The floodplain meadows of Soomaa National Park, Estonia

Vegetation – Dispersal – Regeneration

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Jaan Palisaar

aus Kiel

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Die Arbeit wurde angeleitet von	Prof. Dr. Peter Poschlod
Prüfungsausschuß:	Prof. Dr. Jürgen Heinze
	Prof. Dr. Peter Poschlod
	Prof. Dr. Karl-Georg Bernhardt
	Prof. Dr. Christoph Oberprieler

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A sower went out to sow his seed: and as he sowed, some fell by the way side; and it was trodden down, and the fowls of the air devoured it. And some fell upon a rock; and as soon as it was sprung up, it withered away, because it lacked moisture. And some fell among thorns; and the thorns sprang up with it, and choked it. And other fell on good ground, and sprang up, and bare fruit an hundredfold.

Luke 8, 5–8

A. Foreword

Riverine landscapes are highly dynamic systems with a multitude of interacting processes (Ward et al. 2002). Two aspects characterising riparian landscapes are high levels of natural disturbances and numerous abiotic and biotic gradients which have lead to a number of distinct responses and adaptations in many typical floodplain species. The most obvious agent of disturbance in these landscapes is the flowing water: recurring floods cover the vegetation for considerable times (Blom & Voesenek 1996), and the impact of flowing water or moving ice damages plants and vegetation cover. Flood and ice damage may, however, also be necessary disturbances which create opportunities for establishment (e.g. *Pedicularis furbishiae*, Menges 1990) The most prominent abiotic gradient in floodplains is that of elevation above water table which, however, translates into several derived gradients, e.g. dryness/wetness, flood duration, disturbance intensity and fertility (Day et al. 1988). Taken together, these factors ultimately lead to an exceptionally high diversity of habitats and plant communities. Consequently, riverine landscapes are very rich in species and are thus of high concern for the conservation of biodiversity and ideal subjects for plant ecological research (Blom & Voesenek 1996).

Man started early to use the fertile floodplain landscapes: floodplain forests were among the first that were turned into grasslands, a process that started in Central Europe in the Iron Age (Speier 1994, 1996), possibly even as early as the Bronze Age. For Estonia the first settlement of farmers in floodplains and subsequent formation of grasslands are reported for 2000 BC (Truus & Tõnisson 1998). From this time on floodplains were managed continuously in an extensive way, i.e. low (if any) fertiliser input, minimal land drainage and mostly a single cutting per year for hay (Joyce & Wade 1998). These conditions were favourable for a rich flora and fauna which developed in accordance with the local management regimes but also crucially depended on it. Besides their importance for the conservation of biodiversity there is a growing awareness that intact floodplains and their semi-natural habitats perform important ecosystem functions, such as flood retention, groundwater recharge and water quality improvement (Benstead et al. 1999).

The period of low-intensity farming systems lasted in Europe generally until the 1950ies when agriculture underwent a radical shift towards more intensive practices. Following that time many unproductive areas including floodplain meadows were either abandoned or 'improved', i.e. drained, fertilised, re-seeded etc. All this caused a dramatic loss of habitat and species richness (Joyce & Wade

1998). In Estonia similar developments took place although due to the peculiarities of the soviet agriculture more meadows were managed in an extensive way than in Western European countries.

Ecologists reacted to this developments and there is now a vast body of literature on the management and restoration of heavily degraded grasslands typical for much of Europe (e.g. SCHIEFER 1981; BAKKER 1989; SCHRAUTZER et al. 1996; JOYCE & WADE 1998). However, there is still much to be learnt about the processes acting in original semi-natural systems which still show intact hydrology, natural nutrient levels and a species rich flora. For this reason Estonia – for many decades a largely forgotten country and both politically and linguistically hard to access – seemed a promising study area, as many habitats, communities and species that have become extremely rare or even extinct in Western Europe are *still* quite common here.

Therefore the aim of this study was twofold: in a first part the meadow vegetation of the local floodplains and its relation to important habitat gradients was studied. In a second part processes of dispersal, germination and establishment were assessed on different scales from the single plant species to whole communities. A special focus was placed on the role plant functional traits and whether they may serve as a shortcut to a functional understanding of the observed patterns.

This study therefore has the following structure:

Section B ("Study Area") gives a description of the Soomaa National Park, its physical setting including climate, soils and vegetation, and the former and present land use.

In Section C ("Vegetation types and habitat parameters") the principle types of floodplain grasslands of the Soomaa area are described together with the major habitat factors governing their distribution.

Section D ("Dispersal, regeneration, and the role of plant traits") describes the results of three field studies involving seed traps, a seed sowing study and a disturbance experiment. Plant traits are used to interpret the results of the experimental studies and the vegetation classification in functional terms.

B. Study area

1 Physical setting

Location

The Soomaa National Park (Soomaa Rahvuspark) is situated in the south-west of Estonia, lying at c. 25°03'15'' E and 58°43'12'' N (visitor centre in the middle of the area, see Fig. B.2). It covers an area of 37117 ha and spans the border of Pärnu and Viljandi county. Its natural borders are the Navesti river in the north and the large mire complexes of Kikepera raba, Öördi raba, Valge raba and Kuuresoo in the west, south and east.

Climate

Climatically, Estonia is part of the mixed-forest sub-region of the Atlantic-continental region within the temperate zone, thus characterised by warm summers and moderately mild winters (Paal 1998). The vegetation period with daily temperatures above 5 °C lasts 165–185 days. The climate in the Soomaa area can be characterised as being transitional between the maritime coastal and the more continental eastern regions of Estonia. Fig. B.1 gives a summary of the average climatic conditions in Viljandi, some 30 km east of Soomaa and the conditions in the years discussed in this study (1998–2000). Mean temperature in the study area is 5 °C and average precipitation is 670 mm.

The year 1998, the first year of the study period, was exceptional in being extremely wet (total precipitation for this year: 853 mm). In consequence two summer floods occurred (June and August), rendering field work almost impossible in large areas of the park for a considerable time.

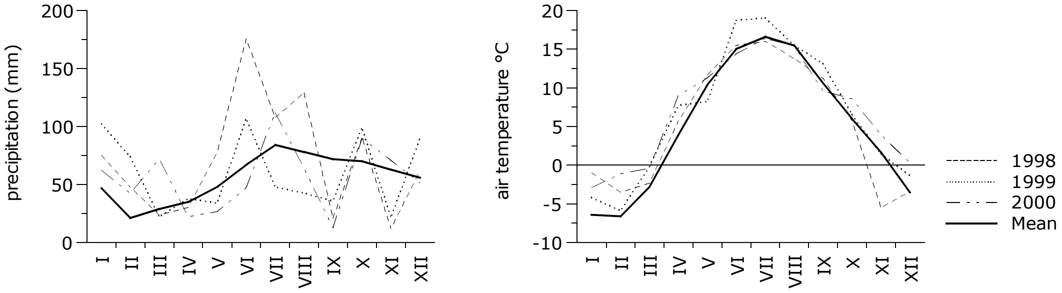


Fig. B.1: Average climatic conditions in the area of the Soomaa NP (Viljandi meteorological station)

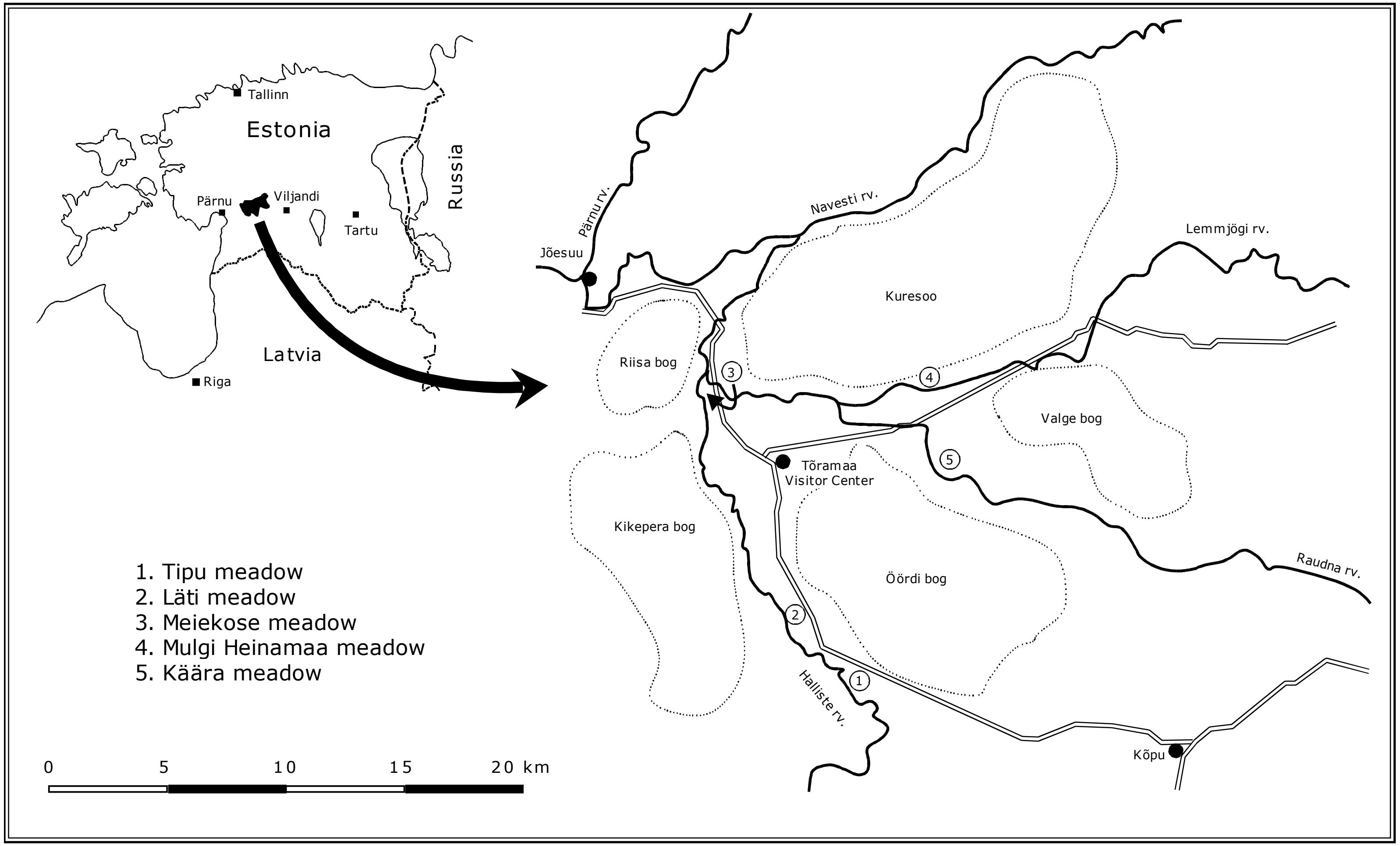


Fig. B.2: Map of Estonia, the Soomaa NP and the major sites visited in this study

Geology and soils

The bedrock in the Soomaa area is made up mainly by middle Devonian sandstone, clay and dolomitic marl (ALLILENDER & ROOSALU 2000). It is overlain by quaternary covers of varying thickness: in the south-east of the area thickness may be 5–10 m while to the north-east it increases to 25–30 m. The quaternary covers consist mainly of glacial lake deposits and moraine.

The main substrate types from which the recent soils of Soomaa floodplains stem are sand, sandy loam and loam (KINK et al. 1996) with loamy substrates covering by far the greatest area. Sand and sandy substrates are found more often in the south and south-east of the park, were the area borders onto post-glacial dune fields. In the floodplains, sandy substrates are located mostly near the river banks were sedimentation is currently low. Loam and loamy substrates are more common in the northern parts of the National Park in the area of the confluences of the rivers Lemmjögi, Raudna and Halliste; generally they are typical for the central floodplains. During the long lasting floods sedimentation is still substantial in this areas. Soil formation in the Soomaa area is largely connected to the hydrological regime. Along the rivers alluvial soils (Fluvisols) can be found: near the river bed sedimentation is strongest and the texture of the soil is more sandy. Consequently soils are often well-drained and at places podzolic (luvic). In the central floodplain, where sediments are finer, soils can remain waterlogged for prolonged periods. In this area gleyic soils of various types can be found. Due to poor drainage peat formation is considerable and so various types of histosols cover the largest part of the park. According to the soil map of the management plan (ALLILENDER & ROOSALU 2000) the following soil types are common in the park area: i) gleyic luvisols and luvisols, ii) dystric (fibric) histosols, iii) eutri-dystric histosols, iv) eutric histosols, v) sod-podzolic or podzolic gleysols, vi) luvi-calcaric and eutri-calcaric gleysols, vii) gleyic sod-podzols, viii) gleyic-rendzic leptosols on calcareous skeletal till and ix) gleyic cambisols or luvisols.

Landscape and hydrology

The Soomaa National Park (NP) lies on the border between Low-Estonia and High-Estonia, in a region called *Estonia intermedia* and further in the *Regio saardeensis* (LIPPMAA 1935). This region is characterised by extensive raised bogs and swampy forests. Its southern part was termed Soomaa, which, in its original sense, covered a greater area than today's Soomaa National Park. The name of the area was well-chosen and already tells a lot about the dominant landscape features: s*oo* in Estonian language means “mire”, *maa* means “land”, so Soomaa is the “Land of mires”.

The landscape of the Soomaa area, as is most of Estonia, is a direct product of the last ice age and the processes during and after the retreat of the continental ice (ALLILENDER & ROOSALU 2000). After the area was freed from the ice cover, an ice-dammed lake formed which covered the area for several centuries. With the disappearance of this lake two characteristic landscape features developed: dune fields marking the shore lines of the shrinking lake (to be found mainly in the southern part of the National Park) and bogs, which developed in shallow depressions in the former lake bottom.

Today's landscape is dominated by the large bog complexes which cover some 30000 ha. These bogs are in a fairly pristine state, except for some peripheral effects from the drainage of nearby forests. Between these mire complexes there is a dense network of rivers which are more or less unregulated and show natural run-off patterns. The Soomaa area experiences regular and extensive floods in spring, causing the locals to speak of a fifth season. Among the topographical features responsible for the floods are:

- the flat relief and small grade of the rivers, causing slow flow, extensive meandering and numerous oxbows lakes
- several small rivers flowing into the main river in a limited area
- neotectonic land upheaval being stronger in the lower than in the middle courses of the Soomaa rivers
- sediment filled and overgrown river beds

These floods can last several weeks and cover more than 100 km^2. Additional floods can occur in wet summers (as happened in 1998) and in autumn.

The floodplains are covered by a mosaic of floodplain forests, fens and semi-natural grasslands. At their maximum extent floodplain grasslands covered around 2000 ha, that is 5.4 % of the area of the National Park. Along the different rivers of the Soomaa area the floodplains show quite distinct morphological and floristic features:

Raudna River

The banks of the upper course are comparably high and steep, consequently floods are only of short duration and of limited extent. Dry and mesic meadows are more common, plants of wetter grounds like *Iris sibirica* or *Gladiolus imbricatus* are rare. There are currently only two farms in Sandra and Kuusekäära in what was formerly a wealthy agricultural area.

Lemmjõgi River

The floodplain of this river is relatively narrow, the river banks are less steep. Floods can rise very quickly after periods of rain, and during the study period the terrain was flooded several times during the summer months. *Iris sibirica* and *Gladiolus imbricatus* are abundant and swampy forests are directly adjacent to the floodplain meadows. Currently there are no permanent settlements nor agricultural activities within the borders of the National Park.

Halliste River

This is the biggest floodplain in the National Park, which is completely flooded during the spring flood. Its banks are lined by extensive stands of *Filipendula ulmaria* and sedges, but also so-called wooded meadows do occur.

Tõramaa River

When building the new gravel road the regime of this river was partly disturbed and parts of the floodplain began to paludify (Allilender & Roosalu 2000). The floodplain is comparably narrow and directly surrounded by forest.

Flora and vegetation

Despite its rather small area Estonia has a very rich and diverse vegetation ranging from dry calcareous vegetation and alvars, various dry, mesic and moist forest types to extensive wetlands, fens and mires. Geobotanically, Estonia is situated on the border between the nemoral and the boreal or, in other words, in the hemiboreal zone (Raukas 1995). The zonal vegetation is boreo-nemoral forest dominated by *Picea abies* with additional *Betula pendula, Populus tremula* and *Pinus sylvestris*. Nemoral forests are only found on exceptionally fertile soils and in a narrow strip along the northern coast at the foot of the glint (Lõhmus 1995). In total forests cover some 45 % of the Estonian area. Due to the humid climate Estonia is rich in wetlands and mires covering 31 % of the country. Around twenty percent of Estonia are covered by grasslands (Paal 1998).

The Estonian flora is made up of 1441 vascular plants (Kukk 1999) and 510 bryophytes (Ingerpuu et al. 1994). 554 vascular plant species and 193 bryophytes have been recorded in the area of the Soomaa NP. Twenty four species are legally protected, eleven are included in the Estonian Red data Book (Allilender & Roosalu 2000). Endangered or protected species relevant for this study are *Dactylorhiza incarnata, D. maculata, Iris sibirica, Listera ovata, Platanthera chlorantha, Primula farinosa, Thalictrum lucidum* and *Viola uliginosa*.

The nomenclature used in this study follows Kukk (1999) for vascular plants and Ingerpuu et al. (1994) for bryophytes.

2 Land use

Historical land use

Archaeological findings indicate that the Soomaa area has been inhabited for several thousand years (Allilender & Roosalu 2000). Earliest findings of arrowheads, fishing-spears and hooks, axes etc. date back to the stone and bronze age. At that time men had probably only a minor influence on the landscape as they lived mainly on hunting and fishing (Küster 1996). Earliest written evidence comes in the form of a map from 1588, where some of the current villages are already mentioned. The villages flourished during the end of the 19th and the beginning of the 20th century when the local population rose to a maximum of around 500 (Allilender & Roosalu 2000). The main agricultural activity was cattle breeding, as the natural conditions were too unfavourable for crops. With the soviet occupation agriculture was concentrated in finally only three collective farms and the population of Soomaa continuously declined due to deportation and abandonment of villages. During the soviet time, many meadows were afforested with spruce, or entirely abandoned. After the end of the soviet occupation the collective farms were closed and management of the floodplain meadows ceased altogether. Private farmers were only mowing a few dozen hectares of meadows in the Soomaa area.

The Soomaa National Park

The Soomaa NP was established on December 8th 1993, its aim being the protection of mires, floodplain meadows and forests of Mid-Estonia. On its current area a Botanical Reserve of the Halliste wooded meadow had been established in 1957, and the main mire complexes Kuuresoo, Valgeraba, Öördi and Kikepera raba had the status of mires reserves since 1981.

Three types of zones with different protection schemes are defined in Soomaa NP: strict nature reserve, special management zone and limited management zone. In the *strict nature reserve* no human interference is permitted and ecosystems are allowed to develop only by natural processes (0.4 % of the park area). *Special management zones* have been established with the intention to preserve or restore natural and semi-natural communities like forests and floodplain meadows and mires (77.3 %). All other areas that do belong to the above mentioned zones (22.2 % of the park area) constitute the *limited management zone*. Economic activity has to comply with the *Protected Natural Objects Act* and the *Protection Rules* (Allilender & Roosalu 2000).

Considering the huge area of former floodplain meadows and the costs of management, the meadows have been divided into four management classes to ensure an optimal allocation of financial resources (Allilender & Roosalu 2000). The meadows assigned to *Management Class I* (209 ha) have the highest priority in management, i.e. they are mown annually and the hay is removed from the meadow. These meadows are found mainly on drier sites, they have a species rich herb layer and their successional status is very good, i.e. typical indicators of abandonment like *Filipendula ulmaria* and various species of *Salix ssp.* are only of small abundance. Most of the meadows discussed in this study belong to this and the next category. Meadows in *Management Class II* (140 ha) are still in a good condition, they are mostly mesic to wet floodplain meadows with a species rich herb layer, that are mown ± every second year to maintain or improve their status. Meadows in *Management Class III* (140 ha) are to be maintained to preserve the character of connected floodplain complexes. They are mostly large sedge communities that need to be mown every third to fourth year to keep them from being overgrown with bushes. Those meadows that have already undergone considerable successional development and that cannot currently be managed form *Management Class IV* (805 ha). Management of the floodplain meadows is done by local farmers on a contract basis.

C. Vegetation types and habitat parameters

1 Introduction

Semi-natural grasslands are among the most species-rich plant communities in Europe (Kull & Zobel 1991), and thus attracted considerable attention by both plant ecologists and phytosociologists. Descriptive and classificatory treatments of grasslands in general and floodplain grasslands in particular date back well to the beginning of phytosociology (Cajander 1903; Cajander 1908; Cajander 1909; Regel 1925; Lippmaa 1931; Steffen 1931; Regel 1936). In the following decades a vast body of information on the synecological and syntaxonomical relations of grasslands and their habitats has accumulated. In Central and Western Europe this has led to a well established, syntaxonomical system of plant communities according to the Braun-Blanquet school of phytosociology, which is recorded e.g. in the currently published *Synopsis der Pflanzengesellschaften Deutschlands* (Dierschke 1996 ff.) with its volumes 3, 8 and 9 (Dierschke 1997; Peppler-Lisbach & Petersen 2001; Burkart et al. 2004) being relevant for the current study. A competing system is that of the so-called *Eberswalde-school* which follows a similar but not identical methodology and nomenclature (Passarge 1996; 1999; 2002); due to its eastern German focus and the similarity of the described vegetation units it is of special interest for this study.

Floodplain grasslands as they are understood in this study, i.e. all regularly flooded graminoid or forb-dominated communities that are at least irregularly mown or grazed or that have obviously been mown or grazed in the recent past, cover a broad range of communities from dry grasslands on sandy soils, mesic and moist grasslands to reed and sedge communities. Many of these communities are easily recognised as members of such alliances as *Nardion*, *Molinion* or *Magnocaricion* although the exact position and circumscription may remain open for debate. Other communities, especially those where *Sesleria caerulea* comes to dominance, are not known in Central and Western Europe and the position of these communities in the established syntaxonomical system will have to be carefully considered.

Estonian vegetation science did not adopt the Braun-Blanquet school of phytosociology with its emphasis on a purely floristic methodology and the creation of a formal hierarchical system. The current classifications of Estonian vegetation in general (Paal 1997), and of floodplain grassland in particular (Krall et al. 1980) are more akin to the other Scandinavian schools of phytosociology in that they put more emphasis on the dominant species in the definition of communities (TRASS & MALMER 1973).

PAAL (1997) uses a hierarchical system with four levels: *site types* at the lowest level, *type groups* and *type classes;* at the highest level PAAL distinguishes eight physiognomic *vegetation types*, i.e. forests, grasslands, mires, vegetation of outcrops, of dunes and sandy plains, of waterbodies, ruderal vegetation and cultivated vegetation. Grasslands are divided into four *type classes*: dry and fresh grasslands, floodplain grasslands, coastal meadows and paludified grasslands. These type classes are defined *a priori* on the basis of broad habitat types. From this follows that very similar or identical communities may be listed within several type classes. Table C.1 gives a summary of the relevant type groups from PAAL (1997). Estonian vegetation scientists like PAAL and LAASIMER (LAASIMER 1965) use a terminology for communities that resembles the classical phytosociological system (e.g. "Nardo-Seslerietum", Table C.1), which, however, is completely independent of its central European counterpart and lacks its strict nomenclatural conventions. KRALL et al. (1980) group the communities of Estonian floodplain meadows into six ecologically and floristically defined *community types*, which are listed in Table C.2. Because of its broad and pragmatic nature this system will be used throughout the study as a baseline for various comparisons.

To my knowledge no attempt has been made so far to apply the Braun-Blanquet-methodology and system to Estonian grasslands. Cursory remarks about Estonian wet grasslands or floodplain grasslands can be found in PASSARGE (1976), ELLENBERG (1996) and DIERSSEN (1996), but in all this cases Estonia is at the periphery of or even outside the area under consideration.

The aim of this study will therefore be (1) to document the variety of floodplain grasslands in the Soomaa area as they have been preserved to the present day and, in a first step, group them into rankless communities; for this the Braun-Blanquet techniques of relevé sampling and table sorting, assisted by multivariate statistical methods, will be used; (2) to document the habitat conditions of the studied floodplain grasslands (soil parameters and groundwater dynamics) in six transects typical for different parts of the Soomaa NP; (3) to assign the described communities to existing Estonian grassland classifications and to existing syntaxa according to the Braun-Blanquet school of phytosociology and to compare these different systems.

This section is not strictly divided into a "Results" and a "Discussion" chapter. As it is common practice in the phytosociological literature, results and their discussion are presented in the same chapters which allows for a more compact and accessible treatment.

Table C.1: Types of Estonian floodplain and paludified grassland (from Paal 1997)

- 2.2.1. Floodplain grassland
  - 2.2.1.1.Fresh floodplain grassland
    - 2.2.1.1.1. Agrostio tenuis-Anthoxanthetum
    - 2.2.1.1.2. Festuco ovinae-Seslerietum
    - 2.2.1.1.3. Nardo-Seslerietum
    - 2.2.1.1.4. Agrostio tenuis-Galietum borealis
    - 2.2.1.1.5. Agrostitetum giganteae
    - 2.2.1.1.6. Nardo-Danthonietum
  - 2.2.1.2. Wet floodplain grassland
    - 2.2.1.2.1. Festuco rubrae-Deschampsietum
    - 2.2.1.2.2. Carici cespitosae-Deschampsietum
    - 2.2.1.2.3. Alopecuretum pratensis
    - 2.2.1.2.4. Alopecuro-Elymetum
    - 2.2.1.2.5. Geranio palustris-Filipenduletum
    - 2.2.1.2.6. Deschampsio-Stellarietum palustris
    - 2.2.1.2.7. Phalarisetum arundinaceae
    - 2.2.1.2.8. Calamagrostietum canescentis
    - 2.2.1.2.9. Caricetum distichae
    - 2.2.1.2.10. Polygono-Cirsietum
    - 2.2.1.2.11. Caricetum acutae
    - 2.2.1.2.12. Caricetum vesicario-rostratae
    - 2.2.1.2.13. Carici paniceae-Seslerietum
    - 2.2.1.2.14. Caricetum diandro-nigrae
    - 2.2.1.2.15. Caricetum appropinquato-cespitosae
    - 2.2.1.2.16. Caricetum elatae
    - 2.2.1.2.17. Drepanoclado-Caricetum lasiocarpae
    - 2.2.1.2.18. Phragmitetum australis
    - 2.2.1.2.19. Phragmiteo-Schoenoplectetum
- 2.4.1. Paludified grasslands
  - 2.4.1.1. Poor paludified grassland
    - 2.4.1.1.1. Caricetum paniceae-nigrae
    - 2.4.1.1.2. Nardo-Danthonietum
    - 2.4.1.1.3. Caricetum elongatae-canescentis
    - 2.4.1.1.4. Polytricho-Nardetum
    - 2.4.1.1.5. Deschampsio-Potentilletum erectae
    - 2.4.1.1.6. Caricetum flavae
    - 2.4.1.1.7. Polygono-Cirsietum
    - 2.4.1.1.8. Geranio palustris-Filipenduletum
  - 2.4.1.2. Rich paludified grasslands
    - 2.4.1.2.1. Scorzonero-Caricetum pallescentis
    - 2.4.1.2.2. Primulo-Seslerietum
    - 2.4.1.2.3. Carici paniceae-Seslerietum
    - 2.4.1.2.4. Nardo-Seslerietum
    - 2.4.1.2.5. Caricetum davallianae
    - 2.4.1.2.6. Caricetum hostianae
    - 2.4.1.2.7. Deschampsio-Ranunculetum acris

Table C.2: Community types of floodplain grassland in Estonia (from Truus & Tõnisson (1998), after Krall et al. (1980) and Aug & Kokk (1983))

Community type	Flooding and moisture conditions	Characteristic plant species
1. Dry floodplain grassland	Dry; occasional flooding	*Sesleria caerulea, Festuca ovina, Nardus stricta, Agrostis capillaris*
2. Moderately moist floodplain grassland	Regularly flooded, well drained	*Agrostis gigantea, Festuca rubra, Alopecurus pratensis, Deschampsia cespitosa*
3. Moist floodplain grassland	Regularly flooded, well drained	*Cirsium palustre, Filipendula ulmaria, Deschampsia cespitosa, Calamagrostis stricta*
4. Wet floodplain grassland with tall sedges	Permanently saturated	*Carex cespitosa, C. acuta*
5. Wet floodplain grassland with tall grasses	Poorly drained to saturated	*Phalaris arundinacea, Deschampsia cespitosa, Calamagrostis stricta*
6. Floodplain marshes	Permanently inundated	*Sesleria caerulea, Carex panicea, C. elata, C. cespitosa, C. lasiocarpa*

2 Methods

2.1 Vegetation

Vegetation survey

For a survey of the different meadow communities, relevés according to the Braun-Blanquet approach were studied across the whole national park. 84 relevés with an area of 25 m² each were placed in representative and homogeneous areas of the floodplains. Cover was estimated according to a modified Braun-Blanquet scale (+: < 1 %, 1a: 1–3 %, 1b: 3–5 %, 2a: 5–12.5 %, 2b: 12.5–25 %, 3: 25–50 %, 4: 50–75 %, 5: 75–100 % (Pfadenhauer et al. 1986)). This scale, rather than the original Braun-Blanquet scale, was chosen because of its more equal distribution of classes, and because the straight-forward numerical interpretation facilitates statistical analysis. For statistical calculations the arithmetic mean of the ranges was used.

Transects

In addition to the broad vegetation survey six transects were placed along the major rivers of the area. This was done to enable a more fine-scale description of the meadow vegetation along the major gradient from river bank to floodplain. The relevés had a size of 4 m² and were placed in homogeneous areas of all distinguishable vegetation types, but at least every 10 m. Plant cover was estimated according to the same scale as above. Along these transects measurements of habitat parameters (groundwater fluctuations, soil parameters) and vegetation characteristics (biomass) were carried out (see below). Also seed traps were placed along these transects (see Section D). Table C.3 gives a summary of some basic characteristics of these transects.

Biomass

Biomass was sampled along five transects near the groundwater gauges. Five subsamples were collected in a plot of 1 m². They had an area of 0.0625 m² each, totalling 0.3125 m² per sample plot. All plant material was collected (bio- and necromass), living plants were clipped near the soil surface. In all subsamples bio- and necromass were separated before drying. Additionally, in three subsamples of each sample the biomass was separated into *graminoids, herbs* and *mosses.* Samples were first air-dried and stored. Before weighing, the samples were dried in a sauna at 60–80 °C until the weight remained constant.

Vegetation analysis

To achieve an initial sorting of the relevés, a TWINSPAN analysis (Hill 1979, using the version modified by Minchin with strict convergence criteria) was performed on the complete data set of 171 samples by 213 species. Nine pseudospecies cut levels were used reflecting the modified Braun-Blanquet scale used in the relevés (0, 1, 3, 5, 9, 19, 38, 63, 88). Otherwise default settings were selected.

In a second step the TWINSPAN classification was validated and complemented by an analysis of species groups. These species groups were created with the help of the COCKTAIL algorithm of Bruelheide as implemented in the Juice software package (Tichy 2002). Species groups are, however, defined here less strictly than in Bruelheide (1995), where a formalised method is used to first construct species groups (which are non-exclusive, i.e. one species can be member of several groups) and then classify relevés by logically combining the presence or absence of these species groups. In the current context species groups are exclusive groups of species that display the same distributional pattern in the studied relevés and can thus be used to define plant communities. Only those species are listed in species groups that occur with a minimum constancy of II (i.e. ≥ 20 %) in at least one community.

Table C.3 Transects in study area with some basic characteristics, listing the current management, length, number of relevés, number of groundwater gauges and number of seed traps.

Site	River	Current management	Length	No. relevés	Groundwater & soil samples	No. seed traps
Tipu	Halliste	mowing	138 m	21	5	–
Läti	Halliste	mostly fallow	170 m	20	6	10 × 5
Halliste puisniit	Halliste	mostly fallow	84 m	11	5	–
Mulgi Heinamaa 1	Lemmjõgi	mowing	46 m	10	4	–
Mulgi Heinamaa 2	Lemmjõgi	mulching/mowing	99 m	12	5	9 × 5
Käära	Raudna	mowing & burning	122 m	13	5	9 × 5

2.2 Habitat parameters

Groundwater

Along all transects groundwater gauges were installed in all major vegetation types (four to six gauges per transect depending on length of transect). Gauges were constructed of PVC pipes 5 cm in diameter and 1.5 m in length. The pipes were perforated on four sides every 5 cm and were closed with a lid to prevent rain, animals and other objects from entering. In some places it was impossible (due to heavy layers of loam) to get the pipe deeper than ca. 50 cm. In other places it was necessary to clear the gauge regularly of entering sandy soil. Readings of groundwater level were performed in 1999 and 2000 every two weeks. In winter and during floods, readings were impossible due to inaccessibility of the sites. In some drier sites the groundwater level sank deeper than the gauge – also in this case no readings were possible.

Soil

At the same sites as the groundwater gauges soil samples were collected and a selection of soil parameters were measured in the laboratory. These parameters were: soil pH, plant available K and P and C/N-ratio. Soil pH-values were measured in a $CaCl_2$-solution (20 g dry soil, 50 g 0.02 n solution). Plant available P and K were extracted with Calcium-Acetate-Lactate. Phosphorus was measured colometrically after staining with a molybdate-vanadate reagent, K was measured by Atomic Absorption Spectrometry. Contents of C and N were determined using the Dumas Method (dry combustion followed by gas-chromatography). Additionally at each sample location the soil profile was inspected with a 1m Pürckhauer soil corer.

Ellenberg indicator values

As actual measurements of habitat factors were available for only a small number of relevés, mean Ellenberg indicator values (IV) were calculated for all relevés. Mean values were calculated for F (moisture), N (nitrogen or fertility) and R (acidity), weighting by abundance was applied and bryophytes were excluded. Indicator values have proven useful to complement or, in cases, even replace direct measurements of environmental variables (DIEKMANN 2003) and are also used successfully outside central Europe, the area they were originally defined for. Interpretation will, however, have to proceed carefully as the different, more continental, climate in Estonia will probably cause different ecological behaviour in some plants. Furthermore, several plant species display a strongly bimodal distribution, especially with respect to soil moisture: *Carex flava*, *C. nigra*, *C. panicea*, *C. pulicaris* and *Sesleria caerulea* are all typical for wet fen communities and are listed with indicator values for moisture of 8 or 9. In the studied meadows, however, these species also occur commonly in the driest grassland types so that the indicator values will be misleading in these cases.

2.3 Statistical methods

The variation of soil parameters in different vegetation types was analysed with a Kruskal–Wallis one-way ANOVA, followed by the Steel-Dwass test (STEEL 1960), a non-parametric multiple comparison procedure equivalent to the Tukey-test. Spearman's rank correlation analysis was used to test the relationship between soil parameters and the species number of the established vegetation. All statistical analyses were performed with the free R package version 1.8.1 (R DEVELOPMENT CORE TEAM 2003), except for the Steel-Dwass test, which was done with the graphing and statistical package KyPlot version 2.0 beta 15 (YOSHIOKA 2001).

The inter-relationship of vegetation and environmental parameters was analysed by means of Canonical Correlation Analysis (CCA). The results are presented graphically in an overlay plot where the position of the samples in ordination space is represented by symbols (species were omitted from the graph as they were not the main focus of this analysis); environmental parameters are represented by arrows pointing into the direction of maximum correlation with variation in species composition. The length of the arrows is an indication of the strength of the correlation. A permutation procedure was used to test whether the eigenvalues were significant. CCA was performed with the VEGAN-package (OKSANEN 2004) within the R statistical package (R DEVELOPMENT CORE TEAM 2003).

3 Results and Discussion

3.1 Species groups

Table C.4 presents a summary of the nineteen species groups that were identified with the help of the COCKTAIL algorithm of Bruelheide and which were used in the classification of the Soomaa floodplain meadows. Mean Ellenberg indicator values (Fig. C.1) show that the species groups cover a wide spectrum of habitat conditions and are thus well suited for the delimitation of vegetation types. While a species group must *per definitionem* consist of at least two species a number of single species displayed distinctive distributional patterns and were also used to define communities: *Campanula glomerata, Taraxacum officinale, Carex acuta, Carex leporina* and *Carex vulpina*.

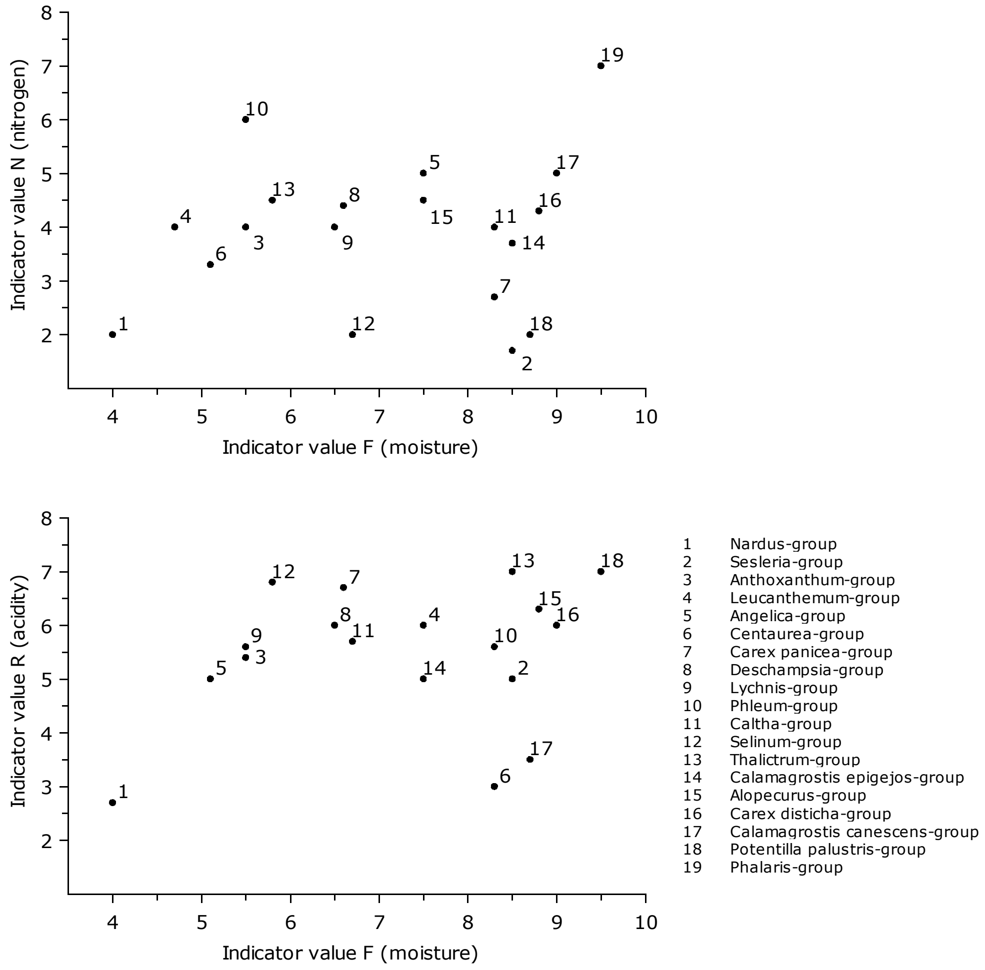


Fig. C.1: Ecological characterization of species groups with the help of mean Ellenberg indicator values for moisture (F), nitrogen (N) and acidity (R).

Table C.4: Species groups with their member species and mean Ellenberg indicator values for moisture (F), nitrogen (N) and acidity (R). Groups sorted from mainly dry to mainly wet habitat preference.

Species group	Members	Mean Ellenberg indicator values		
		F	N	R
Nardus-group	*Danthonia decumbens, Hieracium pilosella, Nardus stricta, Viola canina ssp. canina*	4.0	2.0	2.7
Sesleria-group	*Carex pulicaris, Festuca ovina, Sesleria caerulea*	8.5	1.7	5.0
Anthoxanthum-group	*Anthoxanthum odoratum, Hieracium lactucella, Plantago lanceolata, Rhytidiadelphus squarrosus, Trifolium pratense, T. repens, Veronica chamaedrys*	5.5	4.0	5.4
Leucanthemum-group	*Cerastium holosteoides, Leucanthemum vulgare, Prunella vulgaris*	4.7	4.0	–
Alopecurus-group	*Alopecurus pratensis, Stellaria palustris*	7.5	4.5	5.0
Phleum-group	*Festuca pratensis, Phleum pratense*	5.5	6.0	5.6
Selinum-group	*Campylium stellatum, Iris sibirica, Scorzonera humilis, Selinum carvifolia, Succisa pratensis, Thuidium philibertii, Viola canina ssp. montana*	6.7	2.0	5.7
Thalictrum lucidum-group	*Geranium palustre, Melampyrum nemorosum, Thalictrum lucidum, Trifolium medium*	5.8	4.5	6.8
Calamagrostis epigejos-group	*Calamagrostis epigejos, Carex flava, Equisetum palustre*	8.5	3.7	7.0
Centaurea-group	*Achillea millefolium, A. ptarmica, Agrostis capillaris, Alchemilla vulgaris agg., Briza media, Carex pallescens, Centaurea jacea, Dactylis glomerata, Galium boreale, G. mollugo, Luzula campestris, Potentilla erecta, Stellaria graminea*	5.1	3.3	5.0
Angelica-group	*Angelica sylvestris, Trollius europaeus*	7.5	5.0	6.0
Carex panicea-group	*Agrostis canina, Carex panicea, C. nigra*	8.3	2.7	3.0
Calamagrostis canescens-group	*Calamagrostis canescens, Carex vesicaria, Viola uliginosa*	9.0	5.0	6.0
Potentilla palustris-group	*Calamagrostis stricta, Calliergon cordifolium, Potentilla palustris*	8.7	2.0	3.5
Lychnis-group	*Calliergonella cuspidata, Cardamine pratensis, Climacium dendroides, Lychnis flos-cuculi*	6.5	–	6.0
Deschampsia-group	*Deschampsia cespitosa, Festuca rubra, Filipendula ulmaria, Galium uliginosum, Geum rivale, Lathyrus pratensis, Poa pratensis, Ranunculus acris, R. auricomus, Rumex acetosa, Vicia cracca*	6.6	4.4	6.7
Caltha-group	*Caltha palustris, Galium palustre, Ranunculus repens*	8.3	4.0	5.6
Carex disticha-group	*Carex cespitosa, C. disticha, Juncus filiformis, Valeriana officinalis*	8.8	4.3	6.3
Phalaris-group	*Phalaris arundinacea, Phragmites australis*	9.5	7.0	7.0

3.2 Plant communities

TWINSPAN and subsequent refinement with the help of species groups resulted in 15 communities, which will first be presented as rankless entities (Table C.5). Naming of the communities is still tentative and rather follows the Scandinavian school in using dominant species instead of strict character or differential species. This approach is also advocated by MUELLER-DOMBOIS & ELLENBERG (1974) when communities are not formally placed in the hierarchical system of the Braun-Blanquet-school. Furthermore, it was found during analysis that good character species were rather rare and communities were best defined by the positive and negative combination of species groups.

As there is yet no accepted hierarchical system of Estonian plant communities according to the Braun-Blanquet approach, the communities will be grouped pragmatically into five community types as suggested by KRALL et al. (1980, see Table C.2). According to this system, two communities belong to the dry and both three to the mesic and moist grassland type; seven communities are characterised as wet with either tall grasses or sedges, floodplain marshes were not found in the area. A synoptical table (Table C.6) can be found on page 24.

Table C.5: List of communities of floodplain grassland described for the Soomaa NP

Community No. (Chapter)	Community types and communities
	Dry floodplain grassland
1. (3.3.1.1)	Nardus stricta-Festuca ovina-community
2. (3.3.1.2)	Festuca ovina-Sesleria caerulea-community
	Mesic floodplain grassland
3. (3.3.2.1)	Festuca rubra-Deschampsia-community
4. (3.3.2.2)	Alopecurus pratensis-Galium mollugo-community
5. (3.3.2.3)	Alopecurus pratensis-Deschampsia-community
	Moist floodplain grassland
6. (3.3.3.1)	Sesleria caerulea-Deschampsia-community
7. (3.3.3.2)	Melampyrum nemorosum-Deschampsia-community
8. (3.3.3.3)	Carex cespitosa-Deschampsia-community
	Wet floodplain grassland with tall sedges
9. (3.3.4.1)	Carex disticha-Juncus filiformis-community
10. (3.3.4.2)	Ranunculus flammula-Juncus filiformis-community
11. (3.3.4.3)	Potentilla palustris-Carex disticha-community
12. (3.3.4.4)	Carex acuta-community
13. (3.3.4.5)	Carex elata-community
	Wet floodplain grassland with tall grasses
14. (3.3.5.1)	Phalaris-Phragmites-community
15. (3.3.5.2)	Carex acuta-Schoenoplectus lacustris-community

3.2.1 Dry floodplain grasslands

Two communities of dry grassland *sensu* Krall et al. (1980) were identified in the Soomaa floodplains, i.e. the *Nardus-Festuca ovina-* and the *Festuca ovina-Sesleria caerulea*-community. Both are characterised by the presence of the *Sesleria*-group, of which especially *Festuca ovina* is highly frequent in both communities. This group also occurs characteristically in the moister *Sesleria-Deschampsia*-community but is combined there with different, more moisture-indicating groups. The *Sesleria*-group is here accompanied by the *Anthoxanthum*-group, characteristic for the dry to moderately moist or mesic communities, and by the *Centaurea*-group which forms the common stock of all dry to moist communities.

These dry grassland communities grow on sandy, well drained substrates in the highest parts of the floodplains and are only rarely, if ever, flooded. The groundwater level drops lower than one meter below surface for more than 50 % and rises higher than 50 cm for less than 10 % of the growing season.

3.2.1.1 Nardus-Festuca ovina community

This community can be positively characterised by the presence of the *Nardus*-group, which is more or less lacking in all other communities. The matrix of this community is formed by the two grasses *Nardus stricta* and *Festuca ovina*. Additional highly constant species are *Rhytidiadelphus squarrosus* from the *Anthoxanthum*-group, *Achillea millefolium*, *Luzula campestris* and *Agrostis tenuis* from the *Centaurea*-group and *Deschampsia cespitosa*, *Ranunculus acris* and *Vicia cracca* from the *Deschampsia*-group. The five most dominant species (here and in the description of the following communities only species with a constancy of 50 % or higher are listed) are *Nardus stricta, Rhytidiadelphus squarrosus, Festuca ovina, Festuca rubra* and *Sesleria caerulea*. In the classification of Paal (1997) this community corresponds to the *Festuco ovinae-Nardetum* of the "Dry boreal grassland site type" and partially to the *Festuco ovinae-Seslerietum* and *Nardo-Danthonietum* of the "Fresh floodplain grassland site type".

The *Nardus-Festuca ovina* community is of low growth, being merely between 10 and 30 cm in height. It is clearly dominated by graminoids (mean cover 100 %) and bryophytes (mean cover 65 %) which achieve their highest importance in this community. Forbs are of medium and sedges of low importance, although certain *Carex*-species (*C. nigra, C. pallescens* and *C. panicea*) are quite common.

The *Nardus-Festuca ovina* community can be found on the driest parts of the floodplains that are rarely, if ever, flooded. Their typical habitat are sandy banks along the current or former river beds. The community generally occurs only in small patches as its natural habitat never covers larger areas. Some of these habitats may have been used as building grounds for farmsteads or barns, as flooding is unlikely. In some places the remains of wooden buildings can still be seen and in a few cases charcoal pieces were found in the soil. Nutrient availability as indicated by the Ellenberg indicator value N is the lowest of all studied communities (mean N value 2.3).

3.2.1.2 Festuca ovina-Sesleria caerulea community

This community is similar in composition to the preceding one except for the almost complete absence of members of the *Nardus*-group. It can however – if somewhat weakly – be characterised by the presence of *Campanula glomerata,* which reaches a constancy of III only in this community. The most constant species are *Alchemilla vulgaris agg., Deschampsia cespitosa, Filipendula vulgaris, Ranunculus acris* and *Vicia cracca*. Most of these are members of the *Deschampsia*-group which is the common core of practically all grassland communities. The five most dominant species are *Rhytidiadelphus squarrosus* and *Festuca ovina* (both with a mean cover of 38 %) plus *Sesleria caerulea, Festuca rubra* and *Alchemilla vulgaris agg.* (with a mean cover of 19 %). Being of similar mean height as the preceding community, forbs rather than grasses are the dominant growth form (forbs 99 % and grasses 75 % mean cover) while bryophytes and sedges are of slightly less importance here (50 % and 10 % mean cover). This community is clearly identical with the *Festuco ovinae-Seslerietum* of the "Fresh floodplain grassland site type" listed by Paal (1997).

The groundwater data suggest that this community is slightly less dry than the preceding one, the level dropping for a ca. 20 % shorter period lower than 1 m below surface. In contrast to the *Nardus-Festuca ovina*-community it may cover larger areas of the sandy, well-drained upper parts of the floodplain. Ellenberg indicator values suggest that nutrient availability is slightly better in this community (mean N value 3.1) although data from the soil analysis do not support this (possibly a consequence of the limited number of samples).

Table C.6: Synoptic table of fifteen communities of floodplain grassland recognised for the Soomaa area. Constancy classes III through V indicated by roman capitals, classes I and II indicated by dashes (- and --) for clarity of the overall pattern. Small superscript numbers indicate mean cover.

Community No.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
No. of relevés	6	17	15	25	12	18	9	18	17	3	10	9	2	5	2
Mean species no.	35	38	40	35	24	40	29	30	26	15	27	7	4	10	7
mean cover of grasses (%)	102	75	73	85	60	71	44	51	28	9	24	10	2	81	39
mean cover of sedges (%)	17	10	12	18	13	10	38	47	101	43	73	83	88	0	44
mean cover of forbs (%)	58	99	88	138	76	117	138	103	72	17	62	18	11	39	6
mean cover of bryophytes (%)	65	49	41	20	1	54	29	10	17	6	27	0	0	1	0
No. of soil samples	1	3	2	3	1	2	3	6	2		2	3		1	
pH (CaCl$_2$)	4.9	5.1	5.2	5.3	5.5	5.6	5.3	5.3	5.1		5.1	5.5		6.5	
K (mg/kg)	35	35	94	21	22	21	55	67	44		41	34		59	
N (%)	0.3	0.3	0.4	0.3	0.4	0.6	0.5	0.7	0.5		1.0	0.8		0.4	
C (%)	3.3	3.4	4.5	3.6	4.2	6.9	5.3	7.6	4.9		11	8.6		4.8	
C/N ratio	11	10	9.9	10	9.9	11	10	11	11		11	11		13	
P (mg/kg)	34	16	23	16	33	16	33	35	27		38	35		54	
GW > -50	6.5	7.7	30	2.5	15	28	15	34	33		53	72		18	
GW < -100	79	59	28	79	63	34	28	24	19		2.2	0.5		14	
Ellenberg iv F	6.3	6.4	6.2	6.3	7.0	6.7	6.4	7.8	8.1	8.5	8.1	8.6	9.8	8.4	10
Ellenberg iv N	2.3	3.1	4.0	4.5	4.9	2.8	4.1	4.3	4.4	3.6	4.1	5.2	4.9	6.7	6.8
Ellenberg iv R	4.1	5.5	5.5	6.0	6.0	6.4	6.5	6.4	6.9	4.8	6.4	6.1	6.5	7.1	6.6
<u>Nardus stricta-group</u>															
Danthonia decumbens	$--^{+}$	$-^{+}$	$-^{+}$	.	.	$-^{+}$	.	.	.	.	.	.	.	.	.
Hieracium pilosella	IV^{1b}	$--^{1a}$	$-^{+}$	.	.	$-^{+}$	.	.	.	.	.	.	.	.	.
Nardus stricta	V^{3}	$-^{1a}$	$-^{1a}$	.	.	$-^{+}$	.	.	.	.	.	.	.	.	.
Viola canina ssp. canina	III^{2a}	$-^{+}$	$-^{+}$	$-^{1a}$	$-^{1a}$	$--^{1b}$	$-^{+}$	$-^{1a}$	.	.	.	.	.	.	.
<u>Sesleria caerulea-group</u>															
Carex pulicaris	$--^{1a}$	$--^{1a}$	$-^{+}$	.	.	$--^{1a}$	.	.	.	.	$-^{+}$	.	.	.	.
Festuca ovina	V^{3}	IV^{3}	$-^{2b}$	$-^{2a}$	.	IV^{2a}	.	$-^{+}$	$-^{1a}$	.	.	.	.	.	.
Sesleria caerulea	III^{3}	IV^{2b}	$--^{1a}$	$-^{1a}$	.	V^{3}	$--^{1b}$	$-^{2a}$	.	.	$-^{1a}$	.	.	.	.
<u>Anthoxanthum odoratum-group</u>															
Anthoxanthum odoratum	IV^{1a}	IV^{1a}	V^{1a}	III^{1a}	$-^{2a}$	$--^{1a}$	.	$-^{1b}$	$-^{+}$	.	$-^{+}$	.	.	.	.
Hieracium lactucella	$--^{+}$	$--^{1a}$	$--^{1a}$	.	.	.	.	$-^{1a}$	.	.	.	.	.	.	.
Plantago lanceolata	III^{1a}	III^{1a}	III^{1a}	$-^{1b}$	.	$-^{1a}$	.	.	.	.	.	.	.	.	.
Rhytidiadelphus squarrosus	V^{3}	V^{3}	V^{3}	III^{2b}	.	$--^{2b}$	$--^{3}$	$-^{2a}$	$--^{1a}$	.	.	.	.	.	.
Trifolium pratense	IV^{1b}	III^{1a}	IV^{2a}	$--^{2a}$	.	$--^{+}$	.	.	$-^{1a}$	.	.	.	.	.	.
Trifolium repens	$--^{1a}$	$--^{1a}$	III^{1a}	$--^{1a}$	$--^{1a}$	$-^{+}$	.	.	$-^{+}$	.	.	.	.	.	.
Veronica chamaedrys	V^{1a}	III^{+}	III^{1b}	$--^{1a}$	$-^{+}$	$-^{1a}$	$--^{1a}$	.	.	.	.	.	.	.	.
<u>Leucanthemum vulgare-group</u>															
Cerastium holosteoides	$-^{+}$	III^{1a}	IV^{+}	$--^{+}$	$--^{+}$	$--^{+}$	.	$-^{+}$	.	.	.	.	.	.	.
Leucanthemum vulgare	$--^{+}$	III^{1a}	III^{1a}	$-^{1a}$	.	$-^{+}$	.	.	.	.	.	.	.	.	.
Prunella vulgaris	$-^{1a}$	III^{+}	IV^{1b}	$-^{+}$	.	$--^{+}$	.	$--^{1a}$	$-^{+}$	.	.	.	.	.	.
<u>Taraxacum officinale-group</u>															
Taraxacum officinale agg.	.	$-^{+}$	$-^{1a}$	III^{2a}	III^{2a}	$--^{1a}$	.	$--^{1a}$	$-^{2a}$	.	$-^{1a}$	$-^{+}$	.	.	.
Veronica longifolia	.	.	.	$--^{2a}$	$-^{+}$	$-^{1b}$	.	$--^{1a}$	$--^{1a}$	.	.	$--^{+}$	.	$--^{2a}$	.
<u>Alopecurus pratensis-group</u>															
Alopecurus pratensis	.	$--^{1a}$	$-^{1a}$	V^{2b}	V^{3}	$-^{+}$	.	$--^{2a}$	IV^{2a}	2^{1a}	III^{1a}	$--^{2a}$	1^{1a}	.	.
Stellaria palustris	.	$-^{+}$	$-^{+}$	$-^{1a}$	III^{1a}	.	.	$--^{+}$	III^{1b}	.	$--^{+}$	$--^{1a}$	.	.	.
<u>Phleum pratense-group</u>															
Festuca pratensis	$--^{+}$	$--^{1a}$	V^{1b}	IV^{2a}	III^{2a}	$--^{1a}$	$--^{+}$	$-^{1a}$	III^{1b}	.	$-^{1a}$	.	.	.	.
Phleum pratense	$-^{+}$	III^{1a}	IV^{1b}	V^{2a}	III^{2a}	$-^{1a}$	III^{1a}	$--^{1a}$	III^{1a}	1^{+}	$-^{+}$	.	.	$-^{1a}$	.
<u>Selinum carvifolia-group</u>															
Campylium stellatum	.	$-^{+}$	$-^{+}$	$-^{+}$	.	$--^{1a}$	$-^{1a}$	$-^{+}$	.	.	.	.	.	.	.
Iris sibirica	.	.	.	.	.	$--^{2a}$	$--^{2a}$	$--^{+}$	$-^{+}$	.	$-^{+}$	$-^{+}$	.	.	.
Scorzonera humilis	$-^{1a}$	$-^{2a}$	.	$-^{2b}$	.	V^{2b}	IV^{1b}	.	.	.	.	.	.	.	.
Selinum carvifolia	.	.	.	.	.	IV^{2a}	IV^{2a}	$--^{1b}$	$-^{+}$	.	$-^{1b}$	.	.	.	.
Succisa pratensis	$-^{1b}$	$--^{1a}$	.	$-^{+}$	.	V^{2a}	$--^{2a}$	$--^{1a}$	$-^{1b}$	.	$-^{+}$	.	.	.	.

