharticum*, and seven forb species (*Campanula rotundifolia, Galium verum, G. boreale, Hieracium pilosella, Leontodon hispidus, Prunella vulgaris, Viola arenaria*) had temporally stable and abundant banks of seedlings. Altogether, seedlings were recorded for 65% of species that grew in the plots during the study years (1996–1999). Seedlings occurred for all of the 23 perennial species that were included to the $\mathrm{VTO}_{\mathrm{species}}$ study, except for *Anemone sylvestris*. The frequency of those 23 species was not correlated with the mean abundance of their seedlings in the study plots (r=0.137, p=0.54).

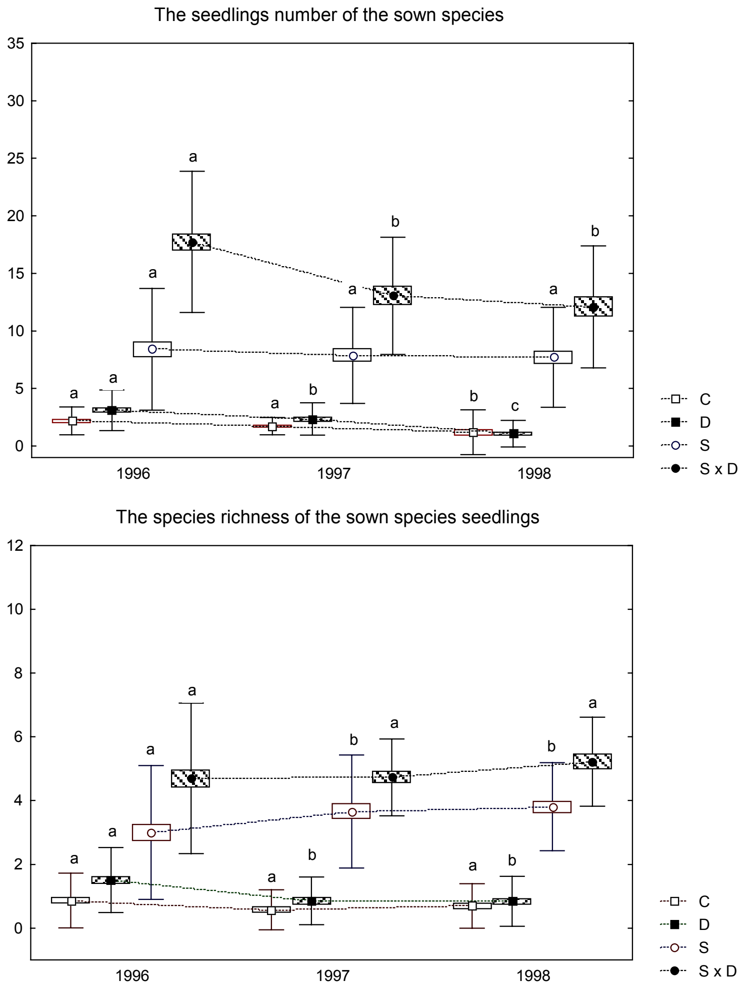
There were no significant differences between the $\mathrm{GTO}_{\mathrm{species}}$ among the 8 forb species; the temporal change in the turnover rate was significant (p=0.008): $\mathrm{GTO}_{\mathrm{species}}$ was higher in the second and third periods characterized by more ambient rainfall and prevailing seedling appearance rather than disappearance events (Figure 2), except in *Campanula rotundifolia* and *Hypericum perforatum*.

Survival of seedlings of perennial species was low, but the rate of mortality decreased in time. From the cohort of 1996, only 6% of seedlings survived up to 1999, though it should be noted that the summers of both 1996 and 1999 were very dry.

Seed limitation and species diversity (II, III)

In the alvar plant community (**II**), sowing of extra seeds of 15 species resulted in a significant increase in the number of seedlings of these species, as well as of the total species richness per plot. At the same time, experimental disturbance increased only the number and species richness of seedlings of sown species, but did not increase the total species richness. In the case of species richness of established vegetation and of seedlings, the interaction between sowing and disturbance was not significant. In the first study year, the interaction of sowing and disturbance had significant effect on the number of seedlings — the highest number of seedlings was observed in sown and disturbed plots. This interaction remained significant over the whole study period only in regard to the number of seedlings of the sown species.

Species richness of the established vegetation in a plot had no impact on the number of sown species that established in the plot. The number of established plant individuals in a plot had no impact on the number of the seedlings of the sown species that established.



The seedlings number of the sown species

The species richness of the sown species seedlings

Figure 3. The change in the number and species richness of seedlings of the sown species from 1996 to 1998, is shown within each treatment combination. The means were compared by Tukey multiple comparisons tests; significant differences are indicated by different letters. C — control, D — disturbance, S — sowing, S × D — sowing and disturbance. Means with standard deviations (whiskers) and standard errors (boxes) are shown.

Among the fifteen species sown in the plots, sowing of additional seeds increased the number of seedlings of seven species, while disturbance had no effect on their number of seedlings. In the case of one species, both sowing of additional seeds and disturbance increased the number of seedlings, though there was no interaction between treatments. For three species, the main effects of sowing and disturbance, but also the interaction of the treatments increased the number of seedlings. Three species did not establish any seedlings neither after the sowing of extra seeds nor in response to applied disturbance.

Year had a significant effect on the number of sown seedlings, but not on their species richness or on total species richness. The number of seedlings declined slightly after the dry summer of 1996, but the speed of changes was not high (Figure 3). A slight decrease in the number of seedlings was recorded for several species. *Plantago lanceolata* was an exception, since the number of its seedlings increased in time.

In another seed addition experiment (**III**), the seed mixture contained fourteen native species, which occurred in dry open calcareous sites in the landscapes nearby (within a 10 km radius), but were absent from the study site, and eleven exotic species of open dry habitats, which did not belong to the regional species pool. Seven exotic species and seven native species established during the first year. In the third year of the experiment, there were still three exotic species with five premature individuals, and three sown native species with sixteen individuals in the plots. Since the experiment was destroyed in the third year for safety reasons, we have no data on whether some of the established plant individuals could have reached the generative stage in the study grassland. These results show that long-distance dispersal both within and between regions may potentially have an impact on species composition in target plant communities. If the relatively best establishing exotic species *Phyteuma scheuchzeri* is classified as casual, one may conclude that transition between different invasion stages corresponds to ten's rule. The species richness of seedlings, taking both local and sown species into account, was higher in plots with higher native established plant species richness.

The effect of various moisture conditions and presence of bryophytes on the establishment of seedlings (IV)

Both irrigation and bryophyte removal increased the establishment of three fescue species in the dry alvar grassland community. In similar moisture conditions, the establishment of seedlings in the presence of the bryophyte layer always remained somewhat lower than on bare soil, indicating the inhibiting effect of the bryophytes. A patch of bare soil offered relatively more favorable conditions for germination and this advantage increased along with the amount of water added. The density of the established vascular plant community did not effect the establishment of seedlings. The significant interaction between year, irrigation and removal of bryophytes indicated the increase in the number of seedlings in all treatments, except in the case of the highest irrigation.

The germination experiment along a concentration of PEG showed that the germinability of the three species did not differ in the distilled water. The rate of germination of *F. pratensis* started to decline already in response to slight drought conditions, but it was more tolerant to water stress than the other two species and retained a remarkable rate of germination over a wide gradient of increasing water stress. *Festuca ovina* was characterized by an abrupt reaction to increasing drought. *F. rubra* retained a rather high rate of germination in moisture conditions that were clearly unfavorable for the other two species, although it could not tolerate as severe water stress as *F. pratensis*.

The establishment of seedlings of *F.ovina* in the microcosm experiment was successful and gave a strong positive response to the ameliorated water conditions. Significantly more seedlings of *F. rubra* were established when the highest amount of water was added. Establishment of seedlings of this species was relatively more limited by the bryophyte layer than for *F. ovina* and *F. pratensis*. In accordance with the germination test, where the number of germinated seeds of *F. pratensis* in favorable moisture conditions (i.e. lower water stress level) remained lower than in the other species, the establishment of its seedlings in the rainy treatment of the microcosm experiment was not as high as in the case of *F. ovina* and *F. rubra*. The mortality of seedlings between 2000 and 2001 was the lowest for *F. ovina*, while in the case of *F. rubra* and *F. pratensis* less than half of the seedlings survived the first year of establishment.