Community No.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
Thuidium philibertii	.	.	$-^{1a}$	$-^{2a}$	.	V^{3}	III^{2b}	$-^{+}$	$-^{1a}$	.	$-^{2a}$	.	.	.	.
Viola canina ssp. montana	$-^{1a}$	$--^{1a}$	.	$--^{1a}$	$-^{1a}$	IV^{1a}	IV^{1a}	$-^{2a}$	.	.	.	.	.	.	.
Geranium palustre-group															
Geranium palustre	.	$--^{2a}$	$-^{1b}$	$-^{1a}$	.	$-^{2b}$	III^{2b}	$-^{3}$	$-^{+}$	.	$-^{+}$	.	.	.	.
Melampyrum nemorosum	.	.	.	.	.	$-^{2b}$	V^{3}	$-^{4}$	.	.	$-^{3}$	.	.	.	.
Thalictrum lucidum	.	.	.	$-^{1a}$	$-^{1a}$	$-^{+}$	V^{1b}	$-^{1a}$	$-^{+}$	.	.	.	.	.	.
Trifolium medium	.	.	.	$-^{3}$	.	.	III^{2a}	.	.	.	.	.	.	.	.
Calamagrostis epigejos-group															
Calamagrostis epigejos	.	$-^{+}$	.	$-^{2a}$	.	III^{2a}	.	III^{2a}	.	.	.	.	.	.	.
Carex flava	-	--	-	-	.	IV	-	--	-	.	-	.	.	.	.
Equisetum palustre	.	.	.	.	.	--	.	--	-	.	-	.	.	.	.
Centaurea jacea-group															
Achillea millefolium	V^{1a}	IV^{1b}	V^{1b}	V^{2a}	$--^{1a}$	III^{1a}	$--^{+}$	.	$-^{1a}$	.	.	.	.	.	.
Achillea ptarmica	IV^{1a}	IV^{1a}	IV^{1b}	V^{2a}	III^{1a}	IV^{+}	$-^{+}$	$--^{1a}$	$--^{1b}$	.	$-^{+}$	.	.	.	.
Agrostis tenuis	V^{1a}	IV^{1a}	V^{1b}	III^{2a}	--	$--^{1a}$	IV^{+}	$-^{1a}$	$--^{1a}$	.	$-^{1a}$	.	.	.	.
Alchemilla vulgaris agg.	V^{2a}	V^{2b}	V^{2a}	V^{2a}	$--^{1b}$	IV^{2a}	III^{2b}	$-^{1b}$	$-^{1a}$	.	.	.	.	.	.
Briza media	IV^{1a}	V^{1a}	V^{1a}	$--^{1a}$	$-^{1a}$	IV^{1a}	$--^{+}$	$-^{+}$	$-^{1a}$	.	$-^{1a}$	.	.	.	.
Carex pallescens	V^{1a}	V^{1a}	III^{1b}	III^{1a}	III^{+}	III^{1a}	$-^{+}$	$--^{+}$	$-^{+}$	.	.	.	.	.	.
Centaurea jacea	IV^{2a}	IV^{2a}	V^{2a}	IV^{2a}	.	V^{2a}	IV^{1a}	$--^{2a}$	$--^{1b}$	.	.	$-^{+}$	.	.	.
Dactylis glomerata	$-^{1a}$	$--^{1a}$	$--^{1a}$	IV^{2a}	$-^{1b}$	$-^{+}$	III^{2a}	$-^{1a}$	$-^{+}$	.	.	.	.	$-^{1a}$	.
Galium boreale	V^{1b}	V^{2a}	IV^{1a}	IV^{2b}	$--^{1a}$	V^{2a}	V^{2a}	III^{2a}	III^{2a}	.	$-^{+}$	.	.	.	.
Galium mollugo	$--^{1a}$	$--^{1b}$	III^{1b}	V^{2a}	$-^{1a}$	$--^{1a}$	IV^{1b}	$-^{1a}$	$-^{1a}$	.	.	.	.	.	.
Luzula campestris	V^{1a}	IV^{1a}	IV^{1a}	III^{1a}	.	III^{+}	$-^{+}$	$--^{+}$	$-^{+}$	.	$-^{1a}$	.	.	.	.
Potentilla erecta	V^{2a}	V^{2a}	IV^{1b}	$--^{1b}$	$-^{+}$	V^{2a}	III^{2a}	IV^{1b}	$--^{1b}$	.	$-^{2a}$	.	.	.	.
Stellaria graminea	$-^{+}$	III^{+}	IV^{+}	IV^{1a}	$-^{1b}$	$-^{+}$	III^{+}	.	.	.	.	$-^{+}$	.	.	.
Angelica sylvestris-group															
Angelica sylvestris	$-^{+}$	III^{1a}	III^{1b}	IV^{2a}	III^{1b}	IV^{2a}	V^{2a}	IV^{2a}	$--^{2a}$	.	$-^{2a}$	$-^{1a}$	.	$--^{2a}$	.
Trollius europaeus	$--^{+}$	III^{2a}	$-^{1a}$	$--^{2a}$	$-^{1a}$	III^{1b}	IV^{2a}	$--^{2b}$	$-^{1a}$	.	.	.	.	.	.
Carex panicea-group															
Agrostis canina	$-^{1a}$	$-^{+}$	$--^{1a}$	$-^{+}$	.	$-^{1a}$	$-^{+}$	$-^{+}$	$-^{1b}$	3^{1a}	$--^{1a}$	.	.	.	.
Carex nigra	IV^{2a}	IV^{1a}	$--^{+}$	$-^{1a}$	$--^{+}$	$--^{+}$	$--^{1b}$	$--^{+}$	$--^{1b}$	2^{1a}	III^{2a}	.	.	.	.
Carex panicea	V^{1b}	III^{1b}	IV^{1b}	III^{2a}	$--^{1b}$	IV^{1b}	$--^{+}$	$--^{2a}$	$--^{1a}$	2^{1a}	IV^{1b}	.	.	.	.
Calamagrostis canescens-group															
Calamagrostis canescens	.	.	$-^{1a}$	.	.	$-^{2a}$	.	III^{2b}	$--^{2a}$	.	$-^{3}$	$--^{2a}$	1^{+}	.	.
Carex vesicaria	.	$-^{+}$	.	.	.	$-^{1a}$	.	III^{+}	$-^{1a}$	.	$--^{1a}$	III^{1a}	.	.	.
Viola uliginosa	$-^{+}$	.	.	.	.	$-^{+}$	.	$--^{2b}$	$-^{3}$	.	$-^{2a}$	.	.	.	.
Potentilla palustris-group															
Calamagrostis stricta	.	.	$-^{+}$	.	.	.	.	$-^{2a}$	$-^{2a}$	.	$--^{1b}$	.	.	.	.
Calliergon cordifolium	.	.	$-^{1a}$	$-^{3}$	.	.	.	.	$-^{3}$	1^{2a}	III^{2a}	.	.	.	.
Potentilla palustris	.	.	$-^{+}$	.	$-^{+}$	.	.	.	.	1^{1a}	V^{2a}	$-^{1b}$	.	.	.
Carex acuta-group															
Carex acuta	.	$-^{+}$	$-^{+}$	$-^{+}$	$-^{+}$	$-^{1a}$	$--^{1b}$	$-^{1a}$	$--^{2a}$	1^{1a}	-	V^{4}	.	.	2^{3}
Lychnis flos-cuculi-group															
Calliergonella cuspidata	$-^{1a}$	$--^{2b}$	$--^{1a}$	$--^{2b}$	$--^{1b}$	IV^{2a}	III^{2a}	III^{2a}	III^{2b}	.	IV^{2b}	.	.	.	.
Cardamine pratensis	$-^{+}$	$-^{+}$	$--^{+}$	$-^{+}$	III^{+}	$--^{+}$	$-^{+}$	$--^{+}$	III^{+}	.	$-^{1a}$	$--^{1a}$	.	.	.
Climacium dendroides	$-^{3}$	III^{2a}	III^{2b}	$-^{2b}$	$-^{1a}$	III^{2b}	III^{2a}	$--^{1b}$	III^{1b}	.	$--^{2a}$	.	.	.	.
Lychnis flos-cuculi	.	III^{+}	$--^{1a}$	III^{1a}	III^{1a}	III^{+}	$--^{1a}$	III^{1a}	IV^{1a}	.	IV^{1a}	$-^{+}$	.	$-^{1a}$	.
Deschampsia cespitosa-group															
Deschampsia cespitosa	V^{2a}	V^{2a}	V^{2a}	V^{2b}	V^{2b}	V^{2b}	V^{2b}	IV^{2b}	V^{2a}	3^{1a}	V^{2a}	$-^{1b}$	.	$-^{+}$	.
Festuca rubra	III^{3}	III^{2b}	V^{3}	V^{2b}	V^{2a}	IV^{1b}	IV^{2b}	IV^{2a}	IV^{2a}	.	IV^{1a}	.	.	.	.
Filipendula ulmaria	IV^{1a}	V^{2a}	V^{2a}	V^{2b}	V^{3}	V^{2a}	V^{2a}	V^{3}	V^{2b}	.	V^{2b}	IV^{2a}	1^{2b}	III^{2a}	.
Galium uliginosum	IV^{+}	IV^{+}	V^{+}	III^{1a}	III^{+}	III^{+}	$-^{+}$	III^{+}	IV^{1a}	.	IV^{1a}	$-^{+}$	.	.	.
Geum rivale	III^{1b}	V^{2a}	V^{2a}	V^{2a}	IV^{2a}	V^{2a}	III^{1a}	V^{2a}	IV^{2a}	1^{+}	III^{1a}	.	.	.	.
Lathyrus pratensis	IV^{1a}	V^{1a}	IV^{1a}	V^{1b}	V^{1b}	IV^{1a}	.	V^{1a}	IV^{1a}	1^{+}	IV^{1a}	$-^{+}$	.	$--^{2a}$	.
Poa pratensis	$--^{+}$	$--^{1a}$	III^{1a}	III^{1b}	V^{1a}	III^{1a}	V^{2a}	III^{1a}	III^{1a}	1^{1a}	III^{1a}	.	1^{+}	.	.
Ranunculus acris	V^{1b}	V^{2a}	V^{1b}	V^{2a}	IV^{1a}	V^{2a}	III^{1b}	V^{2a}	IV^{1b}	.	IV^{1b}	.	.	$-^{1a}$	.
Ranunculus auricomus	IV^{1a}	V^{1b}	IV^{1b}	IV^{1b}	V^{1b}	V^{1b}	IV^{1a}	V^{1b}	V^{1b}	.	V^{1a}	.	.	$-^{+}$	.
Rumex acetosa	IV^{1a}	V^{1a}	IV^{1a}	V^{1b}	III^{1a}	IV^{+}	V^{1a}	III^{1a}	III^{1a}	.	$--^{+}$	.	.	.	.
Vicia cracca	V^{1b}	V^{1b}	V^{1b}	V^{1b}	V^{1b}	V^{1a}	$--^{+}$	IV^{1a}	III^{1a}	.	$--^{+}$	.	.	$--^{1a}$	.

Community No.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
<u>Caltha-group</u>															
Caltha palustris	.	-$^{+}$	-$^{+}$	-$^{+}$	--^{1a}	-^{1a}	.	III^{2a}	III^{2a}	2^{1b}	V^{2a}	IV^{1b}	.	--^{1a}	.
Galium palustre	.	-$^{+}$	-$^{+}$	-$^{+}$	III^{+}	--$^{+}$	-$^{+}$	III^{+}	IV^{1a}	2^{2a}	IV^{+}	--^{1b}	.	-^{1a}	.
Ranunculus repens	.	-^{1a}	--$^{+}$	-^{2a}	--^{2a}	.	.	--^{1b}	IV^{2b}	2^{1a}	III^{2a}	--^{2a}	.	-^{2a}	.
<u>Carex disticha-group</u>															
Carex cespitosa	.	-^{1b}	-^{1a}	--^{2a}	--^{2b}	--^{1b}	III^{3}	V^{2b}	III^{2b}	.	V^{2a}	.	.	.	.
Carex disticha	-^{1a}	--^{1b}	--^{1b}	-^{3}	-^{1a}	-^{2a}	III^{3}	IV^{2b}	V^{4}	3^{2a}	IV^{4}	-^{3}	.	.	.
Juncus filiformis	.	-^{2a}	III^{1b}	-^{2a}	-^{2a}	.	.	-^{2b}	IV^{2b}	3^{3}	--^{2a}	-^{2a}	.	.	.
Potentilla anserina	-$^{+}$	-$^{+}$	--$^{+}$	-^{1b}	-$^{+}$	-^{1a}	.	.	-^{1a}	3^{1a}	-$^{+}$	.	.	-$^{+}$	.
Valeriana officinalis	.	-$^{+}$	-$^{+}$	-^{1b}	III^{1a}	--^{1a}	III^{1a}	IV^{1a}	-^{1a}	.	.	-^{1b}	.	-^{1b}	.
<u>Phalaris-group</u>															
Phalaris arundinacea	.	-$^{+}$	-^{1a}	-^{1a}	.	.	-^{2a}	-^{2a}	.	.	.	III^{2b}	.	V^{4}	1^{3}
Phragmites australis	.	.	-	.	.	--	-	-	.	.	-	-	.	IV	1
<u>further species</u>															
Anthriscus sylvestris	.	.	-$^{+}$	--^{1b}	III^{1a}	.	--^{2a}	.	-$^{+}$	.	.	.	.	III^{1a}	.
Campanula glomerata	.	III^{1b}	-$^{+}$	--^{1a}	.	--^{1a}	--^{1a}	-$^{+}$	.	.	.	.	.	.	.
Carex elata	.	.	.	.	.	-$^{+}$	.	.	.	.	-	.	2^{5}	.	.
Carex leporina	-$^{+}$	-$^{+}$	III^{1a}	-^{1a}	.	.	.	-^{1a}	.	.	.	.	.	.	.
Carex vulpina	.	.	-^{1a}	-^{1a}	III^{2a}	.	.	--^{1b}	--^{1a}	1^{1a}	--$^{+}$	--^{2a}	.	.	.
Poa palustris	.	.	.	-^{1b}	-^{1a}	-^{1a}	-$^{+}$	-^{1a}	III^{1a}	.	-^{1a}	-^{1a}	.	-^{2a}	.
Ranunculus flammula	.	.	.	.	.	.	.	.	.	3^{2a}	.	.	.	.	.
Schoenoplectus lacustris	.	.	.	.	.	.	.	.	.	.	.	-$^{+}$	.	.	2^{2a}
Sium latifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2^{1a}

Table header:
pH measured in $CaCl_2$
K (mg/kg): mean soil content of potassium
N (%): total nitrogen (percentage weight)
C (%): total organic matter (percentage weight)
C/N ratio
P (mg/kg): mean soil content of plant available phosphorus
GW ≥50: percentage of growing season with groundwater table higher than 50 cm below surface
GW ≤100: percentage of growing season with groundwater table lower than 100 cm below surface
Ellenberg iv F: mean Ellenberg indicator value for moisture, weighted by abundance
Ellenberg iv N: mean Ellenberg indicator value for nitrogen, weighted by abundance

Community no.: (1) Nardus stricta-Festuca ovina-com. (2) Festuca ovina-Sesleria caerulea-com. (3) Festuca rubra-Deschampsia cespitosa-com. (4) Alopecurus pratensis-Galium mollugo-com. (5) Alopecurus pratensis-Deschampsia cespitosa-com. (6) Sesleria caerulea-Deschampsia cespitosa-com. (7) Melampyrum nemorosum-Deschampsia-com. (8) Carex cespitosa-Deschampsia cespitosa-com. (9) Carex disticha-Juncus filiformis-com. (10) Ranunculus flammula-Juncus filiformis-com. (11) Potentilla palustris-Carex disticha-com. (12) Carex acuta-com. (13) Carex elata-com. (14) Phalaris arundinaceae-Phragmites communis-com. (15) Carex acuta-Schoenoplectus lacustris-com.

3.2.2 Moderately moist (mesic) floodplain grasslands

Three communities were identified in the data set which can be broadly characterised as moderately moist or mesic according to Truus & Tõnisson (1998), i.e. the *Festuca rubra-Deschampsia-*, the *Alopecurus-Galium mollugo-* and the *Alopecurus-Deschampsia*-community.

3.2.2.1 Festuca rubra-Deschampsia-community

This community still shows strong relations to the dry floodplain communities described above. These three communities almost exclusively share the *Anthoxanthum*-group, indicating mesic and moderately poor conditions. Together with the moderately dry *Festuca ovina-Sesleria*-community this community has the *Leucanthemum*-group in common, but lacks both the *Nardus*- and the *Sesleria*-group. With the second mesic community it shares the *Phleum*-group with *Phleum pratense* and *Festuca pratensis* which suggest conditions somewhat richer in nutrients. *Alopecurus pratensis*, however, is lacking in this community which makes it possible to delimitate it negatively as a separate community. *Carex leporina* may serve as a weak character species of this community, achieving a constancy of III and being almost absent in all other communities. This community corresponds in parts with the *Festuco rubrae-Deschampsietum* of the "Wet floodplain grassland site type" mentioned by Paal (1997) although some of the plants from wetter sites like *Carex cespitosa, Agrostis gigantea* or *Veronica longifolia* are missing here.

The most constant species in this case are *Centaurea jacea, Deschampsia cespitosa, Filipendula ulmaria, Geum rivale, Ranunculus acris* and *Vicia cracca,* most of these belonging to the the ubiquitous *Deschampsia*-group. The most dominant species are *Rhytidiadelphus squarrosus* and *Festuca rubra* with a mean cover of 38 %, and *Climacium dendroides* (mean cover 19 %). *Festuca ovina* may in cases achieve high cover values but is only of low constancy. This community is somewhat more even in the distribution of life forms, with forbs and grasses achieving a mean cover of 88 and 73 %. Bryophytes still contribute a major part of the vegetation with 41 % mean cover while sedges are only of minor importance. Species number is among the highest of the studied communities, reaching a mean of 40.

This community is generally situated lower down in the elevational gradient than the *Festuca ovina-Sesleria*-community, often bordering to wet grassland communities. In the current data set it is only represented by two soil and groundwater samples so that information on the habitat conditions is scarce. Soil samples contained a certain amount of clay and hydromorphic features (grey and rusty patches) were partly present up to a depth of 37 cm. Gauge data show that the groundwater level both rises higher than 50 cm below surface and falls lower than 100 cm for about 30 % of the growing season. Mean Ellenberg indicator value for nutrient availability is 4.0, which is higher than in the preceding two communities but still rather poor.

3.2.2.2 Alopecurus pratensis-Galium mollugo-community

The *Alopecurus pratensis-Galium mollugo*-community differs from the preceding one mainly by the presence of *Alopecurus pratensis* and the absence of both the *Anthoxanthum*- and the *Leucanthemum*-group, indicating more mesic and less nutrient poor conditions. These two communities, however, have in common the presence of *Phleum pratense* and *Festuca pratensis* (i.e. the *Phleum*-group). The main body of the *Alopecurus pratensis-Galium mollugo*-community is formed, as in all dry and mesic communities, by the *Centaurea*- and *Deschampsia*-group.

The six most constant species in this community are *Achillea millefolium* (100 %) and *Deschampsia cespitosa, Festuca rubra, Phleum pratense, Ranunculus acris* and *Vicia cracca* (all 96 % constancy). The characterising *Alopecurus pratensis* has a constancy of 84 %. The five most dominant species are *Alopecurus pratensis*, *Deschampsia cespitosa, Festuca rubra, Filipendula ulmaria* and *Galium boreale* (all with a mean cover of 19 %). In this community forbs clearly dominate over grasses, while sedges and bryophytes achieve both only about 20 % mean cover. This community corresponds to the *Alopecuretum pratensis* described by PAAL (1997). The TWINSPAN analysis suggests the existence of two variants of the *Alopecurus-Galium*-community: in the first variant *Alopecurus* is only present with a mean cover of around 4 % while generally sedges are more important (especially *Carex panicea*). In the second variant *Alopecurus* has a mean cover of 30–40 % and there are a number of differentiating species that achieve higher frequencies: among these are *Campanula glomerata, Campanula patula, Heracleum sibiricum* and *Taraxacum officinale.*

This community can be found on sandy, well drained soils in the centre of the floodplain. Data from the groundwater gauges suggest that conditions in this community are considerably drier than in the preceding one, with levels rising above 50 cm below surface for less than 5 % and dropping lower than 100 cm for nearly 80 % of the growing season. Hydromorphic features were present only in a depth of 77 cm on average. Measured soil parameters are, on the other hand, not much different although mean Ellenberg indicator values indicate somewhat more fertile conditions than in the preceding three communities.

3.2.2.3 Alopecurus-Deschampsia-community

The TWINSPAN analysis resulted in a second set of relevés in which *Alopecurus pratensis* plays a prominent role. They were, however, placed by the algorithm next to the moist *Melampyrum-Deschampsia*- and *Carex cespitosa-Deschampsia*-communities. The main differences to the *Alopecurus-Galium mollugo*-community is the nearly complete lack of the *Centaurea*-group and the high constancy of *Carex vulpina*. Otherwise these relevés share the *Phleum*- and *Deschampsia*-group, but are generally considerably poorer in species than the aforementioned community. In comparison to the other moist communities this one lacks the *Selinum*-group (including the differentiating *Thalictrum lucidum*- and *Calamagrostis epigejos*-groups) on the one hand and the *Caltha*-group on the other hand. Apart from this typical species composition there are two variants of this community where either *Carex disticha* or *Carex cespitosa* become dominant. In both cases *Alopecurus* appears with reduced cover.

The five most constant species are *Filipendula ulmaria* and *Alopecurus pratensis* (100 %), *Lathyrus pratensis* (95 %), *Deschampsia cespitosa* and *Ranunculus auricomus* (both 86 %). The number of dominants is – compared with other similar communities – relatively limited: *Filipendula* and *Alopecurus* are dominant in all of these relevés while *Carex disticha* and *Carex cespitosa* take the place of *Alopecurus* in the two variants.

Habitat conditions of this community are very similar to those of the preceding one, i.e. well-drained sandy soils in the central floodplain. Gauge data indicate that site conditions are slightly wetter here, however no traces of hydromorphic processes were found within the first meter.

3.2.3 Moist floodplain grasslands

Three communities were identified which, according to Truus & Tõnisson (1998), could be classified as moist floodplain grassland, i.e. the *Melampyrum nemorosum-Deschampsia-*, the *Sesleria-Deschampsia-*, and the *Carex cespitosa-Deschampsia*-community. The first two of these show strong similarities, still sharing the large *Centaurea*-group and together being characterised by the presence of the *Selinum*-group, while the third one already shows features of the wet meadow types.

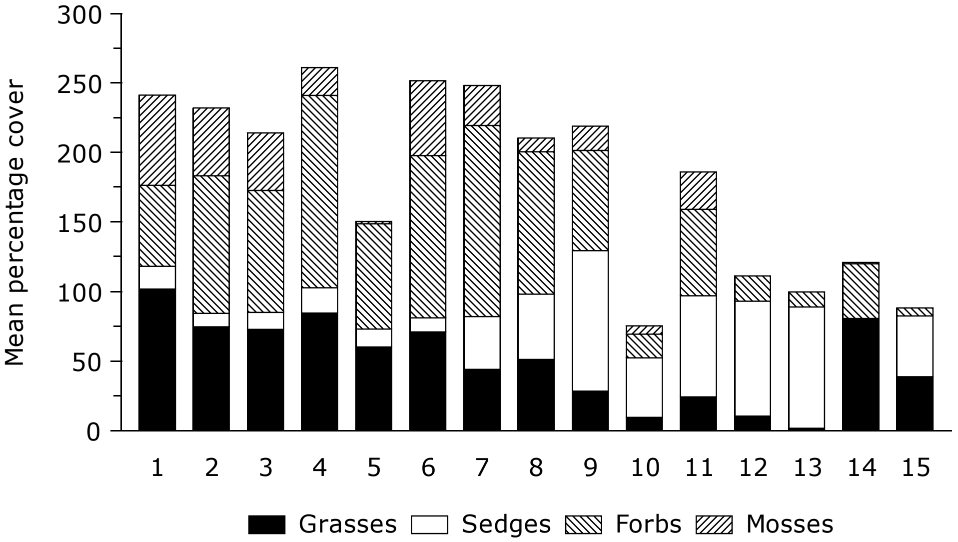


Fig. C.2: Distribution of life forms (grasses, sedges, forbs and mosses) in fifteen floodplain communities. Total values larger than 100 % are caused by the multi-layered structure of the communities and by the use of means of large classes rather than exact values for the calculation of overall cover. Community no.: (1) Nardus stricta-Festuca ovina-com. (2) Festuca ovina-Sesleria caerulea-com. (3) Festuca rubra-Deschampsia cespitosa-com. (4) Alopecurus pratensis-Galium mollugo-com. (5) Alopecurus pratensis-Deschampsia cespitosa-com. (6) Sesleria caerulea-Deschampsia cespitosa-com. (7) Melampyrum nemorosum-Deschampsia-com. (8) Carex cespitosa-Deschampsia cespitosa-com. (9) Carex disticha-Juncus filiformis-com. (10) Ranunculus flammula-Juncus filiformis-com. (11) Potentilla palustris-Carex disticha-com. (12) Carex acuta-com. (13) Carex elata-com. (14) Phalaris arundinaceae-Phragmites communis-com. (15) Carex acuta-Schoenoplectus lacustris-com.

3.2.3.1 Sesleria-Deschampsia-community

As mentioned above, this community and the following one are characterised by the presence of the *Selinum*-group, which contains species like *Selinum carvifolia, Succisa pratensis, Thuidium philibertii* and *Scorzonera humilis*. It is, however, separated from the following community by the presence of the *Sesleria*- and the *Calamagrostis epigejos*-groups and by the absence of the *Geranium palustre*- and the *Carex disticha*-groups. This community shows certain similarities with the *Scorzonero-Caricetum pallescentis* and the *Primulo-Seslerietum* (PAAL 1997), although not all of the characteristic species are present (e.g. *Primula farinosa* is present in the Soomaa NP but so rare, that it isn't included in any relevé). The most constant species of this community are *Deschampsia cespitosa, Centaurea jacea, Galium boreale* and *Ranunculus acris* (all 100 % constancy) and *Geum rivale, Potentilla erecta, Ranunculus auricomus* and *Vicia cracca* (all 95 % constancy). The five most dominant species are *Sesleria caerulea, Thuidium philibertii* and *Climacium dendroides* (all with a mean cover of 38 %) and *Deschampsia cespitosa* and *Filipendula ulmaria* (mean cover of 19 %). In its life form distribution this community is still more similar to the mesic than to the other moist and wet grasslands: forbs are the largest group with nearly 120 % mean cover while grasses reach 71 %. Bryophytes are the third largest group with 56 % mean cover, while sedges are only of minor importance (11 %). Together with the *Festuca rubra-Deschampsia*-community this community features the highest average species number of around 40 species per sample plot.

This community can be found in the central floodplain on poorly drained gleyic soils. Hydromorphic features are common and reach up to a depth of 45 cm. Gauge data are roughly comparable to those of the *Festuca rubra-Deschampsia*-community but mean Ellenberg indicator values for nutrient availability suggest poorer conditions.

3.2.3.2 Melampyrum nemorosum-Deschampsia-community

The *Melampyrum nemorosum-Deschampsia*-community is very similar to the preceding one, as both share exclusively the *Selinum*-group; in fact, both communities could be described as variants of a *Selinum-Deschampsia*-community. It can be positively characterised by the *Thalictrum lucidum*-group, which is almost exclusively confined to this community. In contrast to the *Sesleria-Deschampsia*-community, the *Sesleria*- and the *Calamagrostis*-groups are missing whereas species of the *Carex disticha*-group start to appear, which become more important in the wet grassland communities. This community is similar to the *Melampyreo-Scorzoneretum,* a grassland community of wooded meadows (PAAL 1997) although some of the species indicating drier conditions are lacking in the Soomaa relevés. The most constant species in this community are *Deschampsia cespitosa, Filipendula ulmaria, Angelica sylvestris, Galium boreale* and *Melampyrum nemorosum* all with a constancy of 100 % and *Poa pratensis, Rumex acetosa* and *Thalictrum lu-*

cidum with a constancy of 89 %. The seven most dominant species are *Melampyrum nemorosum*, *Carex cespitosa* and *Carex disticha* (all with a mean cover of 38 %) plus *Deschampsia cespitosa*, F*estuca rubra*, *Thuidium philibertii* and *Geranium palustre* with a mean cover of 19 %. Forbs dominate clearly in this community with a mean cover of 138 %, grasses and sedges being quite similar in their importance (44 and 38 %) and bryophytes covering around 30 %. Species number is significantly lower than in the previous community being only 29 on average.

This community was only found in the area of Halliste puisniit in abandoned wet meadows on poorly drained gleyic soils with a thick underlying layer of clay. Flooding may last exceptionally long in this area as it is near the confluence of the two major rivers of the Soomaa area Halliste and Raudna. Groundwater conditions as indicated by depth of hydromorphic features and gauge data are generally similar to the previous community although conditions may be slightly drier.

3.2.3.3 Carex cespitosa-Deschampsia-community

In contrast to the preceding two moist communities this one almost completely lacks the *Centaurea*-group (except for the two species *Galium boreale* and *Potentilla erecta*, which still occur with higher constancy), which demonstrates its stronger similarities to the wetter grassland communities. These on the other hand share the *Caltha*- and *Carex disticha*-group. The *Carex cespitosa-Deschampsia*-community may be positively characterised – if somewhat weakly – by the presence of the *Calamagrostis canescens*-group: all of its species, *Calamagrostis canescens, Carex vesicaria* and *Viola uliginosa*, occur with a constancy of 3 in this community and are considerably rarer or absent in all other communities. In PAAL (1997) this community corresponds to the *Carici cespitosae-Deschampsietum* of the "Wet floodplain grassland site type". The seven most constant species in this community are *Filipendula ulmaria* (100 %), *Lathyrus pratensis* (94 %), *Ranunculus acris* (88 %) and *Deschampsia cespitosa*, A*ngelica sylvestris*, *Ranunculus auricomus* and *Carex cespitosa* (all 82 % constancy). The five most dominant species are *Filipendula ulmaria* (mean cover of 38 %), *Deschampsia cespitosa*, *Carex cespitosa*, *Carex disticha* and *Calamagrostis canescens* (all with a mean cover of 19 %).

The *Carex cespitosa-Deschampsia*-community can be found in the lower parts of the central floodplain where it can cover large areas. It often borders the *Sesleria-Deschampsia*-community which grows on slightly higher ground, or the *Potentilla palustris-Carex disticha*-community which occupies lower parts of the floodplain. Soils under this community are gleysols or humic gleysols with a moderately developed peat-layer of around 10 cm. Groundwater rises higher than 50 cm below surface for more than 30 % of the growing season and falls deeper than 100 cm for only about 20 %. Hydromorphic features reach up to a depth of 23 cm on average.

3.2.4 Wet floodplain grasslands with tall sedges

Four communities were identified that in the context of Truus & Tõnisson (1998) would be considered members of the category "wet floodplain grasslands with tall sedges", i.e. the *Carex disticha-Juncus filiformis,* the *Potentilla palustris-Carex disticha,* the *Carex acuta-* and *Carex elata*-communities. This group is quite heterogeneous ranging from the more meadow-like communities dominated by *Carex disticha* to the reed-like *Carex elata*-community. A fifth community, the *Ranunculus flammula-Juncus filiformis*-community, may be included here; although it is physiognomically somewhat different, there are floristical relationships to the *Carex disticha-Juncus filiformis*-community.

3.2.4.1 Carex disticha-Juncus filiformis-community

This community is somewhat similar in composition to the following *Potentilla palustris-Carex disticha*-community as both are dominated by *C. disticha;* the two communities are nevertheless quite distinct in their composition and habitat. The *Carex disticha-Juncus filiformis*-community can be characterised by the high constancy of the two naming species and the absence of the *Carex panicea-* and the *Potentilla palustris*-group. In contrast to the following community, *Carex acuta* is of some importance (constancy III with a mean cover of 19 %) and the *Alopecurus*-group is somewhat more prominent. In addition to this the *Lychnis-* and *Caltha*-groups are present: the former can be found in all but the driest communities, the latter is typical for part of the moist and wet communities. The ubiquitous *Deschampsia*-group is also present here, although some of the less competitive species like *Festuca rubra, Galium uliginosum* or *Rumex acetosa* are of lesser importance.

The five most constant species are *Deschampsia cespitosa, Carex disticha* (both 93 % constancy), *Juncus filiformis* (86 %), *Filipendula ulmaria* and *Ranunculus repens* (both 79 % constancy). The five most dominant species are *Carex disticha* with a mean cover of 63 %, *Juncus filiformis* (mean cover 38 %) and *Filipendula ulmaria, Ranunculus repens* and *Carex acuta* (all with a mean cover of 19 %). The mean species number of this community is 20, which is considerably lower than in the two comparable communities (*Carex cespitosa-Deschampsia-* and *Potentilla palustris-C. disticha*-community). Sedges are by far the largest group with around 100% mean cover, followed by forbs with 60 %; grasses and bryophytes are only of minor importance with around 15 % mean cover each.

This community can be found in the lower parts of the central floodplain, but somewhat higher than the following *Potentilla palustris-Carex disticha*-community. Neighbouring communities may be mesic *Alopecurus-* or *Festuca rubra*-communities or reed beds. Soils are gleysols or humic gleysols with a moderate peat layer. Signs of hydromorphic processes are found up to a depth of ca. 40 cm and the groundwater level drops below 1 m for less than 20 % of the growing season.

3.2.4.2 Ranunculus flammula-Juncus filiformis-community

This rather species-poor community can be defined by the occurrence of *Ranunculus flammula* together with members of the *Carex panicea-, Caltha-* and *Carex disticha*-group. The community is dominated by *Juncus filiformis, Carex disticha* and *Ranunculus flammula.* As there were only three samples of this community in the data set, no sound information about the exact frequency of species and about habitat parameters are available. The community is somewhat lower and more open in growth than neighbouring *Carex disticha*-dominated communities. It occurs in small patches or narrow bands in local depressions with poor drainage where water is stagnant throughout most of the year.

3.2.4.3 Potentilla palustris-Carex disticha-community

This community has largely the same stock of plant species as the former one, i.e. the *Carex disticha-*, *Deschampsia-*, *Caltha-*, and *Lychnis*-groups. Notable differences are the presence of the *Carex panicea-* and *Potentilla palustris*-groups which indicate conditions resembling those of fens rather than meadows.

The most constant species in this community are *Filipendula ulmaria, Carex cespitosa* (both 100 %), *Deschampsia cespitosa, Caltha palustris* and *Ranunculus auricomus* (all 92 %); *Carex disticha* and *Potentilla palustris* follow, among others, with a constancy of 83 %. The most dominant species are *Carex disticha* with a mean cover of 63 % and *Filipendula ulmaria, Carex cespitosa* and *Calliergonella cuspidata.* The species number, with a mean of 29, is considerably higher than in the preceding community which otherwise shows strong similarities. The distribution of life forms is somewhat more even in this community, sedges still are the strongest group (81 % mean cover) and forbs the second strongest (70 %). Bryophytes and grasses have both a mean cover of around 30 %.

This community can be found in the lower parts of the central floodplain, often in proximity to reed beds. Soils are gleysols or humic gleysols with a moderate peat layer. Groundwater conditions are wetter than in the preceding communities, with groundwater levels dropping below 1 m for merely 2 % of the growing season and rising above 0.5 m for more than 50 %.

3.2.4.4 Carex acuta-community

The *Carex acuta*-community is one of the species-poor – average species number is around eight – communities dominated by a single species. Besides *Carex acuta* there are only a few other other species that achieve a higher constancy: *Carex vesicaria, Filipendula ulmaria, Caltha palustris* and *Phalaris arundinacea* can be frequently encountered.

This community is common either in the lowest parts of the central floodplain or in narrow bands along the rivers. In both cases the habitat is inundated frequently and for longer periods.

3.2.4.5 Carex elata-community

The *Carex elata*-community is the most species-poor among the studied communities, the average species number being merely four. In between the dominating tussocks of C*arex elata* there are only a few other species of wet grounds like *Lysimachia vulgaris, Calamagrostis canescens* or the omnipresent *Filipendula ulmaria*.

This community is typical for the lowest parts of the floodplains and is most often found in old riverbeds or small rivulets that are only flooded during spring and autumn floods. Soils are humic gleysols which can develop quite thick layers of peat.

3.2.5 Wet floodplain grasslands with tall grasses, reed-beds

Two communities were identified in the current dataset that fit the description given by Truus & Tõnisson (1998) for the category 'wet floodplain grasslands with tall grasses' which could also be described as reed communities. As they are not grasslands *sensu strictu*, that is regularly mown, they were not sampled with the same intensity as the other community types and no sufficient habitat data are available.

3.2.5.1 Phalaris-Phragmites-community

This reed community is easily defined by the presence of the *Phalaris*-group and the absence of practically all other species groups. Average species number is very low (6.7): besides the dominating and naming reed species only a few other species may be found in the shade of these dense stands, e.g. *Veronica longifolia, Filipendula ulmaria, Caltha palustris* or *Ranunculus repens*. In Paal (1997) this community is similar to the *Phalarisetum arundinaceae*, although that community still shows more properties of wet meadows, and to the *Phragmitetum australis*, which, however, in the description of Paal lacks *Phalaris arundinacea.*

This community is common along all rivers of the studied area forming narrow bands. It is usually situated higher than the neighbouring *Carex acuta-Schoenoplectus lacustris*-community but is nevertheless frequently flooded and only in summer for longer periods above the waterline.

3.2.5.2 Carex acuta-Schoenoplectus lacustris-community

This species poor community is dominated clearly by *Schoenoplectus lacustris* and by C*arex acuta*. Other large graminoids that may be present are *Phalaris arundinacea* and *Phragmites australis.* In addition to these there is only a small number of other species, partly terrestrial like *Iris pseudacorus* and partly aquatic like *Hydrocharis morsus-ranae* or *Nuphar lutea.* Paal (1997) describes a *Phragmiteo-Schoenoplectetum* that agrees well with the communities found in Soomaa NP.

The *Carex acuta-Schoenoplectus lacustris*-community is the lowest of the studied communities, being submerged most of the year and rising above the waterline only for short periods in summer.

3.3 Syntaxonomy

In the following chapter possible syntaxonomical relations of the above described communities to established syntaxa will be discussed. Extending the established system of Central and Western European grasslands (e.g. DIERSCHKE 1995) to Estonia poses some methodological problems. PASSARGE (1976) notes that the flora of the hemiboreal and boreal grasslands is generally an impoverished subset of the Central European grassland flora with certain relations to montane grasslands. However, due to differences in climate, species may exhibit markedly different competitive behaviour. For example, species like *Deschampsia cespitosa, Achillea ptarmica* and *Galium uliginosum,* in Central Europe typical for wet grasslands or even character species of the order *Molinietalia,* are here common and often abundant in all grassland types, regardless of nutrient or moisture status. The validity of character species originally described in Central Europe is therefore probably very limited when moving to a distant geographical area, e.g. Estonia. This problem has led to a long-standing debate about the concept of character species in general. One conclusion of this debate is to put a stronger emphasis on the hierarchical level of the alliances rather than the associations, as these promise to be stable over larger geographical areas (MUELLER-DOMBOIS & ELLENBERG 1974). The focus of this chapter will therefore be in most cases to identify an appropriate alliance rather than identifying or creating an association. The latter task would need much more material on a broader geographical scale.

Another way out of the problematic nature of character species is to abandon this concept right away and rather use combinations of species groups to identify syntaxa (as it was done in the previous section). This is the approach of the *Eberswalde-school* centred around Passarge, Scamoni and Hofmann (SCAMONI et al. 1965). The aim is also a hierarchical system analogous to the Braun-Blanquet-system with which it overlaps to some degree (although – due to different methodology – not completely). The new monograph on the plant communities of north-eastern Germany by PASSARGE (1996; 1999) is very interesting from an Estonian perspective as it has an explicitly *baltic* perspective.

However, probably due to the mixed effects of historically long management and recent abandonment (and most recent conservation management) the studied communities of the Soomaa area are far from a floristical equilibrium and so a classification must often remain unsatisfactory.

3.3.1 Nardetalia strictae

Samples with the *Nardus*-group present, i.e. the *Nardus-Festuca ovina*-community, can probably be considered member of the order *Nardetalia* of the class *Calluno-Ulicetea*. *Hieracium pilosella, Luzula campestris, Potentilla erecta* and (here less frequent) *Danthonia decumbens* are character species of the class *Calluno-Ulicetea* (Dierssen 1996). Of the character species Peppler-Lisbach & Petersen (2001) and Dierssen (1996) list for the order *Nardetalia* several are present and abundant in the community under consideration: *Nardus stricta, Carex pallescens* and *Luzula campestris* all achieve a constancy of V and *Nardus* belongs to the most abundant species. On the other hand there are several species (members of the *Centaurea*- and *Deschampsia*-groups) which are considered characteristic of the *Arrhenatheretea* and *Arrhenatheretalia;* considering the overall appearance of the community and the dominance of *Nardus* and *Festuca ovina*, placing the community into the *Nardetalia* seems, however, more convincing. As described by Peppler-Lisbach & Petersen (2001) species of infertile grasslands like *Agrostis capillaris, Festuca rubra, Anthoxanthum odoratum* and *Potentilla erecta* are common in the discussed community as well, and form the common stock of all more or less infertile, dry to mesic grasslands. The further classification is not equally well supported, as character species at the level of the alliance are largely missing - except for *Viola canina*. Nevertheless the presence of *Rhytidiadelphus squarrosus, Rumex acetosa, Festuca ovina, Hieracium pilosella, Plantago lanceolata* and others indicate the communities' membership to the alliance *Violion caninae* and its sub-alliance *Violenion caninae* (Peppler-Lisbach & Petersen 2001). There are, however, species, e.g. the highly frequent *Carex nigra* and *Carex panicea*, that suggest a certain proximity to the alliance *Juncion squarrosi*, and the co-dominant *Sesleria caerulea* indicates some relations to the *Molinietalia.* This, however, does not surprise in the ecological context of a floodplain meadow, where moisture conditions may change within a few meters.

3.3.2 Molinio-Arrhenatheretea

Communities of the studied area are considered members of the class *Molinio-Arrhenatheretalia* if they contain the *Deschampsia*-group but not the *Nardus*-group. By applying this rule, *Nardus*-dominated poor grasslands and stands of large sedges and reeds are excluded. Character species of the *Arrhenatheretea* that span the whole spectrum from dry and poor to wet and nutrient rich meadows are e.g. *Ranunculus acris, Lathyrus pratensis* or *Rumex acetosa.* Other traditional character species of the *Arrhenatheretea* are found in the *Anthoxanthum-, Leucanthemum-* and *Centaurea*-group and in other smaller groups which all have a narrower distribution and can thus be used to delimitate the orders and alliances of this class. Several species, on the other hand, expand their ranges from the *Molinietalia* to cover the whole of the *Arrhenatheretea*, i.e. *Deschampsia cespitosa, Filipendula ulmaria* and *Galium uliginosum.*

The subdivision of the class *Molinio-Arrhenatheretea* is treated rather differently in the various books about German plant communities published recently. The traditional view, as e.g. found in Dierschke (1996), Rennwald et al. (2000) and Oberdorfer (2001) distinguishes two orders: the *Arrhenatheretalia* for mesic grasslands, including four alliances of which only the *Arrhenatherion elatioris* is of interest here; and the *Molinietalia* for moist and wet grasslands which include the *Calthion, Molinion* and *Cnidion*. A contrasting view is found in Passarge (1999), Schubert (2001) and Berg et al. (2004). These authors essentially recognise a further syntaxon for the (sub-)continental floodplain meadows which are either placed in a separate order *Deschampsietalia* (Passarge 1999; Berg et al. 2004) or as a separate alliance *Deschampsion* within the *Molinietalia* (Schubert 2001). Passarge (1964; 1999) goes even further in dividing the *Deschampsietalia* into two separate alliances *Deschampsion* and *Alopecurion.* Another difference relevant in this context is the recognition of a separate syntaxon for the mesic but nutrient-poor meadows characterised by *Festuca rubra*, which Passarge (1999) places in an own alliance *Agrostio-Festucion rubrae*. Furthermore, Passarge (1976) describes a distinct order *Alchemillo-Deschampsietalia* for the boreal grasslands. This opinion, however, does not seem to have met with much approval: Dierssen (1996) e.g. treats the boreal grasslands as members of the established syntaxa from Central Europe. As this study was not meant to be a thorough assessment of the syntaxonomy of the Estonian floodplain meadows, a pragmatic approach was followed based on the greatest similarities to already described syntaxa.

3.3.2.1 Arrhenatheretalia

Festuca rubra-dominated and related communities (Agrostio-Festucion rubrae)

The order *Arrhenatheretalia* in the Soomaa area is represented by the nutrient poor *Festuca ovina-Sesleria-* and *Festuca rubra-Deschampsia*-communities. These relevés are dominated by the graminoids *Festuca rubra, Festuca ovina, Agrostis tenuis* and *Anthoxanthum odoratum* or, in the case of the first-mentioned community, *Sesleria caerulea.* They are together characterised by the members of the *Leucanthemum*-group, lower growing forbs such as *Leucanthemum vulgare, Cerastium holosteoides, Prunella vulgaris, Rumex acetosa* or *Plantago lanceolata,* most of which are character species of the *Arrhenatheretea* or *Arrhenatheretalia.* In contrast to the otherwise similar *Nardus-Festuca ovina*-community these relevés lack species of the *Nardetalia.* Similar poor meadow communities are described by Dierschke (1997) in the form of the *Festuca rubra-Agrostis tenuis-* and *Festuca rubra-Meum*-community, which are, however, considerably less rich in species than the ones found in Soomaa NP. Dierschke lists these communities because of overall similarities in the alliance *Polygono-Trisetion,* although good character species for the level of the association and alliance are missing. While the *Festuca rubra-Deschampsia*-community shows quite strong resemblance with the communities described by Dierschke, the *Festuca ovina-Sesleria*-community is more unique with its relations to both the *Nardetalia* (*Festuca ovina*) and the *Molinietalia* (*Sesleria caerulea*). As the overall species compositions, however, are similar a joint treatment seems justified.

Following Passarge (1978; 1999) these communities may also be placed in a separate alliance *Agrostio-Festucion rubrae* within the *Arrhenatheretalia.* Passarge describes a hydrological variant of the *Plantagini lanceolatae-Festucetum rubrae* (*r. succietosum*) with a number of elements of the *Molinion* and *Deschampsion*, e.g. *Achillea ptarmica, Lychnis flos-cuculi* or *Deschampsia cespitosa*. This agrees quite well with the general species composition of the communities under discussion. In a similar way the *Festuca ovina-Sesleria*-community may be described as an easterly variant with a stronger tendency towards the *Molinion* (*Seslerietum*).

Alopecurus pratensis-dominated and related communities

Another community that may be placed in the alliance *Arrhenatheretalia* is the *Alopecurus-Galium mollugo*-community. Similar communities are described by various authors as common at mesic, nutrient rich floodplain sites with a fluctuating groundwater level (Regel 1925; Steffen 1931; Hundt 1958; Leyer 2002). Common to all these communities is the almost complete absence of characterising species at the level of both associations and alliances, which makes syntaxonomic classification difficult. The same holds true for the relevés sampled in Soomaa NP: *Alopecurus pratensis,* which characterises most of the relevés under discussion, is a character species of the *Molinio-Arrhenatheretea* and so are *Festuca pratensis* and *Taraxacum officinale*. *Phleum pratense* indicates a relation to the *Arrhenatheretalia,* while other character species of this order have a much broader amplitude in the Soomaa samples (e.g. *Achillea millefolium* or *Alchemilla vulgaris*). The occurrence of *Galium mollugo*, which is mainly found in the this community, is the only good indicator of the membership of this community to the alliance *Arrhenatherion.* At the same time it suggests some similarity to the *Galio molluginis-Alopecuretum pratensis* Hundt (1954) 1968 as described by Schubert (2001). Schubert as well as Dierschke (1997), who uses the name *Ranunculus repens-Alopecurus pratensis*-community; both place these communities in the alliance *Arrhenatherion.* In contrast to their descriptions the communities found in Soomaa NP show hardly any features of the *Agropyro-Rumicon*, e.g. *Ranunculus repens* plays only a very minor role here.

Passarge (1964) on the other hand places these communities as a new alliance *Alopecurion pratensis* within the order *Deschampsietalia,* which unite the mesic and moist floodplain meadows of the subcontinental region. Considering the codominance of *Deschampsia cespitosa* in practically all Soomaa samples and – apart from the *Phleum*-group – the lack of species that could be used to characterise the *Arrhenatheretalia* this may also be an appropriate solution.

3.3.2.2 Molinietalia

The order *Molinietalia* as a whole is difficult to define in the current data set; as was mentioned above most of the character species of this order have a much broader ecological amplitude than in Central Europe and may extend into the *Arrhenatheretalia* or even cover the whole class *Arrhenatheretea*. It is therefore necessary to define the order as the sum of its alliances, which are better characterised by differential species.

Molinion

The alliance *Molinion* is represented in the current data set by the *Sesleria-Deschampsia-* and the *Melampyrum nemorosum-Deschampsia*-community. The membership of these communities in the *Molinion* is supported by the high constancy of members of the *Selinum*-group, especially *Succisa pratensis, Selinum carvifolia* and *Scorzonera humilis.* Other common species of the *Molinion* that are frequent in these communities are, among others, *Calamagrostis epigejos, Galium boreale, Iris sibirica* and *Carex panicea. Molinia caerulea* is virtually absent from all relevés but is replaced by *Sesleria caerulea,* a fact that is also described by Dierssen (1996) for the Baltic area. At least the first of the mentioned communities can thus probably be identified as a variety of the *Seslerietum uliginosae* described by Dierssen (1996) Similar communities are described by Kovács (1962) from Hungary, where they grow in various wet and fen-meadows with a species composition basically similar to the Soomaa meadows. Both authors place these *Sesleria*-dominated communities in the alliance *Molinion.*

Interestingly Kovács (1962) cites Palmgren (1915) with the observation of two principal types of *Sesleria*-meadows on the Åland-islands, a typical, lower – coinciding probably with the currently discussed community – and a higher, transitional type which may be identified as the dry *Festuca ovina-Sesleria*-community discussed above.

The second community mentioned here under the roof of the alliance *Molinion*, the *Melampyrum nemorosum-Deschampsia*-community, can be interpreted as an impoverished successional stage and/or a slightly wetter variant of the *Seslerietum. Sesleria* is still present but only of little importance, while on the other hand sedges like *Carex disticha* and *C. cespitosa* gain in importance. Dierssen notes (1996) that *Carex disticha* commonly becomes dominant on abandoned fen meadows which is probably also the case here. This is supported by Lippmaa (1931), who describes a *Scorzonera-Melampyrum nemorosum*-community which resembles the current community and which was typical for moist wooded meadows. *Carex disticha* is suspiciously absent from that description which was based on meadows that were at that time still managed regularly. The differentiating *Geranium palustre* indicates relations to the *Filipendulion,* whereas the abundant

Melampyrum nemorosum may be a relict of the former or the vanguard of a developing floodplain forest of the *Alno-Ulmion*.

Calthion

The *Calthion* is not easily defined in the current data set, as the communities that may be placed here also show strong links to the *Magnocaricion* and may thus be considered successional stages half way between the *Calthion* and *Magnocaricion*. This is supported by the frequent occurrence of *Carex disticha,* which is traditionally considered a character species of the *Magnocaricion* but today is probably most common in abandoned wet meadows (Dierssen 1996; Rennwald 2000). The *Calthion* may be defined in the current data set by the presence of the *Caltha*-group, especially by *Caltha* itself, the only true character species of the *Calthion* in this group, as long as neither *Carex acuta* nor the *Potentilla palustris*-group are present. By this definition communities where *Carex disticha* achieves a frequency of over 80 % and covers on average more than 60 % are excluded from the *Calthion,* they will be treated together with the other *Magnocaricion* communities. Other species commonly considered character species of the *Calthion*, like *Angelica sylvestris, Geum rivale* and *Lychnis flos-cuculi* are found to have a much broader ecological amplitude in the studied meadows thus loosing their indicative power.

Communities dominated by *Carex cespitosa* are treated very differently in the literature. The *Caricetum cespitosae* is classified either as a member of the *Caricion davallianae* (Dierssen 1996), of the *Magnocaricion* (Pott 1995), *Deschampsion* (Schubert 2001), or of the *Calthion* (Celinski 1976; Balátová-Tuláčková & Háberová 1996; Passarge 1999). Placing the *Carex cespitosa-Deschampsia*-community described above in the *Calthion* seems to be the most appropriate solution considering the overall species composition, the presence of *Caltha* and especially the strong presence of the *Deschampsia*-group with its character species belonging to the *Arrhenatheretea* and *Molinietalia,* which form the bulk of this community. The overall character of this community is still that of a meadow, with grasses achieving an average cover of over 50 % and sedges only 41 %, whereas in the other two communities dominated by *Carex disticha* grasses cover only 20–30 % and sedges 80–100 %. Good character species of both the *Magnocaricion* (apart from *Galium palustre* and the only moderately frequent *Carex vesicaria*) and the *Caricion davallianae* are largely lacking. *Carex disticha* must probably be seen here as an indicator of abandonment; it occurs with a frequency of 60–70 % and covers around 20 % on average.

Deschampsion

Apart from the *Alopecurus-Galium mollugo*-community, the second most commonly found community in the data set and in the Soomaa meadows is the *Alopecurus-Deschampsia*-community. The dominance of *Alopecurus* and *Deschamp-*

sia together with a basic set of *Arrhenatheretea*- and *Molinietalia*-species (mainly of the *Deschampsia*-group) and the general lack of further character species at the alliance level resembles the descriptions that Schubert (2001) and Passarge (1999) give of the various *Deschampsietum*-communities, which are placed by these authors in a separate alliance *Deschampsion.* This is partly a synonym of the alliance *Cnidion* into which, according to the authors in Rennwald (2000), most of the various published *Deschampsietum*-communities should be placed. However, since none of the character species commonly recognised for the *Cnidion* is present in the Soomaa samples (only *Viola persicifolia* is present, although very rare and mainly in the *Calthion*) it seems more appropriate to follow the classification of Schubert (2001) and Passarge (1999). Especially the *Ranunculus auricomi-Deschampsietum cespitosae* Scam. 55 (or synonymous *Stellario palustris-Deschampsietum* Freitag 57) as described by Schubert or Passarge is quite similar to the Soomaa relevés: both *Ranunculus auricomus* and *Stellaria palustris* can be found frequently in these samples. *Alopecurus* is relatively abundant in this Soomaa community, sometimes dominating over *Deschampsia*: this may be due to the fact that this community was found mainly on sandy, better drained sites whereas e.g. Passarge (1964) describes the *Deschampsietalia* as generally occurring on soils rich in clay.

As was noted above three variants of the *Alopecurus-Deschampsia*-community may be recognised: a central variant with *Alopecurus* covering 30–70 %, and two variants which are probably hydrologically defined or may be seen as more strongly affected by succession. In each of them either *Carex disticha* or *C. cespitosa* become dominant thus pointing to the corresponding communities in the *Calthion* or *Magnocaricion.*

As already mentioned above, following Passarge (1964) the *Deschampsion* could be united with the *Alopecurion* in a new order *Deschampsietalia*. With respect to the material from Soomaa presented here this appears quite reasonably as these alliances differ only by the presence or absence of the *Centaurea*-group, otherwise being similar in their basic species set.

3.3.3 Caricion nigrae

Indicators of the *Scheuchzerio-Caricetea nigrae* and its lower syntaxa are quite common in the current data set (e.g. *Agrostis canina, Carex nigra, C. panicea*) and moderately acidic to moderately base-rich fens were probably the origin of many of the local wet meadow communities. Although fen communities were not the focus of this study and were accordingly not sampled, the *Ranunculus flammula-Juncus filiformis*-community, which was found in local depressions within wet meadow communities, is probably best placed here, resembling strongly the *Pediculari palustris-Juncetum filiformis* (Jonas 33) Prsg. et Tx. in Tx. 57 described by Passarge (1999). *Pedicularis palustris* was not present in the samples – which moreover are only few and thus hardly representative – but was found at other places in the area at similar ecological situations so that this community can in fact be considered as present.

3.3.4 Phragmito-Caricetea

The syntaxonomical treatment of reed-beds and large sedge communities is slightly easier than that of the *Molinio-Arrhenatheretea.* As these are azonal communities, being more dependent on the local groundwater and soil conditions than on the overall climate, they tend to be more similar over large geographical areas (Walter & Breckle 1991) and the syntaxa recognised in Central and Western Europe will very likely be applicable also in Estonia. Nevertheless, the syntaxonomical treatment especially at the higher levels varies between authors, which is probably caused by their low species numbers and often mono-dominant structure; therefore good character species are naturally sparse.

Magnocaricion

Most *Magnocaricion*-communities are easily identified as they are dominated by a single species of the genus *Carex*. In the current data set these are the *Caricetum elatae* and the *Caricetum gracilis*, which are ecologically and floristically virtually identical with the communities described e.g. by Schubert (2001). A more difficult case are the communities dominated by *Carex disticha,* i.e. the *Carex disticha-Juncus filiformis-* and the *Potentilla palustris-C. disticha*-community. Apart from *C. disticha* as a character species of the *Magnocaricion* there is only *Galium palustre* being of some frequency in both these communities. *Carex elata* is of medium frequency and cover in the first mentioned community, confirming its relation to the *Magnocaricion*, while the second community shows stronger links to the *Caricion lasiocarpae* by the presence of *Potentilla palustris* and *Calamagrostis stricta,* which have their major occurrence here. Both communities, however, also have many elements of the *Arrhenatheretea* and *Molinietalia:* the *Deschampsia*-group is present, although considerably weaker in the first community, and in addition to this *Alopecurus pratensis* attains medium frequency but only little mean cover. However, sedges clearly dominate these communities with 80–100 % mean cover while Poaceae are only of minor importance so that the overall character markedly differs from the other wet grassland communities. The *Carex disticha-Juncus filiformis*-community resembles both the *Polygono amphibii-Caricetum distichae* (although *P. amphibium* is rather rare here) and the *Pedicularis palustris-Juncetum filiformis* (Passarge 1999). The *Potentilla palustris-C. disticha*-community on the other hand shows strong similarity with the *Caricetum intermediae* described by Steffen (1931) and confirmed by Passarge (1999) as a distinct community of the East Prussian region.

A further *Magnocaricion* community is the *Phalaridetum arundinaceae* Libb. 31, which by some authors is placed in a separate alliance *Phalaridion.* The *Phalaris-Phragmites*-community described above obviously stands halfway between this and the *Phragmitetum australis* Schmale 37 as described by Schubert (2001) belonging to the *Phragmition.*

In addition to these communities of the *Magnocaricion* described above, a number of other communities were encountered which were, however, not sampled. Among these communities, which are present in Soomaa NP but probably not common is a community dominated by C*alamagrostis canescens*, resembling the *Peucedano palustris-Calamagrostietum canescentis* Weber 78 and a community rich in *Carex appropinquatae,* which may identified as the *Peucedano palustris-Caricetum appropinquatae* Palczynski 75 (both Passarge 1999). More samples are needed here.

Phragmition

The *Phragmition* is generally considered an alliance of still-water reed-beds, but the reed communities encountered along the Soomaa rivers floristically best fit here. The *Carex acuta-Schoenoplectus lacustris*-community found at the lowest end of the studied transects and extending well below the mean water-line can most likely be placed near the *Scirpo-Phragmitetum* W. Koch 26 as e.g. described by Preising et al. (1990). However, the presence of *Carex acuta* also suggests some similarity with the *Magnocaricion* and the *Caricetum gracilis,* which is often found directly adjacent to this community.

Table C.7: Summary of the suggested syntaxonomical positions of the Soomaa floodplain communities and corresponding communities in Paal 1997

Braun-Blanquet system	**Soomaa communities**	**Estonian vegetation types *sensu* Paal**
Calluno-Ulicetea → Nardetalia → Violion caninae	*Nardus-Festuca ovina*-community	Festuco ovinae-Nardetum[1], Nardo-Danthonietum[4]
Phragmito-Caricetea → Phragmitetalia → Magnocaricion	*Carex acuta*-community	Caricetum acutae[5]
	Carex elata-community	Caricetum elatae[5]
	Carex disticha-Juncus filiformis-community	Caricetum distichae[5]
	Potentilla palustris-Carex disticha-community	(Caricetum distichae[5])
Phragmito-Caricetea → Phragmitetalia → Phragmition	*Phalaris-Phragmites*-community	Phragmitetum australis[5]
	Carex acuta-Schoenoplectus lacustris-community	Phragmiteo-Schoenoplectetum[5]
Scheuchzerio-Caricetea nigrae → Caricetalia nigrae →Caricion nigrae	*Ranunculus flammula-Juncus filiformis*-community	(Caricetum distichae[5])
Molinio-Arrhenatheretea → Arrhenatheretalia →Agrostio-Festucion rubrae	*Festuca rubrae-Deschampsia*-community	Festuco rubrae-Deschampsietum[5], Potentillo erectae-Deschampsietum cespitosae[2]
	Festuca ovina-Sesleria caerulea-community	Festuco ovinae-Seslerietum[4]
Molinio-Arrhenatheretea →Arrhenatheretalia → Arrhenatherion	*Alopecurus-Galium mollugo*-community	Alopecuretum pratensis[5]
Molinio-Arrhenatheretea → Molinietalia → Molinion	*Sesleria-Deschampsia*-community	Carici paniceae-Seslerietum[5]
	Melampyrum-Deschampsia-community	Melampyreo-Scorzoneretum[3]
Molinio-Arrhenatheretea → Molinietalia → Calthion	*Carex cespitosa-Deschampsia*-community	Carici cespitosae-Deschampsietum[5]
Molinio-Arrhenatheretea → Deschampsietalia →Deschampsion	*Alopecurus-Deschampsia*-community	Alopecuretum pratensis[5]

Site types sensu Paal 1997: 1. dry boreal grassland; 2. fresh boreal grassland; 3. dry boreo-nemoral grassland; 4. fresh floodplain grassland; 5. wet floodplain grassland

3.4 Habitat and vegetation parameters

3.4.1 Soil

Depending on elevation and thus upon the hydrological conditions several soil types were found in the Soomaa floodplains (see Fig. C.9 through C.14 for profiles of common soil types). The greatest area, especially the lower lying central parts of the floodplains, is covered by various kinds of gleysols. The lowest parts of these and small depressions are often occupied by humic gleysols and histosols (German *"Anmoorgley"* and *"Niedermoorböden"*) with layers of peat of up to 50 cm thickness. These soils are water-logged throughout the year and the first and longest to be flooded. When moving to higher ground these soils make way to stagnic gleysols (*"Pseudogley"*) on loamy and fluvisols (*"Auengley"*) on sandy substrates. These two soil types are the most common ones in the Soomaa floodplains. The zone influenced by fluctuating groundwater or stagnant flood-water (indicated by rusty stains and greyish coloration) varies from a depth of 70–80 cm on sandy to 20–30 cm on loamy substrates. On the highest areas where sandy substrates dominate cambisols (*"Auenbraunerde"*) have developed. These may occasionally show signs of podsolisation. There, no traces of groundwater influence are found within the first meter of depth.

Fig. C.3 gives a summary of some soil parameters measured in the floodplain grasslands. The small number of samples does not allow for a comprehensive assessment of soil-vegetation relationships but may serve as an indicator of general trends. For the same reason results are presented in relation to community types as described by KRALL ET AL. (1980) and AUG & KOKK (1983) (see Table C.2). This coarser classification, rather than the finer one developed in this study, was used since not all communities were covered by soil samples and in most cases the number of samples would have been to small to calculate meaningful averages. Differences between community types were in most cases not significant (Kruskal-Wallis ANOVA with Steel-Dwass non-parametric multiple comparison) except for total nitrogen and organic carbon: in these cases differences between dry and moist floodplain grassland (type 1 vs. 3) were significant at $p \leq 0.05$. Other soil parameters showed conceivable but non-significant differences between community types, which will be noted below.

Soil pH values were remarkably homogeneous in all community types except for the reed communities (no. 5) which were, however, only represented by one relevé. The mean values lay between 5.0 and 5.5 with relatively little variation and are thus in the range described by SUCCOW (SUCCOW 1988) as *subneutral*. Such values are not uncommon for areas with glacial deposits (ROSENTHAL et al. 1998; LEYER 2002).

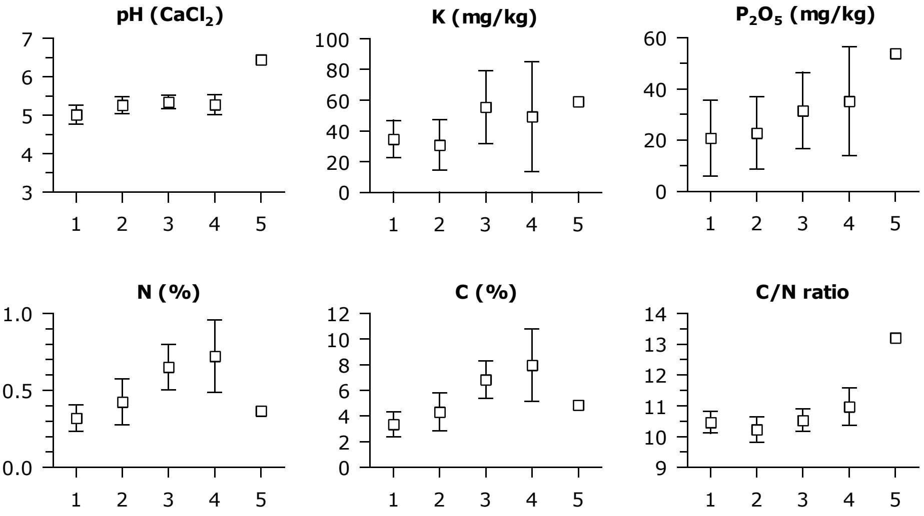


Fig. C.3: Overview of soil properties (mean ± 1 S.D. for pH, plant available phosphorus, potassium, total nitrogen, organic carbon and C/N ratio) for grassland community types according to Krall et al. (1980) and Aug & Kokk (1983): (1) dry floodplain grassland (n = 4), (2) mesic floodplain grassland (n = 6), (3) moist floodplain grassland (n = 11), (4) wet floodplain grassland with tall sedges (n = 8), (5) wet floodplain grassland with tall grasses (n = 1).

The content of potassium showed more variation, both in mean values and in variance itself, the latter increasing considerably with the mean. Lowest values of around 30 mg/kg were found – not surprisingly – in dry and mesic floodplain communities on sandy soils. These samples also exhibited the lowest variation. Moist and wet communities had mean potassium contents of 50 to 60 mg/kg but also exhibited the highest variation with some values being as low as 20 mg/kg, others as high as 100 mg/kg or more. These values are quite comparable to those reported by Burkart (1998) for floodplain meadows along the Havel river; those meadows also exhibited the large variation in the content of potassium, sometimes varying over one order of magnitude within the same plant community.

The content of extractable phosphorus showed a similar general picture, albeit variation was similar in all community types. Communities on drier, sandy substrates (community types 1 and 2) had a mean soil content of phosphorus of around 20 mg/kg while soils on loamy substrates (community types 3, 4 and 5) had mean values of around 40 mg/kg. The observed values lie in the same range as reported by Burkart (1998) for the floodplain grasslands of the river Havel. Content of extractable phosphorus has been shown (Janssens et al. 1998) to be strongly related to species numbers of grassland communities. While a strict humped-back curve could not be proven, species number was negatively correlated to phosphorus content ($r = -0.419$, $p = 0.019$, $n = 31$).

Soil organic matter again follows the same pattern with low mean values of around 4 to 5 % in the dry and mesic, and higher values of 7 to 8 % in the moist and wet communities. The general picture is similar again for total nitrogen: community types 1 and 2 on sandy substrates had mean values of around 0.4 to 0.5 %, while community types 3, 4 and 5 on loamy substrates had mean nitrogen contents of ca 0.7 %. This pattern is probably due to the fact that the drier, more sandy soils are better aerated so that microbial decomposition is stronger here than in the lower lying, wetter soils. The C/N ratio on the other hand showed very little variation between the different community types with all mean values lying between 10 and 11 and comparably low overall variation. These ratios were generally very narrow and are indicative of very fertile or *eutroph* soil conditions (SUCCOW 1988) but data reported in ROSENTHAL et al. (1998) and LEYER (2002) are of the same order of magnitude (in the range of 12 to 16).

While there were apparently some differences in soil parameters, especially between soils on sandy and on loamy substrates, these differences are obviously not very large and exhibit large variation. Generally, all communities can be characterised as rather nutrient-poor. This may have several reasons: none of the studied communities has been subject to significant fertilisation, exceptions may be more intensively used meadows in the direct vicinity of farmsteads. In the ecological context of a floodplain meadow, nutrient-rich sediment input could be expected. However, the direct catchment area of these small rivers is covered in large parts by raised bogs, forests and grasslands so that the actual nutrient input may be quite small.

3.4.2 Groundwater

The habitat factor of overriding importance in the study area clearly is the groundwater regime. Depending on substrate type and position in the floodplain a small-scale mosaic of different regimes may be found that ultimately determine the local vegetation type. On the dry side of the spectrum there are well-drained sandy sites where the groundwater level drops early in the growing season and remains below the range of the gauges used here for most of the summer (see figures Fig. G.3 through Fig. G.8 in the appendix). Even flood events that otherwise caused levels to rise considerably were not detected at these sites. Sites with these kind of groundwater regime are generally covered by low grasslands dominated by *Nardus stricta* or *Festuca ovina.* In the moist to wet communities of the central floodplain, where a thick layer of clay often hampers drainage the groundwater level seldom drops deeper than one meter and is quick to rise by half a meter or more in periods of heavy rain. At these sites communities are mostly dominated by sedges like *Carex disticha* or *C. cespitosa.* In the lowest parts of the floodplains and near the rivers where the vegetation is dominated by reeds and large sedges like *Carex* acuta or *C. elata* the groundwater level is al-

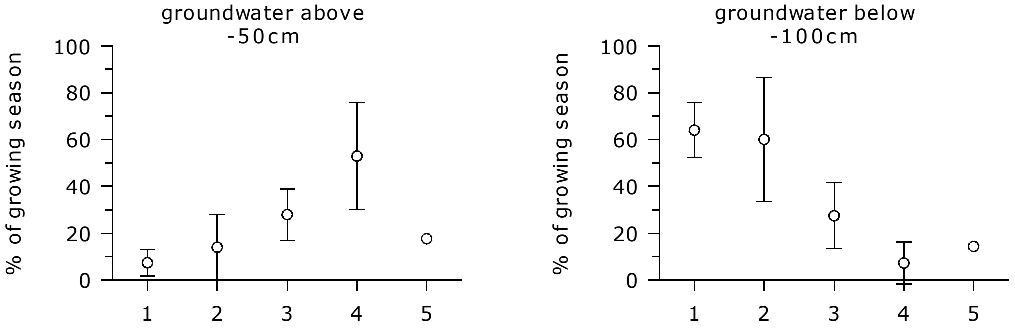


Fig. C.4: Period of time with groundwater higher than -50 cm or below -100 cm, presented as percentage of growing season measured over two years (± 1 S.D.), separately for five grassland types according to Krall et al. (1980) and Aug & Kokk (1983): (1) dry floodplain grassland (n=4), (2) mesic floodplain grassland (n=6), (3) moist floodplain grassland (n=11), (4) wet floodplain grassland with tall sedges (n=8), (5) wet floodplain grassland with tall grasses (n=1).

ways near the surface and the sites may be flooded for longer periods even in summer.

Due to technical limitations of the gauges and inaccessibility of the transects during floods and winter it was not possible to record the groundwater fluctuations constantly throughout the nominal period of measurement of two years. Therefore grassland types were characterised by the period of time the groundwater exceeds or falls below a certain level (Fig. C.4). As was to be expected, dry, mesic, moist and wet communities differ markedly in their groundwater dynamics and even mesic communities experience extended periods of dry conditions with the groundwater level falling below 100 cm depth. This habitat conditions with long periods of flooding in winter and spring on the one hand and rather dry conditions in summer are typical for the (sub-)continental floodplain meadows of the *Cnidion venosi* and *Deschampsion cespitosae* (Ellenberg 1996; Passarge 1999; Dierschke & Briemle 2002).

3.4.3 Biomass

Total biomass and litter varied considerably between sites and between sample plots. Total biomass may be as high as 749.4 or as low as 213.1 g/m^2. Litter mass varied even stronger, from a minimum of 43.5 to a maximum of 817.9 g/m^2. High biomass values were found mostly in reed beds or sedge stands, low values either in dry and poor sites, or in mesic sites in combination with a high litter mass (Fig. C.5). With few exceptions biomass was always higher than litter mass. The exceptions were again found in unmown reed-beds or sedge stands. Absolute biomass values are comparable to those described e.g. by Wheeler & Shaw (1991) and Olde Venterink et al. (2001), both reporting observations from fen and wet grassland vegetation.

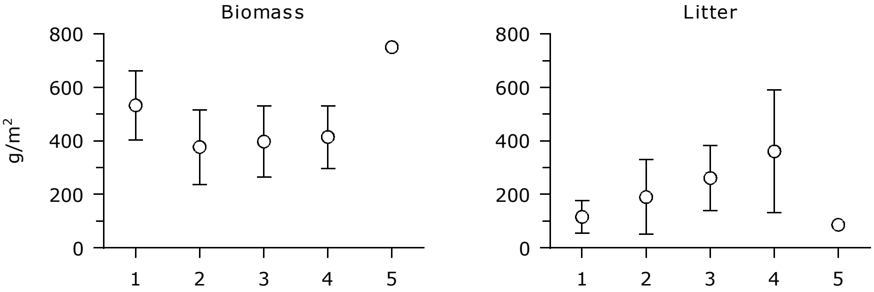


Fig. C.5: Mean biomass and litter mass (± 1 S.D.) for grassland community types according to KRALL et al. (1980) and AUG & KOKK (1983): ((1) dry floodplain grassland (n = 4), (2) mesic floodplain grassland (n = 6), (3) moist floodplain grassland (n = 11), (4) wet floodplain grassland with tall sedges (n = 8), (5) wet floodplain grassland with tall grasses (n = 1).

When looking at the different components of biomass, graminoids generally accounted for the largest part of the total biomass (Fig. G.2 in the appendix). Notable exceptions were found only in two cases: in very dry plots of a mown and partly burned site (Käära) and with moister soil conditions in a fallow (Meiekose). Bryophytes can also achieve considerable proportions of total biomass, mostly in drier sites with lower plant cover. In one case on dry and sandy soil bryophytes even made up the highest proportion of total biomass (Läti). On the other hand bryophytes were virtually absent in the partly burned site which coincided with low litter mass.

Biomass showed no linear relation to total species number of the vegetation or with vascular plant species number. However, litter mass and total species number were strongly negatively correlated (Fig. C.6).

Biomass or, more generally, productivity is considered an important factor in community ecology, both with respect to conceptual and practical questions. It is generally assumed (GRACE 1979, WAIDE et al. 1999) that species density and community biomass are strongly related. GRIME (1979) suggested an unimodal, hump-shaped relation so that species density would be highest at intermediate biomass while very high and very low community biomass would result in reduced species density. While the mechanisms behind this pattern remain debated (e.g. WAIDE et al. 1999, RAJANIEMI 2003) the pattern itself has been shown to exist in several habitats (see WAIDE et al. 1999 for an extensive review and OLDE VENTERINK et al. 2001 for a recent study in comparable habitats).

The results presented here did not unequivocally support a hump-shaped pattern, but a quadratic (parabolic) function fitted to the *total biomass* vs. *total species number* data resulted in an unimodal curve (Fig. C.6a). This relation, however, was not significant. The lack in strong correlation can be explained by the fact that the overriding environmental factor was hydrology while soil properties were rather homogeneous; furthermore, sites with very high productivity, as e.g. reported by Wheeler & Shaw (1991), were completely missing. Therefore, most of the studied meadows were in a range of productivity, where species density is potentially high and other factors like hydrology and management were responsible for the observed differences in species number.

On the practical side, community biomass is considered an important benchmark when planning restoration measures in (wet) grasslands: it has been postulated that positive effects on species number will only be observed when community biomass is below certain limits (Schrautzer et al. 1996). In case of highly fertilised meadows nutrients may have to be removed by a period of intensive mowing. However, in naturally mesotrophic habitats like the studied floodplains this considerations do not apply.

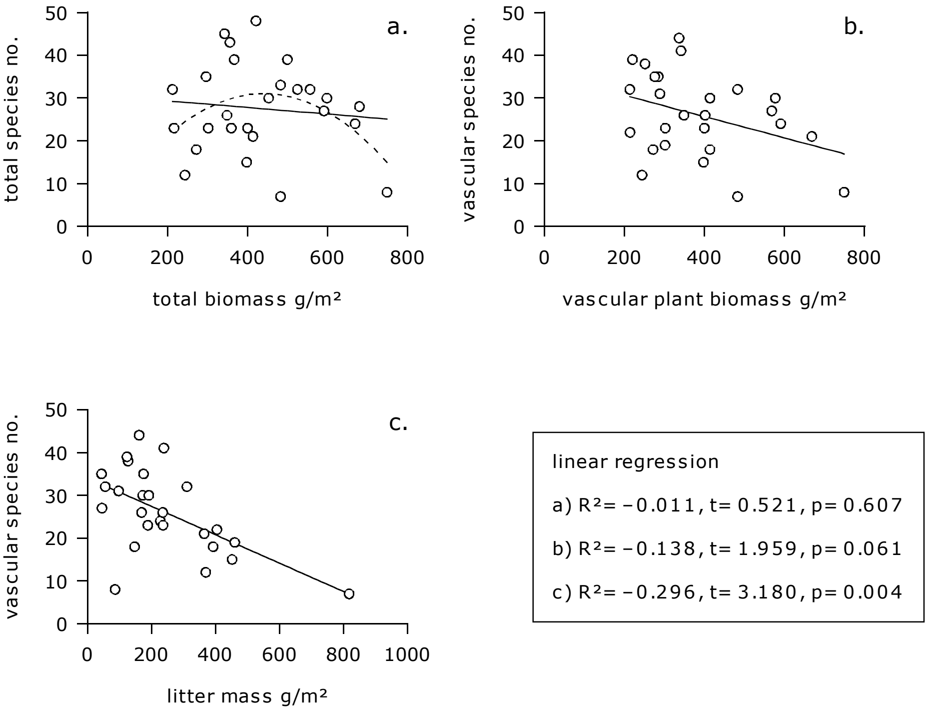


Fig. C.6: Correlation of biomass and litter mass with total and vascular plant species richness. In a.) a quadratic function is fitted to the data (dashed line); the regression, however, is not significant ($R^2=0.143$, $p=0.169$, second order polynomial regression).

3.5 Synopsis of habitat – vegetation relations

As was shown in the previous chapters, the Soomaa floodplain grasslands are a reflection of both the soil and the hydrological conditions and of the former and current land use. It may be assumed that hydrology is the single most important factor in the studied floodplain grasslands resulting in a gradient from permanently water-logged to permanently dry sites and extensive areas with a highly dynamic groundwater table. Flood intensity and duration also translate into a gradient of substrate and fertility: low lying sites, which may be flooded for prolonged periods, are covered with fine, fertile substrates while river banks and ridges are made up of sandy, less fertile substrates. Land use, finally, influences the floodplain vegetation both in the long term – human influence ultimately had been responsible for the development of these grasslands – and in the short term, when management changes or stops altogether. How these factors work together in shaping the current floodplain vegetation will be discussed in this chapter by means of Canonical Correlation Analysis (CCA), Ellenberg indicator values and with the help of a number of landscape profiles across all major floodplains (Fig. C.9 through Fig. C.14).

3.5.1 CCA

To access the habitat – vegetation relations numerically a CCA was run on those vegetation data where habitat information was available (31 samples along six transects, Fig. C.7). The first two axes had eigenvalues of 0.57 and 0.55 respectively, thus representing rather long gradients (which does not come as a surprise considering the breadth of vegetation types involved in the analysis). A permutation test (based on 1000 permutations) showed that the eigenvalues were highly significant ($F = 1.526$, $p < 0.001$). It is apparent that the environmental factors contributing most to the ordination are almost all related to the groundwater dynamics. The strongest factor is the time span the groundwater level drops below or rises above a certain depth (these two factors are of course highly correlated and therefore somewhat redundant). Also correlated positively to the first axis is minimum depth of hydromorphic features and substrate coarseness. Both factors are, directly or indirectly, related to the hydrological conditions and to the topographical position: minimum depth of hydromorphic features, i.e. rust stains and other signs of conditions that are alternately oxidising and reducing, will be greater on higher grounds where groundwater dynamics are weaker. Likewise, substrate coarseness is related to topography and hydrology: lower lying sites will be flooded for longer periods and with lower velocity so that finer material will be deposited. Sites on higher grounds on the other hand will be submerged only in case of more severe floods with higher velocity; in this case also coarser material will be deposited.

Total nitrogen and organic carbon content are negatively correlated to the first axis. Again, these factors are directly related to hydrological conditions, especially to flood duration (which could not be measured directly). Flooded soils will suffer anoxic and therefore reducing conditions, so that the decomposition of organic material is hampered and nitrogen and organic carbon can accumulate. Consequently the first axis differentiates between dry and mesic communities on sandy soils with a mostly low groundwater level and moist to wet communities on low lying sites where the groundwater rises near the surface for prolonged periods.

The second CCA axis separates between reed and tall sedge communities, which are associated with a strong humous top horizon of the soil; and between moist *Molinion* communities which show a correlation to a raised content of potassium. Whether the differences in potassium content are an effect of former management and fertilisation, or simply an effect of insufficient sampling cannot be decided at the moment. For the overall differentiation of the vegetation pH plays only a minor role; the small number of higher values in some plots (Fig. C.3) proved to be non-significant due to the small sample size.

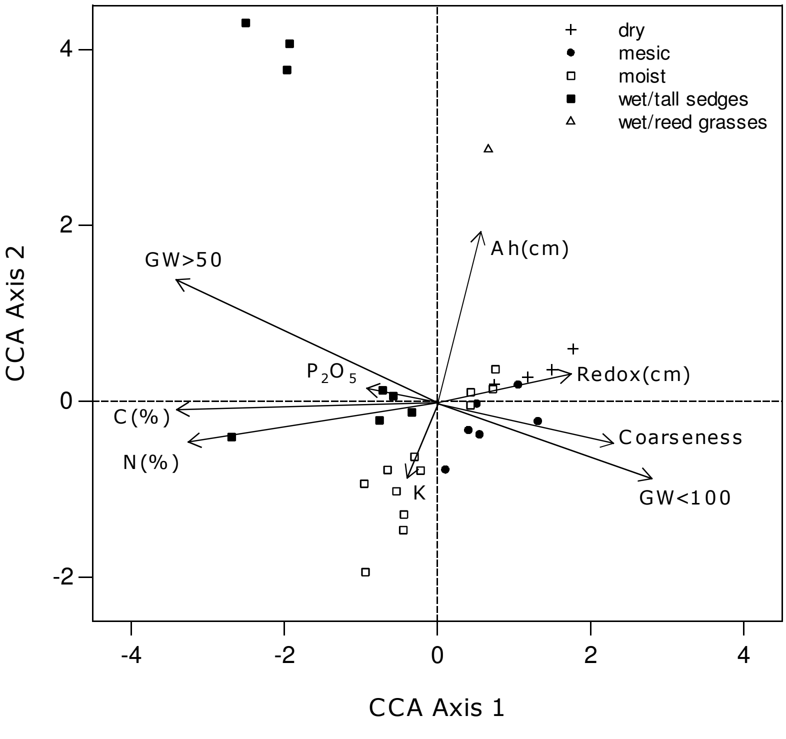


Fig. C.7: Results of Canonical Correspondence Analysis (CCA) based on 31 plots, 140 species and 10 environmental factors related to soil and groundwater dynamics. The graph shown is based on the WA site scores as these tend to be more robust with noisy environmental data (McCune 1997). **GW > 50**: time of the growing season groundwater rises above 50cm below surface; **GW < 100**: time groundwater drops below 1m; **Ah(cm)**: thickness of A or O soil horizon; **Redox(cm)**: depth of first rust stains indicating fluctuating groundwater; **Coarseness**: subjective five-step measure of substrate coarseness from pure sand to pure clay; **K** and **P_2O_5**: soil content of potassium and phosphorus; **N(%)** and **C(%)**: total nitrogen and organic carbon; **pH** measured in $CaCl_2$.

3.5.2 Ellenberg indicator values

Since not all of the rarer communities were covered by soil and groundwater samples Ellenberg indicator values were calculated for all relevés and may serve as a supplementary source of information about the underlying habitat conditions. It must, however, be born in mind that the indicator values might have to be adjusted to the hemi-boreal conditions to be fully reliable.

Generally the calculated mean indicator values suggest somewhat more variation in the environmental conditions than documented by the actual measurements. Mean "R" indicator values (i.e. reaction or acidity, see Fig. C.8) suggest more variation especially with the dry and nutrient poor *Festuca ovina* and *Nardus stricta*-dominated communities on sandy soils being slightly more acidic. Otherwise mean indicator values ranged from 5 to 7 and are thus comparable to the values presented by Böcker et al. (1983) although e.g. values for *Molinion*-communities were somewhat lower in the Soomaa samples. Also the indicator value "N" (nitrogen or general fertility) calculated for all fifteen grassland communities showed more variance: poorest conditions were found in the two dry communities but also in the *Molinion*-communities; highest values were found – not surprisingly – in the reed communities along the river margins. The indicator value "F" (moisture) shows the greatest divergence from the observed patterns: the calculated values suggest that all sites, even those that are considered dry in this study, are at least moist to damp. Only the permanently wet sites are classified in accordance with field observations. This results demonstrate that the concept of indicator values becomes problematic where the underlying environmental factor is highly variable as it is the case with the groundwater table of the Soomaa floodplains. Although extensive areas of these continental floodplains can be rather dry during large parts of the growing season they are subject to a highly dynamic water table and temporary flooding during winter, spring and autumn. This conditions have selected a number of unique species known as *Stromtalpflanzen* (i.e. river corridor plants occurring mainly in (sub-) continental floodplains, see Burkart 2001), although the exact mechanisms behind their distributional pattern remain unclear. These very characteristic species (e.g. *Galium boreale, Thalictrum lucidum, Viola persicifolia*) are joined by a number of species otherwise common under very different conditions (e.g. *Sesleria caerulea, Festuca ovina, Carex pallescens, C. panicea* etc.). Indices based on the arithmetic mean of indicator values of those species will hardly capture the dynamic nature of these environments.

Additionally to the classical indicator values related to basic environmental conditions a fourth indicator value was analysed, which describes the mowing compatibility of grassland plants (Briemle & Ellenberg 1994). The values range from 1 (complete intolerant of mowing, woody species) to 9 (very tolerant of mowing and only competitive under heavy mowing or trampling). Mean values between 1 and 3 are generally found in fallow land or fen meadows mown only once in

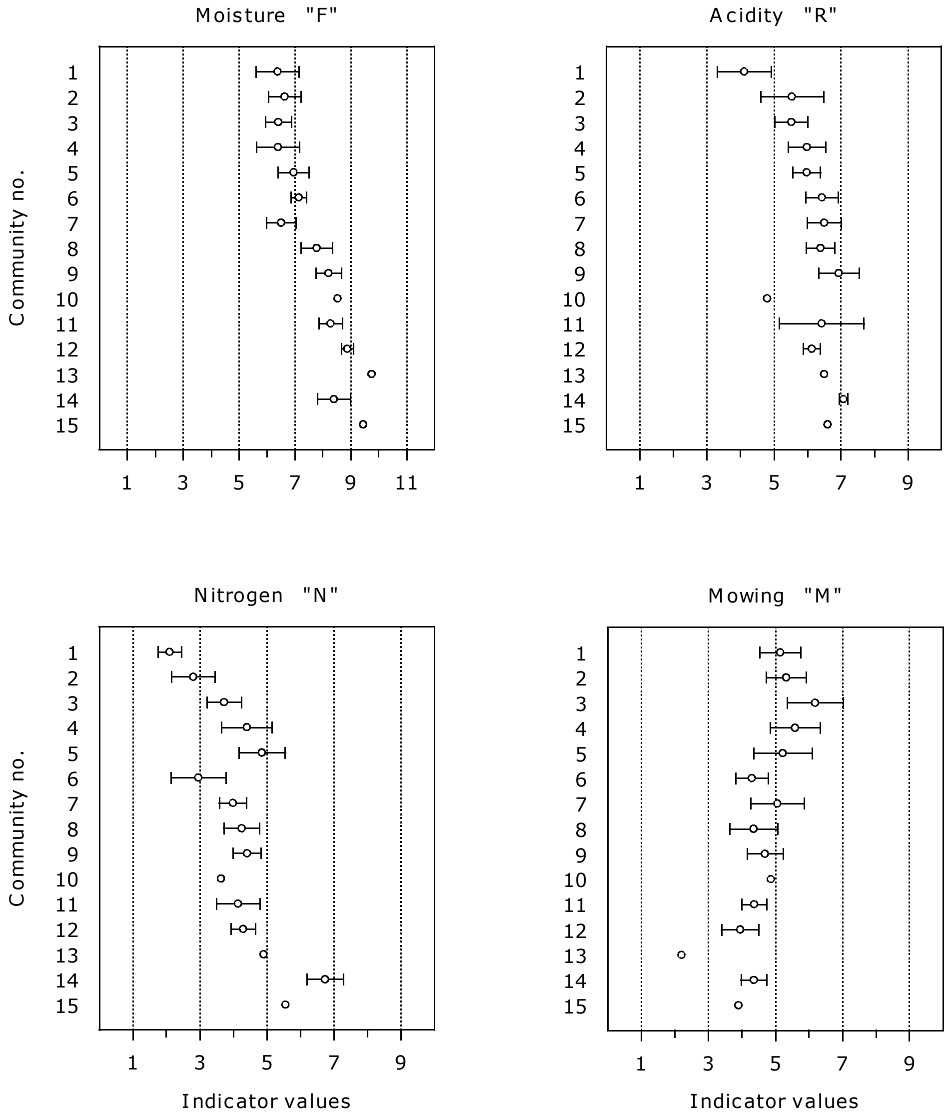


Fig. C.8: Mean Ellenberg indicator values for nitrogen, moisture, acidity and mowing compatibility (± 1 S.D.) for fifteen grassland communities described for the Soomaa floodplains: (1.) *Nardus-Festuca ovina*-community, (2.) *Festuca ovina-Sesleria*-community, (3.) *Festuca rubra-Deschampsia*-community, (4.) *Alopecurus pratensis-Galium mollugo*-community, (5.) *Alopecurus pratensis-Deschampsia*-community, (6.) *Sesleria caerulea-Deschampsia*-community, (7.) *Melampyrum nemorosum-Deschampsia*-community, (8.) *Carex cespitosa-Deschampsia*-community, (9.) *Carex disticha-Juncus filiformis*-community, (10.) *Ranunculus flammula-Juncus filiformis*-community, (11.) P*otentilla palustris-Carex disticha*-community, (12.) *Carex acuta*-community, (13.) *Carex elata*-community, (14.) *Phalaris-Phragmites*-community, (15.) *Carex acuta-Schoenoplectus*-community.

autumn; values between 4 and 6 are characteristic for extensively to moderately intensively used grasslands, whereas values between 7 and 9 are found in intensively managed grasslands. As was to be expected in these floodplain habitats most communities recorded in the Soomaa area have mean values between 4 and 6 indicating mostly extensive grassland. Highest values were found in the mesic F*estuca rubra-Deschampsia*-community which were still mown regularly. This results also support the hypothesis that the *Alopecurus pratensis-Galium mollugo*-community and the *Alopecurus pratensis-Deschampsia*-community are mainly differentiated by their management status.

3.5.3 Vegetation profiles

Tipu transect

This and the following two transects are situated along the Halliste river in sequence from south to north and encompass a large variety of habitat types and current management types. Tipu transect (Fig. C.9) is situated near a farmstead and is still mown regularly, except in very wet summers (like in 1998) when it can become inaccessible. The transect begins with stretches of the *Carex acuta-Schoenoplectus*-community and the *Phalaris-Phragmites*-community below and around the mean water line. The banks of the river are only moderately high and sandy at this point and slope gently to the central floodplain so that there is a broad region of dry and mesic grassland. In the driest parts this is made up mainly by the *Festuca ovina-Sesleria*-community while the more mesic parts are covered by the *Festuca rubra-Deschampsia*-community. In the direct vicinity of the transect, where conditions are mesic and somewhat more fertile, the *Alopecurus pratensis-Deschampsia*-community commonly occurs. In the central floodplain, where a thick layer of clay can be found shortly below the soil surface, *Carex disticha* is the dominating species, which occurs either in the *Carex disticha-Juncus filiformis*-community or in the *Potentilla palustris-Carex disticha*-community. The lowest parts of the Tipu floodplain are covered by the large tussocks of the *Carex elata*-community underneath which a thick layer of fen peat is found. Small flood channels in between the mesic and moist communities are the habitat of the *Ranunculus flammula-Juncus filiformis*-community. Due to the regular management willows and rhizomatous forbs like *Filipendula ulmaria* are rather rare in this meadow.

Läti transect

Läti meadow is situated a few kilometres downstream from Tipu meadow along the river Halliste. It is one of the largest continuous floodplain grasslands in the park area and is for this reason managed to maintain its open character. There are, however, stronger signs of successional processes than in Tipu meadow: willows are scattered over the grassland and highly competitive forbs like *Filipendula ulmaria, Urtica dioica* or *Rumex spec.* are common in most mesic and moist communities. The dry communities on well-drained sandy soils on the other hand seem to respond considerably slower to successional changes: the species number and composition in these dry communities is much more similar in a variety of sites with different management histories.

In the area of Läti meadow (Fig. C.10) the river bank is usually lined with trees (mostly alder), the steep slope facing the river is covered with the species-poor *Phalaris-Phragmites*-community. The part of the floodplain covered with grassland is exceptionally broad in the Läti area and may reach up to 500 m and more. The mesic parts of the floodplain on the broad, sandy river bank are largely covered with the *Alopecurus pratensis-Deschampsia*-community. On slightly higher grounds, which are less exposed to flooding, the *Nardus-Festuca ovina*-community and the *Festuca ovina-Sesleria*-community may be found. On the large Läti meadow these dry communities often occur like small, disconnected islands in a matrix of mostly mesic to moist and rather species poor grasslands. Large areas of the central floodplain are covered by moist and wet communities dominated by tall sedges, in the moist sector this may be the *Carex cespitosa-Deschampsia*-community, wetter sites are characterised by species-poor *Carex gracilis* stands. Broader channels, which are quickly flooded during periods of high water, are typically covered by the *Carex elata*-community.

Meiekose transect (Halliste puisniit)

This transect (Fig. C.11) lies in a region where all major rivers of the Soomaa area join so that floods tend to be especially severe and long-lasting. Consequently the soils are based almost exclusively on fine substrates and gleyic soils prevail.

Halliste puisniit was only recently cleared from shrubs and willows and generally showed the strongest signs of succession. Combined with the special environmental conditions this results in large stretches of rather homogeneous vegetation dominated by *Carex disticha*. In the central floodplain soils are composed completely of pure loam so that the floods last even longer due to lack of seepage; these sites are covered largely by the *Potentilla palustris-Carex disticha*-community and the *Carex disticha-Juncus filiformis*-community. Nearer to the river bank, where the soils contain a certain fraction of sandy material, the *Carex cespitosa-Deschampsia-* and the *Melampyrum-Deschampsia*-community may be found. A characteristic feature of these meadows, which have been abandoned for some ten years, is that certain plant species, especially *Iris sibirica* and *Betonica officinalis*, form dense, tussock-like colonies whereas on managed sites they occur as scattered populations.

Mulgi Heinamaa transects

The floodplain of the Lemmjõgi, along which these transects are situated, is characterised by a rather narrow band of grasslands and a gently sloping river bank. For this reason these meadows are quickly flooded even in summer. Floristically these meadows are of high importance – there are large populations of *Iris sibirica*, *Scorzonera humilis* and *Gladiolus imbricatus* – and consequently they are mown with high priority (including hay removal). The shorter transect MHT1 (Fig. C.12) is situated close to the Mulgi heinamaa bridge and is therefore managed more regularly, the longer transect MHT2 (Fig. C.13) on the other hand shows more signs of abandoning but is also mown if the conditions permit this. It must further be noted that the Lemmjõgi river is quite extreme in its meandering creating very small-scale gradients from permanently wet ox-bow ponds to dry ridges between consecutive bends of the river.

The river bank at both transects is generally lined with a band of *Carex gracilis*, together with various combinations of other reed plants (*Schoenoplectus*, *Phalaris*, *Phragmites*). Within only two to three meters the vegetation changes to a dry *Festuca ovina-Sesleria*-community where *Scorzonera humilis* may form large populations. Where the substrate changes from sand to clay and conditions are more moist the *Sesleria-Deschampsia*-community and the *Carex cespitosa-Deschampsia*-community form species-rich stands. In the lowest areas the grassland communities blend into fens when e.g. the *Potentilla palustris-Carex disticha*-community is joined by species like *Carex appropinquata* or *Carex diandra*.

Käära transect

The Käära transect (Fig. C.14) is situated at the Raudna river in the eastern part of the National Park. This meadow is still managed by a farmer, both mowing and low intensity grazing were observed and the meadow may even be burned in winter. The meadows of this part of the Soomaa area differ from the other studied meadows in that the banks are exceptionally high so that even lower lying areas are often not directly flooded but are more influenced by ascending water.

The steep outer banks are covered by the *Phalaris-Phragmites*-community, which in this case is very species rich, especially in forbs typical of moist to wet meadows. The top of the bank is lined by trees and shrubs, mostly alder and willow but also elm, lime and ash may be found. The dry and mesic ridge of the river bank is characterised by a relatively unique set of species classified as the *Alopecurus pratensis-Galium mollugo*-community which, however, has strong links to the *Festuca rubra-Deschampsia*- and to the F*estuca ovina-Sesleria*-community (but lacks *Sesleria*). The lower parts of the floodplain are again covered by large stretches of the *Carex disticha-Juncus filiformis*-community, small channels or ditches are filled with the *Carex acuta*-community.

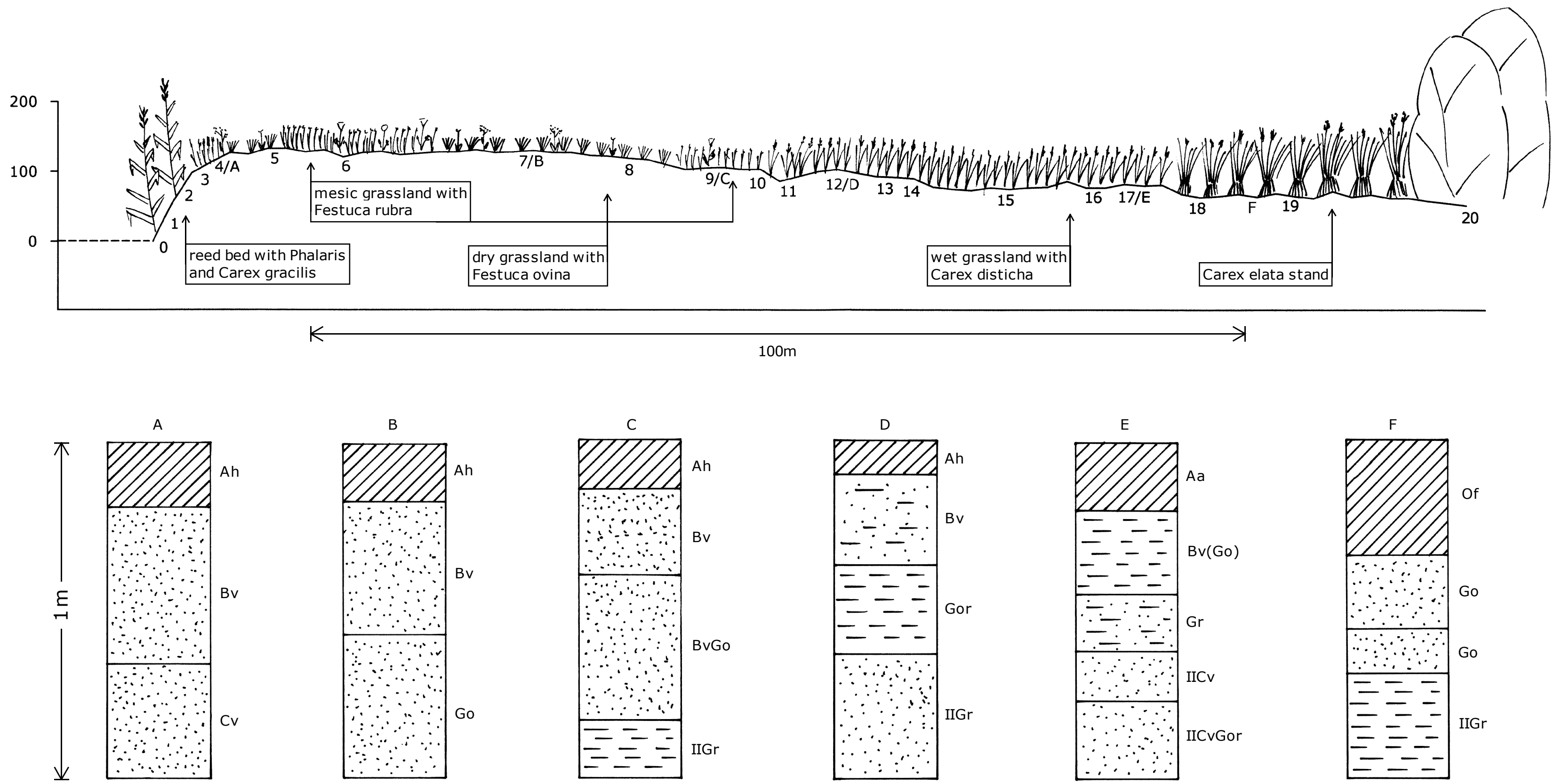


Fig. C.9: Landscape profile near Tipu school at the Halliste River (Tipu transect: TT) with soil profiles at six sample locations (capitals A through F). Nomenclature of soil strata follows AG Boden 1994. Numbers 0 through 20 indicate location of relevés.

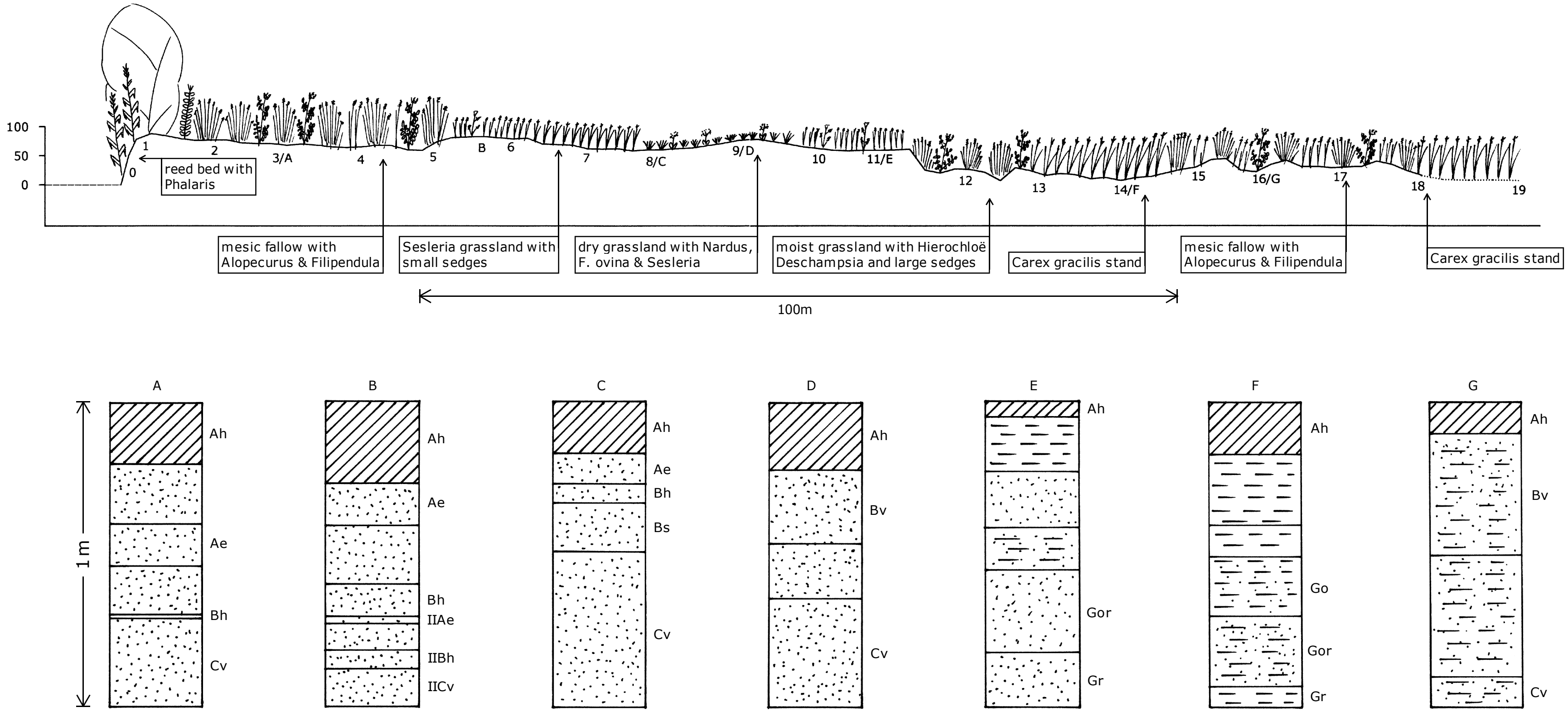


Fig. C.10: Landscape profile of Läti transect (LT) at the Halliste River with soil profiles at seven sample locations (capitals A through G). Nomenclature of soil strata follows AG Boden 1994. Numbers 0 through 19 indicate location of relevés.

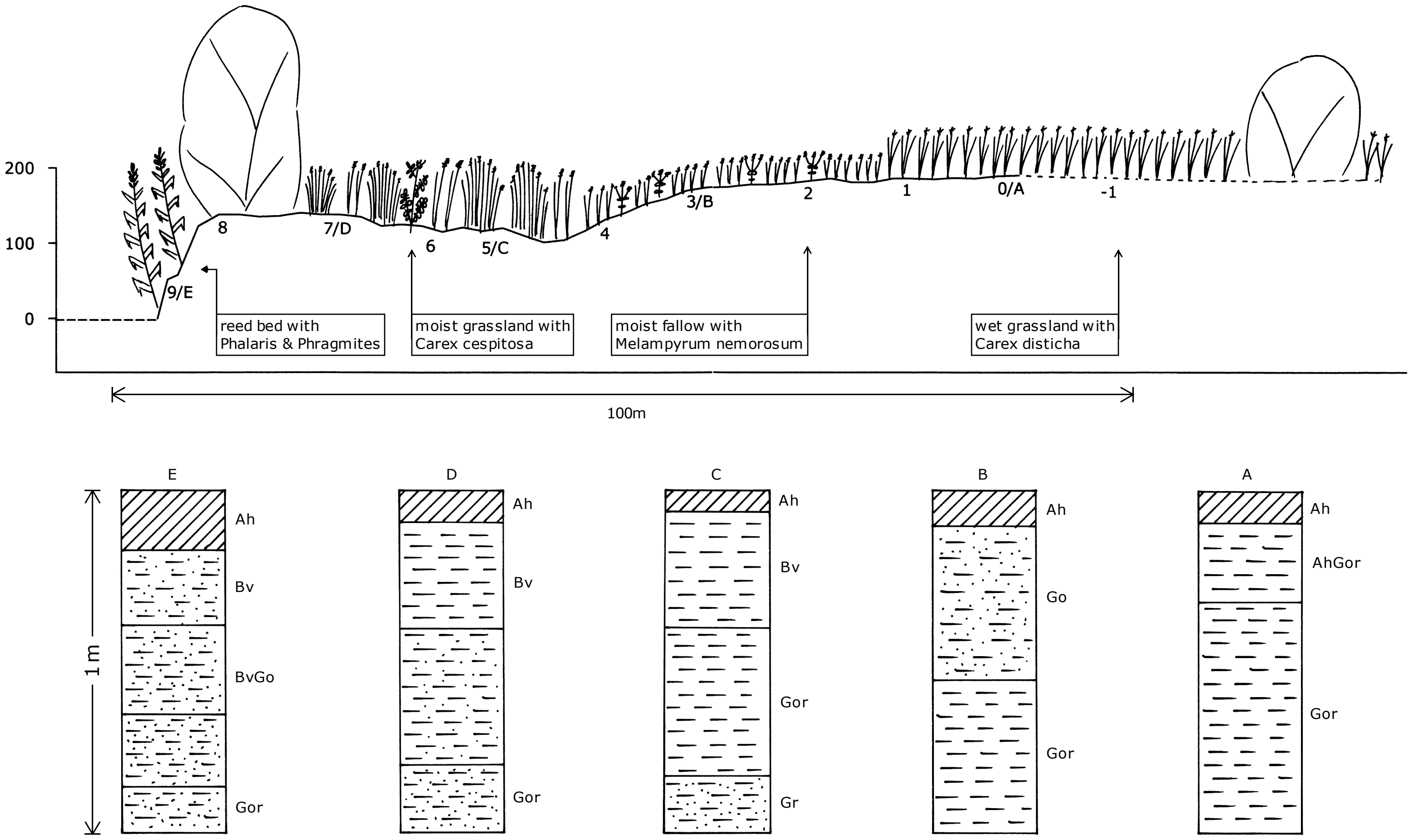


Fig. C.11: Landscape profile of Meiekose transect. (MT) at Halliste river with soil profiles at five sample locations (capitals A through E). Nomenclature of soil strata follows AG Boden 1994. Numbers -1 through 9 indicate location of relevés.

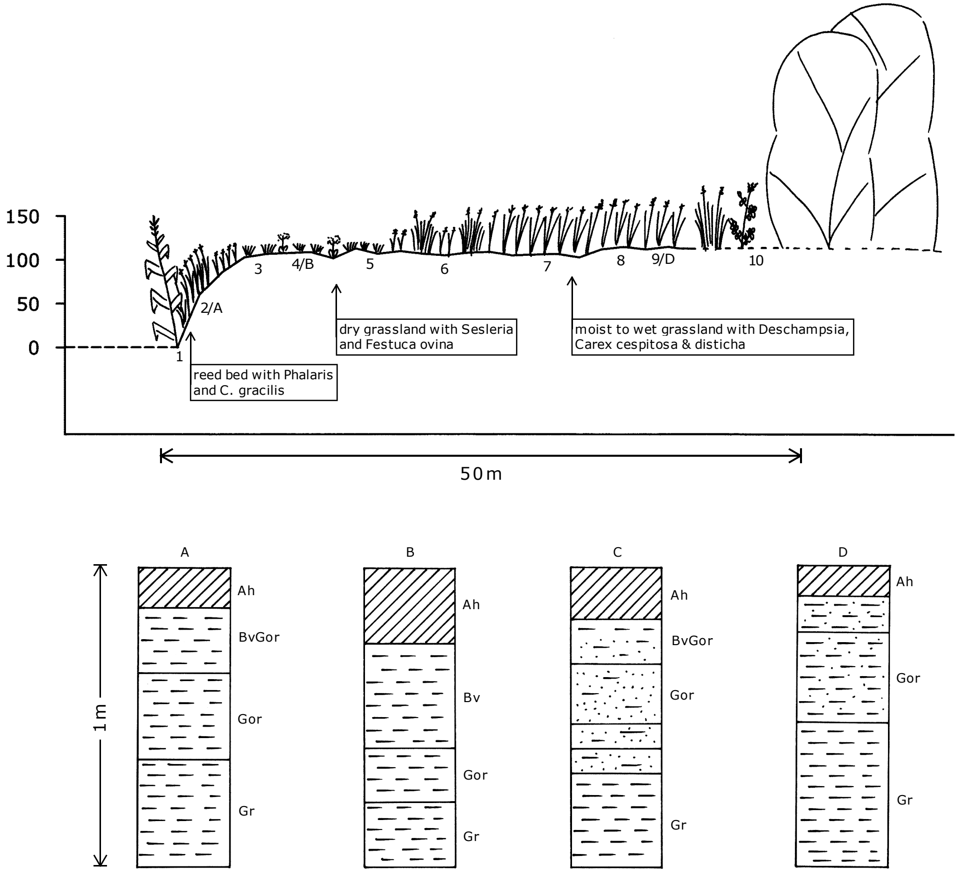
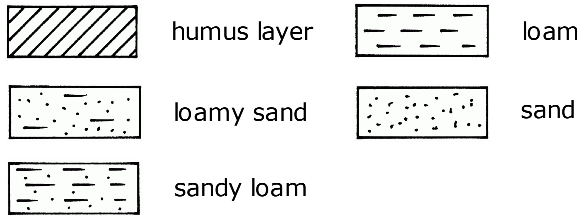


Fig. C.12: Landscape transect at Mulgi Heinamaa transect 1 (MHT1) with soil profiles at four sample locations (capitals A through D). Nomenclature of soil strata follows AG Boden 1994.

Legend for Fig. C.9 through C.14:



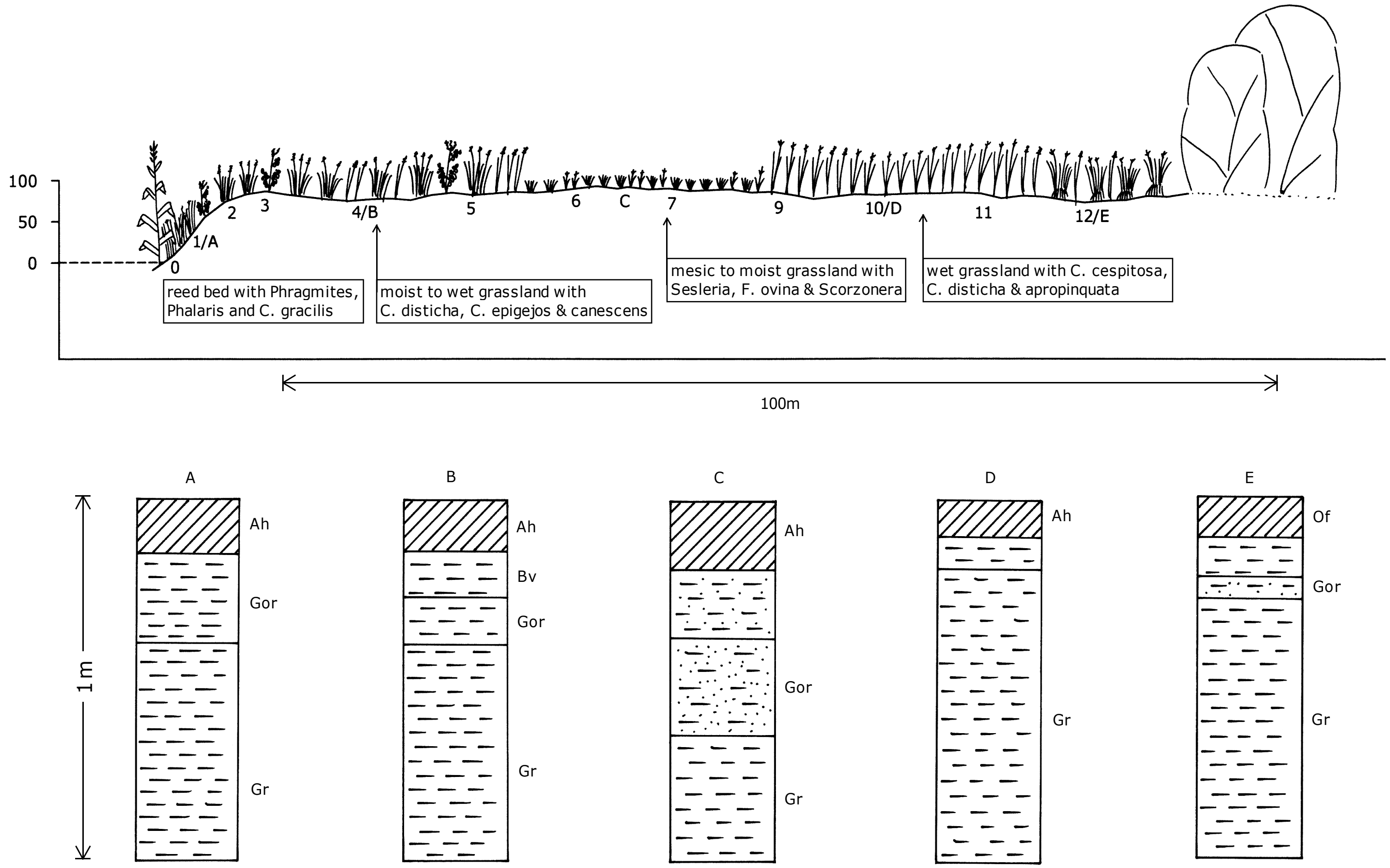


Fig. C.13: Landscape profile at Mulgi Heinamaa transect 2 (MHT2) with soil profiles at five sample locations (capitals A through E). Nomenclature of soil strata follows AG Boden 1994. Numbers 0 through 12 indicate location of relevés.

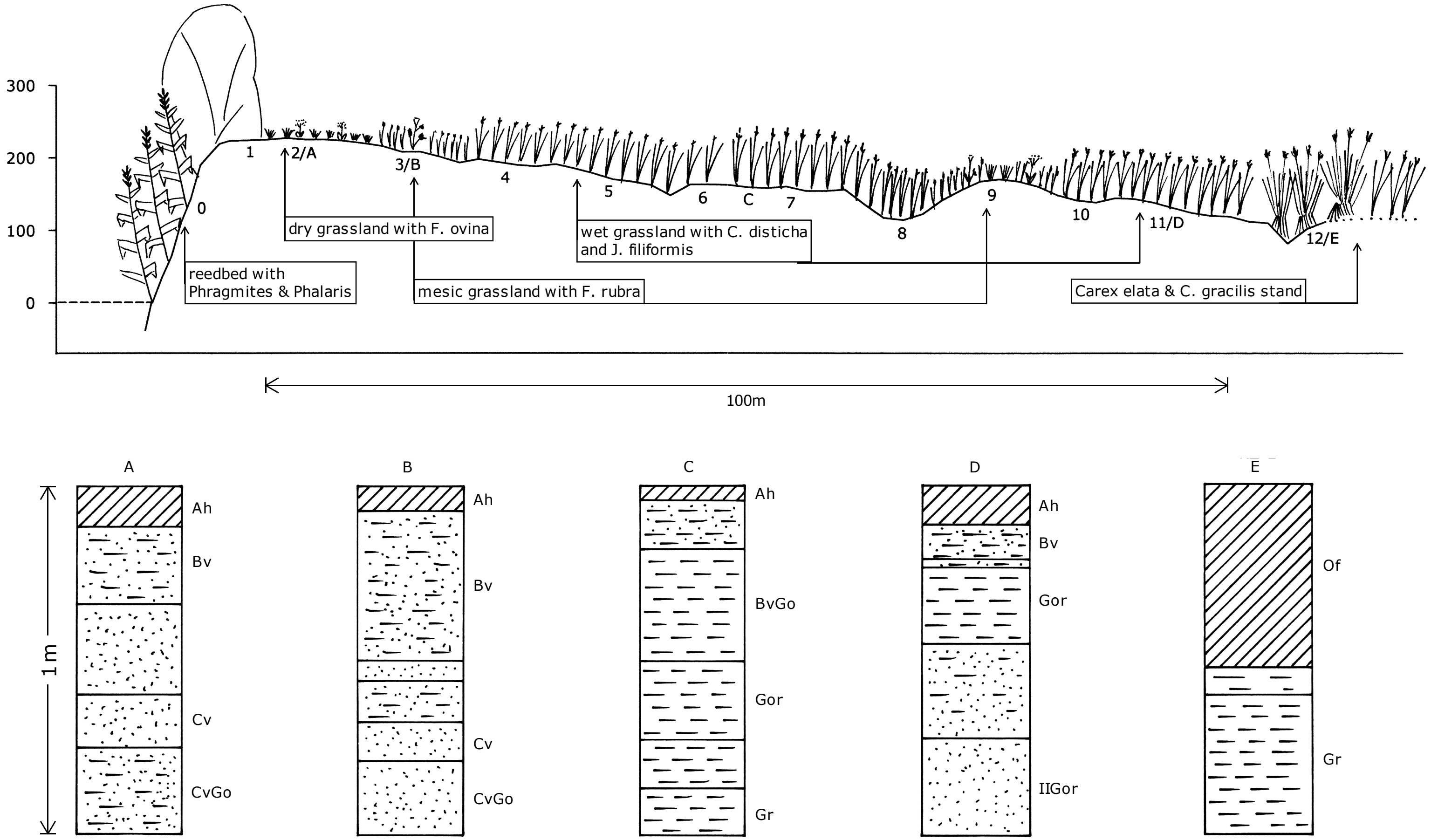


Fig. C.14: Landscape profile at Käära transect (KT) with soil profiles at five sample locations (capitals A through E). Nomenclature of soil strata follows AG Boden 1994. Numbers 0 through 12 indicate location of relevés.