DISCUSSION

The assumption that most of the plant communities display a remarkable small-scale turnover of vegetation (van der Maarel and Sykes 1993, Sykes *et al.* 1994) found support in the case of the dry species-rich alvar grassland. On the one hand, the ratio of unvegetated subplots within 100 cm^2 plots remained rather stable over the study period. Even severe droughts (in 1996 and 1999) did not result in great change in that: at any time nearly one fifth of the plot area was free of rooted plants and apparently open for colonization. The ongoing change in the location of un-vegetated subplots means that arenas for colonization of new plant individuals, either ramets or seedlings, appeared naturally without any evident external disturbances. Our results indicate that seedlings prefer microsites with established vascular plants *in situ*. The rather similar likelihood for ramets to appear either in completely empty subplots or in those where only seedlings were present was very much as expected: evidently, clonal integration makes them less vulnerable to either competition from present vegetation or to abiotically unfavorable conditions. Our study, however, did not show whether the appearance of new ramets was dependent on the presence of adult ramets in the plots. The high values of turnover at species level indicate the occurrence of species replacement within 2 cm × 2 cm subplots, but as the subplots were continuously occupied, these internal subplot dynamics were not reflected in the plot turnover dynamics.

All species of the study area showed some rate of turnover, i.e. the location of their ramets or/and seedlings changed in time. There was no indication that the recorded high turnover could make the existence of a species in a community somehow unstable: the species richness of the whole stand was maintained despite the ongoing natural process where species just “walk away” from previous microsites to new ones, being also able to survive in the different microsites. Communities certainly exhibit some level of spatial variation of resources (e.g. Lundholm and Larson 2003), which makes the local conditions less or more favorable for certain species, but there is no reason to expect that there is only a limited amount of microsites for each species in the community, in which it can gain the competitive superiority over others (Tilman 1994). Instead, the small-scale dynamics of the alvar grassland community resembled a “random walk” through different microsites (cf. van der Maarel and Sykes 1993).

We also assumed that the mobility of species could be regarded as a mechanism enhancing coexistence, since species that are competitively suppressed by other species in particular microsites, may find more favorable conditions in neighbouring microsites. Thus, one might therefore assume that subordinate species with relatively weaker competitive abilities could be characterized by higher mobility, but this hypothesis of coexistence was not convincingly proved in the present study. The average turnover of subordinate species, however, tended to be higher than that of frequent species, but this result remained marginally nonsignificant. It may mean that the spatial mobility of species plays a rather unimportant role in avoiding competition in dry alvar grassland communities and the spatial turnover alone does not provide one a key for explaining different frequencies of species. Alternatively, the relatively higher turnover rate of species could in certain circumstances lead to lower frequency, as the quick turnover of ramets, instead of their persistence, may not be the most favorable strategy in conditions of limited water availability. The generality of such a statement, however, is challenged by the occurrence in the community of certain species (e.g. *Asperula tinctoria, Carex tomentosa*) with both relatively high turnover and frequency. Within the group of species with high frequency, very different rates of vegetative turnover were observed, thus the type and rate of mobility did not contribute directly to the status of the species in the community. In general, we could agree with Klimeš (1999) that small-scale mobility in the species-rich plant community is not directly related to species competitive ability and coexistence.

The natural pattern of colonisation of the free microsites, raised due to both vegetative and generative regeneration, showed that seedlings formed the more mobile component in the grassland, due to their low persistence. The appearance or disappearance of seedlings and ramets in the plots was also related to local weather conditions, so part of the small-scale turnover can be explained by the fluctuations in weather conditions. The alternation of dry and moist vegetation periods had a different impact in relation to vegetative and generative regeneration: there were more unoccupied subplots where seedlings established during the moist summers, while the number of new microsites occupied by ramets was smaller when two humid and presumably favorable summers followed each other than when a rainy summer followed a dry one. However, both processes of new rames and seedlings establishments gave a positive response to increased ambient rainfall and removal of bryophytes.

In the vegetation of the alvar grassland, where the perennials make up the majority of the species, the proportion of species establishing seedlings was still rather high. Despite the fact that many seedling establishment events were not successful and the overall seedling mortality rate was high, the establishments of new individuals by generative regeneration over all species of the plant community were remarkably numerous. Regeneration from seeds thus has an important role in the regulation of the species composition and richness of calcareous grassland communities.