3.6 Nature conservation and management

It has already been stated in the introducing chapters that wet grasslands are among the most endangered habitats in Europe (Benstead et al. 1997; Joyce & Wade 1998; Benstead et al. 1999). At the same time these habitats support a considerable biodiversity both in their flora and fauna. It is stated for Estonia (Benstead et al. 1999) that 20 % of the rare plant species of the Baltic region occur in wet floodplain biotopes; among these are *Angelica sylvestris*, *Iris sibirica*, *Scorzonera humilis*, *Succisa pratensis* and *Valeriana officinalis*, all of which were common in the studied meadows. Other species of the Soomaa floodplains that are either legally protected or are listed in the Estonian Red Data Book (ERDB) are *Gladiolus imbricatus*, *Primula farinosa* and *Thalictrum lucidum*. Also the bird fauna of the Soomaa floodplains is notable for a number of rare and/or endangered species: *Crex crex* (Corncrake) e.g., which is considered globally endangered (Benstead et al. 1999), was commonly heard on all studied meadows. Also *Grus grus*, *Ciconia ciconia* and *Ciconia nigra* (Crane, White Stork and Black Stork), which all depend to some degree on wet grasslands and wetlands in general are found in the Soomaa floodplains and surrounding areas.

Floodplain meadows are generally the result of a long process of human activity (except for those in the far north formed by ice scouring); however, they degenerate quickly once the management stops or is significantly altered. Benstead et al. (1999) identified seven groups of factors which contribute to the degeneration of floodplain meadows and to the loss of diversity. Among these are *changes in agricultural practice* (including intensification and abandonment), *land drainage & flood defence* and *site fragmentation*. Hydrological conditions of the Soomaa floodplains can be considered near-natural with frequent and long-lasting floods so that no measure are necessary in this respect. Also fragmentation does not seem to be a critical issue at the moment: the frequent floods provide an effective measure of dispersal (Wanner 2003) and in three species of conservational interest (*Iris sibirica*, *Trollius europaeus* and *Scorzonera humilis*) no evidence for negative effects of small population size or fragmentation were found (Meier 2000; Schürzinger 2000; Bylebyl 2002). *Intensification* of agricultural use mostly comes in the form of regulation of the water table, application of fertiliser and/or pesticides or even reseeding. Following this measures higher stocking densities or higher mowing frequencies are possible allowing the farmers to achieve higher productivity and finally higher profits. This modifications always result in species poor communities where only few species highly tolerant of grazing or mowing remain. The single most important factor in this context is high nutrient input typical for intensively managed grasslands (Poschlod & Schumacher 1998). It has been repeatedly shown that high nutrient input, leading to high biomass production, is negatively correlated with species richness (Janssens et al. 1998; Joyce 2001).

In much of Central and Western Europe the major losses of wet grasslands date back several decades, the development having started in the 1950ies with the large scale intensification of agriculture (Schrautzer & Wiebe 1993; Joyce & Wade 1998; Poschlod & Schumacher 1998). In effect, only small fragments of the former semi-natural grasslands have remained. Although in Estonia too intensification and abandonment have led to considerable losses in the area of semi-natural grasslands, large areas like the later Soomaa NP were still managed extensively till the beginning of the 1990ies. Reasons for this were the low costs of labour and fuel and the enormous demands in the Soviet Union for agricultural products, whether produced economically or not. According to Leibak et al. (1996) the soviet type of grassland management was sufficient to preserve the Estonian floodplain grasslands and their biodiversity. Consequently Paal (1998) states, that so far no floodplain community has been considered rare, although several may become endangered in the future due to abandonment. Considering the current distribution of floodplain grasslands in Estonia (Truus & Tõnisson 1998) dry floodplain grasslands may be among the more endangered communities as they are generally rare and make up only ca. 5% of the total area of floodplain grasslands. On the other hand, own observations suggest that these dry and rather nutrient poor communities are relatively stable and less prone to rapid invasion of shrubs and clonal forbs like *Filipendula ulmaria*.

The most immediate threat to the Soomaa floodplain meadows obviously is abandonment. A first wave of abandonment took place in the 1940ies when farmers were deported or forced to join collective farms. These meadows were either afforested with spruce or have now developed into young floodplain forests. With regained independence at the beginning of the 1990ies a second wave of abandonment took place when the large collective farms were closed and only a handful of small private farms remained. In between these two larger waves of abandonment smaller areas dropped out of management so that at present there is a mosaic of abandoned meadows ranging in age from some 15 to 65 years.

The successional processes and pathways occurring after abandonment of grasslands are now well studied and understood (Stöcklin & Gisi 1985; Schreiber 1987; Neitzke 1991; Müller et al. 1992; Rosenthal 1992; Jensen 1997; Schrautzer & Jensen 1998). With the cessation of management, changes in the competitive interactions lead to substantial shifts in the species composition of abandoned grasslands. Jensen (1997) described four distinct phases or stages in the succession of wet grasslands: an initial phase (successional stage I) with no substantial changes in the species composition is followed by a phase (stage II) where tall rhizomatous species, which were already present in the initial meadow community, spread considerably. These species produce large amounts of biomass which is not decomposed completely during winter and thus forms a growing layer of litter. By their own underground storage of nutrients and quick clonal growth these species are able to cope with the thick litter layer while less competitive species are excluded from the community. Especially species that have to rely on generative reproduction are not able to establish beneath the litter layer with its unfavourable microclimate and light conditions. Another important effect of abandonment and built-up of a litter layer is that nutrients are retained and accumulated in the community while during management they were removed from the system, only by this allowing the formation of species-rich communities. In the following phase (stage III) competitive species from outside the initial community increasingly invade and come to dominance. The succession can be locked in this stage when litter and dense vegetation prevent further invasion and establishment of woody species. Examples of this community type were observed in the Soomaa area in the form of dense stands of *Filipendula ulmaria, Urtica dioica* and various tall sedges like *Carex disticha*, *C. acuta* or *C. acutiformis*. Usually, however, succession will proceed to stage IV with the invasion of woody species like *Salix ssp.* and *Alnus ssp.* Currently all described successional stages may be observed in the Soomaa NP although the vegetation sampling described in the preceding chapters focused on successional stages I and II.

Optimal management measures depend crucially upon the current status of the meadows, the goals that are to be achieved and upon the financial and technical resources available for management. Different measures are necessary if the meadows are located on highly fertilised and drained fen peat or on moderately fertile floodplain soils with a natural flood dynamic. It is also important to state whether the management is focused on floristic or faunistic diversity or whether the aim is simply to halt succession and maintain an open landscape. Financial resources clearly are the limiting factor so that not all of the roughly 1300 ha of current and former floodplain grassland can be optimally managed to maintain them in or return them into a species-rich, semi-natural state. Therefore the National Park has formulated different goals to optimally allocate the available financial resources. Approximately two thirds of the former floodplain grasslands have undergone such successional changes that with the current resources it will not be possible to maintain them: they will be left to succession. Another 11 % – mostly stands of tall sedges – will be managed infrequently to keep them from overgrowing and to maintain the character of an open floodplain; species richness is not the primary aim in these cases. The remaining 27 % are still in a good to moderately good, species-rich condition and need regular management to maintain or improve their present state.

A number of studies have evaluated the effectiveness of different management variants (Schiefer 1981; Bakker 1989; Rosenthal 1992; Schreiber 1997; Vinther & Hald 2000; Wahlman & Milberg 2002). The general options for grassland management are mowing with or without removal of hay, grazing and burning (Benstead et al. 1997). These methods may further be varied with respect to timing, frequency or combination with other methods.

Burning may seem advantageous in a situation where financial resources are limited and when there is no use for large quantities of hay: large areas can be cleared of coarse vegetation and litter in short time and at low costs. In most cases however, burning has many unacceptable effects on the fauna and flora, so that it can only be recommended when no other management method is feasible. The species number of plants is in most cases negatively affected whereas clonal species and those with organs for underground storage benefit from this treatment; the plant species composition of burnt meadows is reported to be very different from the original communities (BAKKER & DE VRIES 1985; NEITZKE 1991; SCHREIBER 1997; HANSSON & FOGELFORS 2000; WAHLMAN & MILBERG 2002). Own observations on burnt patches in the Sandra area support this; besides the absence of a litter layer, bryophytes were conspicuously absent from communities where they otherwise abundant. Furthermore burning can damage many animal groups like less mobile invertebrates or ground-breeding birds (BENSTEAD et al. 1997). With respect to the Soomaa floodplain meadows, burning is probably only an option in meadows that would otherwise be overgrown by bushes and that have no importance for the conservation of animals or plants. If used at all, burning should be done infrequently and only on parts of the meadows, so that a mosaic of habitat types can develop. Special care has to be taken where meadows border on peat sites as this can result in subterranean fires. Burning could be done in winter when the soil is frozen but snow is absent as this should result in minimal disturbance for the invertebrate fauna.

The Soomaa floodplain meadows were largely used for hay production, but grazing around the farms and aftermath grazing on the more distant sites also occurred (ALLILENDER & ROOSALU 2000). It therefore seems worthwhile to consider reintroducing grazing as an additional management method. There is a growing awareness in Europe that traditional, low-intensity farming systems are the key factor for many highly divers cultural landscapes (BIGNAL & MCCRACKEN 1996). Several studies have shown that low-intensity grazing systems with traditional breeds of domestic animals (also discussed within the framework of pastoralism by TUBBS 1997) can help preserve or restore species-rich semi-natural grasslands (VINTHER & HALD 2000; WAHLMAN & MILBERG 2002; HELLSTRÖM et al. 2003; see also the case studies in Benstead et al. 1999). ITJESHORST & GLADER (1994) studied the use of Galloways in the maintenance and restoration of wet grassland and concluded these can effectively be employed for this task; furthermore grazing was in this case more cost efficient than mowing with additional removal of the hay. At the Swedish Hornborgasjön cattle, sheep and ponies are used successfully to restore and manage lake-side wet grasslands (BENSTEAD et al. 1999). VINTHER & HALD (2000), however, caution that grazing may promote sedges and rushes and thus change the species composition of the communities in undesired ways. These examples show that the introduction of grazing by hardy, traditional breeds of domestic animals in the Soomaa area could be an interesting strategy to manage large areas of floodplain grasslands that would otherwise overgrow with bushes and trees. Several points, however, have to be carefully considered:

- selection of the type of breed and stocking densities can control the impact the grazers have on the grasslands and to which extend woody and other unwanted plants are removed by grazing.
- grazers may have to be excluded for certain times from sites which are important for ground-breeding birds.
- long floods in spring and long and severe winters make it necessary to provide shelter and fodder for the animals and will necessarily raise the costs for this type of management.
- wolves and bears may a problem for animals which are kept outside for most of the year.

In contrast to grazing, where grazers eat selectively rejecting some species and favouring others, mowing affects all species in the same way creating a sward of uniform height. Furthermore one-time mowing allows a large number of species to find a temporal niche and complete their life cycle with seed set and ripening. Therefore extensively mown meadows are often especially rich in forbs, whereas grazed meadows are rather dominated by grasses although certain unpalatable species may become problematic weeds (Dierschke & Briemle 2002).

Mowing currently is the main management method employed in the Soomaa NP. The floristically most valuable sites are mown every year and the hay is removed while floristically less important sites are mown – as time and financial resources permit – less frequently; the hay may have to be left on the sites or is gathered and burned in winter when the ground is deeply frozen (Allilender & Roosalu 2000). Removing the hay from the meadows is generally strongly recommended as it opens the sward for seed germination and favours less competitive species by removing nutrients from the system and preventing the formation of a thick mat of dead plant matter (Benstead et al. 1999). A cost-efficient alternative to mowing plus hay removal could be mulching: the plant matter is cut to small pieces and left *in situ* where it decomposes quickly without forming a thick mat of litter. The drawback of this method is that nutrients are not removed from the system although the spring floods will probably wash away much of the remaining litter. Whether this method is appropriate for the Soomaa floodplain meadows would have to be evaluated in a comparative study which ideally should include all other relevant management methods like burning, mowing with varying frequency and timing and maybe even grazing.

When setting up the time of mowing several points have to be considered: if depletion of nutrients is necessary or the hay is to be used for livestock early mowing in June to July is recommended (Benstead et al. 1999). Rosenthal (1992) notes that on productive fen sites which are mown late in the year tall and rather species-poor stands can develop. Early mowing, however, can be detrimental to ground breeding birds like *Crex crex* or certain plants of conservational interest like *Iris sibirica* so that the timing of mowing has to be adjusted accordingly.

Mowing for grassland conservation has a number of pros and cons which have to be carefully considered when setting up a management plan: mowing can be easily done by local farmers with common machinery and takes only a short time whereas grazing needs an all-year commitment in terms of personnel, finances, buildings etc. Mowing, however, may not be cost-efficient on large wet grassland sites when there is no use for the crop. Grazing on the other hand could be part of a larger scale strategy for the conservation of this old cultural landscape involving e.g. also the appropriate marketing of the products.

D. Dispersal, regeneration, and the role of plant traits

1 Introduction

If a suitable habitat would be the only factor controlling the distribution of a plant species, it should be found at all sites with the right combination of abiotic conditions, i.e. at all sites matching its habitat niche (GRUBB 1977). However, as is e.g. evidenced by many years of (often fruitless) efforts to restore species rich, semi-natural grasslands, suitable habitat conditions are a necessary but by no means sufficient precondition for a plant to grow at a certain place (BAKKER & BERENDSE 1999, VAN GROENENDAEL et al. 2000). As GRUBB (1977) pointed out in his seminal paper, a plant species has also to find a match for what he termed its *regeneration niche*. The regeneration niche encompasses a description of all the specific requirements of a plant during its regeneration cycle, ranging from the production of viable seeds to dispersal in space and time and to germination and establishment.

The *conditio sine qua non* for a species to become established at a certain location is obviously the presence of viable seeds (disregarding the possibility of colonisation by vegetative means at this place, which is of course a highly important mechanism in permanent grasslands (e.g. ERIKSSON & JAKOBSSON 1998, MILBERG 1993) but which was not considered in this study). The species of the local flora (e.g. in this case the Soomaa are) which are capable of growing in the target community were described by ZOBEL et al. (1998) as the *local species pool*, being a subset of the *regional species pool* (e.g. the relevant part of the flora of Estonia or the baltic region); in contrast to these, the species actually growing in the target community are conceived as the *community species pool*.

What may seem trivial can be actually a highly limiting factor once a species has disappeared from the current vegetation due to habitat deterioration or destruction (PRIMACK & MIAO 1992, BAKKER 1999, BISCHOFF 2002), or for other reasons is not present at a newly created site. Plant species may overcome this lack of diaspores by either dispersal in time or dispersal in space (BAKKER et al. 1996; STRYKSTRA et al. 1998; BAKKER & BERENDSE 1999). Put the other way round, it can be hypothesised that a population may either be seed or microsite limited (ERIKSSON & EHRLÉN 1992; COULSON et al. 2001; OZINGA et al. 2005, POSCHLOD & BIEWER 2005, POSCHLOD et al. 2005).

1.1 Seed banks

Dispersal in time – the formation of a bank of viable but dormant seeds in the soil – is a well-known phenomenon in many temperate plant communities (Poschlod 1991; Thompson 1992). Its role for the maintenance of floristic and genetic diversity (Levin 1990) and its potential for the management and restoration of species-rich plant communities (van der Valk & Pederson 1989; Maas & Schopp-Guth 1995; Bakker et al. 1996) has led to a vast amount of research on these topics. Fundamental to the discussion on seed banks is the distinction between three types, i.e. *transient*, *short-term persistent* and *long-term persistent*

(Thompson 1992; Thompson 1993). In the first case seeds persist for less than one year, often much less. This means that all seeds of one cohort germinate immediately after seed shedding or after the next unfavourable season has passed. In the second case (*short-term persistent*) seeds survive longer than one year, but less than five years, i.e. populations are able to bridge years unfavourable for seed set. In the third case (*long-term persistent*) seeds persist for longer than five years in the soil, often even much longer; species with this behaviour are able to bridge unpredictably long periods of unfavourable conditions, e.g. late successional stages, and they are the only ones which are likely to contribute to successful restoration measures.

The size of the seed bank varies considerably between habitats and so does the similarity of the species composition of the seed bank and that of the established vegetation. Generally, the dominant species of habitats with little natural disturbance (woodlands, grasslands, wetlands) do not form long-term persistent seed banks (Thompson 1992). Consequently, there is little similarity between the established vegetation of this habitat types and the respective seed banks. This has been repeatedly shown for permanent, temperate grasslands (Milberg 1993;

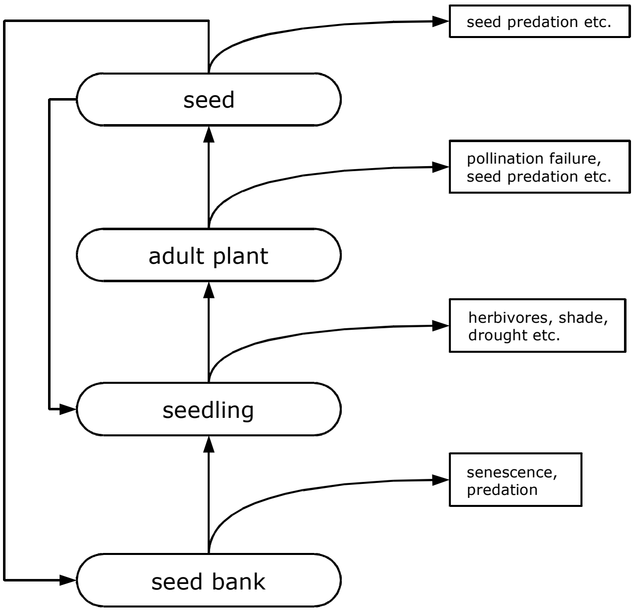


Fig. D.1: Simplified pathway of seed regeneration and possible reasons for failed transition.

Milberg 1995; Edwards & Crawley 1999; Amiaud & Touzard 2004). On the other hand, arable weed communities, heathlands and disturbed wetlands often have extensive and persistent seed banks. However, as Thompson (1992) points out, no community is totally undisturbed and the scale of the disturbances also play an important role in determining which modes of establishment become important. As floodplain grasslands are a mosaic of different habitat types with varying disturbance regimes depending on flooding frequency the role and composition of the seed bank can be expected to vary considerably.

1.2 Seed dispersal

If a species is neither present in the seed bank nor in the established vegetation of a target site, the only chance of getting there by natural means is by the seed rain – another field of intense theoretical and practical research (Howe & Smallwood 1982; Renner 1992; Chambers & MacMahon 1994; Bakker et al. 1996; Bonn & Poschlod 1998; Lehmann et al. 1999). In a variety of habitats seedlings derived from the seed rain play an important role in community regeneration (Peart 1989; van Splunder et al. 1995; Fröborg & Eriksson 1997; Jensen 1998). Whether a species will be part of a community's seed rain depends to a considerable extend on its dispersal mechanism. There are a number of attempts to classify the different dispersal mechanisms and vectors (see Bonn & Poschlod 1998 and references therein). However, until much more is known about actual 'real-world' dispersal processes of individual species in specific habitats all these classification systems have to cope with the problem of inferring dispersal vectors from morphological clues (see Poschlod et al. 2004). These may or may not lead to correct interpretations: our perception of what constitutes a *morphological feature* or an *adaptation* will probably be incomplete or may even be incorrect. Furthermore seeds may actually be dispersed by vectors which they are not adapted to: most seeds will be transported by water for some distance, provided the stream's current is strong enough, and many seeds may be transported by animals when adhering to wet fur or when being part of mud sticking to an animals hooves. Furthermore all seeds below a certain seed weight can be effectively transported by wind although this does not have to be an adaptation but may simply be an effect of the well-known seed-size/seed-number trade-off (Westoby et al. 2002). In many cases, however, morphological features clearly suggest adaptations to certain dispersal vectors (the *pappi* of Asteraceae, wings or plumes to wind dispersal; elaiosomes to dispersal by ants; hooks, barbs and other sticky features to animal dispersal, etc. (Bonn & Poschlod 1998)). Therefore a pragmatic classification based on morphological features seems to be the only feasible approach when the aim is a community-scale comparison of dispersal spectra (e.g. Hodgson & Grime 1990; Willson et al. 1990). Tackenberg (2001) developed an elaborated model to estimate the potential of species for long distance wind dispersal based mainly on the terminal velocity and height of seed release. Additionally Tackenberg formulated a rule-based approach to estimate the overall long distance dispersal potential taking into account also epi- and endozoochory and hemerochory. As the result is a real number and not simply a binary descriptor, as in most classical classifications, it is better able to capture the diversity of processes operating in the real world. Applying this approach to the Soomaa data, however, was beyond the scope of this study. One common outcome of studies of dispersal spectra is that in many habitats a large proportion of species do not have any apparent dispersal mechanism (WILLSON et al. 1990). Also often the species with the greatest dispersal capacity (in space as in time) are ruderal species with little relevance for the management or restoration of species rich communities (e.g. SCHRAUTZER 2004).

Hydrochory is one of the mechanisms which may potentially lead to long-distance dispersal; moreover seed deposition is relatively selective – wetland plants will most likely be deposited again in wetland habitats and not in some totally alien habitat as will unavoidably be the case e.g. with wind-dispersed seeds (BONN & POSCHLOD 1998). An important factor determining which seeds get actually dispersed by running water is the timing of the flood event and of the seed shed (VAN SPLUNDER et al. 1995). It has been repeatedly shown that hydrochory is an important factor structuring plant communities of floodplains from floodplain forests and meadows to aquatic communities (NILSSON et al. 1989; SMITS et al. 1989; NILSSON et al. 1991; SCHWABE 1991; JOHANSSON & NILSSON 1993; KLEINSCHMIDT & ROSENTHAL 1995).

Besides the natural dispersal vectors like wind, water and animals, man has a large influence on dispersal processes (HODKINSON & THOMPSON 1997). Herds of grazing animals have been shown to be effective dispersal vectors in low-intensity farming systems (POSCHLOD & BONN 1998) and even modern mowing machinery may act as a dispersal agent (STRYKSTRA et al. 1997). However, nowadays the influence of man on dispersal processes is probably mainly negative: low-intensity farming systems with their associated seed dispersal have largely disappeared and the ongoing fragmentation of natural and semi-natural habitats has disrupted many natural dispersal processes (MACDONALD & SMITH 1990, POSCHLOD et al. 1996).

Another focus of research on seed dispersal is the question of *seed shadows,* i.e. the spatial distribution of dispersed seeds around the source (WILLSON 1992). Generally, seed shadows are strongly leptokurtic, i.e. a high peak near the source and a long tail monotonically declining from the peak outwards. This pattern implies that most seeds will not travel far from their source, in fact seldom more than a few dozens of meters (HARPER 1977; HOWE & SMALLWOOD 1982; WILLSON 1993). Moreover, that the seed rain will almost exclusively contain species of the local community. This is in line with numerous observations that populations may be in fact dispersal limited (PEART 1989; PRIMACK & MIAO 1992; ERIKSSON 1998; EHRLÉN & ERIKSSON 2000; KUPFERSCHMID et al. 2000; FRANZÉN & ERIKSSON 2003; OZINGA et al. 2005), and even in cases where source populations are directly adjacent to target sites of restorations projects, re-colonisation may be extremely slow (Donath et al. 2003). However, the tail of the seed shadow, i.e. the very few seeds that actually do travel for a longer distance, may still be of great ecological importance for founding new populations or colonising newly created habitats, even if this is difficult to detect (Silvertown 1991; Cain et al. 2000).

1.3 Gap regeneration

Once a seed has arrived at a certain location – whether by seed rain or from the seed bank – it needs a favourable site (a *safe site* sensu Harper et al. 1961, see also Fowler 1988) for germination and establishment. A closed vegetation canopy and even small layers of litter or bryophytes are generally unfavourable for seed germination and seedling establishment (van Tooren 1988; Špacková et al. 1998; Jensen 2003) as they limit the access to vital resources like light and water. There is now a considerable amount of evidence that gaps, i.e. small-scale disturbances in the dominant vegetation canopy, play a great role in offering these *safe sites* and thus provide opportunities for regeneration from seed (Grubb 1977; Pickett & White 1985; Silvertown & Smith 1988; Bullock 2000; but see Grubb 1988 for a differing view where disturbance and regeneration may be uncoupled). Classical examples are forest gaps that are quickly invaded by fast growing but rather short-lived tree species (Brokaw 1985; Qinghong & Hytteborn 1991) but this mechanism has also been described for permanent grasslands (Peart 1989; Bullock et al. 1995; Eriksson & Eriksson 1997; Pakeman et al. 1998; Kalamees & Zobel 2002; Vandvik 2004). Much of this research was carried out in dry calcareous

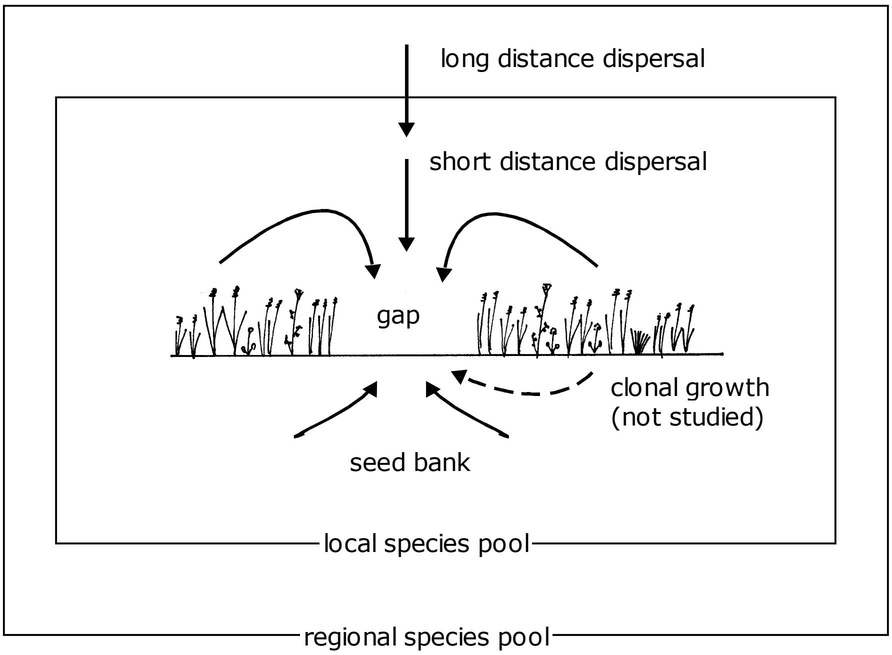


Fig. D.2: Framework of gap regeneration experiment with sources of colonisation and different scales involved.

grasslands, which have a relatively high proportion of short-lived species that rely on regular regeneration from seed (van der Maarel & Sykes 1993; Kupferschmid et al. 2000; Zobel et al. 2000; Kalamees & Zobel 2002). In this type of grassland, permanent creation and re-colonisation of small-scale gaps lead to a high mobility of species and guarantee the coexistence of a large number of species.

In permanent grasslands like the ones under consideration in this study, gaps may arise by various means, at different scales and times in the year. Small-scale gaps may be created by burrowing animals, trampling or ramet death but at small sizes gaps in permanent grassland are most likely filled by vegetative means (Bullock et al. 1995). Larger-sized gaps are frequently created by mowing machinery, by wild boars, and during flooding by ice scouring or large woody debris. All of these disturbances have been observed in the study area. Even though the studied wet grassland communities may be dominated by clonal plants that quickly invade small-scale disturbances, nonetheless a number of plants have to rely on regular or occasional regeneration by seed. According to Ellenberg (1996) clonal growth is of little advantage especially in late mown litter meadows as these are dominated by tussock plants that have to regenerate by seed.

Regeneration by seed is not only a significant process in natural and semi-natural communities, but may also gain importance as a method of grassland restoration. When source populations do not exist or are too remote for unaided dispersal to be effective direct sowing of single target species or seed mixtures is a possible means to re-establish desired species (Benstead et al. 1997; Davies 2002, Poschlod & Biewer 2005).

1.4 Plant trait analysis

In the last decade or so, there is an increasing interest in the use of plant traits and growth-form or functional groups for the analysis of such topics as community response to disturbance, shifts in management practices or global climatic change (Lavorel et al. 1998; Weiher et al. 1999). Analysis of plant traits and functional groups, by abstracting from the individual species and integrating easily obtainable knowledge about multiple species, makes it possible to formulate hypotheses about underlying processes and mechanisms and to make predictions of community responses to the above mentioned environmental changes. Furthermore, by using trait or functional group spectra comparisons across floristic boundaries are possible where purely floristic comparisons would fail due to lack of co-occurring species.

Depending on the object of study various plant characteristics may be used; while the focus of the studies is mostly on 'hard traits' directly related to the factor under consideration (e.g. competitive ability, dispersal ability etc.), these traits are often difficult to assess directly (Cornelissen et al. 2003). Therefore 'soft traits' are used that are easily measured or extracted from the available literature and that are reasonably good correlates of the 'hard traits'. Among the traits that have proved to be useful in the analysis of recruitment processes are seed mass and number, plant height, clonality, life span and history, onset of flowering and seed shedding and dispersal mode (e.g. WEIHER et al. 1999). There is e.g. a well established trade-off between seed size or mass and seed number (HARPER 1977; LEISHMAN 2001; WESTOBY et al. 2002). Generally speaking, a plant can either invest in a large number of necessarily small seeds which may be expected to be more easily dispersed; or a plant may invest in a small number of large seeds which should have advantages in recruitment as they can rely on larger 'on-board' resources to overcome unfavourable conditions (WESTOBY et al. 1996). It may be expected that under varying environmental conditions, e.g. disturbance regimes, different traits or strategies are advantageous. The timing of important life cycle events like seed shedding can have important implications for recruitment success: the shedding of seeds with a certain dispersal mode must coincide with the presence of the respective dispersal vector (e.g. hydrochorous seeds and flood events) or otherwise dispersal will be ineffective (BLOM et al. 1990; VAN SPLUNDER et al. 1995). Likewise, time of germination must coincide with the presence of safe sites to allow for successful recruitment; being too early or too late at the right place might mean leaving the field to competitors. The most well-known strategy scheme in plant ecology is the CSR-scheme of GRIME (1977). It focuses on the plant's ability to cope with competition (C), abiotic stress (S) and disturbance (R) and combines these three basic factors in a triangular fashion. Problematic with this type of strategy schemes is that e.g. *competition* may mean different things for different species or for the same species in different situations and thus the classification may only be valid in the vegetation for which it was developed (LAVOREL et al. 1997).

COLASANTI et al. (2001) noted that "in ecology there are many more actors on the stage than roles that can be played". The concept of using functional (rather than purely taxonomical) criteria for classifying species has a long history in ecology (e.g. WARMING 1896; RAUNKIAER 1937) and consequently there is a multitude of terms in use for often (but not always) similar concepts (life forms, guilds, strategies, functional types, morphological groups, etc.). In a review LAVOREL at al. (1997) recognised four types of functional classifications: (1) *emergent groups*, based on correlations of biological attributes, (2) *strategies*, species having similar traits that are considered adaptive under certain conditions of resource use, (3) *functional types*, species fulfilling similar roles in ecosystem processes, and (4) *specific response groups*, species responding similarly to specific environmental factors. COLASANTI et al. (2001) stress the difference between functional *groups* and functional *types*. Following their definition, functional *groups* share a single important trait leading to functional similarity in this respect; depending on the trait considered, species may belong to several functional groups simultaneously. Functional *types* on the other hand share a collection of traits, which define a unique and exclusive function; consequently a species can only belong to a single functional *type*.

In this study plant functional groups (PFGs) are defined operationally as groups of species sharing a set of traits that are *considered* functional under the given environmental conditions. In this, they largely coincide with the 'emergent groups' of LAVOREL at al. (1997) and the 'functional types' of COLASANTI et al. (2001). Whether the traits are indeed functional and whether the functional groups discovered by multivariate analysis are indeed related to environmental variables will have to be discussed *a posteriori*.

1.5 Questions asked

In a series of three experimental studies various aspects of the regeneration niche of floodplain species were investigated on an individual and on a community scale. In a first experiment a selection of ten typical plants of the local floodplain meadows were sown into artificially created gaps simulating different disturbance intensities. Recruitment success was monitored after one and again after three years. In a second study the differential contribution of seed rain and seed bank to the regeneration after disturbance of the vegetation was studied *in situ*. Experimental patches were created in two different habitat types that selectively excluded either seed rain, seed bank, both of these or none. This two experimental studies were complemented by an observational study using seed traps along three transects to estimate the composition of the seed rain at different locations and time of the year. More specifically the following questions and problems will be discussed in this chapter:

Seed trap study:

1. Which species can be found in the seed rain of three different floodplain meadows? Does the seed rain reflect the different floristic composition along the sampled gradients from the river margins to dry meadow communities? Is the seed rain more similar to its native plant community or to other seed rain samples?
2. Does the seed rain entirely reflect the species composition of the local meadow community or is there evidence for substantial long-range dispersal?
3. Which temporal and spatial patterns can be found in the seed rain?
4. Is the seed rain a random sample of the local meadow community or are certain plant traits (seed weight, height of mature plant, dispersal type, etc.) over- or under-represented? What does this suggest about the processes and mechanisms?
5. What conclusions can be drawn from this results regarding the management or restoration of floodplain meadows?

Recruitment in artificially created gaps:

1. Which species will establish spontaneously in artificially created gaps of two different meadow types?
2. What is the differential role of seed rain and seed bank as a source of establishing seedlings?
3. Are the different seedling assemblages more similar to each other or to their native communities of established plants?
4. Does the trait composition of the seed rain and seed bank reflect that of the native established vegetation, or are there significant differences in the composition? What does this suggest about the mechanisms responsible for the formation of the seed bank and seed rain and about the mechanisms governing gap regeneration?

Seed sowing experiment:

1. Are the selected species able to germinate in the studied meadow communities and what is the influence of different gap types on germination and establishment? Are there species that establish equally well in undisturbed vegetation and on bare ground?
2. How is emergence rate after one year related to establishment success after three years and survival rate? Are good germinators also good survivors?
3. Which role does seed mass play for germination and establishment success? Do heavier seeds, as generally assumed, have an advantage over lighter seeds in less favourable situations?

Plant traits and functional groups:

1. How are traits distributed among the common meadow plants?
2. Are all traits distributed randomly within species or are certain traits intercorrelated, suggesting e.g. trade-offs?
3. Is it possible to arrange species, on the basis of morphological and functional traits, into groups of similar trait composition? Which traits are most important in defining these groups?
4. Are plant functional groups (PFGs) distributed evenly among the floodplain communities or are certain PFGs significantly associated with certain communities? What does these associations suggest about underlying processes acting in those communities?

Taking together the primary results additional questions may be addressed:

1. Is there evidence for populations of floodplain meadows to be either microsite- or seed-limited?

2. What conclusions can be derived from these experiments regarding the maintenance or restoration of species-rich floodplain meadows? What role do seed dispersal and regeneration from seed play in semi-natural grassland communities with near-natural habitat conditions? What does this tell us about the management necessary to preserve these or restore more heavily affected grasslands?

2 Methods

2.1 Seed rain

Seed traps

The seed rain, being an important component of the dynamics of plant populations and communities, is increasingly becoming the focus of both theoretical and practical research. There are various technical solutions to the task of trapping seeds (Kollmann & Goetze 1998) which all have their pros and cons depending on the question asked, the habitat studied and the time and man-power available for processing the traps. For this study it was decided to install a large number of technically simple traps rather than using more elaborate but necessarily fewer traps (Jackel & Poschlod 1994).

In spring 1999 seed traps were installed along three of the above described transects in Soomaa NP (Läti, Mulgi Heinamaa 2, Käära; see Table C.3) to cover typical topographic and moisture gradients in habitat and vegetation. The traps where placed at 10 sample plots along the Läti-transect (at distances of 5, 10, 20, 30 45, 70, 81, 90, 105 and 155 m from the river), and 9 each along the Käära-transect (at 1, 10, 20, 30, 50, 71, 85, 100 and 105 m) and the Mulgi Heinamaa 2-transect (at 1, 5, 10, 20, 30, 40, 55, 70 and 91 m). Four of the 28 plots represent the dry floodplain grassland type (see Table C.2), five belong to the moderately moist, ten to the moist and nine to the wet grassland type with tall sedges.

Seed traps consisted of plastic gardening pots with a quadratic opening of 11 × 11 cm; two of these pots were placed inside each other with the inner one having its bottom removed. Between the two pots a sheet of thin cloth was placed; on emptying the seed traps these sheets were replaced and dried for later identification of seeds. The bottom of the outer pot had holes so that rain water could leave the traps without washing seeds out and slowly rising groundwater could enter the traps from below. The traps acted to some degree like normal soil surface, in that they allowed for secondary dispersal. Five of these traps were placed in a fixed pattern (Fig. D.3) on a 1 m² sample plot thus totalling an

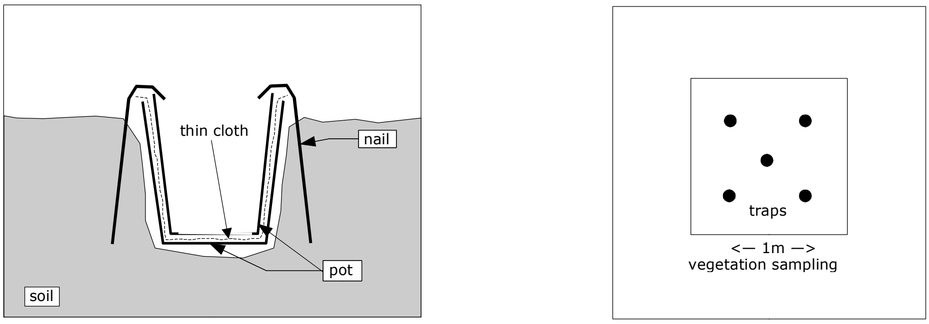


Fig. D.3: Sketch of seed traps used in this study and layout of plots for vegetation sampling and seed trapping area of 605 cm² per sample plot. Seed traps were emptied seven times in 1999 beginning on June 30th and ending on November 15th. The traps were left in the field over winter and were again emptied on May 11th 2000. Identification of seeds was done visually with a dissecting microscope with the help of a reference collection; obviously damaged or empty seeds were not included in the counts.

Seeds in drift material

In August 2000 heavy rainfalls lead to a sudden rise in river water levels which flooded parts of the Mulgi Heinamaa meadows and other lower lying parts of the National Park. Three samples of drift material were collected and checked visually for transported seeds. Subsamples of 100 ml each were analysed quantitatively to get an impression of the seed densities in drift material, the rest of the samples was scanned qualitatively to obtain a more or less complete species list. Although these samples are by no means representative they may serve as an indication of the importance of summer flooding events for seed dispersal.

Vegetation survey

For comparison of the seed trap data with the established vegetation, vegetation was sampled in the 1m² plots around the seed traps before installing the traps. Cover classes were identical to those used in the regular vegetation survey. Seeds found in the traps with the respective adult plants present in these plots are considered to have originated locally with practically no (i.e. ≤ 1 m) dispersal between plant and trap. To assess the possibility of longer range dispersal two additional data sets were used: species presence information from the transect plots, and finally, compiled check lists of whole meadows. The seed traps were generally placed not further than 5 m away from the transect plots so that a plant present here but not in the trapping plots indicates a dispersal distance of up to 5 m.

Data analysis

For the comparison of the established vegetation with the total seed rain or the pooled seed rain of whole transects frequency or mean cover alone would be inadequate measures. A highly frequent species can be of low overall cover and a species with high mean cover (when counting only those lots where the species is present, as is done here) can be infrequent; in both cases the species would contribute little to the overall seed rain. Therefore a measure of *importance* was calculated for each species in the established vegetation by multiplying mean cover and frequency (see also JURKO 1987). This value was used as percentage importance in the analysis of species traits in the seed rain and the established vegetation.

The variation of the species numbers found in the seed rain of different meadow types was analysed with a Kruskal–Wallis one-way ANOVA, followed by the Steel-Dwass test (STEEL 1960), a non-parametric multiple comparison procedure equivalent to the Tukey-test. Spearman's rank correlation analysis was used to test the relationship between the species numbers of seed rain and established vegetation. All statistical analyses were performed with the free R package version 1.8.1 (R DEVELOPMENT CORE TEAM 2003), except for the Steel-Dwass test, which was done with the graphing and statistical package KyPlot version 2.0 beta 15 (YOSHIOKA 2001).

NPMANOVA (Anderson 2003) was used to compare the species composition of the seed rain and the established vegetation, both for the complete data set and various subsets (different sites and grassland types). NPMANOVA is a new method for testing multivariate hypotheses based on any distance measure. The method can handle any one- or two-way ANOVA design. P-values are calculated using permutations of the original data. Bray-Curtis dissimilarity was used on quantitative and on presence/absence transformed data. To independently verify these results a cluster analysis was performed using the group-average algorithm (UPGMA) on a Bray-Curtis dissimilarity matrix. The cluster analysis was performed with the MVA-package, the dissimilarity matrix was calculated with the VEGAN-package (OKSANEN 2004), both of the R statistical package (R DEVELOPMENT CORE TEAM 2003).

Plant traits were used in the analysis of this experiment to assess the role of plant functional characteristics for the distribution of species in the seed rain as compared to that in the established vegetation. For this purpose a multivariate approach was chosen. In addition to the species × plot and species × trap matrices describing the floristic composition of vegetation and seed rain a trait × plot matrix was compiled. This matrix lists the percentage of all species characterised by a certain trait, weighted by species abundance. NPMANOVA (ANDERSON 2003) was used on this matrix, as with plain species compositional data, to test for significant differences in trait composition between seed rain and established vegetation. In a second step the plot × trait matrix was subjected to a Principle Components Analysis (PCA); the loadings (scores) of traits on the PCA axes denoted the traits most strongly associated with each axis. Correlation of the axes with habitat (three experimental sites and four grassland types) and treatment (established vegetation vs. seed rain) was assessed with a Mann-Whitney-U-test. By this two-step approach the association of traits and treatments and habitat could be addressed. All analyses were performed with the R statistical package (R DEVELOPMENT CORE TEAM 2003) together with the MVA-package for multivariate and the CTEST-package for univariate analyses. For a more in depth discussion of the selection of the plant traits, their coding and the analysis of plot × trait matrices see page 92.

2.2 Seed sowing experiment

The effect of different gap types on the germination and establishment of typical floodplain species was investigated by sowing seeds of ten species into experimental plots . All species were perennial forbs or sedges with a wide range of seed and plant traits. The seeds were collected in summer and autumn 1999 at various sites in the park, dried and stored at room temperature in paper bags until used in the experiment. All seeds were sown in the beginning of October 1999 within four days. The number of seeds sown differed according to availability and ranged from 40 to 200.

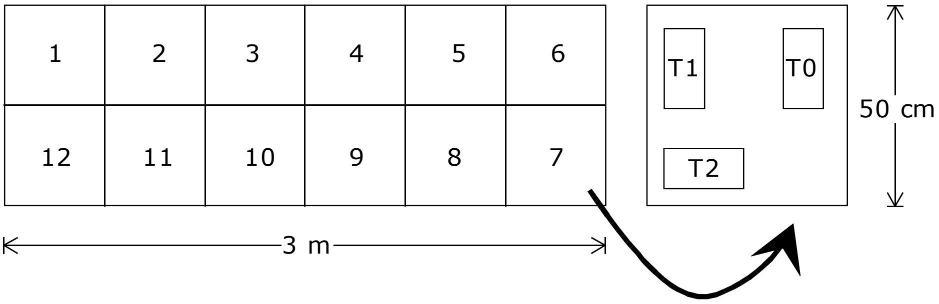


Fig. D.4: Layout of seed sowing plots (ten species plus two controls, randomly assigned) and treatment patches (T1: all vegetation removed, T2: litter and bryophytes removed, T0: intact vegetation)

The experimental plots were 50 × 50 cm in size (Fig. D.4). Twelve of these were arranged in two adjacent rows of six each. In each plot one randomly selected species was sown into three treatment patches of 10 × 20 cm. These patches were arranged systematically to facilitate recovery. Two corners of each plot were permanently marked with PVC tubes into which a wooden frame with wires marking the exact location could be fitted for counting of the seedlings. Two plots were set aside randomly as controls. However, none of the sown species germinated in the controls indicating that all seedlings originated from the seeds initially sown. Displacement of seeds out of the treatment patches was minimal (in the range of < 5 cm) proving that the different treatments were appropriately spaced and did not mix. 14 replicates were set up along all major rivers in the park area on six different meadows. The locations of the plots were selected so that all species could be expected to grow there but it was taken care that none of the sown species was actually present in the experimental plots or within a radius of a few meters.

Three different treatments were applied to the patches before sowing:
- T1: all vegetation removed to the bare soil,
- T2: bryophytes and litter removed, and
- T0: intact vegetation.

When sowing into the patch types T2 and T0 the vegetation was gently brushed so that the seeds would fall down to the ground and could not be easily blown or washed away. The germination and establishment of the sown seeds was followed over a period of three years. Seedlings were first counted in August 2000, giving an estimate of the rate of *emergence* in the field and again in August 2002, allowing to calculate the rate of *establishment* and the *survival* rate. However, at this second date only six out of the original 14 replicates could be recovered, partly due to subsequent management of the sites.

Information on species

Betonica officinalis

This perennial plant is a character species of the alliance *Molinion*. It occurs sporadically in Estonia, mainly in wooded meadows, forest edges and scrubs. In the Soomaa area *Betonica* is rather rare: it was only found in the area of Halliste puisniit on an abandoned wet meadow where it forms massive clusters. Reproduction is by seed and vegetatively by means of rhizomes (KLOTZ et al. 2002) although vegetative spread is slow (KLIMEŠOVÁ & KLIMEŠ 1998). Seed bank type is transient to short-term persistent and in the CSR-strategy scheme the species is classified as a competitive (C).

Carex flava s. str.

A perennial sedge common throughout Estonia and in the Soomaa area in fens and wet meadows. Reproduction is by seed and vegetatively by shortly creeping rhizomes (KLOTZ et al. 2002). Information on seed bank type varies but is probably short term-persistent while the ecological strategy is competitive-stress tolerant-ruderal (CSR).

Table D.1: Meadow species included in the seed sowing experiment and some aspects of their biology.

Species	Seed weight (mg)	CSR life-strategy	Dispersal vector	Life history	No. seeds per plot
Betonica officinalis	1.17	C	UN	clonal perennial	200
Carex flava s. str.	1.06	CSR	AQ	clonal perennial	100
Carex pulicaris	1.81	CSR	UN	clonal perennial	50
Iris sibirica	10.71	CS	AQ	clonal perennial	100
Lychnis flos-cuculi	0.15	CSR	WIc	clonal perennial	200
Scorzonera humilis	2.33	CSR	WIp	clonal perennial	40
Selinum carvifolia	0.93	CS	WIw	non-clonal perennial	100
Thalictrum lucidum	0.87	CS	UN	non-clonal perennial	100
Trollius europaeus	0.51	C	WIc	non-clonal perennial	200
Veronica longifolia	0.10	CS	WIc	non-clonal perennial	200

Carex pulicaris
An inconspicuous perennial sedge typical for fens and fen meadows. In western Estonia common but otherwise rare. In Soomaa it was mostly found in dry meadow types and in *Molinion*-meadows although it may be frequently overlooked due to its small size. All seeds were collected at one site at Tipu school where a large population is found in a base rich fen meadow of the *Caricion nigrae* alliance. It reproduces by seed and vegetatively by short below-ground stems (Klimešová & Klimeš 1998, Klotz et al. 2002). A seed bank is probably absent, the ecological strategy is competitive-stress tolerant-ruderal (CSR).

Iris sibirica §[1]
A conspicuous perennial plant of wet meadows (*Molinion*) and wooded meadows. Occurrence in Estonia is sporadic but in the Soomaa area it is still frequently found in the wetter parts. When the meadows are mown the populations may cover large areas but after abandonment only single large old tussock-like individuals remain with little recruitment between these (Bylebyl 2002). A seed bank is probably absent, the ecological strategy is competitive-stress tolerant (CS). The species is legally protected in Estonia. Seeds are the largest in this experiment with a mean weight of 14.8 mg and are water-dispersed.

Lychnis flos-cuculi
A common perennial plant of wet meadows, wooded meadows and road verges. In Estonia and in the Soomaa area it is very frequent in all appropriate habitats. According to Klotz et al. (2002) regeneration is by seed and vegetatively by short rhizomes (Klimešová & Klimeš 1998). It has a long term persistent seed bank and the ecological strategy is competitive-stress tolerant-ruderal (CSR). Seeds are small with a mean weight of 0.2 mg and are classified as wind-dispersed (WIc *sensu* Grime et al. 1988).

Scorzonera humilis
A perennial character species of the order *Molinietalia*; while rare and strongly protected in Germany, it is common in Estonia, mainly on meadows, wooded meadows, coastal meadows and pine forests. In the Soomaa area it can be found mainly in smaller patches on the dry sandy banks of the floodplain. According to Klotz et al. (2002) regeneration is only by seed, but own observations and Klimešová & Klimeš (1998) suggest that moderate lateral spread is possible. A seed bank is not known to exist, the seeds have a mean weight of 2.3 mg and are wind-dispersed. The ecological strategy is CSR. When collecting the seeds this species was found to produce only few viable seeds which were furthermore heavily infested by seed eating parasites.

Selinum carvifolia
A perennial character species of the order *Molinietalia,* occurrence in Estonia is scattered on meadows and in shrublands. In the Soomaa area it occurs mainly in

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[1] legally protected in Estonia

the lower floodplains which are flooded frequently and for long periods. Regeneration is exclusively by seed (Klotz et al. 2002), a seed bank is absent. The seeds have a mean weight of 1.0 mg and are classified as wind-dispersed (WIw), the ecological strategy is scored as CS.

Thalictrum lucidum §
A perennial species of fen meadows, floodplain forests and shrublands. This plant is protected in Estonia and occurs sporadically in wet meadows, forest edges and shrublands. In the Soomaa area, the species can be found throughout the park but always with low abundance. Regeneration is by seed and vegetatively by rhizomes although lateral spread is probably poor. Information on seed longevity in the soil is not available; the seeds have a mean weight of 0.9 mg and have no apparent morphological adaptations for dispersal. *Thalictrum lucidum* has a competitive-stress tolerant strategy (CS).

Trollius europaeus
This perennial is a character species of the order *Molinietalia*. In Estonia, it is common in meadows, wooded meadows and forest edges of the mainland but rare on the islands. In the Soomaa area *Trollius* is common in all mesic to moist grasslands. Regeneration is by seed and vegetatively although lateral spread is poor. Seeds do not form a persistent seed bank and show no adaptation to long-distance-dispersal; seeds are probably shed by wind and animals from the elongated flower stalks. Mean seed weight is 0.5 mg. The species is described to have a competitive strategy (C).

Veronica longifolia
A perennial species typical for wet meadows and especially *Filipendulion* communities. In the Soomaa area it is common in narrow bands along all rivers. Regeneration is by seed and vegetatively by rhizomes although lateral spread is probably poor. The seeds are very small with a mean weight around 0.1 mg; for this reason the species can be considered wind-dispersed. Information on seed persistence is not available, V. longifolia is described to have a competitive-stress tolerant strategy (CS).

Statistical analysis

Emergence rates in different treatment patches were compared by Kruskal-Wallis one-way ANOVA, subsequent multiple comparison was done with the Steel-Dwass test, a non-parametric equivalent of the Tukey test. Spearman rank correlation was used to relate germination and establishment success to seed weight. All univariate statistics were calculated using the R package (R Development Core Team 2003), except for the Steel-Dwass test, this was computed using KyPlot version 2.0 beta 15 (Yoshioka 2001).

2.3 Disturbance and regeneration

To study the influence of seed rain and seed bank in the recolonisation of disturbed meadow patches an experiment was set up in the Läti meadow. The study plots were selected to reflect two different habitat types in the gradient from dry riverbanks to the moist floodplain. The following criteria were applied to identify appropriate habitat patches: dry patches were mainly dominated by *Festuca ovina* and *Festuca rubra* with *Nardus stricta, Carex panicea* and *Sesleria caerulea* often present. The moist habitat type was characterised by the presence of *Trollius europaeus* and *Geum rivale*. Sedges like *Carex cespitosa* or *C. disticha* could be present but not dominant. Of each habitat type 10 representative replicates were chosen. Due to the very patchy structure of the meadow vegetation, with the 'matrix' being formed by relatively species-poor stands of different *Carex* species (*C. disticha, C. elata, C. vesicaria*), a random selection of plots was impossible. It was attempted to achieve a more or less homogeneous distribution of the study plots over the whole meadow.

Plant cover was recorded in summer 1998 in 2.5 × 2.5 m plots (Fig. D.5). In these plots four 0.5 × 0.5 m treatment plots were permanently marked separated by a 0.5 m wide strip. To prevent seed input from the directly surrounding vegetation and to facilitate access to the plots an area 0.5 m wide around and between the four treatment plots was mown after recording of the species and repeatedly during the period of investigation.

As the aim of this experiment was to separate the influences of the seed rain and seed bank three different patch types had to be created: a first type with only the seed rain serving as seed source, a second with seed rain plus seed bank and a third with only the seed bank. The 'seed rain only'-treatment (T2) was created by placing a deep (30–40 cm) and presumably seed free soil layer on top of of the (inverted) upper soil layer. For the 'seed rain plus seed bank'-treatment (T3) all vegetation and viable plant fragments were carefully removed and the upper soil layer disturbed by raking. An identical treatment was applied to the 'seed bank only'-patches, however in this case the seed rain was excluded by a wooden frame covered with a thin transparent gauze (T4). In addition to this a fourth patch was marked as control with no treatment (T1). Recording of emergent seedlings took place in July and August 1999. Plots were revisited in October for

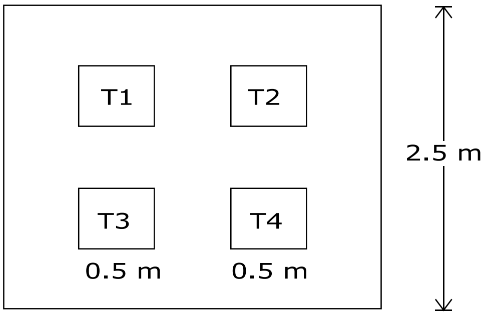

Fig. D.5: Sketch of plot used for disturbance experiment; 2.5 × 2.5 m plot for recording of vegetation and four 0.5 × 0.5 m plot for treatments: control (T1), seed rain (T2), seed rain + seed bank (T3), seed bank (T4) a final inspection. Seedlings were counted, removed and dried for later inspection with the dissecting microscope. Individual plants were left in the field to allow further growth until identification was possible. In order to minimise edge effects only the central 30 × 30 cm were subject of investigation.

Due to difficult identification in juvenile state the following species were pooled: *Viola canina* and *V. montana* are listed as *Viola canina s.l.*; *Luzula campestris* and *L. multiflora* are listed as *Luzula campestris s.l.*

Statistical analysis

To analyse the effects of habitat and treatment on seedling and species numbers, the non-parametric Scheirer–Ray–Hare test (an extension of the Kruskal–Wallis test, see Sokal & Rohlf (1995) for details) was used. The non-parametric Steel-Dwass test (Steel 1960) was used for post-hoc comparison among all treatments. Both tests were performed using the graphing and statistical package KyPlot version 2.0 beta 15 (Yoshioka 2001).

The overall species composition of the established vegetation and the seedling assemblages of the treatment plots was compared with NPMANOVA (Anderson 2003) using Bray-Curtis dissimilarity measure on quantitative and qualitative (presence/absence transformed) data. Additionally a DCA was run (default settings, no downweighting of rare species) to visually assess the similarity of the different assemblages. For this and all other statistical analyses two groups of *Carices*, which were numerous as seedlings but hard to separate in this stage, had to be pooled: *Carex acuta, C. cespitosa* and *C. nigra* were subsumed under the label *Carex sect. Phacocystis*, *Carex flava* and *C. vulpina* were listed as *Carex flava/vulpina*. The DCA was computed with the R statistical package (R Development Core Team 2003) together with the VEGAN-package (Oksanen 2004).

Plant traits were again used in this experiment to assess the possible influence of plant characteristics on the distribution of species and their reaction to different types of disturbance. For this aim a trait × plot matrix was compiled that contained the percentage of each trait found in any of the experimental plots. All trait analyses were based on quantitative data, i.e. abundance of the species (percentage cover for established vegetation and seedling number for experimental plots) was taken into account. NPMANOVA (Anderson 2003) with Bray-Curtis measure of dissimilarity was used on this matrix to test for multivariate differences in the trait composition of the different treatments. After this preliminary analysis the plot × trait matrix was analysed by a Principle Components Analysis (PCA) following the same logic as described for the seed trap study on page 83: the loadings (scores) of traits on the PCA axes denoted the traits most strongly associated with each axis. Correlation of the axes with habitat (moist vs. dry) and treatment (established vegetation vs. seedling assemblages of different origin) was assessed with a Mann-Whitney-U-test. In this way the association of traits and treatments (in this case source of colonisation) could be addressed. All analyses were performed with the R statistical package (R DEVELOPMENT CORE TEAM 2003) together with the MVA-package for multivariate and the CTEST-package for univariate analyses. For a more in depth discussion of the selection of the plant traits, their coding and the analysis of plot × trait matrices see page 92.

2.4 Plant traits

Selection of traits

Analysis of plant traits is used throughout the following chapters as a means to interpret the results of the experiments in functional terms. Therefore a selection of fourteen plant traits (Table D.2) was compiled for the species encountered in the experiments and in the established vegetation of the Soomaa floodplain meadows. Six traits were related to the vegetative and seven traits to the reproductive phase of the plants life cycle. Traits were selected to be of putative importance for the processes under consideration here, i.e. dispersal, germination and establishment, and to be easily extractable from published sources as own measurements were largely beyond the scope of this study. To simplify statistical analysis all traits were scored as interval- or nominal-scaled variables.