The success of regeneration by seed in the studied alvar grassland community depended on both availability and germination of seeds, as well as on the survival of seedlings. Seed limitation was a much more important force behind the pattern of small-scale species richness, while local small-scale disturbances alone did not change the pattern of species diversity in dry calcareous grasslands. First, this result is in good accordance with the studies showing that in grassland communities the fresh (short-distance) seed rain gives the majority of the germination events and that the effect of the seed bank is only minor (Kalamees and Zobel 2002). On the other hand, in our study the disturbances did not result in the more pronounced effect of natural seed rain: disturbance without sowing of extra seeds did not change either the number or richness of the species of emerged seedlings. The sowing treatment was, however, slightly more effective in interaction with disturbance — in the case of some species, there was a significant positive interaction of the experimental treatments, and therefore the number of seedlings of the sown species was also higher if the sowing of seeds and disturbances were applied together. However, the temporal decrease in the number of seedlings of sown species in the plots with both sowing and disturbance treatments and in the pure disturbance treatment indicated that the artificial gaps were associated with relatively less favorable conditions for the survival of the established seedlings. Thus, unvegetated gaps did not present safe sites for seedlings in oligotrophic conditions with low standing biomass of vegetation. Evidently, some shelter from the established plants may be needed for seedling establishment (cf also Ryser 1993). The opposite examples, reporting that bare ground (with no effect from the established vascular plant community layer) is the best ground for regeneration from seeds (Bakker and Olff 2003), come from more productive stands and concern species with better regenerative ability.

Eriksson and Ehrlen (1992) were probably the first to clearly put forward the question, whether plant populations are seed or microsite limited. Later on, there have been a large number of seed addition experiments, focusing on the population dynamics of one or more plant species. These experiments have shown (reviewed by Turnbull *et al.* 2000) that plant populations are more often seed limited than usually assumed. In addition to the population-level studies, the small-scale species richness of vascular plants of the alvar grassland turned out to be significantly seed limited as well. Therefore, presence of seeds and factors contributing to their availability (e.g. occurrence of dispersal vectors, structure of landscape, distance and area of communities with similar ecological conditions, presence of seed predators or pathogens, etc.) have a crucial role in generating the pattern of small-scale species richness in such oligotrophic plant communities. There are a handful of studies that have demonstrated the dependence of small-scale species richness on the availability of diaspores as well (Stampfli and Zeiter 1999, Tilman 1997, Houle and Phillips 1989, Lord and Lee 2001, Xiong *et al.* 2003). Our results are in good accordance with these studies. One exception is the study by Houle and Phillips (1989), however other experiments have been conducted in mesophyte grasslands with higher standing crop than the calcareous grasslands we used for experiments. In an oligotrophic dry alvar grasslands, plant community species composition and richness were clearly seed limited.

The results of our study support the theoretical expectation and the experimental findings that the effect of disturbance on the regeneration of species and species diversity in plant communities with low standing crop is not as important as in communities with higher standing biomass (Kitajima and Tilman 1996, Huston 1999). This expectation has received further support from the experimental studies by Foster (2001, Foster *et al.* 2004), who elaborated the so-called shifting limitation hypothesis. This hypothesis claims that landscape gradients in local plant diversity should reflect shifts in the major regulating factor, from species pools to local ecological processes, as one moves from sites of inherently low to inherently high productivity.

In the mesophyte calcareous grassland, the survival of introduced species was rather low, compared to the results of the experiment in the alvar grassland. The main reason behind this difference is evidently the different nature of the sowing mixtures. The native species in the sowing mixture represented species which were “available” in the vicinity of the experimental grassland, but that had not established there. Grasslands in the study area have been used for centuries (Pärtel *et al.* 1999b) and both the moving of domestic animals and the transportation of hay evidently enhanced seed dispersal (see Poschlod *et al.* 1998; Poschlod and Bonn 1998). Since the study site is characterised by relatively very high species richness (Kull and Zobel 1991), one may assume that most of the species in the surroundings whose ecological requirements correspond to the local conditions have arrived and established in the study grassland already. Hence the present distribution pattern of vascular plant species in the local landscape is evidently not created by dispersal limitation among fragments of dry open calcareous habitats, but rather corresponds to the historical pattern of local site conditions (different land-use practise and related characteristics of soil). As regards the establishment of exotic species, then the short duration of the experiment did not allow us to make far-reaching conclusions. It should be noted that species for the sowing mixture were chosen randomly and were not selected on the basis of ecology and traits that would make them more fitting for the target community. In addition, the vegetation of the mesophyte calcareous grassland under investigation was characterized by higher canopy, standing crop, and cover than the alvar grassland. Previous studies have indicated, however, that the generative regeneration of species in mesophyte grassland communities may be more gap-dependent even in communities with relatively low productivity (Kalamees and Zobel 2002). Also, the shifting limitations hypothesis of Foster *et al.* (2004) claims that the role of disturbances increases along the productivity gradient. Thus, besides other factors, low establishment of sown species in mesophyte calcareous grassland may be explained also by the lack of local disturbances.

There are numerous examples of species invasions onto new areas or continents (Lonsdale 1999, Stohlgren *et al.* 2003, Higgins *et al*. 2003), but the quantitative estimates of the germination, establishment and naturalization of the arrived diaspores and species are practically lacking. There exists a so-called “tens rule”, describing the transition of alien species between phases of the invasion process (Williamson and Fitter 1996), but as far as the initial stages of the invasion process are concerned, this rule is based merely on an "educated guess". More data are evidently needed to give any quantitative estimates here.

As regards the initial hypothesis that the local species diversity *per se* does not set limits to the establishment of species belonging either to the community, local or regional species pools, but that the establishment of diaspores depends on the traits of introduced species and on local conditions, such as the cover of vegetation, then this idea was supported by the results. We did not notice any significant effect of local small-scale richness on the success of introduced species. One has to agree with Stohlgren *et al.* (2003) and Petryna *et al.* (2002) that other factors than species diversity are determining the success of invading species.

Finally, we assumed that the rate of germination and establishment of arrived diaspores in oligotrophic dry calcareous grasslands depends on the interaction of abiotic factors like ambient rainfall and biotic factors like the density and cover of the local plant community. The microcosm experiment with the sowing of three fescue species and manipulation of the level of rainfall showed that the establishment of seedlings and their survival in dry grasslands depends primarily on the amount of ambient rainfall. The turnover of seedlings was also clearly related to the weather conditions: the droughty summer resulted in a high number of microsites from which seedlings disappeared. One may argue that, in dry alvar grassland, regeneration by seed contributes to the frequency and abundance of species in the plant community, and this contribution depends both on species traits and on local abiotic conditions. On the basis of the establishment pattern of the three fescue species, it is possible to conclude that all three species depend to a certain extent on the so-called "window of opportunity" — an unusual combination of environmental factors that makes the regeneration from the seed possible (Jelinski and Cheliak 1992). The most successful species — *F. ovina* — can still recruit relatively more successfully in droughty years, but in the case of more favourable moisture conditions, it can realize this "opportunity" to a much greater extent than the other two fescue species — *F.rubra* and *F.pratensis*. *F. pratensis,* which is more common in mesophyte and fertile conditions, showed the weakest positive response to irrigation treatments in alvar grassland. *Festuca rubra* showed successful establishment only when there was a coincidence of wet year and local disturbance in the bryophyte layer.

We also expected that the bryophyte layer, due to its water retention capacity, acts as ameliorator of the effect of drought. This expectation did not receive support in the experiment — differently from the mechanism suggested by Keizer *et al.* (1985), we did not record any ameliorating effect of the bryophyte layer. On the contrary, the negative effect of the continuous and temporarily almost dry layer of bryophytes was recorded. The bryophyte layer did not act as a reservoir of moisture and shelter against evaporation, but rather created a natural screen that inhibited successful establishment of seedlings and limited vegetative propagation as well. In general, one may conclude that moisture conditions act as the primary factor "screening" local diaspore rain and regulating seedling establishment, but local disturbances may amplify the positive effect of favorable moisture conditions.

The results of the present study showed that the most crucial phase of generative regeneration, and therefore the most important also for the maintenance of diversity, was not so much the germination of "arrived" diaspores, but rather the survival and further growth of established seedlings. The survival of seedlings originating from natural seed rain was estimated both from direct data and with the help of the indirect measure "turnover of seedlings", and we recorded rather low rates of survival. Mortality was highest during the first year after germination, which is associated with the high vulnerability of younger seedlings. Those seedlings that survived the first year also had considerably higher probability to survive the following years. On the other hand, there were only minor changes in the number and species richness of seedlings of sown species after the first year of experimental sowing of 15 species to the alvar community, indicating also that if once well-established, seedlings survive and contribute to the small-scale species richness.

Many biotic and abiotic factors contribute simultaneously to the fate of a seedling: presence of pathogens, granivores and herbivores (Hulme 1996; van der Putten 2003), absence of suitable mychorrhizal fungi in the soil, or inability to form mychorrhiza in time (Smith and Read 1997), competition from established plants, weather conditions, etc. (Fenner 1987). The relatively high mortality of seedlings in the alvar grassland cannot be explained as a response to the competitive effect of neighbouring adult plants, that is usually expected to be much stronger than the competitive effect of plants of the same size. In the conditions of a dry calcareous grassland, no relationship was found between shoot density and the number of established seedlings or there was even a positive relationship — the microsites in the vicinity of established plants were inhabited by seedlings more often than the unvegetated ones. This pattern probably results from the short-distance dispersal of seeds and from the tendency of the vegetation to act as a seed trap, but on the other hand, it indicates that shoot competition was not a prevailing interaction preventing seedling establishment in an alvar grassland community. In the microcosm experiment, in the most favourable water conditions and in the absence of the bryophyte layer, the shoot density of established vegetation was significantly higher than in the other treatments. It was noticed that in the moist treatment, the plant individuals grew larger than usual in the alvar grassland community. This probably intensified the competitive effect of the established vegetation on seedlings, which explains the decrease in their number seen in the second year.