Table D.2: List of vegetative and reproductive plant traits used in the study

Trait	Abbreviation	Code	Description	Source
1. canopy height	HEI	1	<20cm	(8)
		2	21–40cm	
		3	41–60cm	
		4	61–80cm	
		5	>81cm	
2. canopy structure	ROS	L	leafy, no rosette	(7)
		S	semi-rosette	
		R	rosette	
3. established strategy	STR		Grime's CSR strategy scheme	(7)
4. guild	GLD	F	forbs	
		G	graminoids	
		W	woody species	
5. lateral spread	CLO	0	non-clonal, no lateral expansion	(6)
		1	clonal but minimal lateral expansion	
		2	clonal, moderate lateral expansion	
		3	clonal, strong lateral expansion	
6. life cycle	LIF	S	short-lived, annual bi- or pluriannual	(2)
		P	perennial	
7. time of flowering	PHE	1–9	from 1 (earliest spring) to 9 (early autumn)	(1)
8. time of germination	GER	SP	spring	(10)
		SU	summer	
		AU	autumn	
		WI	winter	

Trait	Abbreviation	Code	Description	Source
9. type of reproduction	REP	S	only by seed	(7)
		SSV	mostly by seed, rarely vegetatively	
		SV	by seed and vegetatively	
		VVS	mostly vegetatively, rarely by seed	
		V	only vegetatively	
10. seed bank type	SEB	0	transient	(5) (9) (11)
		1	short-term persistent	
		2	long-term persistent	
11. seed weight	SEW	1	≤ 0.2mg	(4) (7) (14) (15) (17)
		2	0.21–0.5mg	(18) and own
		3	0.51–1.0mg	measurements
		4	1.1–2.0mg	
		5	2.1–10mg	
		6	> 10mg	
12. seed number	SEN	1	few, less than 1000	(12) (13)
		2	numerous, 1000–10000	
		3	very numerous, more than 10000	
13. dispersal vector	DIS	AN	animal-dispersed seeds	(3) (4) (5) (9)
		AQ	water-dispersed seeds	
		EX	explosive dispersal	
		UN	unspecialised seeds	
		WI	wind-dispersed seeds	
14. life form	LF	A	hydrophyte	(7)
		C	chamaephyte	
		G	geophyte	
		H	hemicryptophyte	
		N	nanophanerophyte	
		P	phanerophyte	
		T	therophyte	

Sources of trait data: (1) DIERSCHKE (1995), (2) ELLENBERG et al. (1992), (3) FRANK & KLOTZ (1990), (4) HODGSON et al. (1995), (5) JÄGER & WERNER (2002), (6) KLIMEŠOVÁ & KLIMEŠ (1998), (7) KLOTZ et al. (2002), (8) MOSSBERG et al. (1992), (9) OBERDORFER et al. (2001), (10) PEAT & FITTER (2003), (11) THOMPSON et al. (1997), (12) BOEDELTJE et al. (2003), (13) KLEYER (1995), (14) TWEDDLE et al. (2003), (15) ERIKSSON & JAKOBSSON (1998), (17) BAKKER et al. (1997), (18) SCHÜTZ (2000).

Additional comments on trait definitions:

established strategy: according to GRIME et al. (1988).

seed number: concept and data mainly from BOEDELTJE et al. (2003); missing values were extrapolated from closely related plants and morphological evidence.

dispersal vector: concept and data mainly from GRIME et al. (1988) and HODGSON et al. (1995).

animal dispersal: sub-categories include two types of epi-zoochorous dispersal (ANa: attachment to an animals fur by awns, teeth etc.; ANm: seeds adhesive through mucilage) and short-range dispersal by ants (ANe: seeds with an elaiosome rich in protein and fat); seeds with endo-zoochorous dispersal mechanisms *sensu strictu* (e.g. by ingested berries, nuts etc.) where not present among the species of this study. In the literature (e.g. JÄGER & WERNER 2002) many more species are listed as endo-zoochorous, obviously because viable seeds had been found in animal faeces; in the study area large grazers are only of minor importance (apart from elk) so that the category of endo-zoochorous dispersal is restricted here to the above mentioned cases.

water dispersal: seeds are considered water-dispersed if they possess organs which enhance the buoyancy, i.e. air pockets, corky tissues etc. A special problem are the numerous species of the genus *Carex* present in the Soomaa area. While being of high importance in most studied communities, data on their dispersal types are rather scarce or contradictory. It is generally stated that hydrochory is a common trait in this genus, based on the pocket of air created by the utricle. The question, however, is if this morphological feature can be considered adaptive in all cases, as it is present even in species of dry habitats. As it would require a more in-depth study to resolve the dispersal behaviour of the genus *Carex* it was decided to largely follow Jäger & Werner (2002) and Grime et al. (1988); in these compilations only species of wet to semi-aquatic habitats are listed as water-dispersed.

explosive dispersal: the mother plant has some kind of explosive mechanism to propel the seeds away from it; apart from this mechanism the seeds would otherwise often be classified as *unspecialised*, as they are mostly smooth, round and relatively heavy.

dispersal mode unspecialised: no apparent dispersal mechanism; may of course be due to insufficient knowledge; includes UNag i.e. unspecialised but widely dispersed as a result of agricultural practices.

wind dispersal: morphological traits indicating wind dispersal are minute, dust-like seeds (not recognised in this study, as these seeds are hard to detect by the type of trap used here), wings or strongly flattened seeds (WIw) and long hairs and other structures like the pappus of the *Asteraceae* which result in high surface-to-weight ratios (WIp); a special category differing from the above mentioned two in that it only leads to short-range dispersal is characterised by capsules raised above the surrounding vegetation and shedding rather small seeds when moved by wind or animals (WIc).

Analysis of trait data

Most commonly multivariate analysis in community ecology comes in one of three forms: (1) plot × species matrices are used for ordination or classification of plots on the basis of compositional similarity, (2) plot × environment matrices are used to extract major environmental gradients, often in combination with matrices of the first type, and (3) species × trait matrices are used to detect functional groups. A relatively new approach in community ecology is to directly ask for relations between species traits and habitat or environmental conditions. In the context of this study trait composition was related to the outcome of different treatments (in the case of the experimentally disturbed plots) or to different aspects of the vegetation (established vegetation, seed rain, habitat types as in the case of the seed trap study; both data types are referred to as *treatment variables*). Legendre et al. (1997) termed this the 'fourth corner problem' following it's representation in matrix algebra. Several papers have explored this topic with various uni- and multivariate methods (Díaz et al. 1992; Lunt 1997; Díaz et al. 1999; Mabry et al. 2000; Dyer et al. 2001; Vandvik & Birks 2002; Lamb & Mallik 2003; Deckers et al. 2004).

Principle Components Analysis (PCA) was used to relate treatment variables of the two experimental studies to plant trait composition. Two data matrices, one plot × species and trait × species matrix , were combined into a plot × traits matrix, which was used as the input for the PCA. In this matrix the species are replaced by the percentage of species or seeds/seedlings that are characterised by a certain trait or that belong to a certain functional group. In order to facilitate the estimation of the importance of certain traits for the studied processes, abundance rather than presence/absence data were used. Percentage values were arcsine transformed prior to multivariate analysis. The correlation of treatment and habitat variables with the PCA axes was tested with the non-parametric Mann-Whitney U-test. The PCA axis loadings (scores) identify the traits which contribute most to the variation between plots along this axis which in turn allows to make inferences about the relation between trait and treatment variable. For example, if axis 1 is strongly correlated with the *seed rain vs. established vegetation variable* and the trait state *wind dispersal* loads high on axis 1 it can be concluded that wind-dispersed species play a more important role in the seed rain than in the established vegetation.

In addition to their usage to interpret the results of the field studies plant traits were also tested for inter-correlation and whether they can be condensed into meaningful functional or growth form groups. As traits differed in their type of scale (four traits – HEI, PHE, SEN and SEW – can be considered ordinal even though they are transformed to categories, the rest is nominal) different procedures were followed depending on the combination of scale types. Nominal trait variables were transformed into dummy variables, i.e. into as many binary variables as there were trait states, while ordinal trait variables were used in their original form. Pearson's X^2-test was used for differences between two traits expressed on a nominal scale, p-values were computed by Monte-Carlo simulation with 10000 replicates. Kruskal-Wallis one-way ANOVA was used for trait pairs where one is of nominal and one of ordinal type and Pearson's correlation for two ordinal traits. To account for the high probability of significant results when analysing large numbers of pairwise combinations only strong correlations are reported ($p<0.001$).

Groups of species sharing similar combinations of life history traits, i.e. growth-form or functional groups, were identified by subjecting a species × traits matrix to a cluster analysis using McQuitty's algorithm (also known as WEIGHTED ARITHMETIC AVERAGE CLUSTERING WPGMA, (LEGENDRE & LEGENDRE 1998)) and Euclidean distance measure. Other commonly used algorithms were also tested (Ward's, Group Average), but this method provided the most easily interpretable results. The results of the cluster analysis were compared with a PCA of the same species × trait matrix.

The second approach uses the INDICATOR SPECIES ANALYSIS as suggested by DUFRÊNE & LEGENDRE (1997). This method calculates indicator values for species by combining a species' relative abundance with its relative frequency of occurrence in a set of predefined groups. The resulting indicator values for each species/group-pair range from zero (no indication) to 100 percent (perfect indication). The statistical significance of the indicator values is tested using a Monte Carlo randomisation test. This method was initially developed for plot × species matrices and usage in the ecological literature is so far restricted to this scenario. However, there is probably no conceptual difference when this method is applied to a plot × trait or plot × functional group matrix, as traits and functional groups take the place of species in these types of matrices.

All standard statistical analyses were computed using the R package (R Development Core Team 2003). For univariate statistics including Monte Carlo simulations for Pearson's χ^2-test the ctest package was used, PCA and cluster analysis were performed with the mva package. Indicator Species Analysis was performed with the program IndVal version 2.0 (Dufrêne 2004).

3 Results

3.1 Seed rain

3.1.1 Seed traps

General results

Approximately 76 species with a total of 34423 seeds where collected in the seed traps during the period of roughly one year (Table D.3). The frequency distribution of total seeds per species was highly right skewed: one species alone (*Juncus filiformis*) accounted for nearly 70 % of all trapped seeds and 66 of the 76 species contributed less than one percent each to the total seed count. Second to *Juncus filiformis* (23783 seeds), the most abundant species were *Filipendula ulmaria* (1482 seeds), *Hypericum maculatum* (1186 seeds), *Deschampsia cespitosa* (940 seeds) and *Carex acuta* (804 seeds; see Table D.4 and Table G.10 through G.12 in the Appendix for details). In all of these five species one transect alone was responsible for more than three quarter of the total seed count which underlines the differing species compositions of the three transects.

At the Käära transect the most abundant species were *Juncus filiformis*, *Hypericum maculatum*, *Ranunculus acris*, *Lychnis flos-cuculi* and *Hieracium umbellatum*. At the Läti transect the most abundant species were *Filipendula ulmaria*, *Deschampsia cespitosa*, *Veronica longifolia*, *Potentilla erecta* and *Alnus incana*. Finally at the Mulgi transect *Carex acuta*, *Carex appropinquata*, *Carex cespitosa*, *Betula ssp.* and *Ranunculus auricomus* were among the most abundant species.

Seed densities varied considerably: they covered four orders of magnitude from a minimum of 496 (plot M1) to a maximum of 203501 seeds/m^2 (plot K6). The considerably lower densities in most plots of the Mulgi transect are due to the fact that this meadow had been partly mown during the study period. Although the hay had not been removed seed dispersal had obviously been seriously hampered. Average seed density was 20321 seeds/m^2; however, when omitting three traps (out of 28), which collected huge numbers of *Juncus filiformis* seeds, from analysis, this value is reduced to 6346 seeds/m^2 which is near the median. In the following *J. filiformis* is omitted from the analysis and description if not stated otherwise, as it would grossly distort the results by its sheer number. Highest absolute values obviously occurred in wet meadow types dominated by *Juncus filiformis* and sedges; however, when excluding these three plots, mean seed numbers were roughly equal in all vegetation types.

Species number of seeds per plot ranged from 6 to 24 with a mean of 15.1 and a standard deviation of 4.7. Species number tended to be higher in the drier vegetation types although only the difference between type 2 and 3 (moderately moist or mesic and moist grassland) was significant ($p < 0.05$; Kruskal-Wallis one way ANOVA with Steel's non-parametric multiple comparison). However, species number of established vegetation and of the seed rain were significantly correlated (Spearman's $r = 0.745$, $p < 0.001$). Species number of seeds in the Mulgi transect was, in contrast to the seed numbers, not significantly affected by mowing.

Table D.3: General results of seed trapping for three transects; seed density is calculated as seeds/m^2

	vegetation		seed traps				
	total species no.	mean species no.	total species no.	mean species no.	total seed no.	mean seed density	median seed density
Läti	51	13.6	47	14.5	4681	7738	6579
Käära	57	18.4	55	17.7	27933	51300	14051
Mulgi	58	18.0	46	13.0	1809	3323	1537
total	90	16.6	76	15.0	34423	20321	6579

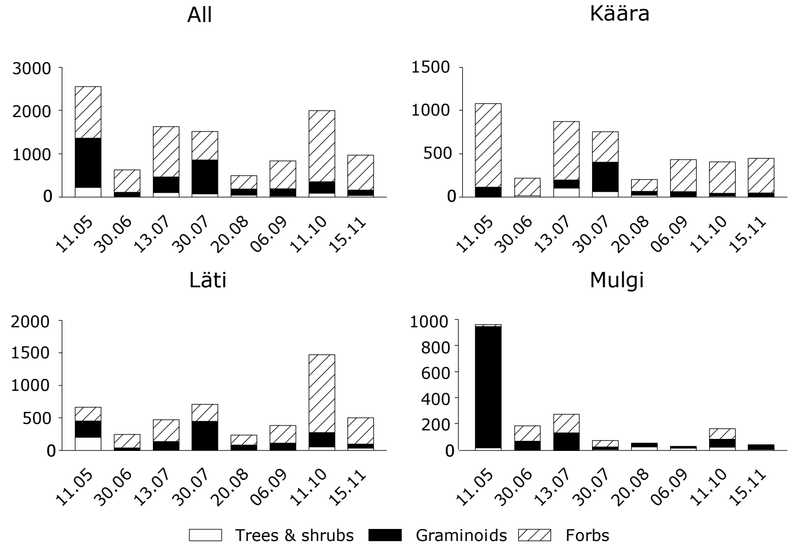

Fig. D.6: Temporal variation of seed rain and contribution of major taxonomic groups (trees & shrubs, graminoids and forbs)

Table D.4: Species found in the seed traps pooled for all three transects, total seed number and percentage of total, seed mass category (see end of table for explanation of categories) and dispersal agent and temporal variation of seed rain (from July 1999 to May 2000).

	Seed rain		Seed traits		Temporal distribution of seed rain – no. of seeds							
	Total seed no.	% of total	Seed mass	Dispersal agent	30.06.	13.07.	30.07.	20.08.	06.09.	11.10.	15.11.	11.05.
1. graminoids												
Agrostis canina	4	0.01	1	ANa	–	4	–	–	–	–	–	–
Agrostis capillaris	24	0.07	1	UN	–	–	2	4	5	6	6	1
Alopecurus pratensis	77	0.22	3	UNag	5	35	17	5	8	2	–	5
Anthoxanthum odoratum	92	0.27	3	ANa	–	44	45	3	–	–	–	–
Briza media	1	0.00	3	UN	–	–	–	–	1	–	–	–
Calamagrostis canescens	21	0.06	1	WIp	–	2	18	–	–	–	1	–
Calamagrostis epigejos	3	0.01	1	WIp	–	–	–	–	–	2	–	1
Calamagrostis stricta	20	0.06	1	WIp	–	5	–	7	5	–	3	–
Carex acuta	804	2.34	3	AQ	1	12	5	–	1	–	1	784
Carex appropinquata	166	0.48	3	AQ	64	91	5	3	1	–	–	2
Carex canescens	4	0.01	2	AQ	–	2	2	–	–	–	–	–
Carex cespitosa	176	0.51	3	AQ	2	–	–	–	–	–	7	167
Carex disticha	158	0.46	3	UN	–	13	101	12	8	6	2	16
Carex flava	11	0.03	2	AQ	–	–	–	–	–	–	–	11
Carex leporina	27	0.08	2	UN	–	–	7	2	1	–	4	13
Carex pallescens	101	0.29	3	UN	–	8	37	18	11	11	6	10
Carex panicea	51	0.15	5	AQ	1	4	2	3	–	4	5	32
Carex pulicaris	3	0.01	4	UN	–	–	–	–	–	–	–	3
Carex rostrata	12	0.03	4	AQ	–	–	–	–	–	–	–	12
Carex vesicaria	19	0.06	5	AQ	–	–	2	–	–	–	–	17
Carex vulpina	24	0.07	4	UN	–	–	20	1	–	1	–	2
Deschampsia cespitosa	940	2.73	1	ANa	–	66	456	69	101	205	29	14
Festuca ovina	43	0.12	2	ANa	–	28	11	1	1	1	–	1
Festuca pratensis	39	0.11	4	UN	–	–	27	6	4	2	–	–
Festuca rubra	2	0.01	3	ANa	–	–	1	–	1	–	–	–
Hierochloe odorata	9	0.03	2	ANa	–	–	3	1	–	–	–	5
Juncus filiformis	23783	69.12	1	ANm/WIm	59	3	33	911	1857	9908	4813	6191
Luzula campestris	46	0.13	3	ANe	–	28	10	1	–	1	4	2

	Seed rain		Seed traits		Temporal distribution of seed rain – no. of seeds							
	Total seed no.	% of total	Seed mass	Dispersal agent	30.06.	13.07.	30.07.	20.08.	06.09.	11.10.	15.11.	11.05.
Phleum pratense	52	0.15	3	ANa	–	–	–	–	13	12	12	15
Phragmites australis	48	0.14	1	WIp	–	–	1	–	2	2	42	1
Poa palustris	14	0.04	1	UNag	1	9	2	–	2	–	–	–
Poa pratensis	26	0.08	2	UNag	–	1	4	3	–	5	1	12
Sesleria caerulea	37	0.11	3	UN	23	6	3	1	–	2	–	2
2. forbs												
Achillea spec.	42	0.12	1	WIw	–	–	–	–	–	8	10	24
Alchemilla vulgaris agg.	45	0.13	3	ANa	1	5	14	3	3	9	9	1
Anthriscus sylvestris	27	0.08	5	UN	–	1	16	4	4	2	–	–
Caltha palustris	5	0.01	3	AQ	3	1	–	–	–	–	–	1
Centaurea jacea	138	0.40	4	UN	1	–	–	41	48	17	7	24
Cerastium holosteoides	27	0.08	1	UNc	–	13	1	–	–	–	–	7
Cirsium heterophyllum	1	0.00	5	WIp	–	–	–	1	–	–	–	–
Epilobium hirsutum	7	0.02	1	WIp	–	–	1	3	2	1	–	–
Filipendula ulmaria	1482	4.31	2	AQ	–	1	14	15	153	720	416	163
Galium mollugo	2	0.01	3	UN	–	–	–	–	1	1	–	–
Geum rivale	97	0.28	4	ANa	1	8	31	8	17	6	5	21
Heracleum sibiricum	1	0.00	5	WIw	–	–	1	–	–	–	–	–
Hieracium pilosella	1	0.00	1	WIp	–	–	–	–	–	1	–	–
Hieracium umbellatum	370	1.08	2	WIp	–	–	–	17	167	151	29	6
Hypericum maculatum	1186	3.45	1	WIc	2	2	4	–	45	61	226	846
Iris sibirica	10	0.03	5	AQ	–	–	–	–	1	7	–	2
Leontodon autumnalis	1	0.00	3	WIp	–	–	–	–	–	1	–	–
Lychnis flos-cuculi	455	1.32	1	WIc	2	333	111	2	2	2	–	3
Potentilla erecta	452	1.31	3	UN	1	169	98	106	13	55	6	4
Ranunculus acris	619	1.80	4	UN	46	180	223	60	37	33	13	27
Ranunculus auricomus agg.	570	1.66	4	UN	303	217	41	6	1	–	–	2
Rhinanthus minor	4	0.01	4	WIcw	–	–	2	1	–	1	–	–
Rumex acetosa	244	0.71	3	WIw	72	149	20	2	1	–	–	–
Rumex thyrsiflorus	1	0.00	4	WIw	–	–	–	–	–	–	–	1
Scorzonera humilis	1	0.00	5	Wip	–	1	–	–	–	–	–	–

	Seed rain		Seed traits		Temporal distribution of seed rain – no. of seeds							
	Total seed no.	% of total	Seed mass	Dispersal agent	30.06.	13.07.	30.07.	20.08.	06.09.	11.10.	15.11.	11.05.
Selinum carvifolia	9	0.03	3	Wiw	–	–	–	–	1	6	–	2
Stellaria graminea	152	0.44	2	UNc	2	4	6	17	38	32	25	28
Stellaria palustris	6	0.02	2	UNc	–	4	1	–	1	–	–	–
Taraxacum sect. Ruderalia	2	0.01	3	WIp	1	1	–	–	–	–	–	–
Trifolium pratense	28	0.08	4	ANa	–	–	2	6	9	9	2	–
Trollius europaeus	148	0.43	4	WIc	85	43	14	2	1	–	2	1
Urtica dioica	61	0.18	1	WI/ANa	–	–	–	–	4	42	5	10
Valeriana officinalis	80	0.23	3	WIpw	–	18	56	5	1	–	–	–
Veronica chamaedrys	3	0.01	1	UNcw	–	–	–	–	3	–	–	–
Veronica longifolia	628	1.83	1	WIc	–	–	–	1	91	470	53	13
Vicia cracca	1	0.00	6	EX	–	–	–	1	–	–	–	–
Viola canina	12	0.03	3	EX/ANe	–	3	3	3	1	2	–	–
Viola epipsila	3	0.01	3	EX/ANe	–	–	3	–	–	–	–	–
Viola uliginosa	5	0.01	3	EX/ANe	2	1	–	–	–	–	–	2
3. woody species												
Alnus incana	288	0.84	2	AQ/WIw	2	2	1	1	4	56	31	191
Betula pubescens	343	1.00	2	WIw	15	105	73	50	24	36	9	31
Salix spec.	4	0.01	1	WIp	–	–	–	–	–	–	–	4

seed mass classes: (1) ≤ 0.2 mg, (2) 0.21–0.5 mg, (3) 0.51–1.0 mg, (4) 1.1–2.0 mg, (5) 2.1–10 mg, (6) > 10 mg

dispersal agents: (AN) animal-dispersed, (AQ) water-dispersed, (EX) explosive dispersal, (UN) seeds unspecialised, (WI) wind-dispersed; for details see appendix to Table D.2.

Temporal variation in seed rain

As much as the seed rain varied spatially it did vary temporally during the study period. The most obvious feature (see Fig. D.6 and figures G.10 through G.15 in the appendix) were three peaks in the number of trapped seeds. A first one appeared in May with the first emptying of the traps, and is most likely explained by the accumulation of seeds during winter and the spring flood. Species that were found mainly this early in the year were *Hypericum maculatum* or *Alnus incana*; the two *Carex* species (*C. cespitosa* and *acuta*) which formed the bulk of this peak arrived at the traps probably by secondary dispersal as these species shed their seeds generally much earlier. A second peak occurred in midsummer around July, typical species in this group were *Trollius europaeus*, *Lychnis flos-cuculi*, *Rumex acetosa* or *Ranunculus auricomus*. Later flowering species with a consequently later seed set and shed formed the third peak in autumn around October with species such as *Filipendula ulmaria*, *Hieracium umbellatum*, *Urtica dioica* or *Veronica longifolia.* Other species dispersed, once the growing season started, throughout the whole year and even, suggested by the presence in the May sample, over winter. Among these species were *Ranunculus acris*, *Stellaria graminea*, *Potentilla erecta* and *Geum rivale*. While tree seeds were dispersed throughout most of the year, though with low absolute numbers, and graminoid and forbs equally contribute to the summer peak, the autumn peak was largely made up of forb species.

Comparison of seed trap data with surrounding vegetation

NPMANOVA indicated highly significant differences between the composition of the seed rain and the established vegetation, both for the complete data set, for the single transects and for most vegetation types (Table D.5). Mean Bray-Curtis dissimilarity of seed traps and their respective vegetation plots ranged from 36 to 94 with a mean of 70 % (see Tables G.10 through G.12 in the Appen-

Table D.5: Results of a NPMANOVA using Bray-Curtis dissimilarity: comparison of the species composition of seed rain and established vegetation, separately for quantitative and qualitative data and for various subsets of the data.

		quantitative		presence/absence	
	N	Dissimilarity	p	Dissimilarity	p
All	28	87.3	0.0002^{***}	72.8	0.0002^{***}
Käära	9	88.8	0.0040^{**}	62.6	0.0530^{ns}
Läti	10	75.5	0.0156^{*}	65.4	0.0022^{**}
Mulgi	9	86.4	0.0012^{**}	74.7	0.0018^{**}
dry	4	81.9	0.2770^{ns}	57.4	0.1988^{ns}
mesic	5	78.6	0.0270^{*}	51.5	0.1248^{ns}
moist	10	76.5	0.0030^{**}	69.9	0.0002^{***}
wet / large sedges	9	90.2	0.0036^{**}	72.9	0.0136^{*}

dix). Similarity was generally higher (or dissimilarity lower) when presence/ absence-transformed data were used in statistical analysis, i.e. a considerable part of the dissimilarity described above can be attributed to species abundance whereas correspondence of plain species composition was much greater. Differences between vegetation and seed rain were not significant in the dry and mesic vegetation types.

Species numbers in the seed traps were strongly correlated with that in the 1m^2 vegetation plots around the traps (Spearman's rho = 0.745, $p \leq 0.001$), also seed number in the traps was correlated with the species number of the established vegetation (rho = 0.430, $p < 0.05$). Furthermore seed number of individual species was significantly correlated (rho = 0.334, $p < 0.001$) with the species' importance in the vegetation (a combined measure of frequency and cover) but not with mean cover itself.

Cluster analysis showed that lower-level branches were mostly occupied by *either* seed rain *or* vegetation samples (Fig. D.7). There were only five (out of 28 possible) pairs of related vegetation and seed rain samples that clustered together on the lowest level branch (M1, M9, K1, K9, L8). All of these plots represented rather species-poor *Magnocaricion* communities.

Of the 99 species present in all vegetation plots 23 did never occur in the seed rain. Of these, twelve were either so rare or of so little cover that they may easily have escaped sampling by the seed traps. Among the remaining eleven more common or more abundant species were *Angelica sylvestris, Potentilla palustris, Galium boreale, G. palustre, Geranium pratense, Lathyrus pratensis* and *Succisa pratensis*. All these species have rather large seeds, two are animal-dispersed (ANa: *G. boreale, Succisa*), another two are self-dispersed (EX: *Lathyrus, Geranium*), the others are either wind or water-dispersed. Other species were only lack-

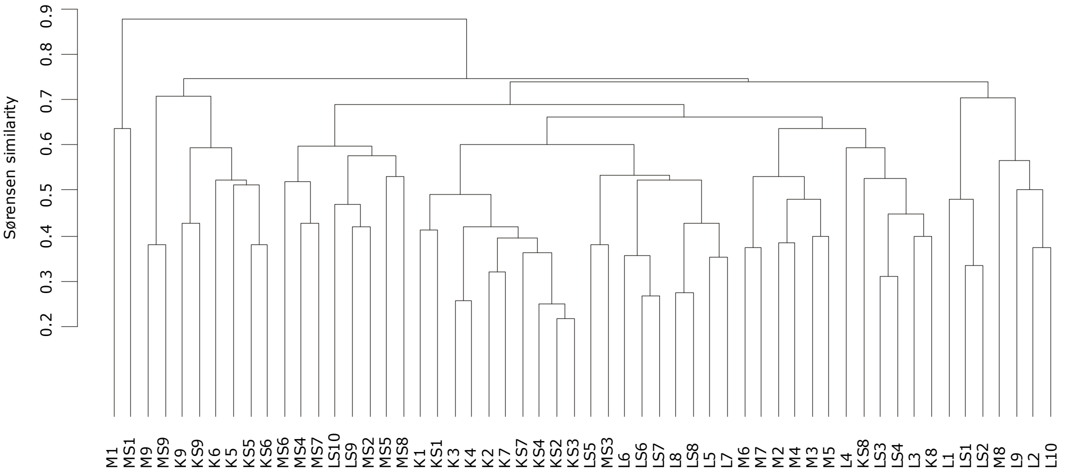

Fig. D.7: Diagram of UPGMA cluster analysis of established vegetation and seed rain using Sørensen similarity; labels of the type M1 denote vegetation samples, those of the type MS1 seed rain samples ing in the seed rain of some of the transects but were found at other places so that their partial absence is probably a sampling effect and needs no intrinsic explanation.

Twelve of the 74 species found in the total seed rain were not present in the vegetation of the sample plots. Most of these were only present with few seeds and the plants are generally small and rather inconspicuous in higher vegetation so that they likewise may have escaped sampling. The remaining species are either clearly adapted to wind dispersal (*Alnus, Betula, Epilobium*) or to dispersal by running water (*C. rostrata*). These species are the best cases in the current study for seed dispersal spanning a distance of up to 100m and more.

When considering each plot separately an average of 51 % of the species of the established vegetation were also present in the seed rain. This value didn't change much for different vegetation types but was considerably lower in the mown Mulgi Heinamaa transect. On the other hand an average of 46.6 % of the seed rain came from outside the surrounding 1m^2 plot. Significantly higher values were found in the moist grassland and values were lower than average in the mesic sites.

Dispersal agents

Wind-dispersed seeds predominated in the total seed rain (37.1 %, with *Juncus filiformis* excluded), followed by water-dispersed seeds (28.5 %), seeds with no apparent dispersal syndrome (23.7 %) and seeds classified as animal-dispersed (13.5 %). Seeds with an explosive dispersal mechanism played only a very minor role (0.2 %). This proportions varied quite considerably between the three transects: wind-dispersed seeds were the dominant group only at the Käära transect (mostly due to large numbers of *Hypericum* seeds collected in the drier parts of this meadow) whereas water-dispersed seeds predominated at the other two transects (Fig. D.9 and D.8 and Fig. G.16 through G.18 in the Appendix). In Mulgi Heinamaa large numbers of *Carex* seeds were collected during winter or spring which most likely were deposited by flood water. The Läti transect generally showed stronger signs of abandonment with a high abundance of *Filipendula ulmaria* which is also classified as water-dispersed.

In contrast to the seed rain the established vegetation as a whole was dominated by species with hydrochorous seeds, followed by species without apparent dispersal vector and animal-dispersed species. Again this proportions are quite different in the three meadows: only in the Mulgi Heinamaa site hydrochory was the dominant syndrome, caused by the high importance of *Filipendula* and species of the genus *Carex*. In the Käära site species without apparent dispersal vectors predominated (41.6 %) but only because *Carex disticha* is classified in this way[2]. On the Läti meadow animal-dispersed species (30.9 %) and species without

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[2] The only published data on *Carex disticha* come from Frank & Klotz (1990) who classify this species as wind, animal (adhesive) and self dispersed. Since, however, the more conservative

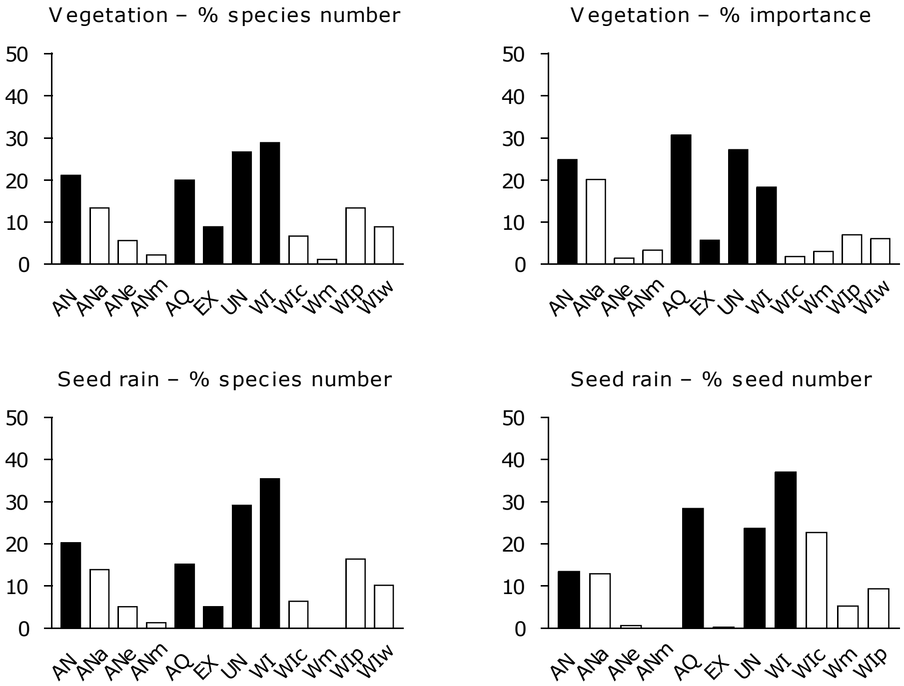

Fig. D.8: Distribution of dispersal vectors including sub-types in seed rain and established vegetation presented as percentage species number and percentage abundance; for explanation of dispersal categories see Table D.2.

dispersal vector (29.9 %) dominated in the vegetation, here it was mainly due to *Deschampsia* (AN) and *Alopecurus* and *Sesleria* (UN).

Animal-dispersed species (AN) were generally more common in the drier vegetation types both in the established vegetation and in the seed rain; however, this relation was not significant. Most animal-dispersed species in the current data set belonged to the subcategory of epizoochorous species that attach their seeds by some means of hooks or other structures to an animals fur. Half of these were grasses and half forbs, the most numerous were *Deschampsia, Geum* and *Anthoxanthum*. A small number of species, of which one – *Juncus filiformis* – was the most numerous species in the seed rain, belonged to a second subcategory of epizoochorous species that attach themselves by means of mucilage. Endozoochorous dispersal in the strict sense, i.e. with berries or other organs especially adapted to being eaten, were not present in the studied vegetation.

Wind-dispersed seeds (WI) showed no clear preference for any vegetation type, they occurred in comparable quantities in drier and wetter sites. In the established vegetation the subcategory WIp with plumed or otherwise hairy seeds was most common, followed by plants with winged seeds (WIw). Typical

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approach of Grime et al. (1988) was applied and there were no indications of hydrochory to be found in the literature it was classified as 'without dispersal vector' (UN).

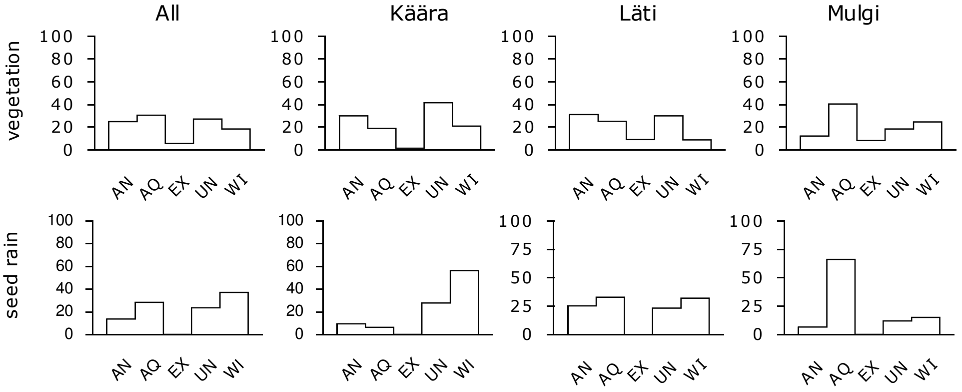

Fig. D.9: Distribution of dispersal vectors in established vegetation (percentage importance) and seed rain (percentage seed number) for complete date set and three transects; for explanation of dispersal categories see Table D.2.

species of the WIp category were grasses or composites, e.g. *Hieracium* or *Calamagrostis*, or other forbs like *Valeriana*. Winged seeds were found mostly among forbs (e.g. *Rumex acetosa*, *Achillea* or again *Valeriana*) or among the woody species, which were also the most numerous here (*Alnus* and *Betula*). In the seed rain WIp was still most common with respect to species number, but category WIc (small seeds shed from capsules) was by far the most numerous group in terms of seed number. This was largely due to species like *Hypericum maculatum*, *Lychnis flos-cuculi* or *Veronica longifolia*, that – when present – commonly shed shed large numbers of small seeds.

Plants with **water-dispersed (AQ)** seeds showed a perceivable but again non-significant preference for moist to wet sites, both in the established vegetation and in the seed rain. The genus *Carex* alone was present with eight species, while the single most numerous species in this category was *Filipendula*. While other water-dispersed forbs were present in the vegetation (e.g. *Angelica sylvestris*, *Iris sibirica* or *Comarum palustre*) they were remarkably rare in the seed rain.

Species with **no apparent dispersal syndrome (UN)** were roughly equally common in all vegetation types, whether counted as species or seeds. Typical species of this category were *Carex disticha* and a number of other *Carex* species, *Ranunculus acris* and *R. auricomus*, *Potentilla erecta* and *Centaurea jacea*.

Other plant functional traits

An initial NPMANOVA (Table D.6) showed that, as with plain species composition, there were significant differences between the established vegetation and the seed rain regarding trait composition. However, not all comparisons were significant (probably partly due to small sample size) and similarity between the two components was considerably higher than in the analysis of the species

Table D.6: Results of a NPMANOVA using Bray-Curtis dissimilarity: comparison of the trait composition of seed rain and established vegetation, separately for quantitative and qualitative data and for various subsets of the data.

		quantitative		presence/absence	
	N	Dissimilarity	p	Dissimilarity	p
All	28	32.9	0.0002***	13.1	0.0002***
Käära	9	31.6	0.0162*	10.6	0.0236*
Läti	10	31.7	0.0126*	12.8	0.0022**
Mulgi	9	30.8	0.0528^{ns}	14.8	0.0058*
dry	4	27.4	0.1744^{ns}	10.0	0.0334*
mesic	5	25.2	0.0346*	8.5	0.0075*
moist	10	29.7	0.0052**	13.4	0.0002***
wet / large sedges	9	34.4	0.0118*	14.6	0.0330*

composition (Table D.5); similarity was again even higher when considering presence/absence-transformed data.

The contribution of individual traits to these observed patterns of different trait composition was traced with an ordination approach. The first three axes of the plot × trait PCA explained 16.3, 14.5 and 12.9 % of the total variation in the original data matrix (Table D.7). Axes 1 and 2 represented a combined gradient of site and vegetation type with axis 1 mainly reflecting a habitat gradient from dry to wet and axis 2 separating weakly between sites; axis 3 distinguished clearly between seed rain and established vegetation.

The results of the PCA suggest that the main differences in the trait composition of the established vegetation are found in flowering phenology, canopy height, lateral spread, dispersal vector and reproductive mode (Table D.8). Drier vegetation types are characterised by plants that flower earlier than in wetter types, are of smaller stature, are capable of moderate lateral spread, reproduce by seed only and are dispersed by animals. Wetter vegetation types on the other hand are characterised by plants of larger stature that reproduce both by seed and vegetatively, are capable of strong lateral expansion, flower somewhat later and are water-dispersed. Differences on axis 2 are not as easily explained, they probably reflect the complex relationships of habitat conditions and management (or lack thereof as in the case of the site Läti, where the effects of abandonment are stronger). Traits that contributed most to the variation between established vegetation and seed rain were guild, lateral spread, seed weight and number and time of germination. The seed rain was generally dominated by wind-dispersed species with large numbers of light-weight seeds. Furthermore these species tend to lack the ability of lateral expansion and germination in spring and woody growth form are more common than in the established vegetation. In the established vegetation graminoid species were more important, furthermore species with strong lateral spread and fewer but heavier seeds.

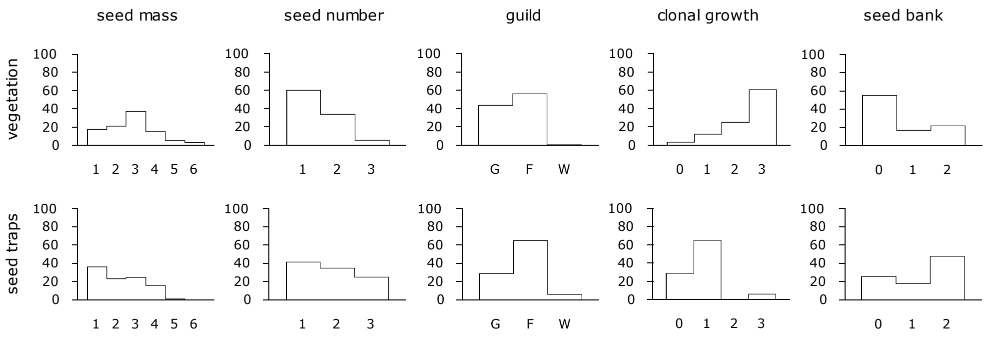

Fig. D.10: Distribution of life history traits in established vegetation (percentage importance) and total seed rain (percentage seed number); for explanation of trait categories see Table D.2.

Table D.7: Correlation of PCA axes scores with treatments and habitat; as variables are categorical significance was tested by a Mann-Whitney U-test; values are mean PCA axis scores for the given category, significant results with $p \leq 0.001$ are marked bold, those with $p \leq 0.05$ are marked italic. Vegetation types after KRALL et al. (1980) and AUG & KOKK (1983), see Table C.2.

Axis	1	2	3
% variance	16.3	14.5	12.9
Käära	– 0.380	– 0.940	– 0.002
Läti	0.213	**2.007**	0.142
Mulgi Heinamaa	0.144	*– 1.290*	– 0.156
Seed rain	0.530	*– 0.841*	**– 1.905**
Established vegetation	– 0.530	*0.841*	**1.905**
VegType 1	*– 3.059*	– 1.237	0.385
VegType 2	*– 2.529*	0.972	– 1.193
VegType 3	*1.110*	**2.106**	– 0.449
VegType 5	*1.536*	**– 2.330**	0.991

Table D.8: Plant traits with highest loadings on the first three axes of a PCA on a plot × trait matrix

trait	loadings	trait (continued)	loadings
axis 1 (dry vegetation – to moist/wet vegetation +)			
time of germination: autumn	–0.262	lateral spread: 2	–0.209
canopy height:2	–0.256	dispersal by water	0.208
time of flowering: 5	–0.244	reproduction by seed only	–0.210
seed bank short-term persistent	–0.241	canopy height: 5	0.200
time of germination: winter	–0.237	dispersal by animals	–0.170
seed weight: 4	–0.228	seed number: 3	0.160
reprod. by seed & vegetatively	0.220	time of flowering: 7	–0.150
lateral spread: 3	0.210		
axis 2 (experimental sites: Käära & Mulgi H. + to Läti –)			
strategy: C	0.314	seed weight: 3	–0.192
seed number: 2	0.258	dispersal explosive	0.189
seed weight: 2	0.257	flowering time: 3	–0.187
seed bank: long-term persistent	–0.240	seed weight: 6	0.186
flowering time: 8	0.240	reprod. mostly seed & vegetatively	0.185
strategy: CS	–0.222	strategy: CSR	–0.181
canopy height: 5	0.220	time of germination: summer	–0.168
seed bank: transient	0.204	seed number: 1	–0.165
guild: forbs	0.195	guild: graminoids	–0.161
axis 3 (seed rain – to establ. vegetation +)			
time of flowering: 4	0.256	seed number: 1	0.215
dispersal by wind	–0.244	seed bank: transient	0.196
guild: graminoids	0.241	time of germination: summer	0.194
lateral spread: 1	–0.239	seed number: 3	–0.189
guild: woody species	–0.235	lateral spread: 0	–0.185
lateral spread: 3	0.218	seed weight: 1	–0.181
seed weight: 3	0.216	time of germination: spring	–0.174

3.1.2 Drift material

A considerable number of seeds was found in the drift material collected in August 2000 comprising a total of 21 species (plus a small number of unidentified seeds). The mean density of seeds – as calculated from three samples of 100ml – was 4140 seeds per litre drift material. The most common species in the drift material were, in descending order, *Ranunculus repens*, *Betula* sp., *Carex* sp. (Sect. Phacocystis), *Carex disticha* and *Alnus incana* (Table D.9). When following the classification of dispersal vectors established above the four main vectors AN, AQ, WI and UN were distributed – considering the small sample size – with roughly even shares. It could, however, be argued that *Carex disticha* is also water-dispersed as it shares with all other species of this genus the particular structure of the utricle with its enclosed pocket of air; this should lead to an enhanced floating ability, whether this is an actual adaptation or not. In this case water-dispersed species would be clearly dominant in the drift material, especially among the common species mentioned above.

Table D.9: Summary of seeds found in three samples of drift material collected in August 2000 in Mulgi Heinamaa: pooled seed number, percentage of total seeds, dispersal vector. Species with a seed number of zero were not found in the three 100ml samples but only in the qualitative scanning of the drift material.

	seed number	% of total	dispersal vector
Alchemilla spec.	0	0	ANa
Alnus incana	15	1.2	AQ/WIw
Betula spec.	424	34.3	WIw
Carex disticha	81	6.6	UN
Carex flava	1	0.1	AQ
Carex panicea	5	0.4	AQ
Carex Sect. Phacocystis	91	7.4	AQ
Carex vesicaria	9	0.7	AQ
Lychnis flos-cuculi	0	0	WIc
Lycopus europaeus	1	0.1	AQ/AN
Myosotis scorpioides	0	0	UN
Potentilla erecta	4	0.3	UN
Ranunculus auricomus	9	0.7	UN
Ranunculus repens	597	48.0	AQ/AN
Rumex spec.	0	0	WIw
Schoenoplectus lacustris	0	0	ANa
Sium latifolium	1	0.1	AQ
Stellaria spec.	0	0	UN
Trifolium spec.	1	0.1	ANa
Valeriana officinalis	1	0.1	WIpw
Viola spec.	0	0	EX/ANe
total	1240		

3.2 Seed sowing experiment

3.2.1 General results

Nine out of the ten initially sown species were able to germinate in the experimental plots. The exception was *Carex flava* with hardly any germination; it will not be considered in the following discussion. Emergence in the first year ranged from 7.3 % (*Iris*) to 38.6 % (*Selinum*) in the plots with the vegetation completely removed (T1), from 3.3 % to 23.1 % in the plots with litter and bryophytes removed (T2; same species as above) and from 0.6 to 14.4 % in the intact vegetation (T0; *Veronica* and *Betonica*). Mean germination rates varied considerably between the three treatments: in all species germination rate was lowest in T0 and highest in T1 (see Table D.10 and also Fig. G.19 in the Appendix). In most species – the only exception is *Selinum carvifolia* – the difference between T1 and T2 was not significant, but differences between either T1 or T2 and T0 were always significant (Kruskal-Wallis ANOVA with subsequent non-parametric multiple comparison), in most cases even highly significant (see Table D.11). No significant differences were found in 2002 but this may be partly due to the small number of replicates in this comparison. None of the sown species germinated in the control plots so that the investigated species can be considered limited by seed availability.

All species were able to some extent to germinate in the undisturbed vegetation; five species, however, had very low mean germination rates of under 2 % with very little variation. In the remaining four species mean germination rates ranged from around 4 % (*Thalictrum* and *Trollius*) to 7.9 % (*Selinum*) and 14.4 % (*Betonica*). Variation in germination rate was considerable in this species.

Table D.10: Results of seed sowing experiments; mean percentages ± SD of germination in first year and surviving seedlings in third year after sowing. Experimental treatments: (T1) vegetation completely removed, (T2) litter and bryophytes removed, (T0) intact vegetation.

	Seedling count 2000			Seedling count 2002		
	T1 (%)	T2 (%)	T0 (%)	T1 (%)	T2 (%)	T0 (%)
Betonica	30.1±12.9	23.1±13.2	14.4±11.4	9.5± 6.2	9.3± 5.7	2.9± 3.7
C. flava	0.9± 2.1	0.4± 1.1	0.1± 0.3	0.2± 0.4		
C. pulicaris	19.7±20.9	6.9± 9.1	1.7± 4.2			
Iris	7.3± 8.8	3.3± 8.2	0.7± 1.9	8.6± 9.2	6.3± 7.2	0.8± 1.1
Lychnis	24.3±17.4	16.5±14.2	1.0± 2.0	4.3± 5.1	3.3± 4.8	0.7± 1.6
Scorzonera	16.4±17.1	6.3± 7.9	0.7± 2.1	5.6± 4.3	0.6± 1.3	
Selinum	38.6±16.8	20.6±12.9	7.9± 7.2	11.2± 4.3	7.8± 3.0	4.2± 4.6
Thalictrum	14.1± 8.5	10.3± 5.1	4.3± 5.1	5.3± 7.1	5.0± 6.2	1.5± 2.7
Trollius	18.3±12.2	15.3± 8.4	4.1± 4.0	3.7± 3.7	2.3± 2.9	0.3± 0.3
Veronica	22.0±12.5	16.8 ± 6.5	0.6 ± 2.0	2.6 ± 4.3	1.0 ± 1.2	

Table D.11: Comparison of germination rates in different treatment patches using the Steel-Dwass test; n.s. = not significant, * = significant at $p \leq 0.05$, ** significant at $p \leq 0.01$, *** = significant at $p \leq 0.001$. Experimental treatments: (T1) vegetation completely removed, (T2) litter and bryophytes removed, (T0) intact vegetation.

	Emergence (2000)			Establishment (2002)		
	T1 vs. T2	T1 vs. T0	T2 vs. T0	T1 vs. T2	T1 vs. T0	T2 vs. T0
Betonica officinalis	n.s.	*	n.s.	n.s.	n.s.	n.s.
Carex flava	—	—	—	—	—	—
Carex pulicaris	n.s.	**	n.s.	—	—	—
Iris sibirica	**	***	n.s.	n.s.	n.s.	n.s.
Lychnis flos-cuculi	n.s.	***	*	n.s.	n.s.	n.s.
Scorzonera humilis	n.s.	***	*	n.s.	n.s.	n.s.
Selinum carvifolia	*	***	**	n.s.	n.s.	n.s.
Thalictrum lucidum	n.s.	**	**	n.s.	n.s.	n.s.
Trollius europaeus	n.s.	**	**	n.s.	n.s.	n.s.
Veronica longifolia	n.s.	***	***	n.s.	n.s.	n.s.

3.2.2 Establishment

Eight out of the ten species managed to establish in the experimental plots, i.e. they were present in the plots upon second inspection in August 2002. Apart from *Carex flava*, whose nearly complete failure to germinate was already mentioned, *Carex pulicaris* did not establish at all, although in this inconspicuous species the danger of overlooking is very high. Highest rates of establishment were found in *Selinum*, *Iris* and *Betonica*, all of these with values around 10% (Table D.10, Fig. G.19). Establishment was again highest in the treatments T1 and lowest in T0 (when it occurred at all). While this observation holds true for all species, the pattern is partly different when survival rate of the seedlings is calculated for the period August 2000 to August 2002. In this case survival in a number of species (*Selinum*, *Thalictrum*, *Iris* and to a lesser degree *Lychnis* and *Betonica*) is actually higher in treatment T2 than in T1, i.e. higher in vegetated plots with litter and bryophytes removed than on bare soil. In *Selinum* survival of the seedlings is even higher in T0, that is in undisturbed vegetation, than in the open patches (Table D.10). However, none of these differences is actually significant (Kruskal-Wallis ANOVA, $p>0.05$)

A special case is *Iris sibirica* with its survival rates of seemingly 1000 % and more: while in all other species it can be assumed that most (if not all) seedlings originated in the first season after sowing, in *Iris* germination lasted at least for two years.

Establishment and seed weight

Emergence rate was not significantly correlated with seed weight, though there may be a slightly negative relation. However, rate of establishment after three years and survival rate were both significantly correlated with seed weight (Fig. D.12). There were no significant differences between treatments when considering seed weight, i.e. large-seeded species didn't perform significantly better in closed vegetation than small-seeded species.

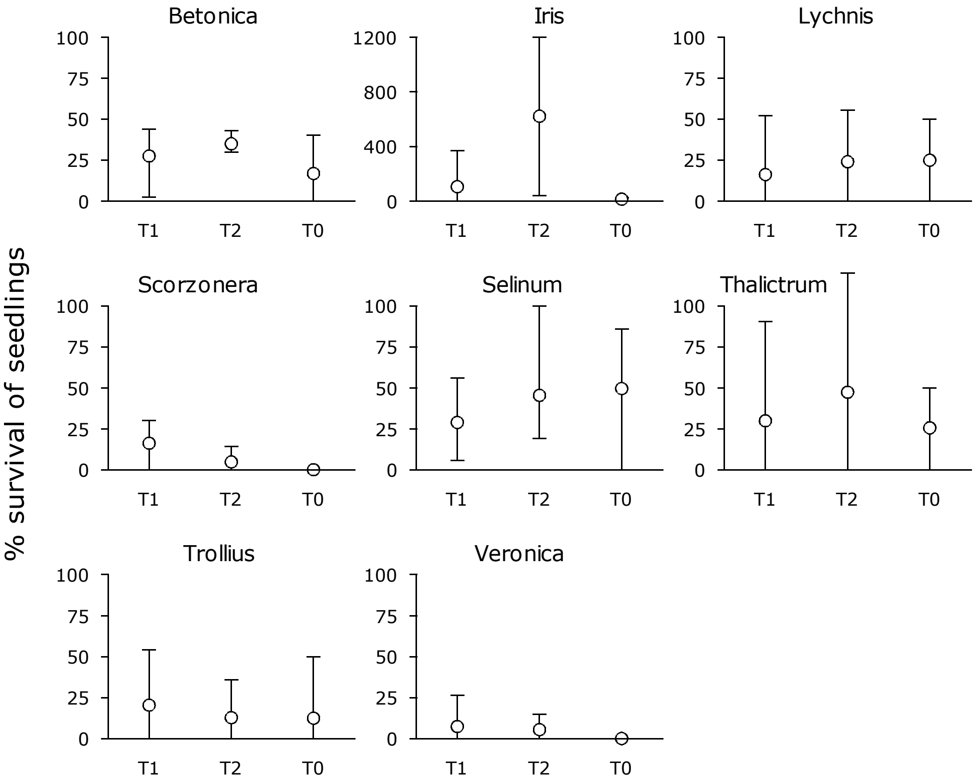

Fig. D.11: Percentage survival of seedlings from August 2000 to August 2002 in different treatment patches: T1 vegetation completely removed, T2 litter and bryophytes removed, T0 intact vegetation; due to small sample size (n = mostly 5) only mean and range are presented

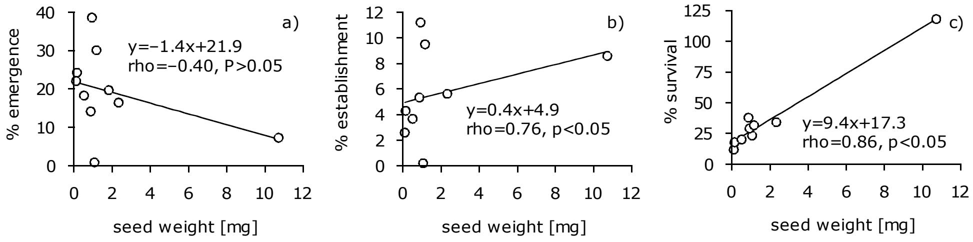

Fig. D.12: Relation between seed weight and (a) rate of emergence, (b) rate of establishment and (c) survival of seedlings calculated using Spearman rank correlation index. C. flava and C. pulicaris were omitted in (b) and (c) due to insufficient data. Lines are best-fit least-square linear regressions.

3.3 Disturbance and regeneration

3.3.1 General results

The local grassland vegetation around the experimental plots, as sampled in the 2.5 × 2.5 m plots, consisted of 92 species, 50 of these where dicots and 40 monocots. Eighty-two of these occurred in the moist community type and 74 in the dry type. Mean species number was 30.7 in the dry and 33.8 in the moist plots. The dry vegetation was dominated by *Festuca ovina, F. rubra, Sesleria caerulea* or *Nardus stricta* and thus belonged to the 'dry floodplain grassland type' *sensu* TRUUS & TÕNISSON (1998). The moist plots were dominated by the grasses *Deschampsia cespitosa* and *Festuca rubra*; forbs like *Geum rivale* and *Filipendula ulmaria* played a much more prominent role than in the dry plots.

A total of 4504 seedlings of approximately 61 species were counted in the experimental plots; 4363 of these were determined to species or at least to genus level, 141 seedlings were undeterminable and were thus omitted from analysis. The number of species and seedlings occurring in the controls was negligible; besides a small number of forbs, almost exclusively of the locally abundant species, it was not possible to distinguish more seedlings, especially of grasses or sedges. In the dense vegetation these were – when present at all – virtually invisible. As the absolute numbers of seedlings in the controls were so small they were not included in the analysis. Patch type T3, which received input from both seed rain and seed bank, was in all aspects (species and seedling number, species composition) approximately the sum of the other two types so that it will not be discussed in detail. It does, however, support the concept of the experimental setup. Seedling establishment in the undisturbed control plots was negligible, an observation which underlines the fact that for most species gaps are a necessary prerequisite for establishment in this type of dense grassland vegetation. Invasion of clonally propagating plants from the surrounding vegetation was observed but the centre of the plot which was used for analysis was affected in only a few, very obvious cases.

Table D.12: Results of disturbance experiment: mean seedling and species numbers and standard deviation

	mean seedling number / m^2 ± S.D		mean species number / plot	
	dry	moist	dry	moist
seed rain only (T2)	267.8 ± 321.1	230.0 ± 344.4	3.1 ± 1.7	2.9 ± 2.0
seed rain + bank (T3)	965.6 ± 474.4	1623.3 ± 896.7	14.7 ± 5.2	17.8 ± 4.5
seed bank only (T4)	836.7 ± 546.7	1042.2 ± 531.1	9.7 ± 5.0	14.1 ± 3.4

Table D.13: Composition of seedling plots, separately for total seedling count, treatments and habitat types. Species with seedling counts lower than 10 and with dubious identity were omitted, see Table G.13 in the Appendix for a complete list. Dispersal vector (AN = animal, AQ = water, EX = explosive, UN = unspecified, WI = wind) and persistence type (T = transient, SP = short-term persistent, LP = long-term persistent) are also indicated. Experimental treatments:: (T2) seed rain only, (T3) seed rain & bank, (T4) seed bank only.

	Disp. vector	Persist. type	total	moist			dry		
				T2	T3	T4	T2	T3	T4
Deschampsia cespitosa	AN	SP	734	153	206	21	167	176	11
Ranunculus auricomus	UN	SP	717	79	305	270	–	42	21
Carex panicea	AQ	LP	300	1	138	71	–	64	26
Ranunculus repens	AQ/AN	LP	226	–	136	45	–	32	13
Carex flava	AQ	LP	221	1	42	37	–	23	118
Viola canina s.l.	EX/AN	LP	212	–	71	25	–	46	70
Lychnis flos-cuculi	WI	LP	202	–	79	60	–	40	23
Carex pallescens	UN	SP	170	–	53	25	1	59	32
Agrostis capillaris	UN	LP	140	3	23	–	–	9	100
Potentilla erecta	UN	LP	120	–	38	36	–	22	24
Alchemilla vulgaris	AN	T	117	–	24	4	–	38	51
Rumex acetosa	WI	LP	103	19	37	4	17	26	–
Festuca rubra	AN	T	101	4	–	2	29	66	–
Carex nigra	AQ	SP	100	–	42	23	1	31	3
Luzula campestris	AN	LP	97	1	16	16	9	44	11
Galium uliginosum	UN	T	82	–	35	42	–	5	–
Ranunculus acris	UN	SP	78	–	29	21	–	12	16
Sesleria caerulea	UN	T	65	1	32	19	3	8	2
Veronica chamaedrys	UN	LP	60	–	–	–	6	14	40
Cerastium holosteoides	UN	LP	59	–	15	10	–	28	6
Trifolium repens	AN	LP	48	–	12	7	–	19	10
Danthonia decumbens	AN	SP	40	–	–	6	–	1	33
Carex pulicaris	UN	T	37	–	4	25	–	–	–
Anthox. odoratum	AN	T	33	–	9	9	1	10	4
Prunella vulgaris	AN	LP	20	–	4	4	–	9	3
Mentha arvensis	AQ	LP	16	1	5	9	–	–	1
Carex vesicaria	AQ	LP	15	–	–	1	–	3	5
Juncus sp.	AN/WI	LP	14	–	3	–	–	4	7
Poa pratensis	UN	LP	11	–	9	–	–	1	1
Carex hirta	AN	T	10	–	10	–	–	–	–
total seedling count			4363	270	1461	844	241	869	678
total species count			61	14	41	34	12	40	32

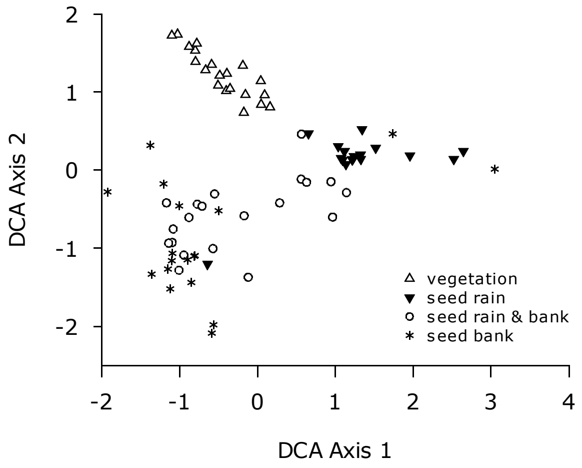

Fig. D.13: DCA scatterplot based on established vegetation and seedling data

The most abundant species in the seedling plots were (in descending order): *Deschampsia cespitosa, Ranunculus auricomus, Carex panicea, Ranunculus repens, Carex flava, Viola canina* and *Lychnis flos-cuculi* (Table D.13). Differences in the most abundant species between habitats and treatments were noticeable but a small group of species recurred in all subsets: in dry plots the five most abundant species were *Deschampsia cespitosa, Carex flava, Viola canina, Agrostis capillaris* and *Festuca rubra,* while in the moist plots these were *Ranunculus auricomus, Deschampsia cespitosa, Carex panicea, Ranunculus repens* and *Lychnis flos-cuculi*. The seed rain was dominated by *Deschampsia cespitosa, Ranunculus auricomus, Rumex acetosa, Festuca rubra* and *Luzula sp.* while in the seed bank the most common species were *Ranunculus auricomus, Carex flava, Agrostis capillaris, Carex panicea* and *Viola canina.*

Seedling densities calculated per 1 m^2 varied from a mere 22 to a maximum of 3478. The mean input of seedlings by seed rain was 249 seedlings m^{-2} and 939 seedlings m^{-2} from the seed bank (averages of dry and moist plots). Slightly higher mean values were generally found in moist compared to dry sites (Table D.12). A non-parametric two-way ANOVA (Scheirer-Ray-Hare test) confirmed this observation: differences between treatments (T2 vs. T4, but not T3 vs. T4; Steel-Dwass multiple comparison) were highly significant, however those between habitat types were not significant; the interaction term was not significant either. Essentially the same patterns of similarity were found for species numbers.

Practically all seedlings belonged to perennial species (99.7 %), with the exception of 15 seedlings of four species (*Angelica sylvestris, Barbarea sp., Euphrasia sp.* and *Peplis portula*) which had either an annual, biennial or pluriannual life cycle. Dicot and monocot species were distributed very evenly in the total data set (49.3 % dicots, 50.7 % monocots of all seedlings) but were unevenly distributed between treatments. While in T3 and T4 there was no significant difference in the mean proportion, in T2 (seed rain only) there were significantly more monocot (79.4 %) than dicot seedlings (20.6 %; $p \leq 0.01$, Wilcoxon signed rank test).

3.3.2 Comparison of species composition

Detrended Correspondence Analysis (DCA, Fig. D.13) was used to visualise the overall species composition of the established vegetation and the seedling assemblages. Axis 1, which separates between the seed bank and seed rain derived seedling assemblages, has a length of 4.98 S.D.s, axis 2 has a length of 3.83 S.D.s and separates between seedling plots and established vegetation. The length of the gradients suggests that vegetation and experimental plots and seed rain and seed bank communities are very dissimilar, having only few species in common. Accordingly the NPMANOVA (see Table D.14) indicated highly significant differences between treatments ($F = 13.16$ with $p = 0.0002$ for quantitative and $F = 20.09$ with $p = 0.0002$ for qualitative data); differences between habitats were only significant for quantitative data ($F = 3.17$ with $p = 0.0114$). Also the interaction term was significant only for quantitative data ($F = 2.20$ with $p = 0.0022$).

Bray-Curtis dissimilarity between vegetation and seedling data was very high, ranging generally from 85 to 95 %; dissimilarity between the seed rain (T2) and seed bank (T4) was equally high. Similarity of plain species composition (Sørensen index) was generally higher and similarity was in both cases higher between vegetation and seed bank than between vegetation and seed rain (Table D.14).

Of the 75 species in the dry vegetation plots 12 occurred in the seed rain and 28 in the seed bank, while of the 83 species in the moist vegetation plots 12 occurred in the seed rain and 27 in the seed bank. Thirty-seven species found in the established vegetation did not occur in the seedling plots. Fifty-four species did occur both in the established vegetation and in the seedling plots. Seven species were present in the seedling plots but not in the established vegetation (*Barbarea sp., Cardamine sp., Crepis paludosa, Euphrasia sp., Peplis portula, Plantago major* and *Viola uliginosa* (Table G.13 in the Appendix), all of them, however, in

Table D.14: Mean Bray-Curtis dissimilarity between established vegetation and seedling assemblages, separately for qualitative and quantitative data; significant differences at $p \leq 0.001$ as indicated by NPMANOVA shown by asterisks (T2 seed rain only, T3 seed rain & seed bank, T4 seed bank only).

	quantitative			presence/absence		
	all	moist	dry	all	moist	dry
vegetation × T2	88.1*	83.1*	93.2*	86.0*	86.6*	84.2*
vegetation × T3	80.8*	78.8*	83.6*	60.8*	61.7*	59.0*
vegetation × T4	88.0*	85.3*	90.3*	68.8*	65.6*	71.8*
T2 × T3	77.1*	81.5*	70.7*	78.5*	80.6*	75.5*
T2 × T4	94.0*	90.9*	94.7*	82.6*	80.0*	84.0*
T3 × T4	76.0	62.7	82.8	52.6	42.0	61.1

small quantities of only a few seedlings. Six of these species are quite common in the surrounding vegetation with the exception of *Peplis portula*, a species of the Isoëto-Nanojuncetea, i.e. wet communities of small rushes; in Estonia this species is rare although not legally protected. *Viola uliginosa* occurs sporadically in Estonia and is legally protected (category III, Kukk 2004). Five of these species were found in the moist habitat type and only two more or less exclusively in the dry type.

When focussing on the three different treatments two species occurred exclusively in the seed rain plots, i.e. *Alopecurus pratensis* and *Helictotrichon pratensis*. On the other hand five species were confined to the seed bank plots: *Cardamine pratensis*, *Cirsium heterophyllum*, *Geum rivale*, *Thalictrum flavum* and *Viola uliginosa*. Again, however, all these species occurred in very small numbers and so this results are not significant. Except for *Deschampsia cespitosa*, *Rumex acetosa* and *Festuca rubra* all of the more abundant species occur significantly more often in the seed bank than in the seed rain.

3.3.3 Species traits

Twelve species traits (vegetative traits: canopy height, canopy structure, established strategy, guild, lateral spread; reproductive traits: dispersal vector, flowering phenology, reproductive type, seed bank longevity, seed weight, seed number, time of germination) were surveyed for possible differences between established vegetation and seedling assemblages. Pronounced differences in cer-

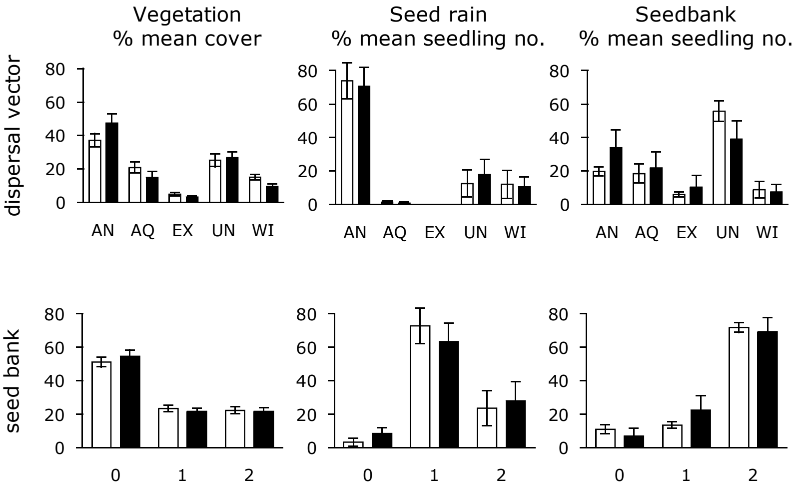

Fig. D.14: Distribution of dispersal vectors and seed bank types in established vegetation and seedling assemblages originating from different sources (seed rain vs. seed bank). Dispersal vectors: animal (AN), water (AQ), explosive (EX), unspecialized (UN), wind (WI). Seed bank types: transient (0), short-term persistent)1), long-term persistent (2). Open bars show data for moist, filled bars for dry sites, percentage mean cover and percentage mean seedling number ± one standard-error.

tain species traits might suggest possible mechanisms influencing the regeneration process. An initial NPMANOVA on the plot × trait matrix suggested highly significant differences in the trait spectra between treatments (F = 17.70, p = 0.0002) and significant differences between habitats (F = 3.00, p = 0.027); there was no significant interaction term. For visual inspection of the seed rain and seed bank data see Fig. D.14, a complete set of trait spectra may be found in the Appendix (Fig. G.20).

Ordination of plots by traits

The first four axes of the plot × trait PCA explained 35.2, 13.2, 7.0 and 6.3 percent of the variation in the original matrix. The first and second axis were clearly related to treatments in a way very similar to the DCA results based on purely floristic data presented above (Fig. D.15): treatments T2, T3 and T4 are positioned along axis 1 with high positive scores for T2 (seed rain only) and high negative scores for T4 (seed bank only). T3 largely overlaps with T4 as was the case with plain species compositional data. Axis 2 distinguishes between established vegetation (T0, high positive scores) and seedling assemblages (negative scores, especially T4). Axis 3 and 4 are both loosely associated with habitat but as this axes only explain around seven percent of the total variance each the overall effect of habitat on trait distribution is low.

The PCA axis loadings of plant trait states suggest that the seed rain (positive loadings on first axis, see Table D.15) is largely composed of rather large, late flowering species with a short-term persistent seed bank, numerous small seeds which are often animal-dispersed. This characterisation coincides with the fact that the grass *Deschampsia cespitosa* is by far the most numerous component of the seed-rain-based seedlings. In contrast to this the seed bank is associated with traits like small numbers of seeds, vegetative and generative reproduction and unspecialised dispersal, indicated by negative loadings on the first axis (Table D.16). Furthermore species in the seed bank tended to be forbs rather than

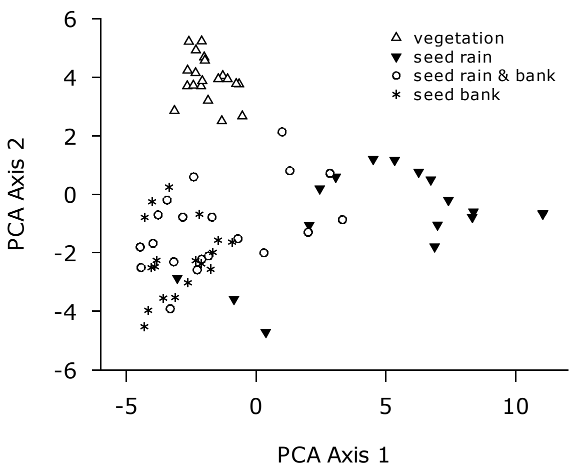

Fig. D.15: PCA scatterplot based on a plot × trait matrix.

graminoids; moreover strategies with a ruderal component are more common in the seed bank. Highest positive loadings on the second axis were found for the traits *canopy height 5*, *seed bank 0* and *seed weight 6*. In addition to these *flowering time 7*, *reproductive type V*, and *germination time WI* also had rather high negative loadings on the second axis. Negative loadings were generally not as high as the positive ones: only *seed bank type 2* and *established strategy CSR* reach comparable values. In contrast to the seedling assemblages the established vegetation is thus characterised by species that reproduce exclusively by vegetative means, have only a transient seed bank and have heavy seeds. Axis 3 and 4 were loosely related to habitat (negative loadings: moist habitat). Among the traits that seem related to moister habitats are wind and water-dispersed seeds and spring germination whereas plants from drier sites are of smaller stature and tend to be animal-dispersed or with explosive dispersal (*Viola ssp.*).

Table D.15: Results of a plot × trait PCA. Correlation of PCA axes scores with treatments and habitat; as variables are categorical significance was tested by a Mann-Whitney U-test; values are mean PCA axis scores for the given category, significant results with p ≤ 0.001 are marked bold, those with p ≤ 0.05 are marked italic.

Axis no.	1	2	3	4
% variance explained	32.0	12.7	6.8	6.6
Habitat (moist)	0.003	–0.211	*–0.470*	*–0.589*
Establ. vegetation	–1.863	**3.929**	0.017	–0.098
Seed rain only	**6.013**	–0.778	–0.549	0.508
Seed rain & bank	–1.468	*–1.164*	0.309	–0.275
Seed bank only	**–2.980**	**–2.207**	0.248	–0.150

Table D.16: Ten plant traits with the highest loadings on the first four axes of a plot × trait PCA

trait	loadings	trait	loadings
axis 1 (seed rain + to seed bank –)		*axis 3*	
canopy height: 4	0.222	canopy height: 3	–0.324
reproduction by seed only	0.218	reprod. mostly by seed, seldom veg.	0.315
seed bank short-term persistent	0.213	dispersal by wind	–0.305
time of flowering: 8	0.210	dispersal explosively	0.296
seed number: 2	0.206	time of germination: summer	0.256
seed number: 1	–0.206	seed number:: 3	0.240
reproduction by seed & veg.	–0.197	reprod. mostly veg., seldom by seed	0.238
seed weight: 1	0.190	dispersal by animals	0.224
strategy: C	0.186	canopy height: 1	0.217
dispersal by animals	0.184	reproduction by seed & vegetatively	–0.195
axis 2 (establ. vegetation + to seed bank only –)		*axis 4*	
seed bank transient	0.314	canopy height: 2	–0.303
seed weight: 6	0.303	canopy height: 1	0.282
canopy height: 5	0.281	dispersal by water	–0.279
reproduction vegetatively only	0.243	canopy structure: leafy	0.272
time of flowering: 7	0.236	lateral spread: 1	–0.268
time of germination: winter	0.224	canopy structure: semi-rosette	–0.252
seed bank: long-term persistent	–0.222	seed weight: 4	–0.250
strategy: CS	0.208	seed weight: 5	–0.246
lateral spread: 0	0.205	time of germination: spring	–0.222
strategy: CSR	–0.195	strategy: S	–0.208

3.4 Plant traits

For a general analysis of plant traits in the Soomaa floodplain meadows a subset of floodplain species that occurred at least three times in the complete relevé data set was compiled; this subset consisted of 135 out of a total of 213 plant species (see Table G.14 in the Appendix). This set of species was still rather large, but choosing a smaller subset would have meant missing many species typical for less-common but nonetheless characteristic floodplain communities. Preliminary multivariate analyses with smaller data sets showed that in theses case especially the rarer functional types were lost so that larger data set was used for analysis.

Perennials were by far the largest group (93 %) whereas annuals and other short-lived species played only a very minor role (7 % or nine species). Likewise did most species belong to the hemicryptophyte life form (81 %), followed by geophytes (12 %); all other life forms were below 5 % each. 63 % of the species in this data set were forbs, only 33 % were graminoids (thirteen of this 45 graminoids or 10 % are sedges, however, another thirteen species of the genus *Carex* were present in the samples but too rare to be included in this list).

Not surprisingly for permanent grassland nearly half of the species (43 %) were capable of strong lateral expansion, and ca. 30 % were characterised by poor or completely lacking clonal spread. 27 % of the species had moderate lateral spread, this category also encompasses the tussock forming species. The trait *canopy height* was more evenly distributed with a peak in the 21–40 cm class (32 %), the other classes all scored around 15–20 %. More than half of the species (55 %) were classified as semi-rosette plants, 34 % as leafy and only 10 % are true rosette plants.

According to Grime's CSR-strategy scheme (Grime 1977) nearly all species had to some degree a competitive strategy: 34% of the species were pure competitors, 21 % were stress tolerant competitors (CS) and 39 % had a CSR strategy. Ruderals were completely missing, there was one competitive-ruderal (CR) and two stress tolerators (S) and ruderal stress tolerators (SR) each.

According to the data compiled in the Biolflor database (Klotz et al. 2002) nearly thirty percent of the species regenerated exclusively or predominantly by seeds whereas more than sixty percent reproduced equally well generatively and vegetatively; only 6 % of the species reproduced exclusively or predominantly by vegetative means. More than half of the species for which data was available (Peat & Fitter 2003) germinated in spring, around twenty percent in summer and autumn.

As most species relied to various degrees on reproduction from seed, seed traits were presumably among the most important traits governing population and community regeneration. In the coarse classification scheme for seed number used here over 60 % of the species were scored as having few, i.e. up to a thousand seeds per plant, 23 % had numerous seeds and ten percent had very numerous seeds (considerably more than ten thousand). Seed weight was rather evenly distributed with most categories ranging from 15 to 30 % and seeds with a weight of 0.51 to 1.0 mg being most common (33 %). Seeds with a weight above 10 mg were very rare (*Vicia cracca* and *Lathyrus pratensis*). Another important seed trait in the context of population regeneration and site restoration is the ability (or lack thereof) to form a persistent seed bank. Around forty percent of the species considered here were either classified as having a transient or long-term persistent seed bank, thirteen percent had a short-term persistent seed bank.

The distribution of dispersal vectors was already discussed in more detail in the preceding chapters so that only a general overview will be given here. Both animal- and wind-dispersed species accounted for some 30 % of the complete species set, followed by species without any obvious dispersal mechanism (25 %) and water-dispersed species (19 %).

Data for flowering phenology were extracted from Dierschke (1995) although these data were compiled for the Central European flora. Own observations, however, largely confirmed the relative phenology so that the usage of this data seems justified. There was a continuous stream of flowering plants from early spring to midsummer peaking in early summer (PHE.6).

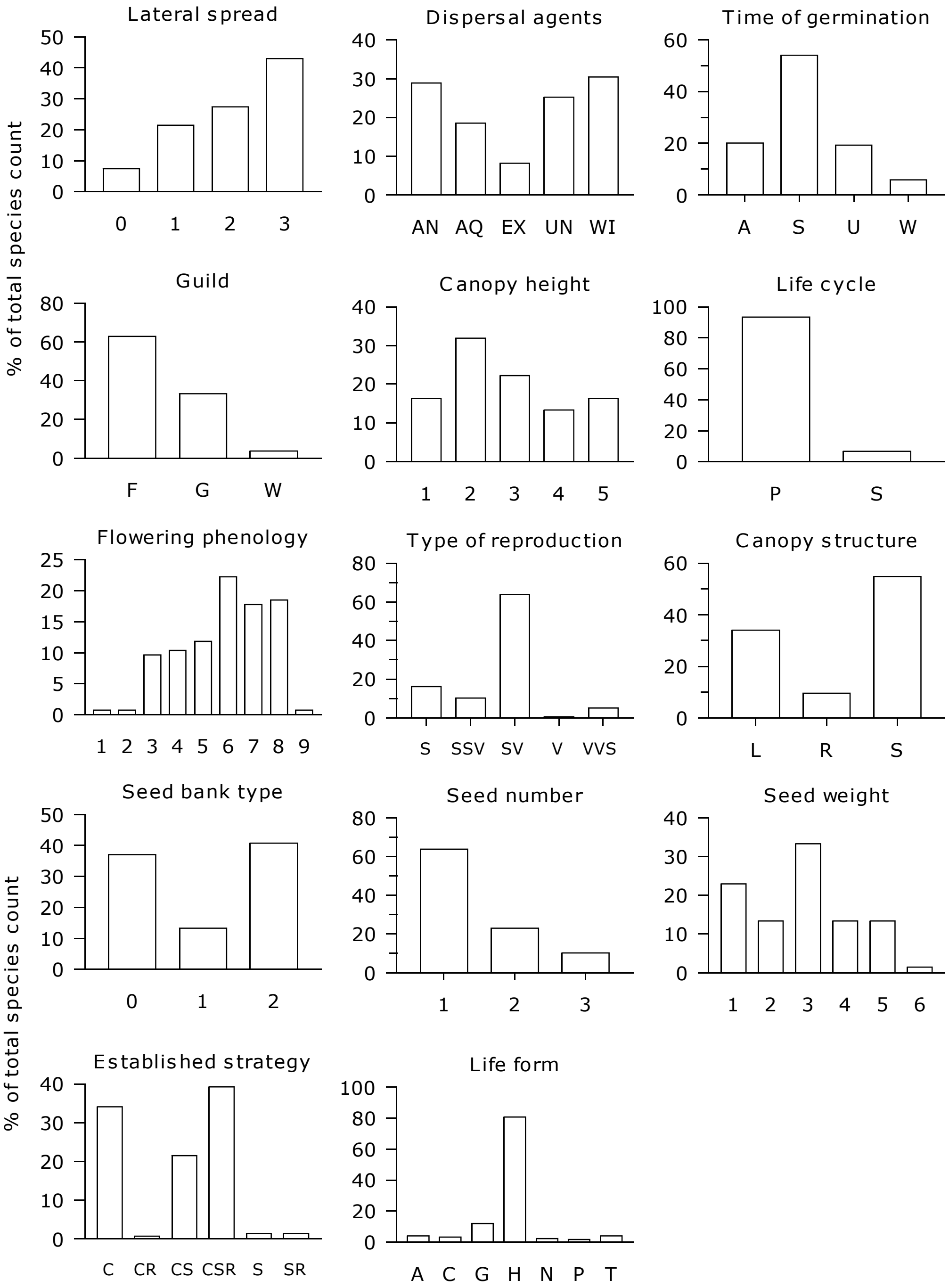

Fig. D.16: Percentage distribution of plant traits of the 135 most common plants in the Soomaa floodplain meadows. For definition of trait categories see Table D.2.

Inter-correlation of traits

Statistical analysis revealed that several of the studied plant traits were inter-correlated, i.e. certain trait states tend to occur together more often or less often than could be expected by chance alone (Table D.17). Dispersal vector e.g. was correlated with seed number and seed weight while seed number and weight were negatively correlated. Lateral spread was correlated with several other life history traits like guild, life cycle and reproductive mode. Further analysis of single trait states (Table D.18) showed e.g. strong correlations of non-clonal growth with short life cycle and reproduction mainly by seed. Anemochory is positively correlated with seed number and (although with lower significance) negatively with seed size. Other reproductive traits do not show such strong correlations, however seed bank type SEB.0 (transient seed bank) is correlated with high seed weight (SEW.5) and greater plant height (HEI.5).

Table D.17: Inter-correlation of plant traits. Pearson's χ^2-test was used for correlations between two traits expressed on a nominal scale, Kruskal-Wallis one-way ANOVA for trait pairs where one is of nominal and one of ordinal type and Pearson's correlation for two ordinal traits.

	Test	Test statistic	Probability
CLO vs. GLD	χ^2	38.3	$p < 2.2$ E-16
CLO vs. LIF	χ^2	69.0	$p < 2.2$ E-16
CLO vs. REP	χ^2	89.8	$p < 2.2$ E-16
GLD vs. ROS	χ^2	26.0	$p = 8.0$ E-04
LIF vs. REP	χ^2	43.0	$p < 2.2$ E-16
DIS vs. SEN	K-W	33.7	$p = 8.5$ E-07
DIS vs. SEW	K-W	20.1	$p = 4.8$ E-04
GLD vs. HEI	K-W	21.4	$p = 8.7$ E-05
GLD vs. SEN	K-W	21.7	$p = 7.5$ E-05
HEI vs. ROS	K-W	14.0	$p = 9.3$ E-04
HEI vs. STR	K-W	77.0	$p = 3.5$ E-15
HEI vs. SEN	Pears.	0.551	$p = 1.9$ E-13
PHE vs. SEN	Pears.	0.275	$p = 9.2$ E-04
SEN vs. SEW	Pears.	-0.495	$p = 2.5$ E-10

Table D.18: Correlation of trait states involving nominal variables using Pearson's correlation index; only cases with r ≤ |0.3| and p < 0.0001 are reported

	Test statistic	Probability
CLO.0 vs. LIF.S	0.642	p < 2.2 E-16
CLO.0 vs. REP.S	0.489	p = 6.4 E-11
CLO.3 vs. REP.S	-0.373	p = 1.6 E-06
CLO.1 vs. REP.SSV	0.321	p = 3.7 E-05
CLO.0 vs. REP.SV	-0.383	p = 6.1 E-07
CLO.1 vs. REP.SV	-0.321	p = 3.7 E-05
CLO.3 vs. REP.SV	0.404	p = 1.2 E-07
GLD.G vs. ROS.L	-0.306	p = 8.6 E-05
LIF.S vs. REP.S	0.416	p = 5.1 E-08
LIF.S vs. REP.SV	-0.350	p = 6.0 E-06
DIS.WI vs. SEN	0.517	p = 3.0 E-12
HEI vs. STR.C	0.467	P = 5.3 E-10
HEI vs. STR.CSR	-0.587	p = 4.3 E-16

further correlated trait combinations with slightly lower significance: CLO.1 vs. GLD.F (+), CLO.0 vs. REP.V (+), LIF.S vs. REP.V (+), DIS.WI vs. SEW (−), HEI vs. ROS.R (−), HEI vs. STR.CS (+), SEB.0 vs. SEW.5 (+), SEB.0 vs. HEI.5 (+), SEB.2 vs. GER.S (+) and SEB.2 vs. GER.A (+)

Growth-form or functional groups

Cluster analysis using McQuitty's method was applied to analyse the matrix of 135 floodplain species by 59 traits. Two different cut-off levels of the cluster dendrogram and the resulting functional groups were examined. At the lower cut-off level nine functional groups emerged, that were defined mostly by guild membership (forbs or graminoids), growth height, lateral spread, canopy structure, seed number and seed weight (see Fig. D.17, Table D.19 and Table G.14 in the Appendix). A tenth cluster existed at the same cut-off level which, however, consisted only of *Cerastium holosteoides*. Graminoids were mainly found in one large cluster (PFG 3) of clonally propagating plants of medium height; this group, however, was somewhat inhomogeneous due to the membership of many forbs and further subdivision did not lead to more homogeneous groups. The most homogeneous group was probably that of tussock forming grasses (PFG 7) which consisted of eight relatively similar species. A small number of further graminoids was found together with forbs and woody species in PFG 8 mainly due to their small and numerous seeds. Forbs were a much more diverse group which were spread over several clusters. Medium sized forbs were divided according to dispersal agent (PFG 1 and 2, both semi-rosette growth), strong lateral expansion plus non-rosette growth (PFG 4) and large seed mass (PFG 5). Another group of forbs was defined by its small stature, CSR strategy and small seed number (PFG 6). All these groups of perennial species were separated on the highest cut-off level from a cluster of eight short lived species , i.e. annuals, biennial and pluriannuals (PFG 9).

Choosing a higher cut-off level with a total of five clusters (plus *Cer. holosteoides*) left PFG 7, 8 and 9 (tussock grasses, small-seeded wind-dispersers and short-lived non-clonals) but fused PFG 1 and 2 (medium sized non-clonal forbs) and PFG 3, 4, 5 and 6 (forbs and grasses with strong lateral spread).

Table D.19: General characterisation of plant functional groups (PFG) from McQuitty's cluster analysis. With a higher cut-off level PFGs 7, 8 and 9 remain unchanged, while PFGs 1 & 2 and 3 through 6 are fused.

PFG	No. of species	Attributes and typical species
1	17	medium sized forbs, wind-dispersed, semi-rosette growth, seeds numerous (SEN.2), lateral spread restricted, reproduction generatively and vegetatively (SV), germination spring or autumn, strategy C or CSR (e.g. *Taraxacum* sp., *Achillea millefolium, Rumex acetosa, Hieracium umbellatum*)
2	13	mostly medium sized forbs, animal-dispersed, semi-rosette growth, seeds few (SEN.1), seed bank mostly transient, lateral spread restricted, reproduction mostly by seed (S), strategy C or CSR (e.g. *Alchemilla vulgaris, Centaurea jacea, Knautia arvensis, Succisa pratensis*)
3	35	medium sized forbs and graminoids with strong lateral spread, semi-rosette growth, seeds few, reproduction by seed and vegetatively (SV), germination mostly spring, strategy mostly CSR (e.g. *Carex* sp., *Agrostis* sp., *Anthoxanthum odoratum, Galium boreale, Ranunculus repens*)
4	11	forbs of differing size with strong lateral spread (CLO.3), non-rosette growth, seeds numerous (SEN.2), seed bank short or long-term-persist., germination mostly spring, strategy mostly C or CS (e.g. *Filipendula ulmaria, Phalaris arundinacea, Betonica officinalis, Stellaria* sp.)
5	8	forbs of mostly medium height, moderate to strong lateral spread, seeds few but heavy, strategy mostly C or CS (e.g. *Geranium* sp., *Iris* sp., *Lathyrus, Vicia*)
6	15	small forbs (HEI.1), mostly strong lateral spread, dispersal mostly by animals or explosive (*Viola*), seeds few (SEN.1) and of medium weight (SEW.3), seed bank mostly long term persist., strategy CSR (e.g. *Galium palustre, Prunella vulgaris, Hieracium pilosella, Viola* sp.)
7	8	tussock grasses (e.g. *Dactylis glomerata, Deschampsia cespitosa, Nardus stricta*)
8	14	plants of medium to large height with small, very numerous wind-dispersed seeds; strategy mostly C or CS (e.g. *Hypericum maculatum, Juncus* sp., *Calamagrostis* sp.)
9	8	short lived forbs, no or poor lateral spread, germination excl. spring; may be subdivided into annuals and biennials + pluriennials (e.g. *Angelica sylvestris, Heracleum sibiricum, Rhinanthus minor*)

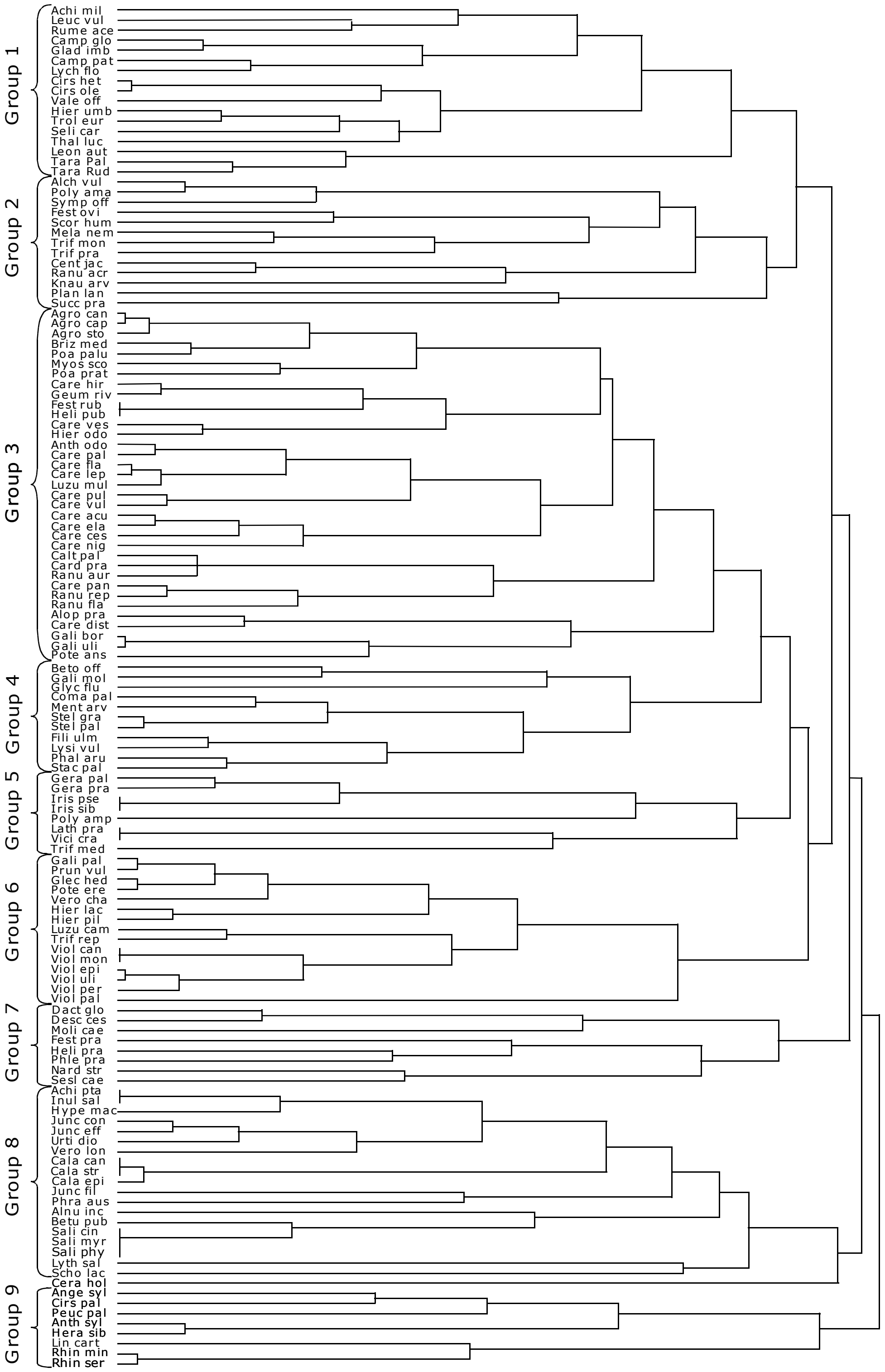

Fig. D.17: Dendrogram showing agglomerative clustering (McQuitty's method) of 135 floodplain species according to a selection of vegetative and regenerative traits.

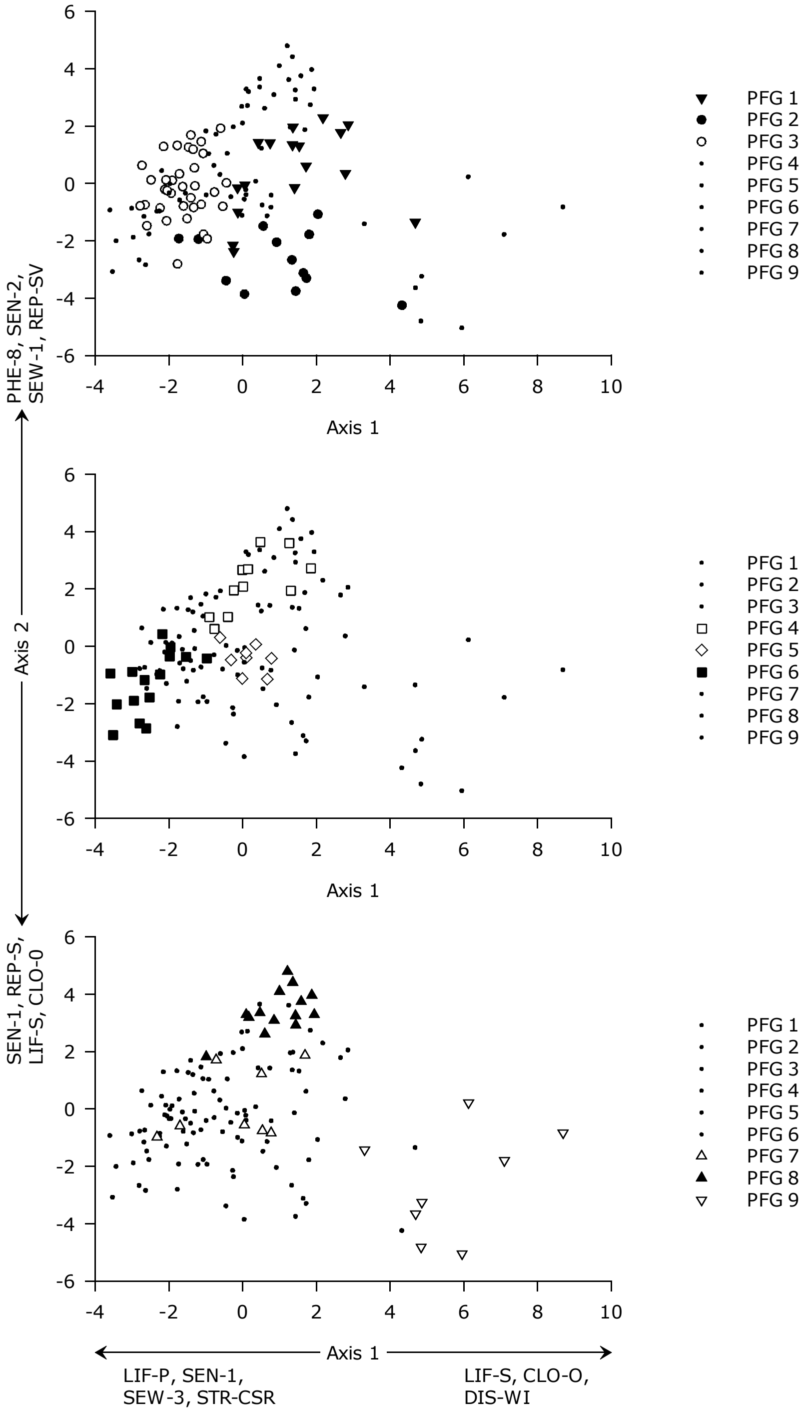

Fig. D.18: PCA scatter plot of a trait matrix of 130 herbaceous meadow species with overlay of 9 functional groups (PFG) from cluster analysis (for explanation of PFGs see Table D.19 on page 125). For better clarity, the graph is split into three parts. Arrows indicate significant correlations between PCA axes and plant traits (CLO: vegetative spread; DIS: dispersal vector, LIF: life span; PHEN: flowering phenology; REP: reproductive mode; SEN: seed number; SEW: seed weight, STR: life strategy; for detailed explanation of traits see Table D.2 on page 90.

As the results of the cluster analysis did not indicate how well the groups were separated a PCA was run with the same trait matrix (Fig. D.18). The first two axes explained 8.9 and 7.8 % of the total variation. The first axis represented a gradient from perennial CSR strategists with few but heavy seeds to short-lived, non-clonal plants that were mostly wind-dispersed. The second axis described a gradient from short-lived, non-clonal plants with few seeds that reproduced mostly by seeds to late flowering plants with many light-weight seeds that reproduced by seed and vegetatively. PFG 2, 8 and 9 of the cluster analysis were well defined on the first two axes which supported their relatively unique trait composition. Axis 3, adding another 6.4 % of explained variation, separated moderately well between PFG 3, 6 and 7.

Functional groups and plant communities

Spectra of functional groups for the different community types present in the study area (Fig. D.19) show that the most common group in most communities is *group 3* with plants of medium height (20–60 cm) and strong lateral spread. These clonally propagating perennials obviously form the matrix of most of the studied grassland types. In dry grassland communities *group 2* is most abundant which is largely due to the prominence of tussock forming *Festuca ovina*, the only graminoid in this growth-form group. In reed communities (*Phalaris-Phragmites* community) competitive forbs with strong lateral spread become dominant (*group 4*), besides the dominant grasses which belong to *group 8* because of their large numbers of small seeds. Further growth-form groups which achieve greater abundance are *group 2* and *7* in dry to most communities and *group 4* in the moist to wet communities with tall sedges and grasses. It is interesting to note that it is the moist grassland communities (*Sesleria-Deschampsia-*, *Melampyrum-Deschampsia-* and *Carex cespitosa-Deschampsia*-community) that are most divers in terms of growth-form groups, i.e. all described groups are present and differences in abundance are comparably small.

The strength of the association between functional groups and plant communities as described in previous chapters of this study was estimated with the help of INDICATOR SPECIES ANALYSIS (Table D.20). The analysis shows that most communities are characterised by a unique combination of functional groups. Furthermore seven out of nine functional groups are significantly associated with one certain community so that they can be considered an analogue of an indicator species. The dry *Nardus-Festuca ovina*-community is characterised by two indicator groups, PFG 6 with small, clonal forbs (e.g. *Viola* sp., *Prunella vulgaris*) and PFG 7 with tussock grasses like *Nardus stricta* and *Festuca ovina*. The dry *Festuca ovina-Sesleria*-community on the other hand is characterised by animal-dispersed, non-clonal forbs (group 2, e.g. *Centaurea* or *Knautia*), which is also abundant in the first mentioned community, however here PFG 6 and 7 are much less abundant.

The mesic *Festuca rubra-Deschampsia*-community does not posses a proper indicator group but is otherwise rather similar to the two dry communities with group 6 and group 2 being the most characteristic ones. Wind-dispersed, non-clonal forbs like *Taraxacum* or *Rumex acetosa* (PFG 1) are indicative of the mesic *Alopecurus-Galium mollugo*-community, also characteristic for this community is group 9 with short-lived non-clonal plants like *Angelica* or *Heracleum*. The *Alopecurus-Deschampsia*-community, which was floristically somewhat difficult to classify and possibly is an impoverished successional stage of other mesic to moist meadow communities, was also hard to define with regard to it's PFG composition.

In the two moist Molinion-communities (*Sesleria-Deschampsia-* and *Melampyrum-Deschampsia*-community) PFG 2 with medium sized, animal-dispersed non-clonal forbs is equally important. The communities differ, however, in that the *Sesleria-Deschampsia*-community is dominated more strongly by tussock grasses (PFG 7) while the *Melampyrum-Deschampsia*-community is characterised by PFG 9 with short-lived, non-clonal forbs. Both of these communities have no statistically significant indicator groups. The third moist community, which floristically was defined by the dominance of *Carex cespitosa* and *Deschampsia cespitosa*, was significantly characterised by PFG 5, medium height, clonal forbs with few and heavy seeds.

The wet reed and sedge communities show a completely different pattern of plant functional groups than the dry, mesic and moist meadow communities. They are largely composed of plants with strong lateral spread (PFG 3 and 4) but differ in their seed production: the reed communities (*Phalaris-Phragmites*-and *Schoenoplectus*-community) are dominated by species that produce large quantities of small and mostly wind-dispersed seeds (PFG 4 and 8). Sedges on the other hand, which dominate in the remaining communities produce fewer and larger seeds (PFG 3).

On the other hand, two functional groups, i.e. group 5 with large-seeded clonal forbs and group 9 with short-lived, non-clonal forbs, are equally rare in all communities so that they do not serve as indicator groups.

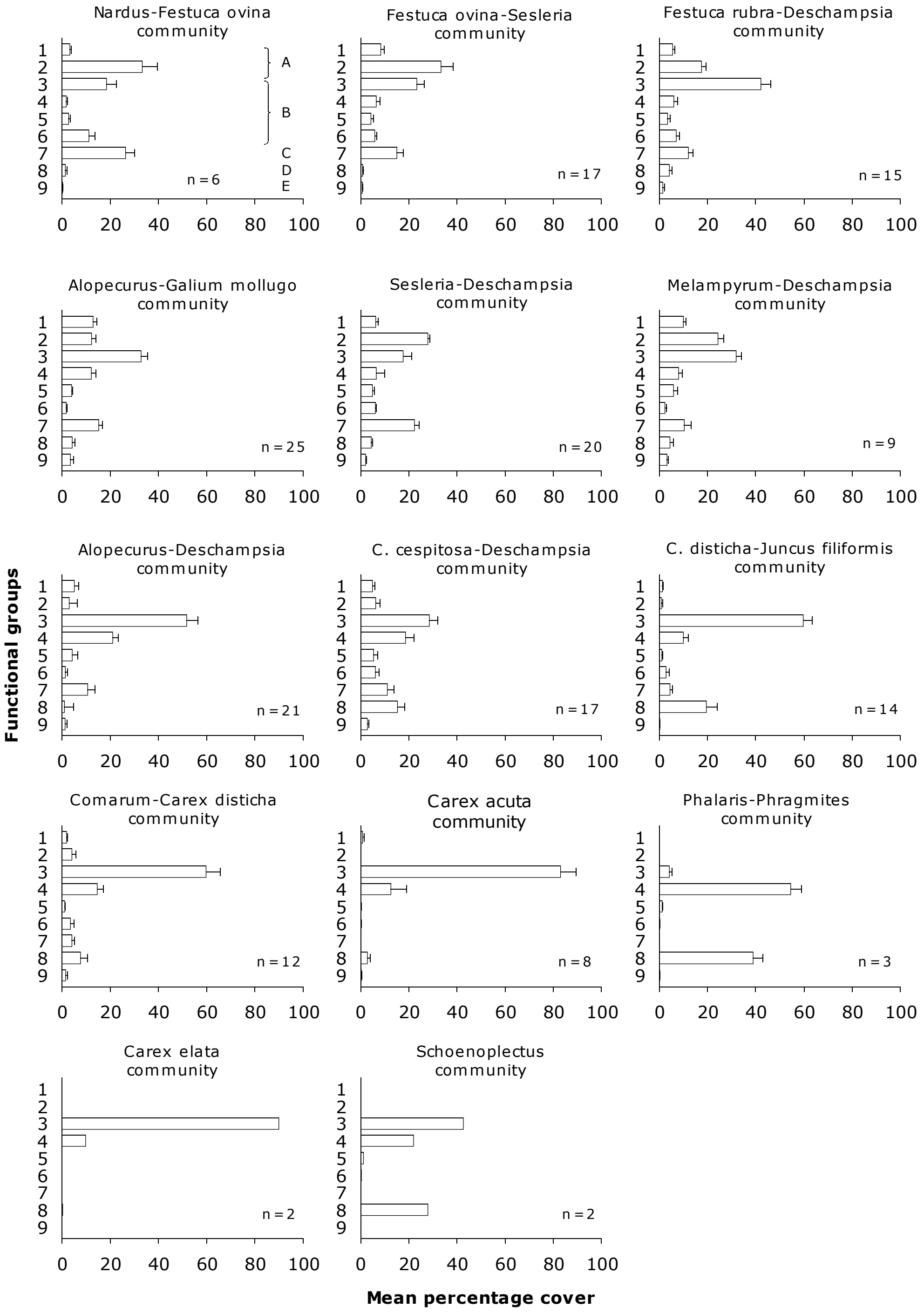

Fig. D.19: Distribution of functional groups in grassland communities of Soomaa NP (mean percentage cover ± 1 standard error, for definition of groups see Table D.19, p. 125). Roman capitals A–E in top left graph indicate functional groups resulting from a higher cut-off level in cluster analysis.

Table D.20: Results of Indicator Species Analysis of the functional group (PFG) composition of 171 vegetation samples. Indicator Value (IV) representing % of perfect indication and significance (p) resulting from Monte Carlo tests with 1000 permutations. Maximum values per row are marked italic.

			Indicator value in plant community no.													
	max. IV	p	1	2	3	4	5	6	7	8	9	10	11	12	13	14
PFG 1	21.5	0.008*	5	14	9	***21***	10	15	8	7	1	3	0	0	0	0
PFG 2	20.5	0.042*	20	***20***	11	8	17	15	2	3	0	2	0	0	0	0
PFG 3	15.4	0.006*	3	4	7	6	3	5	9	5	10	10	14	0	***15***	7
PFG 4	26.7	0.009*	1	3	3	6	3	4	10	9	4	7	6	***27***	2	5
PFG 5	13.9	0.403	7	11	9	10	12	12	11	***14***	2	3	0	1	0	1
PFG 6	23.1	0.017*	***23***	12	14	3	13	4	2	11	4	6	0	0	0	0
PFG 7	20.1	0.004**	***20***	11	9	12	17	8	7	7	3	3	0	0	0	0
PFG 8	29.4	0.030*	0	0	2	2	3	1	0	11	15	4	1	***29***	0	21
PFG 9	18.6	0.175	0	2	6	16	10	***19***	4	13	0	4	0	0	0	0

Plant communities: (1) Nardus-Festuca ovina, (2) Festuca ovina-Sesleria, (3) Festuca rubra-Deschampsia, (4) Alopecurus-Galium mollugo, (5) Sesleria-Deschampsia, (6) Melampyrum-Deschampsia, (7) Alopecurus-Deschampsia, (8) Carex cespitosa-Deschampsia, (9) Carex disticha-Juncus filiformis, (10) Comarum-Carex disticha, (11) Carex acuta, (12) Phalaris-Phragmites, (13) Carex elata, (14) Schoenoplectus

4 Discussion

4.1 Methodological considerations

The results presented in this study were all obtained by means of field studies; although it would have been desirable for more accurate results to supplement these investigations by laboratory studies (e.g. germination tests for accurate maximum germination rates under controlled conditions or more precise estimates of seed bank composition) this option was not available under the given conditions in Soomaa NP. Upon discussing potential limitations of environmental field studies EBERHARDT & THOMAS (1991) distinguish between eight categories of field studies with decreasing amount of control exerted by the observer ranging from fully controlled and replicated experiments down to sampling for patterns. For the study of complex natural systems they suggest a mixed approach of sampling studies for observing the larger system, observational studies to contrast certain components and small-scale experiments for detailed analysis. This approach was partly followed in this study of regeneration processes in floodplain meadows. The role of seed dispersal was estimated in an observational study with four transects and deliberately placed seed traps. Special care was taken to sample all relevant vegetation units over the whole area of the National Park. The relative importance of seed bank and seed rain as sources for regeneration was approached by a second observational study, which combined features of a sampling approach with experimental control of the conditions of the sample plots. Validity of this results is – strictly speaking – restricted to the Läti meadow where all experimental plots were located. Extension of the experiment over the whole area of the National Park was not possible due to logistic reasons. Finally a controlled and replicated experiment was used to study the germination of selected species under three different environmental conditions. These studies may not offer the rigourous strength of inference that controlled experiments of more narrow focus can achieve but they nevertheless seemed worthwhile to explore regeneration processes under the natural conditions of large-scale and species-rich semi-natural grasslands.

Estimates of seed bank and seed rain composition and density have to cope with several methodological problems. Their validity depends upon a number of preconditions which are not always easy to fulfil in field studies where ‘manpower’ is a limiting factor. Both seed rain and seed bank are subject to large temporal and spatial variation (PARKER et al. 1989; NATHAN & MULLER-LANDAU 2000) which ideally have to be accounted for in some way if the estimates are to be meaningful. The temporal variation in the seed rain was addressed as part of the underlying question by leaving the seed traps in the field for a whole growing season and emptying it several times. The temporal variation of the seed bank is usually addressed by repeated sampling throughout the year which, however, was not applicable in the case of this study. Since the experimental plots, which were used for the estimation of the seed bank composition, were set up in autumn and acted like a real-world disturbance they integrated over time and thus captured the seedlings emerging over a longer period of nearly one growing season. Spatial variation of the seed rain was addressed at two scales: at the local scale five seed traps rather than one were placed at each sample location and the results pooled to give a compound data set. At the regional scale four transects were set up and all discernible community types were included in a stratified sampling approach. A more serious problem is that of sufficient size of sampling area. Strykstra et al. (1998) produced a graph relating sampling area and chance of detecting seeds with a given density. To detect e.g. a species with one seed per square meter with a 95 % chance a sample area of ca. 3m² would be needed. On the other hand, with the sampling area used in this study a species with a density of ca. 40 seeds/m² has a 95 % chance of detection and a species with one seed/m² has only a 5 % chance. It is therefore inevitable that rarer species or those few seeds travelling over long distances may be missed by this approach, a problem termed 'Dorothy's Dilemma' by Silvertown (1991) by analogy with Dorothy in the land of Oz who found it difficult to find a way to the end of the rainbow (i.e. the end of the dispersal curve). Nonetheless this approach should provide a useful picture of the seed rain of the more common species.

Classifications of species according to their actual or presumed vector of dispersal (e.g. the one by Grime et al. (1988) used in this study) offer a convenient way of addressing community scale questions of dispersal processes. By condensing the information on a great number of species they help seeing the forest for the trees, i.e. perceiving patterns that would otherwise be hidden beneath a mass of individual facts. It must, however, be kept in mind that these classifications are likely to be incomplete or insufficient. The mostly binary nature of these classifications, i.e. a species is *either* wind-dispersed *or* not wind-dispersed with no possibility to consider multiple dispersal vectors or gradual differences, is highly artificial (Tackenberg 2001) and a considerable number of species will in fact be polychorous (Bonn & Poschlod 1998). To a certain extend this was taken into account in cases where multiple morphological adaptations were very obvious. Furthermore seeds may be transported by agents to which they were not adapted to and certain dispersal vectors may not be present at the right time or location (van Splunder et al. 1995). Therefore dispersal spectra derived from these classifications will always remain approximations and will need to be examined carefully.

4.2 Seed rain

The phenomenon 'seed rain' can be approached in the field from two directions: from the seed source and from the target area (Silvertown 1991). In the first case the focus is on single plants and on the seed shadows they produce. In this way very precise estimates are possible of the distance seeds of the given species may travel under the actual site conditions, and whether a species of conservational interest is able to reach a site that is to be restored or diversified. Bischoff (2002) e.g. found in a study of *Silaum silaus* and *Serratula tinctoria* in floodplain grasslands that, after transplantation into sites where the species were currently not present, dispersal distances were minimal and autonomous re-establishment in target areas was unlikely. Bullock et al. (2003) studied *Rhinanthus minor*, a grassland species also present in the Soomaa floodplain meadows, and found that dispersal agents and distance varied considerably according to management and habitat conditions – a result that cautions against too simplistic interpretations of dispersal spectra where species are assigned to only one dispersal agent. In the second approach, which was followed here, the focus is more on community-wide patterns of seed dispersal and its implications for the structure and diversity of the community. While seed traps have a fairly long history in the study of forest dynamics and are also used frequently to monitor old field succession (Kollmann & Goetze 1998, Poschlod & Jordan 1992) there are relatively few studies using seed traps in temperate grass- and wetlands.

Seed rain density

The observed seed densities of 3323 to 51300 (or 8157 when three occurrences of the super-abundant *J. filiformis* are omitted) seeds m^{-2} are well in the range of those published in the literature (Table D.21) although those values vary considerably over three orders of magnitude. In two seed rain studies conducted in wet grassland (Fischer 1987; Jensen 1998) *Juncus spp.* were by far the most abundant species found in the traps; this corresponds to the data presented here. Trap design seems to play an important role in determining the overall seed yield: most studies used a design where seeds, once they entered the trap, were not able to leave it again (funnel or sticky surface) and here the highest seed densities were reported. In the study by Skoglund (1990) and in the study presented here open traps were used where seeds were able to enter and leave the trap, thus simulating secondary dispersal (Chambers & MacMahon 1994). Total seed numbers were somewhat lower here. Another source of underestimation will probably be total sampling area. Fischer (1987), Jensen (1998) and Jackel & Poschlod (1994) all used greater overall sampling areas in their studies and where able to retrieve on average larger numbers of seeds.

Table D.21: Estimated seed rain densities in temperate grasslands compiled from the literature. Multiple entries per study indicate results from different sample locations.

Source	Habitat	Trap design	Time	Estimated density m^{-2}
Rabinowitz (1980)	tall grass prairie	64 cm^2 sticky traps, no replicates	26 weeks	19726
Fischer (1987)	Molinietalia-community	2500 cm^2 funnel traps, 10 replicates	6 months	65300
Skoglund (1990)	wet grassland/forest	120 cm^2 box traps, no replicates	1 year	1216 8923
Jackel & Poschlod (1994)	calcareous grassland	79 cm^2 funnel traps, 15 replicates	1 year	11786 9634
Jensen (1998)	wet grassland	314 cm^2 funnel traps, 6 replicates	7 months	56926
Kalamees & Zobel (1999)	wooded meadow	226 cm^2 funnel traps, no replicates	6 months	420
present study	floodplain meadow	121 cm^2 box traps, 5 replicates	1 year	7738 51300 3323

Similarity of seed rain and established vegetation

Comparisons between the composition of the established vegetation and the local seed rain (and also the local seed bank) are hampered by the fact that there is no direct link between a plant's abundance in the vegetation and its contribution to the seed rain or seed bank. Seed production of species varies over several orders of magnitude so that a highly abundant plant could in theory produce only few seeds and vice versa. Ideally, seed production of all involved species should be recorded parallel in any seed rain and seed bank study; this was, however, beyond the scope of this study (but see Perttula 1941 for a very thorough community-wide study of this type). It was therefore not surprising that the analysis on the base of abundance data indicated significant differences between seed rain and vegetation at all levels of comparison. This problem does of course not apply when comparing species composition on the base of presence/absence data, which was also done and which resulted in considerably higher similarities. Still, in most cases seed rain samples were found to be more similar to other seed rain samples of the same transect than to the respective vegetation plots. This differs markedly from the findings of Jensen (1998) who observed in a similar habitat and with comparable methodology that seed rain always clustered together with the respective vegetation plots. Jensen concluded that this high similarity, which is also described by other authors (Peart 1989; Poschlod & Jordan 1992), was a result of the very limited dispersal distance which, in turn, is caused by the lack of dispersal vectors other than wind. In the study described here considerable parts of the transects were flooded during winter so that hydrochory can be expected to play an important role during this time. In fact it is the moist and wet communities that showed lower overall similarity. Furthermore parts of the transects were mown during the experiment which may have introduced another vector of dispersal; in the mown Mulgi Heinamaa transect Sørensen similarity was in fact lower than in the other two transects.

Temporal variation of seed rain

Two real and one apparent peak in seed numbers were observed during the one year study period. Part of this variation may stem from the uneven sampling intensity – it had not always been possible to empty the traps at regular intervals due to adverse weather conditions. However, the study of Perttula (1941) confirms many of the observations made about the timing of seed dispersal. *Hypericum maculatum* and *Alnus spp.* for example were found to be largely responsible for the peak in spring which obviously collected all winter dispersed seeds and these species are in fact classified by Perttula as *Winterausstreuer* (species shed in winter). Examples of species shed in mid- to late summer, the second in peak, were *Ranunculus auricomus, R. acris, Rumex acetosa, Geum rivale* or *Carex pallescens*, an observation in agreement with Perttula who lists these species as *Hochsommer-, Spätsommer-* or *Sommer-Herbstausstreuer* (species shed in midsummer, late summer or in summer and autumn). There are only few comparable studies: Rabinowitz (1980) also found two peaks of seed dispersal in a study in a North American tall grass prairie whereas Poschlod & Jordan (1992), Poschlod & Jackel (1993) and Jackel (1999) observed only one peak in midsummer when working in mainly calcareous dry grasslands. The only comparable study in wet meadows by Jensen (1998) also reports only one peak in July and August although species composition and richness of vegetation and seed rain are quite similar to those of this study. Maybe differences in management or climate lead to this different temporal patterns.