CONCLUSIONS

The present study indicated that, in a dry species-rich alvar grassland with standing biomass of 170 g/m^2, the important forces structuring the community are the abiotic conditions determining the water availability and the limited regeneration of plant populations. Local small-scale species richness was not an important determinant of the germination of arrived diaspores and the establishment of seedlings.

The small-scale species diversity of vascular plant species in the dry calcareous grassland was clearly seed limited, but not microsite limited. The presence of free microsites had rather a secondary role in the formation and maintenance of species richness in the oligotrophic alvar community. Vice versa, the significant decrease in the number of sown species seedlings in disturbed plots (a pattern not seen in the case of undisturbed plots) indicates that such microsites do not favour the survival of seedlings.

For several reasons, seed limitation was not clearly expressed in a mesophyte calcareous grassland community. Success of establishment of sown exotic and native (not belonging to the community species pool) species was low, but it was not associated with the established species richness or its density *in situ*.

In the alvar grassland, free microsites were constantly being created by the small-scale turnover of the vegetation, but establishment of seedlings of many species was more confined to the microsites in the close vicinity of established plants. Though the density and species richness of the established vegetation did not negatively impact the establishment of seedlings in the alvar grassland the bryophyte layer turned out not to be the ameliorator of water conditions for seedlings but rather a natural screen decreasing significantly the regeneration of vegetation. Therefore, evidently if microsites empty of vascular plants but covered in a thick bryophyte layer occur, they do not represent the favourable conditions for regeneration. Moreover, the negative relationship between the density of the established ramets and the presence of bryophytes indicates that patches densely covered with bryophytes evidently also suppressed the vegetative spread of clonal plants.

The type of small-scale spatial turnover of species did not directly contribute to the status of the species in the community, leading to the conclusion that interspecific spatial interactions do not explain the coexistence of species in the alvar grassland. There was no clear evidence of the expected differential spatial dynamics of frequent and subordinate species. Higher turnover could be expected to be a more unfavorable strategy for species in dry calcareous grasslands, but no generalised statement of that could be made.

The vegetation of the dry alvar grassland was characterized by considerable generative regeneration: established seedlings were recorded for more than half of the species. This indicates that, despite the rather high mortality of seedlings, especially in the first years of life, recruitment by seed can have a high importance for diversity. In favorable years, with enough precipitation (e.g. over 150 mm summed over months of summer), species may find their "windows of opportunity" *sensu* Eriksson (1997b) and establish successfully, contributing to the persistence and genetic diversity of the population as well as to the species richness of the stand.

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SUMMARY IN ESTONIAN

LUBJARIKASTE NIIDUKOOSLUSTE SEEMNELINE UUENEMINE JA SELLE SEOS LIIGILISE MITMEKESISUSUSEGA

Läbi aastakümnete on taimeökoloogid püüdnud leida seaduspärasusi, mille abil seletada ja ennustada liigirikkuse erinevusi ja muutumist ajas ning ruumis. Peamiselt on koosluse liigirikkust seostatud taimedele kasvuks vajalike ressurssside — valguse, vee ja mullas leiduvate toitainete — hulga ning varieeruvusega koosluses ning jaotumisega liikide vahel. Kõige sagedamini on uuritud liigirikkuse muutumist produktiivsusgradiendil. Koosluse produktiivsuse tõustes eeldatakse liikidevaheliste interaktsioonide muutumist ebasümmeetrilisemaks, kus eelise omandavad kiirema- ja kõrgemakasvulised liigid. Liikide kooseksisteerimise seletamiseks on otsitud mehhanisme, mis lubaksid konkurentselt nõrgematel liikidel koosluses püsima jääda ehk teisisõnu, vähendaksid konkurentsi mõjusid. Võimalikuks mehhanismiks on peetud looduslikke või inimtekkelisi protsesse (näiteks häiringud), mis vähendavad konkurentselt tugevamate liikide mõju koosluses ja muudavad ressursse kättesaadavaks ka konkurentselt allasurutud liikidele.