Dispersal vectors and other species traits

If seed dispersal would be a random process with all species having an equal chance of being transported and deposited, the seed rain should be a random sample of the local vegetation with respect to species and trait composition. The results of this study, however, suggest that this is not the case. It was generally observed that species that possess some mechanism to enhance dispersal were more abundant in the seed rain than in the established vegetation. The trait spectra and also the trait ordination indicated that wind and also water-dispersed seeds were more prominent in the seed rain whereas the reverse was true for animal-dispersed species and those without apparent dispersal vector. Under the given conditions of an open and frequently flooded grassland this pattern is not surprising as wind and water – universally present throughout most of the year – are probably the most effective dispersal agents. Especially wind dispersal has received considerable attention recently, caused partly by its omnipresence, by its relatively easy parametrisation and by the fact that practically all seeds may be dispersed by wind to some extent (Poschlod et al. 2005). Tackenberg (2001) was able to show that considerable dispersal distances may be achieved, provided the seeds are lifted by convective updrafts (see also Tackenberg et al. 2003b, but see Soons et al. (2004) who rather stress the importance of horizontal wind speed for long-distance dispersal in grasslands). These results are contrary to the common notion based on direct measurements of dispersal, that most seeds will be dispersed only short distances (e.g. Harper 1977; Howe & Smallwood 1982; Willson 1993).

Animal-dispersed species and those without apparent dispersal vectors on the other hand were less abundant in the seed rain than in the established vegetation. Fischer et al. (1996), Kiviniemi (1996) and Stender et al. (1997) studied animal dispersal by domestic cattle and sheep by directly counting seeds attached to fur or hoofs and were able to show that in this way considerable numbers of seeds were dispersed over distances of up to several hundred meters. At present, this dispersal vector probably plays only a minor role in the Soomaa area, as large grazers except for the elk are largely missing. However, in former days the Soomaa floodplain meadows were used for cattle grazing and herds were driven for aftermath grazing even to remote meadows (Allilender & Roosalu 2000) and further on to distant market places. So it may be assumed that in former times this mode of dispersal played some role in community dynamics, even more so as meadows formed more or less continuous bands along most rivers. Animal dispersal may have helped to homogenise the meadow vegetation whereas nowadays meadows are mostly disconnected patches within a matrix of forests, fens and mires (Bonn & Poschlod 1998). Besides this exo-zoochorous dispersal animals may transport seeds by ingesting them and depositing them later together with the dung. It has been repeatedly shown (Bonn & Poschlod 1998) that cattle dung may contain large numbers of viable seeds. Janzen (1984) even argues that this is not a chance event but was actually selected for so that the foliage has the role otherwise played by fruits actively promoting ingestion and dispersal.

There is a small but growing number of studies reporting spectra of dispersal vectors for whole communities. However, to my knowledge there is none that simultaneously studied the established vegetation and seed rain in the way as it was done in this study. Jurko (1987) probably still has the most complete list of (abundance based) dispersal spectra of temperate plant communities. The data are not fully comparable as Jurko listed diplochory and polychory as independent categories without resolving which actual dispersal vectors were involved. His results, however, indicate that *Magnocaricion* communities are generally dominated by wind-dispersed species, followed by diplochorous and hydrochorous species. *Molinietalia* communities on the other hand are mostly characterised by diplochorous, anemochorous and polychorous species. Mesic and dry grassland communities are more heterogeneous in their trait composition but the *Anthoxantho-Agrostietum* (sensu Jurko), which probably comes close to many mesic grasslands in the Soomaa area, is described as being dominated by polychorous and diplochorous species followed by anemochorous and boleochorous species. Two generalisations seem possible: apart from diplo- and polychory, anemochory is the most abundant mode in most grassland types, whereas zoochory, especially in its epizoochorous variant, seldom scores higher than a few percent importance. McIntyre et al. (1995) reported spectra based on species number for Australian temperate grasslands. Here by far the largest group are species with undefined dispersal type, followed by adhesively dispersed, and only then by wind-dispersed species. Dupré & Diekmann (2001) studied Swedish coastal and dry calcareous grasslands and found zoochory and anemochory to be the most common dispersal forms in both grassland types. Schrautzer (2004) lists dispersal spectra based on qualitative data for sociological species groups common in various wet- and grasslands. Species from wetland communities (*Phragmitetea*, *Scheuchzerio-Caricetea* and *Molinietalia*) have a high proportion of hydrochorous (decreasing in above order) and anemochorous species (increasing in above order). Unspecialised species are relatively rare in these groups but common in species groups typical for more disturbed fen sites (*Lolio-Potentillio*, *Artemisietea* and *Molinio-Arrhenatheretea*). In these groups wind and animal-dispersed species are also of considerable importance.

All these studies derived the dispersal spectra from the composition of the established vegetation, mostly with the aim of testing the assumption that the community structure is influenced by the process of seed dispersal. A more straightforward approach would be to calculate dispersal spectra directly from the seed rain composition. This, however, is still rarely done so that no data for direct comparison are available from temperate grasslands. Two studies are available from alpine communities (Ryvarden 1971; Spence 1990) where wind-dispersed species and those with apparent dispersal vector account for the largest part of the local seed rain.

Considering the variation in trait composition found even within one transect the differences between spectra from various sources are not surprising. Furthermore, divergent definitions or conceptions of dispersal vectors (e.g. are all species of the genus *Carex* hydrochorous or only those living in aquatic and semi-aquatic habitats; how are polychorous species treated, etc.) may result in contradicting spectra, especially when communities are rather species poor. Thus, it seems important for future research to rely on a set of agreed trait definitions (e.g. Weiher et al. 1999; Cornelissen et al. 2003) to facilitate comparison between different studies. It also has to be kept in mind that the dispersal spectra reported here are based on morphological clues and do not necessarily accurately reflect the actual dispersal processes. Higgins et al. (2003) even argue that non-standard dispersal, i.e. by other means than by those suggested by obvious morphological adaptations, may be actually be more important for long-distance dispersal events.

Considering other plant and seed traits a number of interesting patterns were found. Seeds in the seed rain tended to be smaller than in the established vegetation. The trade-off between *seed size* and dispersal ability is well established (Rees 1993): heavier seeds will reach higher terminal velocities when falling and thus have smaller chances of being lifted up by small gusts of wind (Tackenberg 2001). *Canopy height* on the other hand showed no differences between seed rain and vegetation (with the obvious exception of the trees *Betula* and *Alnus*, which also have by far the highest seed numbers); although it could be assumed that the height of seed release influences the distance a seed may travel, this is probably of minor importance within herbaceous communities. This observation is confirmed by the modelling approach of Tackenberg (Tackenberg 2001, Tackenberg et al. 2003a), who found seed weight, and thus terminal velocity, to be more important in promoting dispersal ability. Soons et al. (2004), however, report height of seed release to be among the most important factors in determining seed dispersal in grasslands and stress the importance of individual plants extending above the general vegetation canopy. Another trait where the observed differences are easily explained is *seed number*: although the classification used in this study is rather coarse, species with large numbers of seeds are apparently more common in the seed rain than would be expected from the established vegetation. Boedeltje et al. (2003) also found in a seed trap study in a lowland stream that seed production was the best predictor for the variation in the diaspore pool. Partly this pattern is explained by the seed number/seed weight trade-off (Eriksson & Jakobsson 1999; Leishman 2001; Westoby et al. 2002): investment of the plant in larger seeds inevitably means reducing the number of seeds and *vice versa*, so that the greater proportion of many-seeded species follows logically from the dominance of species with low seed weight. Moreover, species with higher numbers of seeds have a higher probability of being trapped so that the detected pattern is partly a sampling effect. On the other hand, producing large quantities of minute seeds may in fact be one of the most effective means of reaching currently unoccupied sites (Thompson et al. 2002). Remarkable differences are also found in the distribution of *types of clonal growth*: while the established vegetation is dominated by plants with strong and moderate clonal growth these types are rather rare in the seed rain which is dominated by species with poor or lacking lateral expansion. Clonal growth and high dispersal ability can probably be interpreted as opposing strategies: at the one end of the spectrum persistence at a given site and population maintenance by means of clonal growth is favoured, at the other end colonisation of new habitats by means of seed dispersal (Jackel & Poschlod 2000; Frey et al. 2001; Maurer et al. 2003). Another variable in the system of interrelated life history traits is seed dormancy and the ability to form a persistent seed bank. Rees (1996) points out that species with the capability of clonal growth tend to have less dormant seeds. This is reflected in this study by the observation that the established vegetation, which was seen to be dominated by species with strong clonal growth, was likewise dominated by species with largely non-dormant seeds.

Drift material and hydrochory

The results of the seed trap study provided little *direct* evidence for the role of hydrochory. Although it is obvious that seeds were deposited in the traps by the river during periods of flooding (a short period in summer at the Mulgi Heinamaa transect and during the spring flood) the design of the traps did not allow for the separation of different dispersal vectors. Two approaches are frequently followed to selectively study the seed dispersal by rivers: the use of specialised traps to sample seeds directly from the flowing water (Bill et al. 1999; Andersson & Nilsson 2002; Boedeltje et al. 2003; Wanner 2003; Vogt et al. 2004), and the sampling of sedimented drift material (Schwabe 1991; Kleinschmidt & Rosenthal 1995; Wanner 2003; Vogt et al. 2004). Employing specialised drift nets was beyond the scope of this study but the results of the rather cursory samples collected in summer 2000 compare well with the thorough study about hydrochorous dispersal done by Wanner (2003) in the same area of Soomaa NP. Wanner both used traps in the river and analysed drift material from the river margins. Naturally, she was able to retrieve larger numbers of species and seeds but the maximum seed numbers per litre drift material are quite comparable to those found in this study (both three to four thousand seeds per litre). Both studies also agree in some of the most common species found in the drift material, namely *Carex* spec. and *Ranunculus repens*. Many other species reported by Wanner (2003) were simply not available at the time the samples were taken, which again stresses the importance of timing and proper location in the case of water dispersal (van Splunder et al. 1995). A result also confirmed by the study of Wanner (2003) is the non-specific nature of water dispersal (see also van der Pijl 1982). Species of all major dispersal types had been found in the drift material while Wanner found no relation between abundance in seed traps or drift material and floating ability. This emphasises again what was said above about the shortcomings of conventional classifications of dispersal vectors: while some vectors can be highly specific (e.g. endozoochory) others may transport seeds whether they have special morphological adaptations or not (e.g. strong wind or running water). A related point that needs to be stressed is the fact that, while dispersal is generally seen as a positive force connecting species and habitats, there is also the possibility that seeds are removed from the system and deposited at entirely unsuitable sites. Seeds landing on the surface of a river running in its normal bed may be transported over long distances but the chance that they reach a favourable site may be rather small. It has in fact been shown, at least for fragmented dry grassland communities, that selection may favour traits enhancing persistence rather than dispersal (Jackel & Poschlod 2000; Maurer et al. 2003).

4.3 Seed sowing experiment

General results of seed sowing studies

A growing number of studies have investigated seed germination behaviour under the field conditions of grass- and wetlands. Some of these studies are concerned with the germination behaviour of single, often endangered species (e.g. COLLING et al. 2002; OVERBECK et al. 2003). A number of studies approach more conceptual questions of community dynamics, community invasibility or seed vs. microsite limitation (e.g. TILMAN 1997; KOTOROVÁ & LEPŠ 1999; KŘENOVÁ & LEPŠ 1996; KUPFERSCHMID et al. 2000; TURNBULL et al. 2000; FRANZÉN 2001), whereas other studies examine aspects of habitat restoration or diversification (e.g. PATZELT et al. 1997; BUDELSKY & GALATOWITSCH 1999; COLLING et al. 2002; ISSELSTEIN et al. 2002; HÖLZEL & OTTE 2004; Lindborg 2005; see also Table D.22).

The absolute emergence rates observed in this study (Table D.10) agree well with those found in other seed sowing studies conducted in semi-natural grasslands; in most cases maximum germination rates range from 25 to 50 % (MAAS 1988; THOMPSON & BASTER 1992; ŠPACKOVÁ et al. 1998; KIVINIEMI 1999; KOTOROVÁ & LEPŠ 1999; JAKOBSSON & ERIKSSON 2000; ISSELSTEIN et al. 2002) while in this study values range roughly from 20 to 40 %. In contrast to these field studies greenhouse or incubator studies generally achieve much higher germination rates of up to 100% (GRIME et al. 1981; GROSS 1984). The reasons why over half of the seeds in field experiments generally fail to germinate may be various. If it can be assumed that all sown seeds were viable at the outset of the study (viability had not been tested in the lab but had been assessed visually and manually) then the most likely explanation is that the conditions of the experimental plots were not sufficient for breaking the dormancy (FENNER & THOMPSON 2005). Seed predation may be another major 'bottleneck' in seedling recruitment (JONGEJANS et al. 2006, see also EHRLÉN & ERIKSSON). A third reason for failed germination are fungal pathogens (SCHAFER & KOTANEN 2004); these are mainly debated in the context of mortality of buried seeds but fungal infection was observed especially in *Thalictrum lucidum* in a large fraction of the collected seeds. HARPER (1977) stressed the fact that at the scale of a seed the environment is extremely heterogeneous and even a worm cast or fallen leaf can influence the fate of a seed. At one experimental site leaves from nearby trees tended to accumulate especially in the artificial gaps so that seedling emergence was strongly impaired.

MEIER (2000) conducted studies on the population biology of *Scorzonera humilis* in Soomaa NP and found germination rates in the laboratory of 51–92 %. COLLING et al. (2002) studied germination and establishment of *S. humilis* in several *Calthion* and *Molinion* meadows of Belgium and Luxembourg and observed average germination rates in mown but otherwise undisturbed sites of 24.8 %; both of this is higher than in the experiment described here including the treatment with vegetation completely removed which generally lead to highest germination rates. In *Scorzonera*, however, it was especially difficult to collect enough viable seeds as these were heavily infested by seed eating parasites (Meier 2000).

Iris sibirica showed a peculiar germination behaviour: although the species and the closely related *I. pseudacorus* are not known to form a short- or long-term persistent seed bank (Thompson et al. 1997) germination took place over a prolonged period of at least two years, i.e. rate of establishment after three years was found to be higher than rate of emergence after one year. In all other species studied it can be assumed from the observed decline in seedling numbers that all germination, if any, took place in the first year after sowing. Dymes (1920) describes a similar behaviour for *I. pseudacorus* where 20 % of the seeds germinate in the second year after shedding. The basis of this behaviour may be maternal effects on the ripening seed which finally lead to differences in the strength of dormancy (Gutterman 1992). Generally *Iris sibirica* and *I. pseudacorus* are known to exhibit very low overall germination rates (Falinska 1986; Sutherland 1990; Bylebyl 2002).

Why *Carex flava* performed so badly in germination and establishment in the field remains unclear as there may be several reasons: the sample of seeds chosen for sowing may have been accidentally of low quality although this seems unlikely since seeds were collected from several large populations and mixed before sowing. It is more likely that the conditions in the experimental gaps were not suitable for germination so that they didn't constitute a ‘safe site’ for this species. As was already noted above, species of the genus *Carex* are known to have quite distinct germination requirements including cold stratification and fluctuating temperatures with a relatively high absolute temperature level (Grime et al. 1981; Schütz 2000). Experimental gaps were relatively small so that it seems possible that due to overriding edge effects gaps were not enough ‘gap-like’ and e.g. temperature fluctuation were dampened so much as to be ineffective for this species. It is interesting to note that *Carex flava* was among the most abundant species to germinate in the experimentally disturbed plots (Table D.13), although it emerged almost entirely from the seed bank. These experimental plots were larger (50 × 50 cm) and only the central part of it was sampled so that the conditions may have been more ‘gap-like’ there. Maas (1988) describes a similar seed sowing experiment in fen meadows where two *Carex* species, among them *C. flava*, exhibited similarly poor regeneration, however he doesn't comment on possible reasons. Also Schmid (1984) reports very restricted germination rates in species of the *Carex flava*-group. Grime et al. (1981) on the other hand found weak primary dormancy and high germination rates in *Carex pulicaris* which agrees with the findings of this study. According to Schütz (2000) many Carices show high levels of primary dormancy which results in extremely low germination rates but which also is the reason why many Carices form long-term persistent seed banks. Another reason for failed germination in Carices is suggested by Budelsky & Galatowitsch (1999). They found that dry storage of seeds may considerably reduce germinability in several species of *Carex* and recommend wet-cold storage to maintain the viability of *Carex* seeds. Seeds for this study were collected in 1998 and were stored dry at room temperature so that they may have already lost their viability. More detailed laboratory studies are needed to establish whether this mechanism also applies to *Carex flava*.

Studies with a comparable scope and with partly identical species were done by Špacková et al. (1998) and Kotorová & Lepš (1999). They found maximum germination rates for *Lychnis* of ca 40 % (24.3 ±17.4), for *Betonica* of ca 30 % (30.1 ± 12.9) and for *Selinum* of ca 30 % (38.6 ± 16.8; values in brackets are own results, mean percentage ± 1 SD). For *Trollius europaeus*, *Thalictrum lucidum* and *Veronica longifolia* there are no such comparable studies or information available.

Table D.22: Selection of seed sowing studies in temperate grasslands.

Source	Habitat	Species	Results
Colling et al. (2002)	Molinion and Calthion grasslands	*Scorzonera humilis*	germination and survival positively correlated with soil moisture and negatively with productivity; population ageing due to lack of recruitment
Franzén (2001)	dry–mesic grassland	*Anth. vuln., Cent. jac., Filip. ulm., Prim. ver., Dianth. delt., Hypoch. mac., Trif. aur., Succ. prat.* in different combinations	recruitment higher in more species-rich mixtures and lower in plots with higher ramet density
Isselstein et al. (2002)	fen meadow & species-poor rush-pasture	*Carex ovalis, Cirsium dissectum, Molinia caerulea, Succisa pratensis, Holcus lanatus*	better germination & establishment in fen meadow, soil disturb. most important for germination, canopy removal most important for establishment
Jakobsson & Eriksson (2000)	mesic (?) semi-natural grassland	50 species of semi-natural grasslands	significant positive effects of gaps in 16 species, recruitment success positively related to seed size, all germinating species seed-limited
Jones & Hayes (1999)	species poor mesic grassland with different management	*Achill. mill., Cent. jac., Plant. lanc., Prun. vulg., Stach. off.* (local and non-local provenance)	best establishment in unfertilised sward, local seeds perform in some cases better
Kiviniemi (1999)	mesic road verges, gap treatment	17 species of semi-natural grasslands	better germination and recruitment in gaps
Kotorová & Lepš (1999)	species-rich Molinion meadow with different gap types	*Ach. ptarm., Ang. syl., Bet. off., Car. hart., Car. pall., Cirs. palu., Hier. umb., Lych. flo., Lys. vulg., Sang. off., Seli. var., Succ. prat.*	better recruitment in more open gaps, gap effects decrease with seed weight, germination strongly density dependent
Křenová & Lepš (1996)	oligotrophic wet meadow with different disturbance treatments	*Gentiana pneumonanthe*	highest germination in open gaps, lowest in closed vegetation; recruitment only in open gaps
Kupferschmid et al. (2000)	dry abandoned grassland with different management and gap types	32 species of Southern Prealp grasslands	better germination in gaps and managed plots, established vegetation reduced germination but in some cases improved survival
Lindborg (2005)	four grassland types of different management history (ex-arable, semi-natural, abandoned)	six target species (grazing indicators) and six generalist species (indicators of ceased grazing)	better germination in grazed than abandoned grassland, target species with better germination in semi-natural grasslands, germination density dependent

Source	Habitat	Species	Results
Maas (1988)	two fen meadows of different management intensity plus cutting treatment	*Primula farinosa, Pinguicula vulgaris, Schoenus ferrugineus, Carex flava, Carex panicea, Molinia caerulea*	better germination in cut plots, non-clonal plants with higher germination, rate of establishment generally low
Overbeck et al. (2003)	mown and abandoned fen meadow with gap treatment	*Succisella inflexa*	lower germination rates in abandoned meadow, positive effects of gaps and negative effects of litter on germination, partial positive effects of mosses on survival
Petrů & Lepš	wet/fen meadow with different gap types	*Pedicularis palustris, P. sylvatica*	better germination in gaps
Špacková et al. (1998)	species rich Molinion meadow, with disturbance treatments	*Selinum carvifolia*	best germination in plots with vegetation completely removed and with mosses removed
Thompson & Baster (1992)	mesic grassland	ten Umbelliferae (*Anthriscus sylvestris, Daucus carota, Heracleum sphondyleum*, etc.)	germination in undisturbed sward, only four species established after three years

Effects of gaps and litter & moss removal on seedling emergence and establishment

Fenner (1978) suggested that probably "no seed of any species can establish in a completely closed turf". It may be questionable whether this statements holds true in this absolute form as there is probably no such thing as a "completely closed turf" in reality. All natural communities are subject to some kind of disturbance at some spatial scale and exhibit spatial heterogeneity at all scales (Sousa 1984). However, a large number of seed sowing studies including this one have demonstrated the negative effect of established vegetation and litter on the germination of seeds and enhanced germination rates in artificially created gaps (Maas 1988; Špacková et al. 1998; Kiviniemi 1999; Kotorová & Lepš 1999; Kupferschmid et al. 2000; Petrů & Lepš 2000; Isselstein et al. 2002; Jensen & Gutekunst 2003; Overbeck et al. 2003). Established vegetation shades seeds and seedlings which develop under its cover, it changes the spectral composition of the passing light, and dampens fluctuations in temperature. All these effects may prevent seeds from germinating or seedlings from establishing. Thus, it is not surprising that all of the studied species emerged best in the completely open gaps, followed by plots with litter & mosses removed while emergence in established vegetation was always lowest. Nevertheless, there were differences between species in their reaction to treatments. For example, *Betonica officinalis* performs comparatively well in all three treatments and emergence is reduced in closed vegetation – compared to open gaps – only by ca. 50 %. *Selinum carvifolia* and *Lychnis flos-cuculi*, which perform both comparatively well in open gaps and treatments with mosses & litter removed are reduced by 80 and 95 % respectively in closed vegetation. In the study of Jensen & Gutekunst (2003), *Lychnis flos-cuculi* showed absolutely no germination under litter layers of different thickness. Kotorová & Lepš (1999), who studied a similar set of species under comparable conditions found the same strong reduction in emergence in closed vegetation, however in their study *Betonica officinalis* and also *Selinum carvifolia* had, like all other species, emergence rates well below 5 %. The reasons why *Betonica* performed so well in this experiment may be various: subtle differences in environmental conditions during seed ripening or germination can have pronounced effects on dormancy and dormancy breaking (Baskin & Baskin 1988; Schütz 2000). Kotorová & Lepš (1999) found differences of up to 100 % between years for germination rates of *Selinum carvifolia* under identical experimental conditions, a result which may stand as a warning to cautiously interpret field studies like this one.

Published results on the role of a moss layer on seed germination are ambiguous: the effects may be both positive or negative. In dry grasslands effects tend to be rather positive as the moss layer may protect seeds and seedlings from desiccation (During & van Tooren 1990; Ryser 1990). Another positive effect may be protection from seed predators (van Tooren 1988). In mesic to wet grasslands, where desiccation is less of a problem at least in parts of the year a moss layer more likely has negative effects on seed germination. It may prevent seeds from reaching the soil surface; especially smaller seeds with little resources will fail to produce a long enough root to get into contact with the soil and and thus secure water uptake (Harper 1977). In addition to this, the same detrimental effects described for a closed vegetation canopy (i.e. shading, altered red/far-red ratio of light) also apply for a moss layer. It is therefore not surprising that germination was generally lower in the plots where litter and mosses were removed than in the completely open plots.

Survival and establishment are distinct processes that may or may not be correlated with germination. Conditions that were favourable at the time of germination may have changed or may not be suitable for the establishing plant. On the other hand conditions that were not optimal for germination may turn out to be more favourable for establishment and further growth. This seems to be the case in several of the species in this experiment. It was observed in *Iris sibirica*, *Selinum carvifolia* and *Thalictrum lucidum* that survival rate was highest (differences were, however, not significant) in the plots with mosses & litter removed whereas germination rate was, as with all other species, highest in open gaps. Although absolute rate of establishment was still higher in open gaps, those seeds that did germinate under semi-open conditions obviously had better chances of survival. This discrepancy may be explained by assuming that the established vegetation (minus litter & mosses) provides some sort of protection or niche that only becomes relevant once a seed has germinated. Besides the negative impacts of competition for space and light, neighbouring plants may offer protection against desiccation, frost or mechanical damage by water or ice. Similar observations were made by Kupferschmid (2000) where low germination but high survival rates were found in tussocks of *Molinia arundinacea*.

Seed vs. microsite limitation

The question, which factors ultimately determine the distribution of plant species has been framed in the concept of "seed vs. microsite limitation" (e.g. Eriksson & Ehrlén 1992). The concept states that the distribution of populations may either be limited by the availability of suitable microsites for germination and establishment, or by the availability of seeds. These two alternatives are not thought to be mutually exclusive but can rather be seen as the two extremes of a continuum. In the case of microsite limitation, alteration of habitat conditions (e.g. by disturbance or management) should enable or promote establishment in contrast to unaltered conditions. On the other hand, seed limited species should be able to germinate and establish at a suitable site if seeds are added. The results of this study, although not specifically aimed at unambiguously answering this question, suggest that the studied species are to different degrees either seed or microsite limited (or both). *Betonica officinalis* and *Selinum carvifolia* e.g. were both able to germinate and survive even in the undisturbed sward of the floodplain meadows. This implies that these species should be able to colonise similar but unoccupied sites, if they were able to reach them by seed. This can be seen as an indication of seed limitation. Other species like *Lychnis flos-cuculi*, *Scorzonera humilis* and *Veronica longifolia* were only able to germinate and establish when the established vegetation was disturbed or completely removed. This suggests that, even if seeds of these species were present they would not be able to recruit as long as the appropriate microsite is lacking. Note, however, that more focused experiments like adding seeds to existing populations would be necessary to clearly establish what limits the distribution of these species. It must also be taken into account that other factors like herbivory (slug herbivory: see Overbeck et al. 2003) and unpredictable climatic effects may have influenced the outcome of the sowing experiments.

Effects of seed size on seedling emergence and establishment

It is generally acknowledged that seed size is linked to a number of other life history features such as seed number, seed dispersal and seed germination and establishment. It is both theoretically plausible and empirically proven in a number of studies that larger seed size is advantageous for establishment success, especially in shaded situations or when the seedling has to cope with layers of litter (Gross 1984; Westoby et al. 1996; Turnbull et al. 1999; Westoby et al. 2002). In this study maximum establishment and survival rate were indeed found to be positively correlated with seed weight, whereas emergence was probably slightly negatively related. The positive relation of seed size and establishment success can probably be attributed to a 'reserve effect' (Westoby et al. 1996) where larger amounts of nutrients stored in the seed enable the seedling to better cope with hazards like shade, drought or damage.

In in greenhouse study with a large number of fen meadow species Jensen & Gutekunst (2003) reported a significant positive relation between seed size and germination in the presence of litter. Likewise, Kotorová & Lepš (1999) found larger-seeded species to perform better under competitive conditions of oligotrophic wet meadows, similar results were reported by Jakobsson & Eriksson (2000). The experiment presented here was not able to reproduce this relation; however, sample size of species was probably too small so that random effects masked this pattern. Schütz (2000) mentions a critical value of ca. 1 mg seed weight for successful establishment in undisturbed vegetation. This is insofar supported by this study that all species that do show substantial emergence or establishment in the undisturbed plots have seeds of around 1 mg or larger, although there were larger-seeded species that did not perform well in closed vegetation. Shipley & Parent (1991) on the other couldn't find any association between seed size and three germination attributes among 64 wetland species, although Shipley et al. (1989) had found such associations; they attribute this to the fact that annuals – which were not present in the 1989 study – often have smaller seeds and germinate more vigourously and so may confound the effect of seed size alone.

Grime et al. (1981) report in their extensive comparative study on germination characteristics a decline of germination rate with increasing seed weight. This supports the trend observed in this study which, however, was not strong enough to be statistically validated. Why smaller seeds should have larger initial germination rates is less well understood than the positive relation of seed size and establishment. It may have to do with the generally more opportunistic life strategy of small seeded species which is a result of the well known seed size–seed number trade-off (Westoby et al. 2002). Moles & Westoby (2004) stress the point that while large-seeded species may gain a short-term competitive advantage over smaller-seeded species this does not necessarily counterbalance the advantage gained by smaller-seeded species by the larger number of seeds. It must, however, be noted that the results of Grime et al. (1981) stem from controlled laboratory studies and may be not directly comparable with the results presented here.

Implications for habitat restoration and management

As a consequence of the ongoing fragmentation of European semi-natural habitats, dispersal processes that once connected different sites are becoming increasingly disrupted (Poschlod & Bonn 1998). Once a species is locally extinct and there is no seed bank from which it could recover, chances are very low that it will re-colonise the site, even if habitat conditions are optimal (e.g. Bischoff 2002). Therefore, deliberate introduction of species by seed sowing is discussed in the conservation literature as a measure to increase the floristic diversity of species-poor grasslands or to completely re-create grasslands e.g. on formerly arable land (e.g. Manchester et al. 1998, Benstead et al. 1997, Jones & Hayes 1999, Walker et al. 2004).

The results of this study confirm that seed sowing may be a feasible method to (re-)introduce target species into impoverished grasslands: typical species of wet grasslands were able to establish in the existing sward, provided that they were sown into gaps, which most species seem to require. It must, however, be noted that this study was not able to prove the long-term establishment of the sown species; when visiting some of the experimental sites after 5 years it was in most cases not possible to locate the experimental plots which were completely overgrown by clonal species. Whether any of the sown species had successfully established at that time is not clear, at least no flowering individuals were seen, but it seems evident that gap size has to be sufficiently large to guarantee conditions of low competition for seedlings to firmly establish (see also Bullock et al. 1995).

Important issues that need to be considered are the seed source and the method of seed introduction. If the focus is on (re-)creating species rich grassland ‘from scratch', it is probably more practicable to use hay collected from nearby species rich sites as seed source and spread it on the target site. On highly productive ex-arable sites it may be necessary to remove the topsoil. Using this method, PATZELT et al. (1997) and HÖLZEL & OTTE (2003) were able to re-establish species rich fen- or floodplain meadows. When the aim, on the other hand, is the (re-)introduction of certain target species, then the selective sowing of pure seeds or even planting of pot-grown plants is more appropriate (MAAS 1988, BENSTEAD et al. 1997, JONES & HAYES 1999, DAVIES 2002). It is generally advised to use seeds from local stock as these are supposed to be better adapted to the local conditions (LIPPITT et al. 1994) and to prevent genetical 'contamination' of local populations.

Even if seeds have not to be introduced but sites are managed conventionally for conservation, the results of this study suggest that regeneration from seed is of great importance for the maintenance of many species of floodplain meadows. To enhance opportunities for germination and establishment it should be considered to deliberately create small-scale disturbances or gaps in the established sward. As mentioned above, size is an important issue here: gaps have to be large enough to allow firm establishment, but not too large so that the sward might get damaged in the next flooding season. Both livestock grazing and mowing machinery may help in providing these gaps (COULSON et al. 2001).

4.4 Disturbance and regeneration

In addition to the seed sowing experiment, establishment in vegetation gaps was also approached in a second experiment: the spontaneous seedling flora was monitored in artificial gaps that allowed either seed rain, seed bank or both to act as source of colonisation. This was achieved by seed exclosures and replacement of top soil. While these methods offered a relatively convenient way of addressing this topic they are subject to a number of imponderables. The use of seed exclosures will probably alter the micro-environmental conditions like temperature and its fluctuations, and humidity. This in turn may have implications for seed germination and seedling survival. In fact, seedlings under the exclosure, i.e. those stemming entirely from the seed bank, often grew rather vigourous which may be attributed to reduced desiccation stress. The exchange of topsoil with soil from lower horizons was used to obtain a seed bank-free substrate for establishment from the seed rain. It was assumed that at the same time soil chemical and physical properties would remain relatively unaltered and be comparable between the different treatments. Although every care was taken to separate the two soil horizons during the preparation of the plots small contamination of the seed-free horizon by topsoil cannot be completely ruled out. There may have also been slight differences in soil properties between top- and deeper soil layers: the deeper horizon sometimes was somewhat more sandy in texture and seemed to have a lower organic content. There was, however, no possibility to test for these differences in the laboratory but Pakeman et al. (1998) found no significant differences between soil horizons in a similar experiment.

Seed rain

The size and role of the seed rain in temperate grasslands was already discussed in the preceding chapters. Using seed traps seed densities of several thousand up to several ten thousand seeds per m^2 are commonly found (see Table D.21 on page 135 for an overview) whereas in this experiment mean values where in the range of a few hundred only. Still the seed rain accounted for 20–25 % of the total seedling community. Several reasons may account for this much lower estimates: one important factor is probably seed predation by rodents and arthropods and early seedling abortion. Another reason may be that many seeds failed to germinate and thus escaped sampling. Conditions may simply have not been favourable for germination, but more important for many species that dispersed in early or mid summer was probably the lacking cold stratification so that they remained dormant. At least in the case of *Deschampsia cespitosa* – the most abundant species in the seed rain plots – it can be assumed that the seeds were still dispersed in autumn directly after the experimental plots were installed: in the seed trap study this species was found to disperse till very late in the year. In a similar experiment conducted in Swedish semi-natural wet grasslands Milberg (1993) found only a few seedlings of *Taraxacum officinale* in the seed rain plots; the reason for this nearly complete failure to detect species in the seed rain is probably that Milberg established the experimental plots in spring so that only early flowering and dispersing species had a chance to germinate in the disturbed plots; furthermore, seedlings were monitored for only three months. Many species that were dormant during the study period were probably missed. Pakeman et al. (1998) on the other hand, in a study in acidic grasslands, detected with the same methodology a rich seed rain which accounted for ca. 40 % of the developing plant cover; in this case, however, establishment was monitored over an entire year. Another important source of colonisation in this study were rabbit pellets, that accounted for another 15 % of the seedling assemblages. It seems unlikely that this type of zoochory plays a comparable role in the Soomaa grasslands. A third study using top soil replacement and disturbance treatments to monitor the seed rain and seed bank was done by Edwards & Crawley (1999) in species-poor acidic grassland. In contrast to all other mentioned studies, there the seed rain was by far the dominating source of colonisation (ca. 700 seedlings per m^2), while practically no seedlings emerged from the seed bank. The authors monitored the plots for 22 months after the creation in May; disturbance in the 'seed bank + seed rain' treatment, however, was only slight so that many seeds may have not been able to germinate. The very different outcome of these otherwise similar experiments demonstrates the importance of the exact timing and type of disturbance for the success or failure of seed dispersal (in space and time) and subsequent establishment.

The composition of the seed rain as it appeared in this disturbance experiment differed quite significantly from that derived from seed traps. Apart from being much poorer in species it lacked even species that were highly abundant in the seed traps such as e.g. *Filipendula ulmaria*. One reason for the different species composition may be that the seed traps where directly placed within the undisturbed vegetation and thus even seeds with poor dispersal capacity were easily trapped. To reach the experimental gaps seeds had to bridge a distance of up to 0.5 m which probably was already to much for many seeds.

Seed bank

The seed bank of temperate grasslands is an intensively studied subject: a large number of field studies have shown that grasslands may have a large persistent seed bank although the similarity to the established vegetation is often low (Thompson 2000). Furthermore many of the abundant species are often ruderals or belong to different successional stages (Bekker 1998). However, most of these studies use greenhouse methods to assess the total seed content of soil samples. While this type of study is able to give a fairly precise estimate of the total soil content of viable seeds it does not address the question under what conditions this seed bank will recruit into the established vegetation. Thompson (2000) cautions that "the apparent presence of a seed bank does not guarantee that it plays much part in regeneration". The actual contribution of the seed bank to the colonisation of bare soil is treated in only a few studies by monitoring the recolonisation of deliberately disturbed experimental plots (Eriksson & Eriksson 1997; Edwards & Crawley 1999; Kalamees & Zobel 2002; Touzard et al. 2002; Amiaud & Touzard 2004).

Studies in wet grasslands using greenhouse or comparable methods commonly describe seed densities in the range of 10 000 to 80 000 seeds/m² (Fischer 1987; Drückhammer & Wriedt 1996; Jensen 1998; Jutila 2002). Wagner (2003) e.g. studied the seed bank of two floodplain meadows of the Soomaa area using the improved method of ter Heerdt et al. (1996). In total he was able to retrieve ca. 53 species with an average of 14 000 seeds and approximately 10–17 species per m². Considering the different methodology it is surprising that the mean number of species found in each seed bank sample is quite comparable to the numbers presented here (14.1 ± 3.4 species/m²). Obviously the estimates of species numbers are of the correct order of magnitude. The seedling densities reported in this study are on the other hand more in line with other studies using in situ germination experiments like those by Milberg (1993), Pakeman et al. (1998) and Edwards & Crawley (1999) who found densities of a few hundred to a few thousand seeds per m². As for the seed rain the reasons for the much lower densities are probably failure to germinate under the experimental conditions and premature death prior to sampling.

One factor which is often considered to influence the seed bank composition and size is soil type and especially soil water content. In this study it was found the the seed bank of moist sites was considerably more rich in species and seeds than that of the dry sites. This observation is supported e.g. by the findings of FISCHER (1987) who studied the seed bank of moist, mesic and dry grasslands in Central Germany. He found that the seed bank of the *Molinietalia* meadow was – with ca. 70000 seeds per m^2 – by far richer in seeds than the *Arrhenatheretum* (<10000 seeds/m^2) or *Gentiano-Koelerietum* meadow (ca. 5000 seeds/m^2). HÖLZEL & OTTE (2001) also found much higher seed densities with longer flood duration in a study of flood-meadows along the Upper Rhine. An explanation often discussed for this difference is the anoxic condition of moist and waterlogged soils (BEKKER et al. 1998), which are thought to reduce seed ageing. While the studied Soomaa meadows are in fact regularly flooded they also experience extended periods of desiccation of the upper soil horizons; it was mostly these soil layers that where disturbed in this experiment. It therefore seems unlikely that soil conditions are responsible for the observed differences in seed density. HÖLZEL & OTTE (2001) concluded that differences are due to shifts in the dominant plant strategies that go along with changes in habitat conditions.

A common feature of most studies in wet grasslands is the extremely large number of *Juncus* seedlings found in those seed banks (FISCHER 1987; DRÜCKHAMMER & WRIEDT 1996; JENSEN 1998; FALINSKA 1999; BEKKER et al. 2000; WAGNER et al. 2003), even when rushes are absent from the established vegetation (FISCHER 1987). With its large numbers of small seeds *Juncus* is a typical candidate for a long term persistent seed bank. It is therefore surprising that in the current study *Juncus* was completely lacking from the seed bank although it was present in the vegetation (*J. effusus*, *J. filiformis*). Also in the seed trap study it was the most abundant genus. The reasons for this absence of *Juncus* in the seed bank are unclear. Either conditions for germination were unfavourable in the experimental plots (which seems unlikely) or *Juncus* is in fact absent in this rather stable grasslands with a long and undisrupted history of management (RICE 1989). In WAGNER's study (WAGNER et al. 2003) *Juncus* was also missing from the seed bank of the plot still under management.

Table D.23: Selection of studies on seed banks and gap regeneration in temperate grasslands.

Source	Habitat	Procedure	Results
Amiaud & Touzard (2004)	grazed marsh wetlands and oldfield	a) seed bank sampling, b) recolonisation of 2500 cm^2 gaps	>20000 seeds m^{-2} in seed bank, little similarity between seed bank & vegetation; recolonisation of gaps mainly vegetatively
Bullock et al. (1995)	species-poor fertile pasture	plots with grazing treatment and 3, 6 and 9 cm diameter gaps	up to 17000 ramets m^{-2}, 59 % of establishing ramets from seed, small gaps filling fastest
Edwards & Crawley (1999)	species-poor acidic grassland	gap (225 cm^2) recolonisation from seed bank and seed rain	only few species in seed bank, recolonisation mainly from local seed rain
Eriksson & Eriksson (1997)	4 pastures with different management history	a) seed bank sampling, b) recolonisation of 400 cm^2 gaps	little similarity between seed bank & vegetation, seedling recruitment enhanced by disturbance
Jensen (1998)	abandoned Calthion meadows of different successional stages	a) seed bank sampling, b) seed traps	a) wet grassland species in seed bank decreasing rapidly during succession, little prospect for restoration; b) seed rain exclusively of local origin, important for succession but little prospect for restoration
Jutila (2003)	coastal wetland meadows	undisturbed plots (400 cm^2) in grazed and ungrazed sites, comparison with seed bank and vegetation	total of 44 species with ~4 species per plot and ~1500 seedling m^{-2}, poorer in grazed plots; seedling assemblages more similar to vegetation than to seed bank
Kalamees & Zobel (2002)	calcareous grassland	gap (100 cm^2) recolonisation from seed bank, seed rain & clonal growth	84 species from seed, 5.4 seedlings per plot from seed bank, 4.1 from local and 2.7 from longer distance seed rain, 2.7 clonal shoots per gap
Milberg (1993)	semi-natural flood grassland	a) seed bank sampling, b) gap (2500 cm^2) recolonisation from seed bank and seed rain	up to ~7000 seeds and 17 species in seed bank; gap recolonisation mainly from seed bank but generally poor
Pakeman et al. (1998)	species-poor acidic grassland	gap (2500 cm^2) recolonisation from seed bank, seed rain and rabbit pellets	44 species from seed; 45 % cover from seed bank, 40 % from seed rain, 15 % from rabbit pellets
Touzard et al. (2002)	eutrophic alluvial wetland	a) seed bank sampling, b) recolonisation of 1 m^2 herbicide gaps	up to 19000 seeds m^{-2} in seed bank, little similarity between seed bank & vegetation; recolonisation of gaps also from seed bank

Also other ruderal species like *Gnaphalium uliginosum*, *Poa trivialis*, *Polygonum* or *Sagina*, which make up a considerable part of the seed bank (when omitting the omnipresent *Juncus*) in the studies e.g. of Fischer (1987), Jensen (1998) or Wagner (2003) were conspicuously absent from the disturbed plots of this study. Hölzel & Otte (2001) report a similar observation from their study of floodplain meadows: weedy and ruderal species were mostly absent from the samples from the functional floodplain. On the other hand most of the dominant species like *Ranunculus repens* or *Lychnis flos-cuculi* and many species of the genus *Carex* are known to form persistent seed banks and are commonly found in the seed bank of similar wet grasslands (Jensen 1998; Touzard et al. 2002; Wagner et al. 2003; Schrautzer 2004). There were, however, also species in the seed bank plots that are classified as short term persistent or even transient (*Ranunculus auricomus, R. acris, Alchemilla vulgaris*), although classifications are often equivocal. The presence of species that should not be able to form a persistent seed bank may on the one hand be due to contaminations which entered during the installation of the plots or during the following months; the second possibility can large be ruled out as the patterns were very obvious in the case were it indeed had happened. On the other hand, seedlings largely originated from the upper few centimetres of the soil where it is most likely to find seeds with with a low longevity.

The results of seed bank studies in grasslands commonly lead to the conclusion that the seed bank is not able to help in restoring species to the established vegetation once they are lost from the community (Milberg 1995; Jensen 1998; Hölzel & Otte 2001; Wagner et al. 2003). Most typical grassland species of high conservation value have only a short term persistent seed bank and the abundance of weedy and ruderal species in the seed banks of impoverished wet grasslands hampers the establishment of desired species (Drückhammer & Wriedt 1996). In focusing on the species that actually recruit in plots of open soil this study, however, suggests that the seed bank may indeed play an important role in community dynamics of species-rich semi-natural grasslands. Smaller disturbances are most likely re-colonised quickly by vegetative means from the surrounding vegetation (Bullock et al. 1995) but larger gaps are obviously filled to a considerable degree from the seed bank and seed rain. The study described here makes it possible to estimate the relative contribution of both components: it appears that the seed bank accounts for 70–80 % and the seed rain for 20–30 % of the seedling assemblages. In the moist sampling plots the seed bank was slightly more important than in the dry plots. This corresponds to the general observation of larger seed banks in wet habitats (Harper 1977); waterlogged, anoxic conditions in themselves favour the preservation of seeds, but also many typical wetland plants (like *Juncus* spp.) produce very high numbers of seeds. Kalamees & Zobel (2002) conducted a similar experiment in calcareous grassland which also confirms this general observation: in their case of mesic grassland seed rain contributed most to the colonists (46 %), followed by seed bank (36 %) and clonal growth (18 %). Milberg (1993) on the other hand found in a study of wet lake-side grassland that most seedlings originated from the seed bank (~60 %) while 40 % originated from the seed rain. In this study, however, seedlings covered after three months only around 1 % of the disturbed ground while vegetative re-growth clearly dominated the patch.

Species traits

The trait composition of the seed rain were already discussed in the seed trap study so that here a short comment will suffice. There, it was found that the seed rain consisted mostly of wind-dispersed species with large numbers of small seeds and a lack of strong lateral expansion. The established vegetation on the other hand was dominated by species with heavier but fewer seeds with the ability of strong lateral expansion. In the seed rain plots, the most abundant species – *Deschampsia cespitosa* – is classified as animal-dispersed and the few other abundant species are from all major dispersal types. However, due to the small number of species that developed in these plots the dispersal spectra cannot be expected to be very informative. During the long period of exposure in autumn and winter and spring wind, rain, snow and flood water may have transported any seeds regardless of their dispersal mode (SKOGLUND 1990). Moreover, all the abundant species were also frequent and abundant in the surrounding vegetation so that this is probably the overriding factor rather than certain traits.

Seed bank data with their larger overall species numbers are probably better suited to analyse the trait composition. Some of the results of the ordination analysis are well supported by ecological theory and field evidence. The dominance of forbs in seed banks is also reported in the studies by WAGNER (2003) or JUTILA (2003) and in the review by RICE (1989). A common explanation for this patterns is the fact that in perennial grasslands ruderal species, which usually are numerous in seed banks, tend to be forbs. This was also demonstrated by the PCA, as species with a ruderal component in their life strategy (strategies CR and CSR) were largely confined to the seed bank whereas the established vegetation was dominated by competitive species (strategy C). The result that species in the seed bank tend to have smaller seed numbers is rather surprising: common observation suggests that smaller seeds are more likely to persist in the seed bank (THOMPSON 2000) and the well-known trade-off predicts that smaller seeds come in larger numbers (WESTOBY et al. 2002). Another trade-off, however, is confirmed by this study: theory predicts that dispersal in space and persistence are opposing strategies (THOMPSON 2000) so that 'good dispersers' cannot be 'good persisters' at the same time. Accordingly it was observed that species in the seed bank tend to have no special adaptations for dispersal whereas the seed rain was found to be dominated by wind and water-dispersed species.

4.5 Plant traits

Intercorrelation of traits

The role of plant traits in the context of seed dispersal and gap colonisation has already been discussed in the preceding chapters. This section approaches the question how traits are correlated, whether they allow the classification of species into functional groups and how these group are distributed in the plant communities.

Correlations among traits may arise for different reasons. Some trait combinations are impossible for obvious bio-physical or morphological reasons: tiny herbaceous species can hardly produce acorn-sized seeds so that, at least at the ends of the trait spectra, seed size and growth height can be expected to be correlated. Other trait combinations are governed by trade-offs, when investment in one morphological or physiological structure reduces the available resources for other structures. A well-known example for this, which was also established in this study, is the seed size (or mass)–seed number trade-off (Crawley 1997; Jakobsson & Eriksson 2000; Westoby et al. 2002). Producing a larger number of seeds with a given amount of resources means reducing the average size of the seeds and increasing the size likewise means reducing the number. Another correlation related to seed morphology was established for the studied species set between seed weight and seed bank type. Thompson et al. (1993) showed that small, compact seeds are more likely to build up a persistent seed bank than heavy, irregular shaped seeds. This relation is so well established that seed size and shape may serve as a short-hand indicator of seed bank longevity. They argue that this is most likely due to the fact that small, spherical seeds will be incorporated more easily into the soil, which will also provide some protection against predation. This may, however, be also partly due to a simple sampling effect: smaller seeds generally come in larger numbers which in turn increases the probability of finding a viable seed in a seed bank sample. The same argument also holds true for the relation between seed size and dispersal ability.

Related to the basic principle of trade-offs is the concept of strategies; these may be understood as different (or even opposing) answers to the same problems a plant may face during its life cycle (Venable & Brown 1988). It is e.g. generally assumed that dispersal in space and dispersal in time, i.e. the formation of a persistent seed bank, are opposing strategies with which a plant may avoid or escape unfavourable conditions or periods (Venable & Brown 1988). The validity of this assumption is, however, still debated (Thompson 2000) and the data of this general trait analysis could neither support or reject it. One result of the seed trap study, however, was that species with a long-term persistent seed bank were more abundant in the seed rain than those with a transient seed bank while in the established vegetation it was the other way round. This apparent contradiction with theoretical predictions may be explained by the fact that smallseededness is considered favourable for both dispersal and persistence in the soil (Thompson et al. 1993; Tackenberg 2001). And indeed seed dispersal by wind was found to be positively correlated with seed number which in turn was negatively correlated with seed weight.

A similar case can be seen in the correlations between clonal spread (CLO) and reproductive mode (REP). Reproduction by seed and clonal spread may be interpreted as opposing strategies: a species can seek its advantage either in the vegetative exploitation of a favourable site or in the (repeated) colonisation of new sites by seeds (see also the life strategy system of Frey & Hensen (1995) and Frey (2000) with its antagonistic strategies "perennial stayers", "fugitives" or "shuttle species" which rests on the same concept). Consequently it was found that lack of lateral spread (CLO.0) was positively correlated with exclusive reproduction by seed (REP.S) and strong lateral spread (CLO.3) positively with REP.SV and negatively with REP.S. For the same reason clonal growth and life history are correlated so that short-lived plants are always non-clonal.

Growth-form or functional groups

A major problem in the analysis of patterns and processes in ecological communities is the large number of species, potentially obscuring underlying patterns of interest. A possible solution to this problem is the condensation of species into groups sharing certain functional traits which presumably fulfil similar functional roles in the communities (Duckworth et al. 2000). The term 'functional group' has gained wide usage and acceptance although it may be more appropriate to talk of 'trait' or 'attribute groups' (Willby et al. 2000) so long as the actual functional significance is only hypothesised. Attempts to assemble species into non-taxonomic groups can be traced back more than a century to von Humboldt (1806) and Grisebach (1872). Many of the classical functional group schemes like Raunkiaer's system of life forms (Raunkiaer 1937), McArthur & Wilson's system of r- and K-selection (McArthur & Wilson 1967) or the CSR strategy scheme of Grime (1977) are built top-down, or in a *deductive* way; i.e. species are assigned to a preconceived system of strategies (Duckworth et al. 2000). The opposite way of constructing functional groups bottom-up or in an *inductive* way is a relatively new approach made possible by the availability of appropriate multivariate techniques and databases of plant traits. While the deductively derived classifications can *per definitionem* claim some universal validity (at least in the floristic domain for which they were constructed), inductive classifications are context-dependent and rest on the selection of traits and species used for their construction.

A number of studies used this *inductive* approach in recent years, both on field data and with experimental results (Grime et al. 1988; Díaz et al. 1992; Leishman & Westoby 1992; Boutin & Keddy 1993; Golluscio & Sala 1993; Lunt 1997; Jackel 1999; Kleyer 1999; Mabry et al. 2000; Willby et al. 2000; Deckers et al. 2004).

An early approach to data-driven classification of functional types was presented by Grime et al. (1988) who analysed 273 herbaceous species from the Sheffield region, described by 27 regenerative and vegetative traits. The resulting 12 clusters were mainly based on regenerative traits like seed-size and germination characteristics. The authors reported strong correlations among regenerative and among vegetative traits but only weak correlations between vegetative and regenerative traits. Jackel (1999) used Ward's clustering method to analyse 38 species of dry acidic grassland and found five clearly defined functional groups based on a mixture of vegetative and generative traits. Jackel also used ordination techniques to supplement the cluster analysis as it was done in this study. She found that for several different sets of species seed weight, seed bank type and growth height were most strongly correlated with the first axes, i.e. these traits represented the major gradients of variation in trait-space. Deckers et al. (2004) also used Ward's clustering in the analysis of hedgerow communities. In separate analyses for woody and herbaceous species they found a total of six functional groups: woody species were divided into two groups, mainly according to generative traits, while herbaceous species formed four clusters defined largely by vegetative traits and habitat preference, a trait not included in the analysis of Soomaa plant communities. Díaz et al. (1992) on the other hand used TWINSPAN and DCA ordination to identify supra-specific groups within montane grassland species based mainly on morphological traits; they distinguished six ‘species modes’ reflecting annuals, two types of forbs and three types of graminoids including tussock grasses.

In this study the number of entities of the floodplain flora was reduced from 135 species (which already were a selection of the more common species) to nine or five functional groups, depending on the chosen cut-off level. On the five-group level groups were defined by only three traits. The most fundamental split of the cluster analysis was between short-lived species on the one and perennial species on the other hand, a result also supported by the PCA ordination, where the short-lived species formed a very distinct group. In functional terms this is indeed a fundamental differentiation: being short-lived in a mainly perennial community means that establishment from seed has to be successful regularly or the species will go locally extinct. Perennial species on the other hand can hold a position, once established, for considerable times, even if conditions are no longer favourable for establishment (remnant populations *sensu* Eriksson (1996) and can often expand vegetatively. Therefore it can be expected that for short-lived species regenerative traits are more crucial for long-term survival, while for perennial species vegetative traits are of an overall higher importance.

At the next split a group of species was separated which was defined by the possession of small, very numerous wind-dispersed seeds. Internally this group was still rather inhomogeneous, being comprised of forbs, graminoids and woody species. Grime (1979) recognises a similar combination of traits and described these species as fugitives, exploiting landscapes with spatially unpredictable disturbances (see also Frey & Hensen 1995). However, in the species involved here there were no strict ruderals, these species were mostly competitives although species like *Urtica dioica* and the different species of *Salix* have, in a way, a ruderal component in their strategy. A third compact group was defined as grasses without lateral expansion, i.e. tussock grasses; together with the short-lived forbs this is probably the most homogeneous group in the studied sample. This group was most strongly associated with the dry and mesic vegetation types and especially in the very driest grasslands this type of species (e.g. *Nardus stricta*) formed the matrix of the community.

The remaining bulk of the species was divided at the five-group level according to the capability of lateral spread. It is well-established (Stöcklin 1992) that a clonal growth form has a number of advantages: (a) vacant space like disturbed patches can be quickly invaded and population size can be rapidly increased, (b) mortality in young ramets is lower than in young seedlings, thus risk of establishment is much lower, (c) dense clonal patches can prevent other plants from establishing and (d) high mobility and plasticity allows the effective exploitation of spatially heterogeneous resources. A large group, making up slightly more than half of the whole species set, is characterised by moderate to strong lateral expansion. By its sheer size this group is highly heterogeneous and at the nine-group level it was split into four sub-groups. The largest of these (PFG 3) contains most of the common grasses and Carices forming the matrix of nearly all dry to moist communities; proving the notion that there is a trade-off between vegetative and regenerative reproduction, most of these clonal species have only few seeds. The other three groups of strongly clonal species are characterised by specialised seed traits (seed number and seed size which were already discussed above) although they remain ecologically heterogeneous.

The remaining group at the five-group level is made up mainly of medium sized forbs which are characterised by their restricted capability of lateral spread. This group contains most of the conspicuous forbs typical for dry to moist grasslands like *Leucanthemum vulgare*, *Lychnis flos-cuculi*, *Centaurea jacea* or *Succisa pratensis*. Again seed traits distinguished between sub-groups at the lower cut-off level: one group was characterised by numerous, wind-dispersed seeds, the other by larger, animal-dispersed seeds. Both modes of dispersal are capable of bridging larger distances.

The overall results of this study, i.e. a small number of well defined groups (short-lived species, tussock and matrix grasses) plus a larger number of heterogeneous or ‘fuzzy’ groups, are confirmed by the findings of other studies. A number of studies (Leishman & Westoby 1992; Golluscio & Sala 1993; Lunt 1997) reported problems in finding distinct species groups; especially Leishman & Westoby (1992) were not able to sub-divide perennial forbs into smaller units. Noble & Gitay (1990) caution that we should not expect to find a universally useful functional classification. Nygaard & Ejrnæs (2004) also stressed the fact that this type of 'unsupervised' classification, based exclusively on trait × species matrices, is highly dependent on the input data, i.e. the selection of species and of traits. This is probably also the reason why the classification presented in this study proved to be somewhat 'unstable': choosing a different clustering algorithm (e.g. Ward's or UPGMA) or even changing the input order of the species resulted in different classifications of which the chosen one was the most plausible in ecological terms while it was not necessarily the only 'correct' one. This also suggests that the overall functional differentiation of species in the studied floodplain grasslands is actually small. This is not surprising as all studied vegetation types were perennial grasslands dominated by herbaceous and largely clonal species with only a few woody or short-lived species; this already implies a somewhat limited functional diversity.

E. Summary

Vegetation types and habitat parameters

Based on the phytosociological method of Braun-Blanquet, but aided in the analysis by multivariate methods, the floodplain meadows and related communities of the Soomaa NP were surveyed and in selected locations important habitat parameters like groundwater dynamics and a number of soil parameters were recorded. A total of 171 relevés were studied, 84 of these were located all over the park and 87 along six transects, which were placed at all major rivers of the area. Along each transect four to six groundwater and soil sampling sites were located.

The vegetation survey resulted in the description of 15 meadow, reed and sedge communities occurring commonly in the Soomaa floodplains. In the driest areas that are rarely if ever flooded the *Nardus-Festuca ovina*-community and the *Festuca ovina-Sesleria*-community can be found. These communities grow on mostly sandy and rather nutrient-poor soils of river banks and small ridges. Three communities were identified which cover large areas of the central floodplain on mesic and mostly well-drained soils: the *Festuca rubra-Deschampsia*-community, the *Alopecurus-Galium mollugo*-community and the *Alopecurus-Deschampsia*-community. Three communities were described, which are found in the central floodplain under moist conditions on mostly poorly-drained soils: the *Sesleria-Deschampsia*-, the *Melampyrum nemorosum-Filipendula*- and the *Carex cespitosa-Deschampsia*-community. A large number of communities can be found on permanently wet sites along the river margin, in small depressions and in the lowest parts of the central floodplain. These are dominated by sedges and reed grasses. Among the mostly sedge dominated communities are the *Carex disticha-Juncus filiformis*-community, the *Ranunculus flammula-Juncus filiformis*-community, the *Potentilla palustris-Carex disticha*-community and the two species poor communities dominated by either *Carex acuta* or *Carex elata*. Among the common reed communities are the *Phalaris-Phragmites*- and the *Carex acuta-Schoenoplectus lacustris*-community.

In a comparison of the so far rankless communities with the established phytosociological system of Central Europe and with the communities described by PAAL (1997) possible correspondences and differences in classification were sought. It was concluded that most communities can conveniently be placed in the established syntaxonomical system, at least at the level of alliances. It was found that the rather species-poor sedge and reed communities showed the greatest correspondence with Central European syntaxa. True meadow communities of the *Arrhenatheretalia* and *Molinietalia* were easily recognisable but showed distinct properties setting them apart from their Central European counterparts; especially the habitat fidelity of several species (e.g. *Deschampsia cespitosa*) was rather weak so that they could not be used as character species as in Central and Western Europe. Communities with *Sesleria caerulea* were found to be unique to the Baltic area but could be placed inside the *Molinion* alliance. The Estonian school of phytosociology differs from the Braun-Blanquet school in that it stresses dominants and builds the system top-down from broad habitat types to communities, instead of using purely floristic features (bottom-up approach). Therefore a complete 1:1 congruence of both systems is not possible.