Uue vaatenurga liigirikkuse varieeruvuse põhjustele on avanud nn. liigifondi kontseptsioon, mis arvestab liigirikkuse kujunemislugu lokaalkoosluses, sh. pikaajalisi ja suuri ruumiskaalasid puudutavaid protsesse nagu liigiteke, liikide levimine, lokaalkooslusi aegade jooksul mõjutanud tegureid jmt. Sellekohaselt lähtuvad erinevused taimekoosluste liigilises mitmekesisuses eelkõige abiootilisest keskkonnast ja sellest, kui paljudele liikidele on need tingimused ressursinõudluse poolest sobivad. Taolised liigid moodustavad selle koosluse jaoks lokaalse (koosluse ümbruskond) või regionaalse (laiem piirkond, ka nt. riik) liigifondi. Järelikult mõjutavad liigilist mitmekesisust koosluses ja pinnaüksusel oluliselt ka liikide levimisvõime ja -võimalused ning kooslusesse lõimumise õnnestumine. Sellise hüpoteesi paikapidavust võimaldavad hästi kontrollida külvikatsed. Külvi positiivse mõju avaldumine liigilisele mitmekesisusele viitab sellele, et konkurentsed interaktsioonid ei piira uute taimede ja/või liikide lisandumist proovipinnale. Kui külvi mõju ei avaldu, võib see tähendada, et lokaalkoosluse tingimused ei vasta külviliikide ressursinõudlustele või et koosluses valdavad taimede vahel negatiivsed interaktsioonid, mis idandite ellujäämisvõimalusi vähendavad.

Soontaimede liigirikkus on Eesti lubjarikastel muldadel kasvavatel taimekooslustel märkimisväärselt suur. Nende niidukoosluste geograafiline paiknemine Eestis on seotud Ordoviitsiumi ja Siluri lubjakivi aluspõhjaga ja seepärast leiab selliseid pärandkooslusi Lääne- ja Põhja-Eesti rannikualadel, Muhumaal, Saaremaal, Hiiumaal ja paljudel Lääne- ja Põhja-Eesti saartel. Taimeökoloogide tähelepanu pälvib nende madala ja hõreda taimestuga õhukestel muldadel kasvavate koosluste suur liigiline mitmekesisus. Käesolevas töös uuriti, millest sõltub taimekoosluse (seemneline) uuenemine ja millist mõju see avaldab koosluse liigilisele mitmekesisusele. Täpsemalt otsiti vastust järgmistele küsimustele: (1) missugune on loopealse taimestiku ruumiline muster ja kuidas see ajas muutub ning kas sealne kõrge liigiline mitmekesisus on seotud vähemsagedaste liikide võsude kiirema asukohamuutusega, mis lubab neil eeldavasti vähendada teiste liikide võimalikke negatiivseid mõjusid; (2) kas lubjarikka taimekoosluse väikeseskaalalist liigirikkust limiteerib leviste või sobivate “mikropaikade” (s.o. vajalike ressursside ja sobivate bioloogiliste interaktsioonide) puudumine; (3) kas lokaalkoosluse liigirikkus piirab uute liikide kooslusse lisandumist; (4) kas samblarinne loob seemneliseks uuenemiseks paremaid tingimusi, muutes need kuivaperioodidel idanditele soodsamaks?

Siinse töö tulemustest selgus, et lubjarikaste niidukoosluste taimestiku liigirikkusele avaldasid olulisimat mõju abiootilised keskkonnatingimused, eelkõige sademete hulk, ja leviste olemasolu, samas lokaalne väikeseskaalaline liigirikkus ja võsude tihedus seemnelisele uuenemisele mõju ei avaldanud.

Ligikaudu 20% 100 cm^2 prooviruutude pindalast oli iga-aastaselt soontaimede poolt asustamata, kuid selliste asustamata paikade muster muutus prooviruudul igal aastal. Seega näib koosluses olevat piisavalt vabu kohti, kuhu taimed levida ja juurduda saavad. Sellele vaatamata asustasid idandid rohkem selliseid 2 cm × 2 cm osaruute, mis olid eelnevalt soontaimede poolt juba asustatud. Rametite väikesel ruumiskaalal ümberasetumise määr erines liigiti märkimisväärselt. Selget seost liigi esinemissagedusega (mõõdetud kui esinemisprotsent prooviruutudel) uuritud parameeter ei ilmutanud. Ka ei õnnestunud leida toetust kirjanduses viidatud võimalusele, et väiksema sagedusega liigid asetavad oma rameteid suhteliselt kiiresti ümber uutesse ruumipunktidesse ja see lubab neil teiste liikide konkurentseid mõjusid vähendades koosluses edasi kasvada. Kuigi vähest tendentsi suuremale võsude ümberpaigutumise määrale võis väiksema sagedusega liikide puhul märgata, liigi esinemissagedus uuritavas koosluses sellega oluliselt ei seostunud. Nii võibki järeldada, et loorohumaal ei ole liigi väikeseskaalaline mobiilsus otseselt seotud konkurentsivõimega ega oma olulist tähtsust liikide kooseksisteerimise seisukohast.

15 loopealseliigi seemnete katselise lisamise korral 100 cm^2 prooviruutudele suurenesid oluliselt nii nende idandite arv ja liigirikkus kui ka liikide koguarv. Taimestikku tekitatud väikesepinnalised häiringukohad ei põhjustanud liigirikkuses märkimisväärseid muudatusi, mis ühelt poolt viitab sellele, et ressursside hõivatus ei ole loopealse taimekoosluse liigirikkust piiravaks teguriks, teisalt aga annab taas kinnitust teistegi autorite seisukohale, et seemnepanga mõju lubjarikaste niitude uuenemisel on üsna tagasihoidlik ja idanemist on oodata värske seemnevihmaga saabunud seemnetest. Samas oli seemnete lisamine mitme liigi puhul efektiivsem häiringutega katsetöötluses, mis kokkuvõttes põhjustas ka nende katsetöötluste interaktsiooni positiivset mõju külviliikide idandite koguhulgale. Siiski hakkas idandite arv häiringutega külviruutudes teisel, s.t. külvijärgsel suvel langema, sama toimus ka külvita, kuid häiringuga

töötluseruutudes. Häiringuta külviruutudes sarnast muutust ei täheldatud. Selline tulemus näitab, et häiringukohad ei pruugi siiski pakkuda idandite kasvuks sobivaid tingimusi, kuna taimkatte eemaldamisega kaob ka selle vari, mis suudaks põuatingimusi leevendada.

Lubjarikkal pärisaruniidul osutus koosluses seni mittekasvanud soontaimeliikide katseline lisamine vähetulemuslikuks. Ühelt poolt on siin põhjuseks külvatud liikide valimine juhuslikkuse printsiibil — liike ei valitud nende ökoloogilist sobivust pärisaruniidu tingimustele arvesse võttes. Puududa võisid ka idandite kasvuks ja ellujäämiseks olulised interaktsioonid, vajalikud keskkonnaimpulsid idanemispuhkuse lõpetamiseks või idanema hakkamiseks jms. Teisalt võisid seemnelise uuenemise edukust pärisaruniidu uurimisalal vähendada ka taimkatte suurem biomass ja katvus pinnaühikul võrreldes loopealsega, kus külvi mõju selgelt ilmnes. Loopealsel ega ka pärisaruniidul ei avaldanud lokaalse taimestiku võsude tihedus ega liikide arv pinnaüksusel seemnelisele uuenemisele olulist mõju, pärisaruniidul olid kõrgema liigirikkusega prooviruudud hoopis invasioonile avatumad. See tulemus ei toeta ökoloogia klassikalist hüpoteesi, nagu piiraks koosluste invasioonilisust (võimet lõimida uusi liike) selle liigiline mitmekesisus, mida on otseselt seostatud konkurentsete interaktsioonide intensiivsusega. Nagu leiti siinses töös, nii on teisedki viimasel aastakümnel tehtud uurimused näidanud, et kuigi invasioonide edukust on raske ennustada, ei tohi invasioonilisuse ja liigirikkuse vahelist negatiivset seost reegliks pidada.

Kui prooviruutudel kasvanud soontaimed pigem soosisid kui välistasid idandite moodustamist, siis samblarinne pärssis oluliselt katses kasutatud aruheinte (*Festuca ovina, F. pratensis, F. rubra*) seemnelist uuenemist. Oluliselt sõltus seemneline uuenemine sademete hulgast, millest võib eeldada, et sajurikastel suvedel võivad kõik kolm liiki, eriti aga *F. ovina*, edukalt uueneda ja esinemissagedust ja ohtrust suurendada. Idanemisedukus prooviruutudel oli üldiselt hästi seostatav taimeliigi arvukuse ja sagedusega loopealsel.

TÄNUSÕNAD

...selle ühe kummarduse sees
on veel üks kummardus
mu südames

J. Viiding

Käesoleva töö valmimise eest olen kõige enam tänu võlgu oma juhendajale, professor Martin Zobelile, kes kannatliku ja targa meelega on siinkirjutaja töid suunanud.

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