Dispersal, regeneration, and the role of plant traits

In a set of three experimental studies various aspects of the regeneration dynamics of floodplain plants were assessed. Seed traps were used to study the composition of the local seed rain, in a seed sowing study the *in situ* germination of ten species in different gap types was investigated and a third study examined the role of seed bank and seed rain in the colonisation of artificial gaps. Data were also analysed in view of the role of plant traits and functional groups.

Seed rain

A total of 140 seed traps in groups of five were placed at 28 sample locations along three transects. 34423 seeds of ca. 76 species were collected during one year of sampling; the distribution of species was highly skewed with only five species accounting for 84 % of the total seed count. Median seed density was 6579 seeds/m^2 with no significant differences between habitats. Mean dissimilarity between seed rain and the respective vegetation plots was 70 % and difference was significant for most partitions of the data set (transects, vegetation types). However, both species number of seeds and seed number itself were significantly correlated with the species number of the established vegetation indicating some basic resemblance of species composition.

Approximately half of the seed rain (both species and seeds) originated from the direct neighbourhood (1m^2 around traps) of the seed traps but only very few species came from outside the studied transects; those were either wind-dispersed (*Alnus*, *Betula*, *Epilobium*) or water-dispersed (*Carex rostrata*). Roughly one quarter of the species of the established vegetation never did occur in the seed rain. These were either rare or of low cover. Of the remaining species of this category most were rather large-seeded or otherwise poorly dispersed. Temporal variation of seed rain was considerable with three distinct peaks in the course of one year. Two peaks in mid-summer and autumn mirrored the flowering phenology, the third in spring collected all seeds dispersed during winter and spring flood. The distribution of dispersal agents was rather even in the pooled data set of the established vegetation and seed rain but showed substantial variation between transects and between seed rain and vegetation of the same transects. Generally, wind- and water-dispersed species were more important in the seed rain whereas animal-dispersed species and those without apparent dispersal agent were underrepresented in the seed rain. Multivariate analysis of a plot × trait matrix revealed that established vegetation, seed rain and different vegetation types were each characterised by a distinct combination of vegetative and generative traits. The established vegetation is mainly dominated by graminoid species and those with fewer but heavier seeds and the ability of strong lateral expansion; the seed rain on the other hand is dominated by wind-dispersed species with large numbers of light-weight seeds and a lack of strong lateral expansion. Analysis of samples of drift material collected in August 2000 demonstrated that the rivers may transport considerable numbers of seeds and species: 21 species and more than 4000 seeds per litre drift material were found which belonged to all major dispersal types.

Seed sowing experiment

Ten species typical of the Soomaa floodplain meadows (*Betonica officinalis, Carex flava, Carex pulicaris, Iris sibirica, Lychnis flos-cuculi, Scorzonera humilis, Selinum carvifolia, Thalictrum lucidum, Trollius europaeus, Veronica longifolia*) were sown into experimental plots with different disturbance treatments and into the undisturbed vegetation.

Most of the studied species were able to germinate and establish in the experimental plots; emergence rate in the first year generally declined in the order bare soil (T1) > bryophytes & litter removed (T2) > intact vegetation (T0), which agrees with findings from similar studies and is explained in terms of differing competitive situations. No significant differences between treatments were found for establishment after three years and for survival; however, both values tended to be lowest in intact vegetation (T0). In some species, however, survival tended to be higher in the semi-open conditions of treatment T2, which is discussed in terms of sheltering effects. Three species stand out, although for opposite reasons: both *Carex* species performed very badly with low emergence after one and next to no establishment after three years; *Iris sibirica* on the other hand performed very well and had a prolonged period of germination which obviously lasted for at least two years. Seed weight was not directly correlated with seedling emergence; it was, however, significantly correlated with establishment and survival. Implications of seed sowing studies for habitat restoration are discussed and it is suggested that deliberate (re-)introduction of species by seed may be a valuable method to overcome seed limitation.

Disturbance and regeneration

Twenty plots (ten each in a dry and a moist meadow type) with three experimental treatments were set up to study the role of the seed rain and seed bank in the re-colonisation of gaps in the meadow vegetation. Soil inversion was used to exclusively measure the seed rain; exclusion of the seed rain by cages covered by nylon mesh allowed the assessment of the seed bank. A disturbed but uncovered plot and an undisturbed control received input from both seed bank and seed rain.

4363 seedlings of ca. 61 species were identified in the experimental plots. Seed rain and seed bank differed significantly in their contribution to the seedling flora: the seed bank generally was four to five times richer in both species and seeds. Species and seedling numbers in treatment type 3, which received input from both seed bank and seed rain, were approximately the sum of the two single components. Only few seedlings emerged in the undisturbed control plots proving the importance of gaps for regeneration in these meadows. Ingrowth of clonal plants was restricted mostly to the margins of the plots, the central area used for sampling was not affected.

Mean seedling density per m² was 249 in the seed rain plots and 939 in the seed bank plots; mean species number was 3.0 and 11.9 respectively. Differences between habitats were significant only for the seed bank: the seed bank of moist sites was both larger in seeds and in species. Seed rain and seed bank were both dominated by a small number of species: the seed rain mostly by *Deschampsia cespitosa*, the seed bank by *Ranunculus auricomus*, *Carex flava* and *Agrostis capillaris*. However, only few species were exclusively confined to either seed rain or seed bank and those that were, were found only in small numbers. Virtually all seedlings belonged to perennial species; monocot and dicot species were evenly distributed in the seed bank, but the seed rain was clearly dominated by monocots. Similarity between the established vegetation and the seedling assemblages was very low (5 to 15 %); the seed bank was slightly more similar to the vegetation than the seed rain, especially when considering qualitative data.

Analysis of life history traits suggested that the established vegetation was largely characterised by species with a transient seed bank, heavy seeds and exclusively vegetative reproduction; the seed bank assemblage on the other hand consisted of species which reproduce equally by seed and vegetatively and have small numbers of seeds. Conclusions about the seed rain were not so well supported as they were based largely on one species (*Deschampsia*).

Plant trait analysis

The data collected for the functional analysis of the experimental results was also used for a general assessment of trait distribution and functional group differentiation of the grassland vegetation as a whole.

Correlation analysis showed that a number of traits like clonal growth, reproductive mode, guild membership, seed number and weight etc. were inter-correlated. These correlations are explained in terms of general bio-physical constraints and trade-offs. A cluster analysis of a trait matrix of 135 floodplain species resulted in nine morphologically and functionally defined groups of species (PFGs); by choosing a higher cut-off level five groups remained that where defined mostly by guild membership (forb vs. graminoid), life-history (short-lived or monocarpic vs. perennial), lateral spread and seed size and number. PCA confirmed these results by extracting life-history, seed number and weight, mode of regeneration and dispersal vector as the major components of the trait matrix. Functional groups were distributed unevenly within the different grassland communities described in previous chapters. PFG 3 (forbs and graminoids with strong lateral spread) proved to be the most common group in most communities, but PFG 2 (forbs with restricted lateral spread) dominated in dry grasslands and PFG 8 (larger forbs and graminoids with numerous wind-dispersed seeds) dominated in some reed and sedge communities. Indicator Species Analysis confirmed the distributional patterns of PFGs by showing that seven out of nine PFGs were significantly related to certain plant communities.

Conclusion

The three experimental studies presented in this thesis approached the population dynamics of floodplain species from different directions with a special focus on regeneration by seed. Summing up the results, it may be concluded that i) considerable numbers of seeds are dispersed in the grassland systems, predominantly by wind and water, although mostly over short distances only, ii) the seed bank plays a major role in the filling of gaps provided they are large enough so that clonal species cannot pre-empt the open space, and finally iii) gaps and small-scale disturbances may play an important role in the maintenance of species richness in these communities dominated by clonal plants by opening "windows of opportunity" for seedling recruitment. Plans for habitat management should take into account the requirements for seedling recruitment and should, if necessary, deliberately create the necessary conditions and help species in reaching appropriate habitats.

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G. Appendix

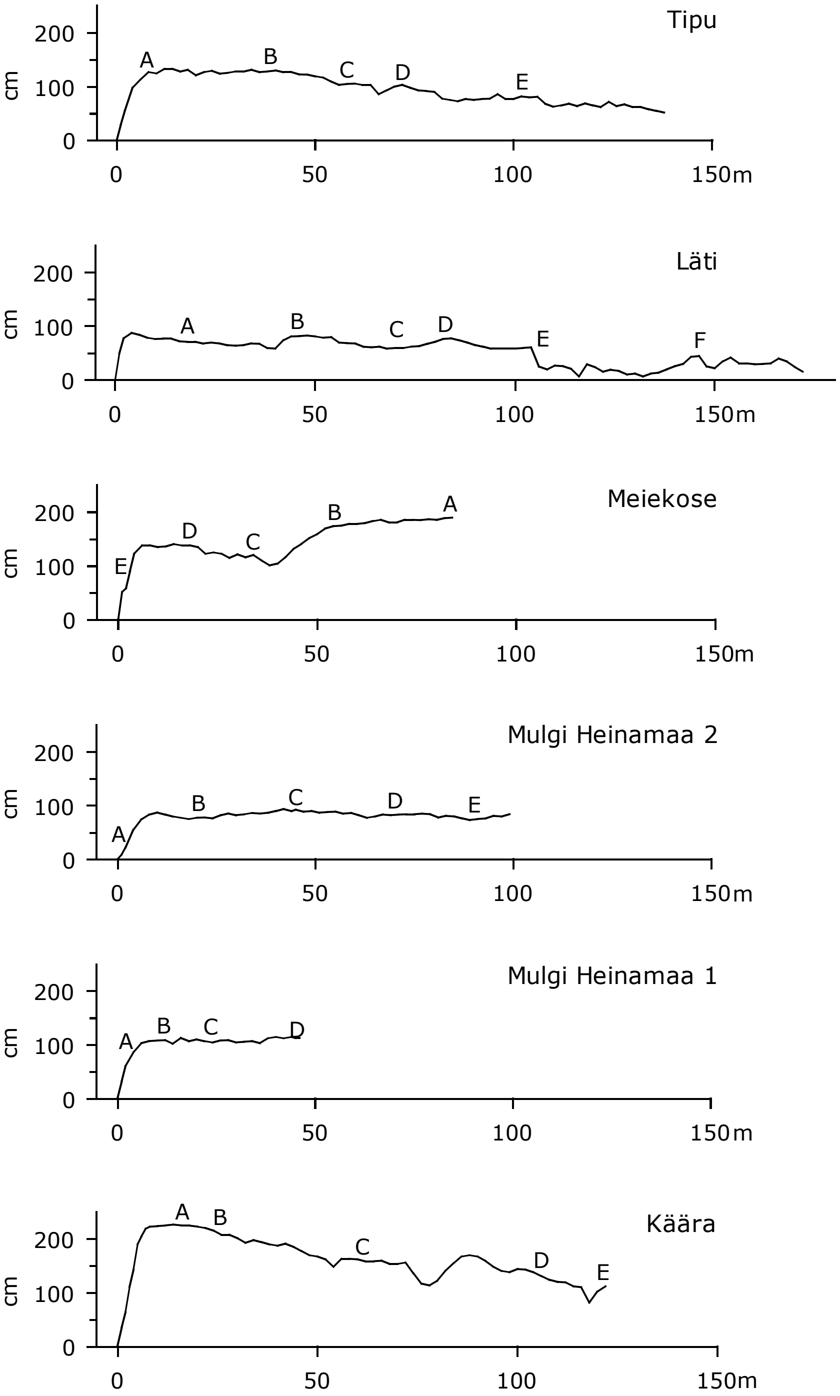


Fig. G.1: Sketches of transects with position of gauges and locations for soil and biomass sampling

Table G.1: Raw data of soil analysis (pH, potassium, total nitrogen, organic carbon, C/N ratio and plant available phosphorus

Plot	pH ($CaCl_2$)	K (mg/kg)	N (%)	C (%)	C/N Ratio	P (mg/kg)
KT-A	5.07	24.0	0.22	2.44	10.95	16.89
KT-B	5.15	14.9	0.33	3.28	10.01	13.37
KT-C	5.09	48.8	0.38	4.16	11.03	36.23
KT-D	5.13	33.0	0.61	6.36	10.40	9.85
KT-E	5.20	46.0	0.90	10.75	11.96	60.84
LT-A	5.48	21.8	0.43	4.26	9.87	32.71
LT-B	5.53	24.0	0.49	5.18	10.47	16.89
LT-C	5.36	42.8	0.39	4.24	10.82	32.71
LT-D	4.91	34.8	0.31	3.27	10.68	34.47
LT-E	5.39	78.3	0.76	7.70	10.09	48.53
LT-F	5.37	41.9	0.66	6.68	10.13	46.78
MT-A	5.23	62.4	0.56	6.04	10.82	18.65
MT-B	5.26	59.5	0.44	4.82	10.93	39.74
MT-C	5.18	80.1	0.63	6.31	10.08	46.78
MT-D	5.53	26.6	0.45	4.68	10.35	13.37
MT-E	6.45	59.1	0.37	4.85	13.21	53.81
MH1-A	5.66	34.4	0.64	7.15	11.25	4.58
MH1-B	5.59	26.7	0.62	6.74	10.81	25.68
MH1-C	5.21	49.4	0.63	6.63	10.59	27.44
MH1-D	5.27	50.4	0.71	7.32	10.31	22.16
MH2-A	5.67	20.4	0.73	7.98	10.91	39.74
MH2-B	5.56	70.1	0.98	9.89	10.10	55.57
MH2-C	5.53	18.7	0.66	7.05	10.66	11.61
MH2-D	5.07	88.5	0.72	7.94	11.07	36.23
MH2-E	4.96	19.9	1.02	11.66	11.46	29.19
TT-A	4.82	17.5	0.20	2.06	10.09	6.34
TT-B	4.97	43.5	0.38	3.87	10.24	9.85
TT-C	4.98	58.7	0.41	4.03	9.92	9.85
TT-D	5.35	130.2	0.49	4.93	10.04	36.23
TT-E	5.15	61.7	1.01	10.82	10.72	64.36

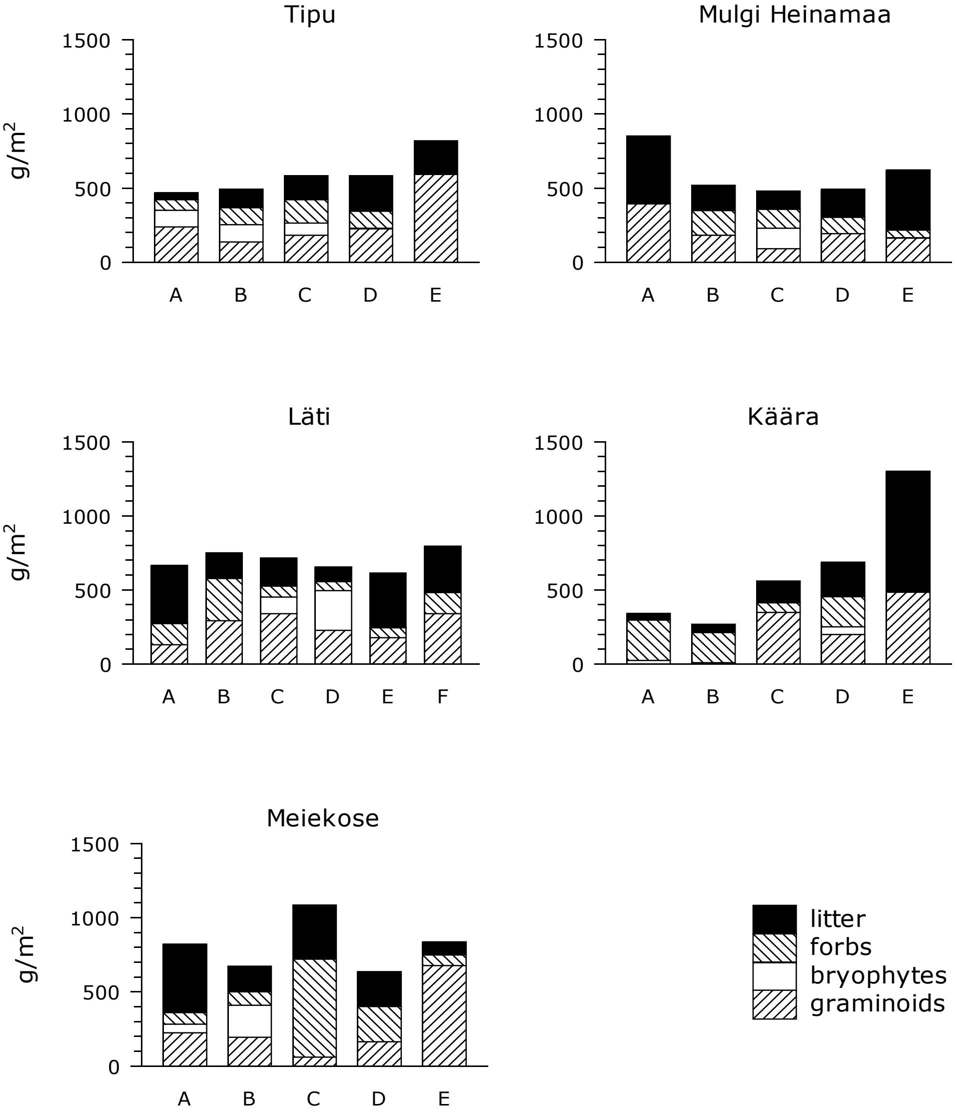


Fig. G.2: Detailed results of biomass measurements at 26 transects locations. Abbreviation of transects: Tipu (TT), Mulgi Heinamaa (MHT), Läti (LT), Käära (KT), Meiekose (MT). Classification of transect locations: dry floodplain grassland (LT-C, LT-D, TT-A, TT-B), mesic floodplain grassland (KT-A, KT-B, LT-A, LT-B, LT-F, TT-C, TT-D), moist floodplain grassland (LT-E, MHT-B, MH-C, MHT-D, MT-A, MT-B, MT-C, MT-D), wet floodplain grassland with tall sedges (KT-C, KT-D, KT-E, MHT-A, MHT-E, TT-D, TT-E), wet floodplain grassland with tall grasses (MT-E)

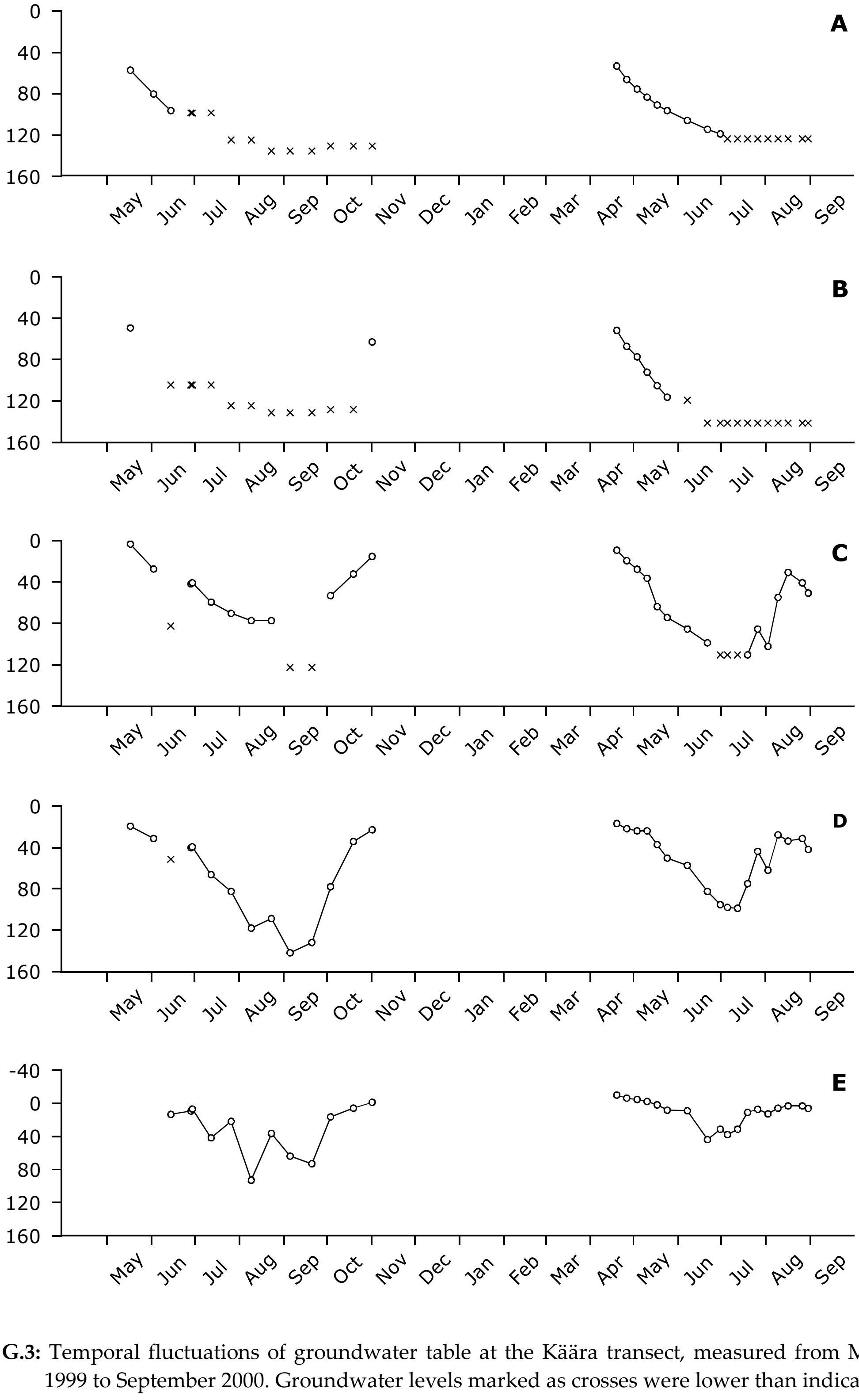


Fig. G.3: Temporal fluctuations of groundwater table at the Käära transect, measured from May 1999 to September 2000. Groundwater levels marked as crosses were lower than indicated but could not be determined accurately.

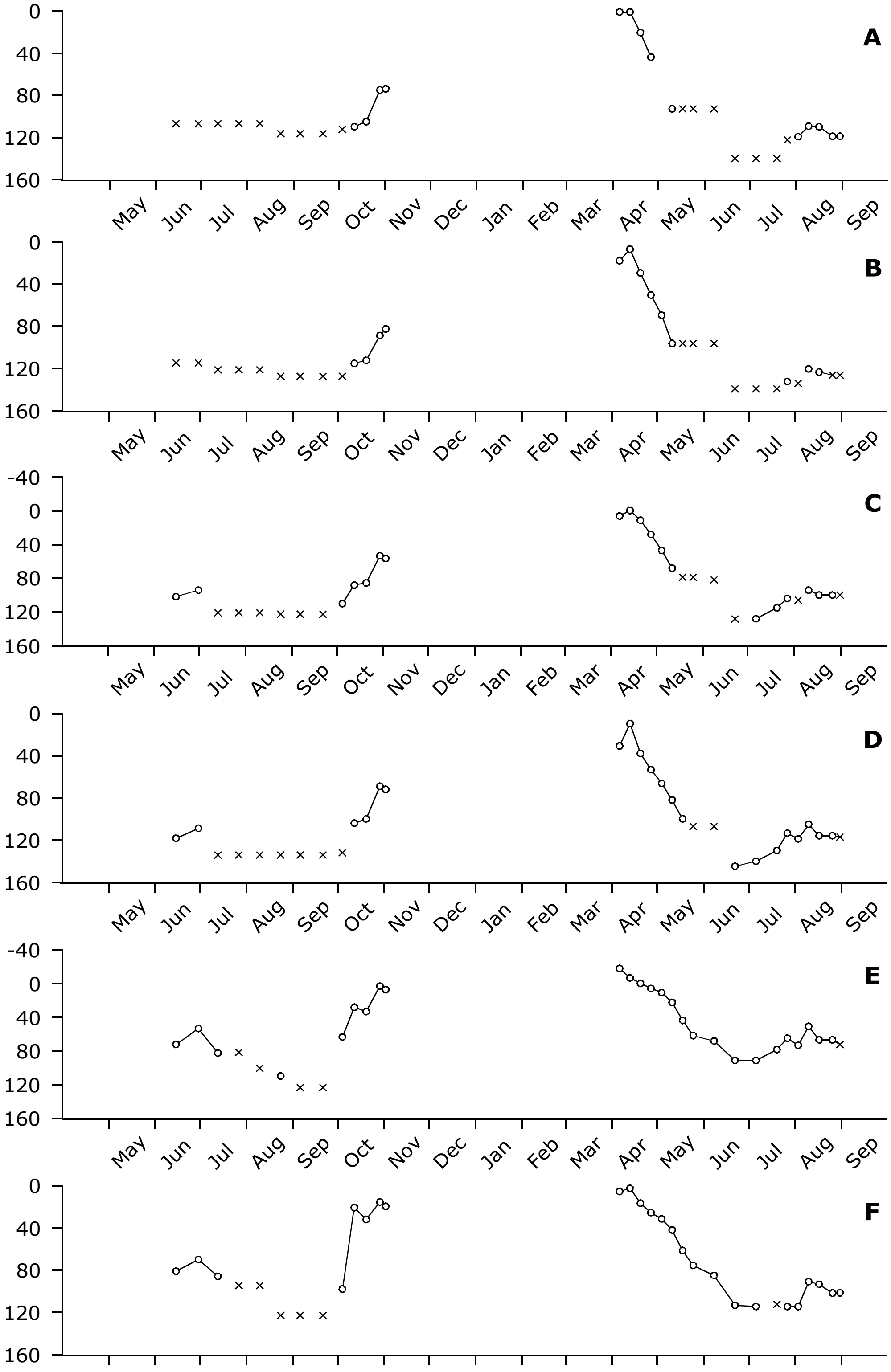


Fig. G.4: Temporal fluctuations of groundwater table at the Läti transect, measured from May 1999 to September 2000. Groundwater levels marked as crosses were lower than indicated but could not be determined accurately.

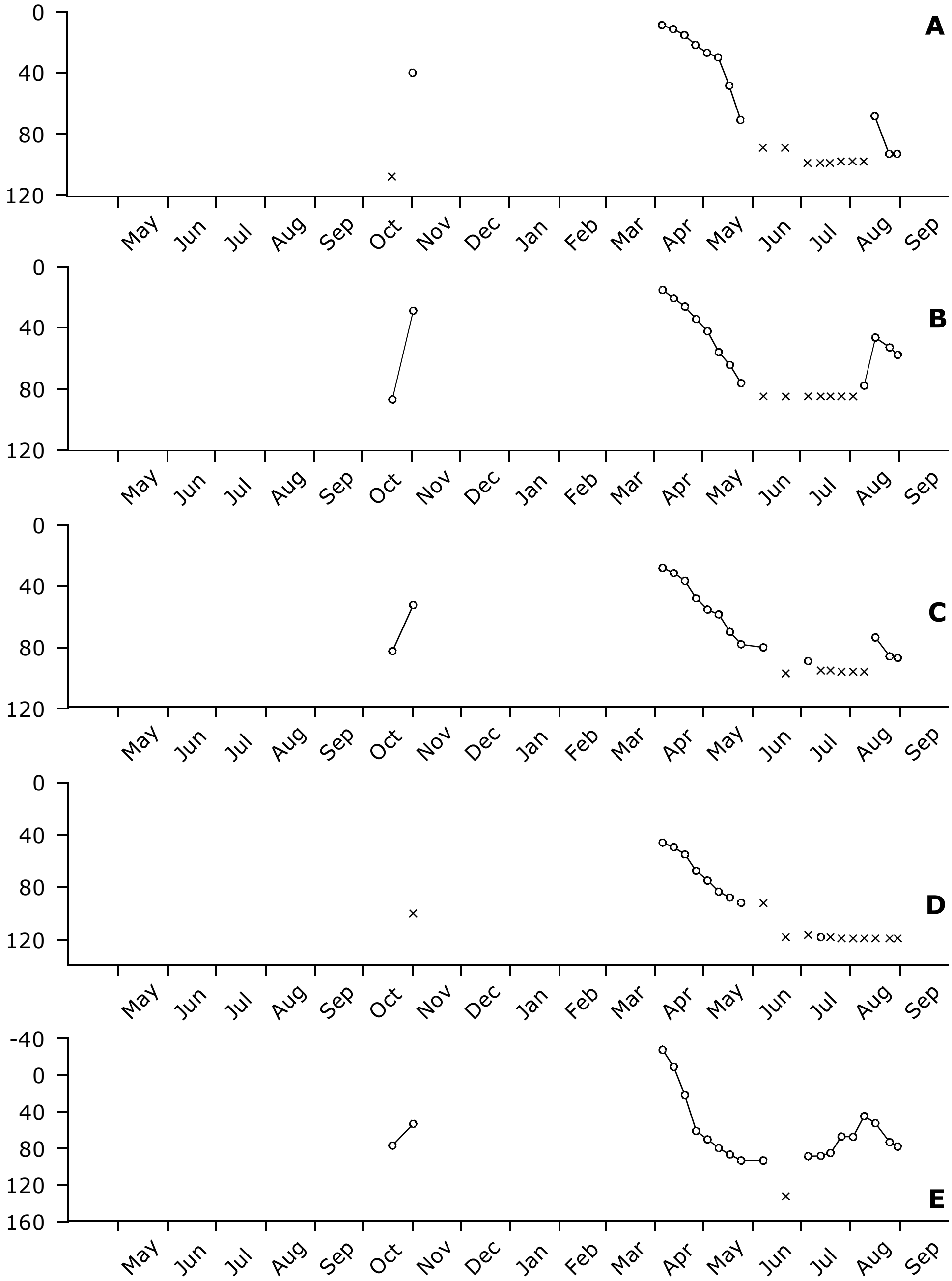


Fig. G.5: Temporal fluctuations of groundwater table at the Meiekose transect, measured from May 1999 to September 2000. Groundwater levels marked as crosses were lower than indicated but could not be determined accurately.

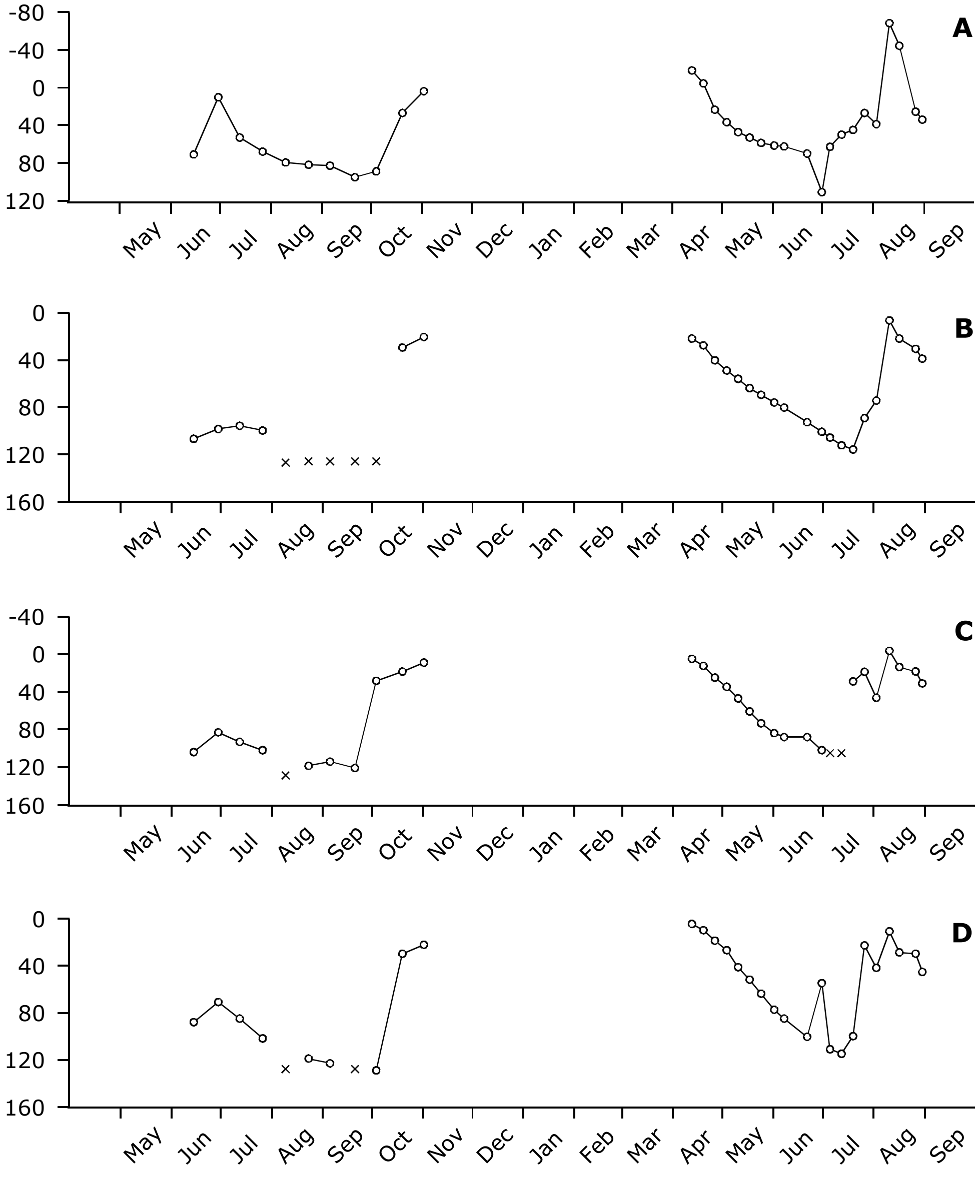


Fig. G.6: Temporal fluctuations of groundwater table at the Mulgi Heinamaa 1 transect, measured from May 1999 to September 2000. Groundwater levels marked as crosses were lower than indicated but could not be determined accurately.

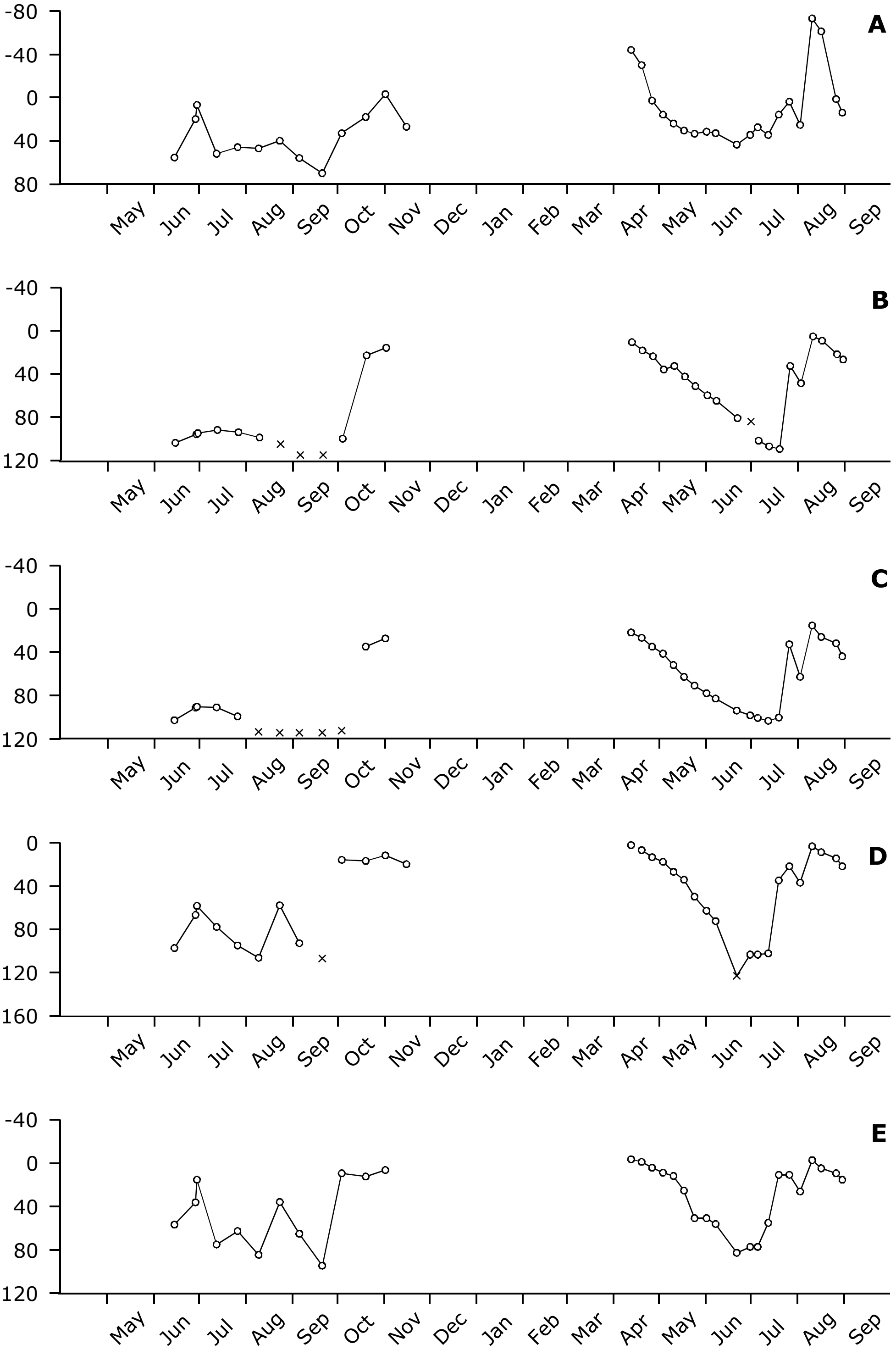


Fig. G.7: Temporal fluctuations of groundwater table at the Mulgi Heinamaa 2 transect, measured from May 1999 to September 2000. Groundwater levels marked as crosses were lower than indicated but could not be determined accurately.

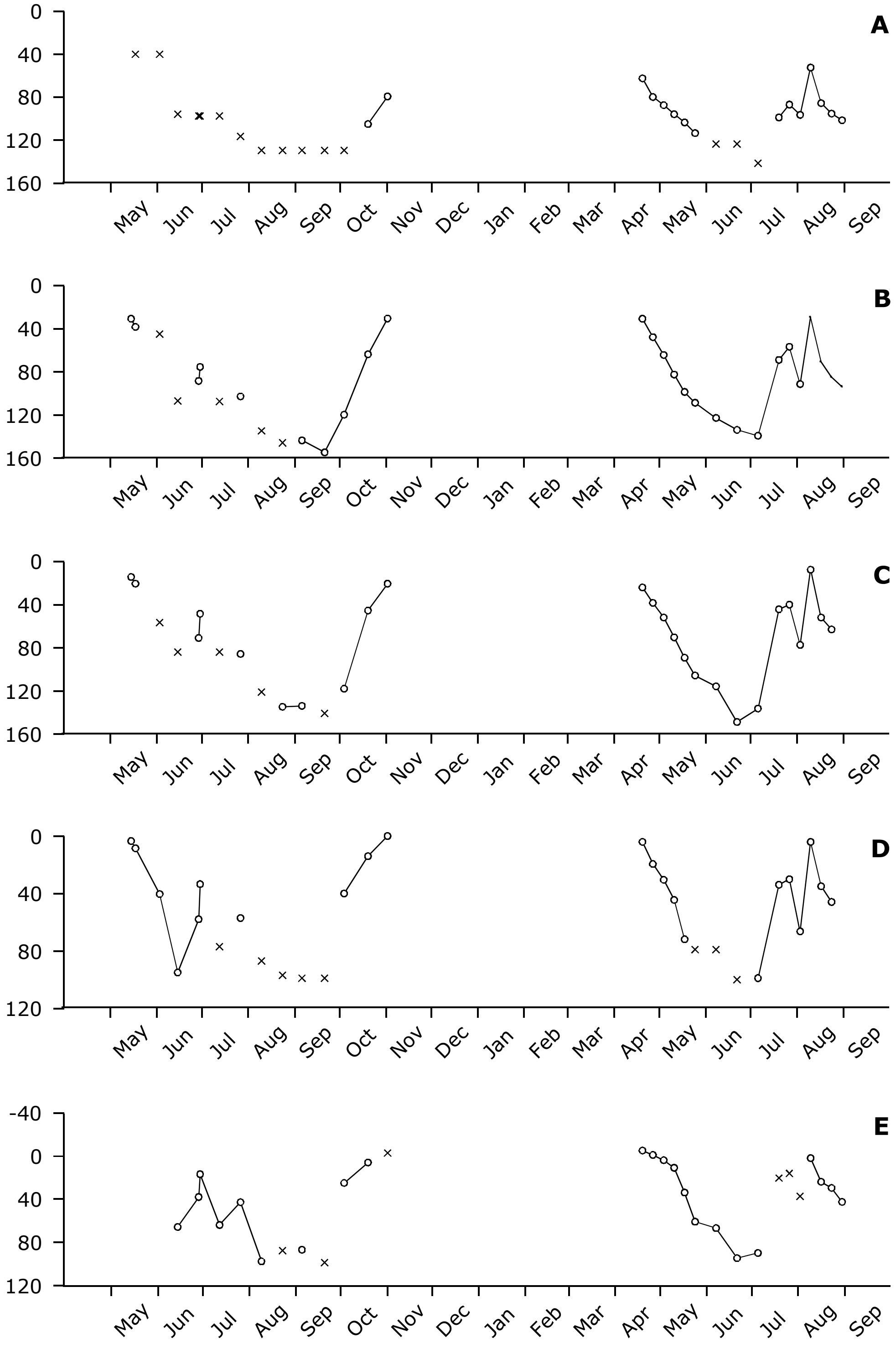


Fig. G.8: Temporal fluctuations of groundwater table at the Tipu transect, measured from May 1999 to September 2000. Groundwater levels marked as crosses were lower than indicated but could not be determined accurately.

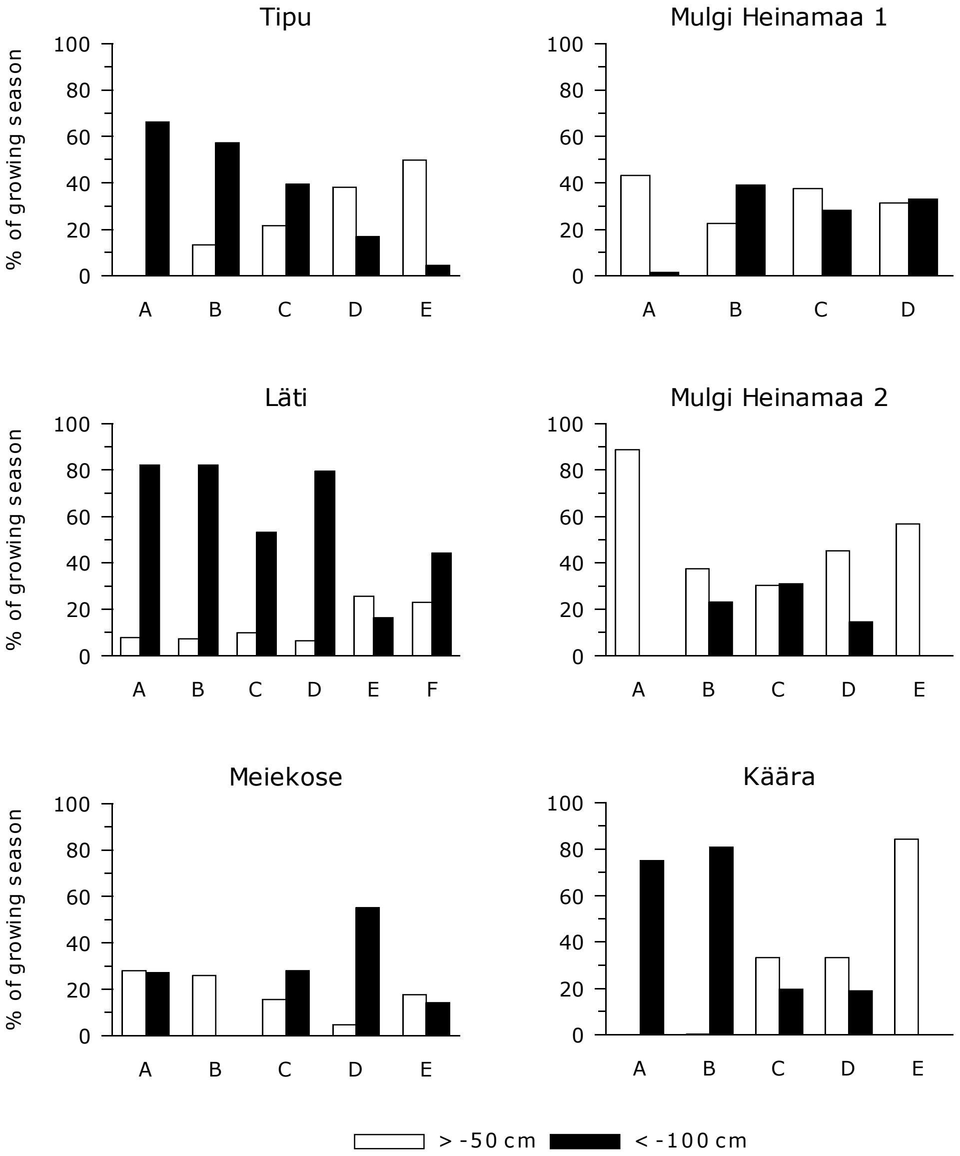


Fig. G.9: Results of groundwater measurements over two years: percentage time of growing season with groundwater higher than 50 cm (open bars) or lower than 100 cm (filled bars).

Table G.2: Nardus-Festuca ovina-community

Column no.	1	2	3	4	5	6
Species no.	32	27	45	32	39	34
Total cover (%)	90	100	100		100	100
Graminoids (cover %)	80	95	90		80	90
Forbs (cover %)	40	50	40		50	40
Mosses (cover %)	10	90	90		70	60
Nardus stricta-group						
Nardus stricta	4	3	2b	2b	2a	2a
Hieracium pilosella	2a	1a	1a	.	.	+
Viola canina ssp. canina	.	2a	1b	.	.	1b
Danthonia decumbens	.	.	+	.	.	+
Sesleria caerulea-group						
Festuca ovina	.	3	3	3	3	4
Sesleria caerulea	.	.	.	3	3	2a
Carex pulicaris	.	.	+	.	1b	.
Anthoxanthum odoratum-group						
Rhytidiadelphus squar.	2a	3	3	4	4	4
Veronica chamaedrys	.	1a	1a	+	+	+
Anthoxanthum odoratum	1a	.	1a	+	+	.
Trifolium pratense	2a	.	+	.	1b	+
Plantago lanceolata	.	+	1a	.	.	1a
Hieracium lactucella	.	.	.	.	+	+
Trifolium repens	1a	.	.	.	1a	.
Centaurea jacea-group						
Achillea millefolium	1a	+	1b	1b	+	1a
Agrostis tenuis	1b	+	1a	1a	1a	1a
Luzula campestris	1b	2a	1a	1a	+	+
Alchemilla vulgaris agg.	2a	.	2a	2a	2a	2a
Carex pallescens	1b	+	+	1a	.	1a
Galium boreale	.	2a	+	2a	1a	1a
Potentilla erecta	2b	2a	2a	.	1b	2a
Achillea ptarmica	2a	.	+	.	+	+
Briza media	1a	.	+	+	1b	.
Centaurea jacea	+	.	1b	+	2b	.
Galium mollugo	.	1b	.	.	.	+
Dactylis glomerata	.	.	.	1a	.	.
Stellaria graminea	.	.	.	.	+	.
Deschampsia cespitosa-group						
Deschampsia cespitosa	1b	2a	1b	2b	1a	1b
Ranunculus acris	1b	1b	1a	2a	1a	+
Vicia cracca	2a	1b	1a	2a	+	1a
Filipendula ulmaria	.	.	+	2a	+	1a
Galium uliginosum	1a	.	+	.	+	+
Lathyrus pratensis	1b	.	+	.	+	+
Ranunculus auricomus	.	+	.	1b	1a	+
Rumex acetosa	+	1a	1b	1b	.	.
Festuca rubra ssp. rubra	2b	.	4	.	+	.
Geum rivale	.	.	+	2a	.	+
Poa pratensis	.	.	+	.	+	.
Carex panicea-group						
Carex panicea	1b	+	1a	2a	.	+
Carex nigra	2b	.	+	1b	1b	.
Agrostis canina	1a	.	.	.	.	.
Further species						
Campanula patula	.	+	.	.	+	.
Equisetum arvense	.	.	+	+	.	.
Festuca pratensis	.	.	.	+	+	.
Helictotrichon pratense	.	.	.	.	+	+
Leucanthemum vulgare	.	.	+	.	+	.
Rhinanthus angustifolius	+	.	+	.	.	.
Salix bicolor	1b	.	1b	.	.	.
Trollius europaeus	.	.	.	.	+	+
Viola palustris	.	.	1b	.	.	+

Miscellaneous species

Agrostis stolonifera LT-9:1a; Angelica sylvestris A98-49:+; Aulacomnium palustre A00-23:3; Betula pubescens B A00-10:+; Calliergonella cuspidata A00-10:1a; Cardamine pratensis A98-36:+; Carex disticha LT-9:1a; Carex flava A00-23:1a; Carex hartmanii A00-10:1a; Carex leporina A98-49:+; Carex pilulifera A00-10:2b; Cerastium holosteoides A98-36:+; Climacium dendroides A98-49:3; Helictotrichon pubescens LT-9:+; Hylocomium splendens A00-23:1a; Hypericum maculatum A98-49:1b; Knautia arvensis A00-23:1a; Mentha arvensis LT-9:+; Phleum pratense A98-40:+; Pleurozium schreberi A00-23:1a; Polytrichum commune A00-23:3; Potentilla anserina A98-40:+; Prunella vulgaris A98-36:1a; Salix caprea A98-49:1a; Salix cinerea LT-9:+; Salix myrsinifolia A00-10:1b; Scorzonera humilis A98-49:1a; Succisa pratensis A98-49:1b; Viola canina ssp. montana LT-9:1a; Viola uliginosa A98-36:+

Column no. & plot ID:

1) A00-10; 2) A00-23; 3) A98-49; 4) LT-9; 5) A98-36; 6) A98-40

Habitat parameters:

LT-9: pH 4.9; C/N 10.7; K (mg/kg) 34.8; N (%) 0.31; C (%) 3.3; P (mg/kg) 34.5; GW > -50: 6.5;
GW < -100: 79.5

GW > -50: groundwater table higher than 50cm below ground for given percentage of growing season
GW < -100: groundwater table lower than 100cm below ground for given percentage of growing season

Table G.3: Festuca ovina-Sesleria-community

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Species no.	35	38	38	39	50	41	36	32	43	47	40	44	28	45	36	38	24
Total cover (%)	100		100		100	100	100		100	100	100	100		100	100	100	
Graminoids (cover %)	40		40		80	50	70		30	30	50	80		80	50	40	
Forbs (cover %)	60		60		60	50	80		70	70	75	60		70	60	60	
Mosses (cover %)	90		80		80	70	10		1	70	0	90		100	10	1	
Sesleria caerulea-group																	
Festuca ovina	4	4	3	4	3	2b	2b	2b	1b	2b	2b	4	5	.	.	.	.
Sesleria caerulea	2b	2b	2a	1b	1b	2b	4	4	2b	.	.	.	.	2b	2b	1a	2a
Carex pulicaris	.	+	.	+	+	+	.	.	.	.	+	.	.	1b	.	.	.
Anthoxanthum odoratum-group																	
Rhytidiadelphus squar.	5	4	5	4	1a	4	2a	2a	+	3	.	5	4	5	2a	+	.
Anthoxanthum odoratum	1a	+	1b	+	1a	+	.	+	+	1a	.	+	.	1a	1a	+	.
Plantago lanceolata	+	.	+	.	+	1a	.	.	+	1a	1a	2a	1a	1b	.	.	.
Trifolium pratense	1a	1a	+	1b	1a	+	.	.	.	1a	.	2a	.	1a	.	+	.
Veronica chamaedrys	+	+	.	1a	.	.	+	.	1a	+	.	+	1a	.	+	.	.
Trifolium repens	.	1a	.	.	.	.	.	+	.	+	.	2a	1a	+	.	.	.
Hieracium lactucella	+	.	.	1a	.	1a	.	.	.	.	.	.	1b	.	.	+	.
Leucanthemum vulgare-group																	
Leucanthemum vulgare	+	.	+	1a	+	.	.	.	1a	+	+	1a	1a	+	.	.	.
Cerastium holosteoides	.	+	.	1a	+	.	.	.	.	+	+	1b	+	1a	.	.	.
Prunella vulgaris	+	1a	.	+	.	+	.	.	.	+	.	1a	+	.	.	.	.
Centaurea jacea-group																	
Alchemilla vulgaris agg.	2b	3	2b	2a	2b	1a	+	1a	2a	2b	2a	3	2a	1a	2b	1a	1a
Galium boreale	.	2b	2a	2a	2a	1a	.	2a	2a	1b	3	2b	+	1b	1b	1b	2b
Potentilla erecta	2a	1a	1b	1a	2a	2a	.	2a	2a	+	1b	2a	.	2a	1a	2a	2a
Briza media	1a	1a	1a	1a	+	1a	+	+	1a	1a	1a	1a	.	1a	1a	.	.
Carex pallescens	+	+	+	+	+	.	1a	1a	+	+	+	2a	.	1a	+	.	1a
Achillea millefolium	2a	1b	1b	2a	.	2a	1a	1a	1b	.	1a	1a	1a	1a	.	.	1b
Achillea ptarmica	+	.	+	.	+	+	.	1b	1b	1a	+	1a	+	.	1a	1a	2a
Centaurea jacea	2b	2b	2b	2b	1b	2a	.	.	.	2a	2b	2a	1b	2b	1a	1a	.
Luzula campestris	1a	+	1a	+	1a	+	.	.	.	.	+	2a	+	1a	1b	.	+
Agrostis tenuis	.	+	.	1a	1a	1b	1a	.	1b	1b	1a	.	1b	1a	.	.	1a
Stellaria graminea	.	+	.	+	+	.	.	.	+	+	.	+	+	.	.	.	.
Galium mollugo	.	+	+	.	.	.	2a	.	.	.	.	2a	.	.	.	+	.
Dactylis glomerata	1a	.	.	+	.	.	1a	.	.	.	+	.	.	.	.	.	.
Deschampsia cespitosa-group																	
Deschampsia cespitosa	1a	+	2a	+	2b	1a	2b	2b	2a	1b	2b	2b	1b	1a	2b	1b	2b
Filipendula ulmaria	1a	+	2a	1a	2b	2a	3	2a	1b	2a	2b	2a	+	1a	1b	2b	2b
Ranunculus acris	2a	1b	2a	1b	2a	1b	1b	2a	1a	1a	1a	2a	+	1a	2a	2a	2a
Vicia cracca	1b	1a	1b	+	1a	1a	1a	2a	+	+	+	1b	+	1a	1b	1b	2b
Geum rivale	+	.	1b	1a	1b	2a	2a	1b	+	1a	2b	2b	.	+	2b	1b	2a
Lathyrus pratensis	.	1a	1a	1a	1a	+	+	1a	+	+	.	1a	+	1a	1b	+	1b
Ranunculus auricomus	2a	1b	2a	.	1a	1a	1a	1b	1a	1a	+	1b	.	1a	2a	1a	1b
Rumex acetosa	.	.	+	1a	1a	+	1a	1a	+	+	.	2a	+	1a	1a	1a	1a
Galium uliginosum	1a	+	+	+	1a	+	.	+	+	1a	.	+	.	+	1a	.	+
Festuca rubra ssp. rubra	.	.	.	.	1b	1b	2a	2a	1b	.	.	3	.	5	2b	+	2b
Poa pratensis	+	.	1a	.	.	.	.	.	.	1a	.	.	.	.	1b	+	.
Phleum pratense-group																	
Phleum pratense	+	.	.	.	1a	+	1a	.	1a	+	+	+	.	+	1a	.	.
Festuca pratensis	.	+	.	.	1b	.	.	.	1a	1a	.	.	+	.	2a	.	.
Angelica sylvestris-group																	
Angelica sylvestris	.	+	.	.	1a	.	1a	.	+	1a	2a	.	.	1a	.	+	.
Trollius europaeus	.	.	1b	.	.	.	2b	.	2a	2a	+	1b	.	+	.	.	.

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Carex panicea-group																	
Carex nigra	.	+	+	1a	+	+	.	1a	+	.	+	.	.	1a	1b	.	1a
Carex panicea	.	.	.	+	2a	.	1b	1b	.	+	2a	1a	.	1a	+	.	1b
Agrostis canina	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Selinum carvifolia-group																	
Viola canina ssp. montana	.	.	.	.	.	.	.	1a	1a	1a	.	.	.	1a	1a	1b	.
Succisa pratensis	.	.	.	+	1a	.	.	.	.	.	1a	.	.	1b	.	.	.
Scorzonera humilis	.	.	.	.	.	.	.	.	.	.	.	2b	.	+	.	.	.
Campylium stellatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Lychnis flos-cuculi-group																	
Lychnis flos-cuculi	.	+	1a	.	+	+	.	.	.	+	+	.	.	.	1a	1a	+
Climacium dendroides	.	.	1a	.	3	.	1a	.	+	3	.	.	.	1a	.	+	.
Calliergonella cuspidata	.	.	.	.	3	.	.	3	+	.	.	1a	.	.	+	+	.
Cardamine pratensis	.	.	.	.	+	.	+	.	.	+	.	.	.	.	.	.	.
Further species																	
Campanula glomerata	1a	.	1a	+	.	.	+	.	1b	+	+	2b	.	+	1a	.	.
Cerastium arvense	+	.	+	.	.	+	.	.	+	.	.	.	.	.	1a	+	.
Cirsium heterophyllum	.	.	.	.	1a	2a	2b	+	.	.	.	.	.	.	.	2a	.
Geranium palustre	.	1b	.	2a	.	1a	.	.	+	2b	.	.	.	.	.	.	.
Luzula multiflora	.	.	.	.	.	.	+	+	+	+	.	.	.	.	.	+	.
Alopecurus pratensis	.	.	.	.	.	1a	.	.	+	.	.	.	.	.	1b	+	.
Carex disticha	.	1a	.	.	1b	.	.	.	.	+	.	.	.	.	.	2a	.
Carex flava	.	.	.	.	.	+	.	.	.	.	+	2a	.	+	.	.	.
Helictotrichon pratense	.	.	.	1a	.	.	1b	.	.	+	.	.	.	+	.	.	.
Hieracium pilosella	.	+	.	.	.	.	1a	.	.	+	.	1a	.	.	.	.	.
Carex acuta	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.
Carex cespitosa	.	.	.	.	.	.	.	.	.	+	.	.	.	.	1a	2a	.
Equisetum arvense	.	+	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.
Galium palustre	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	+	.
Helictotrichon pubescens	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+
Heracleum sphondylium	.	1a	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.
Hypericum maculatum	.	.	.	.	+	.	.	.	+	.	.	2a	.	.	.	.	.
Stellaria palustris	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	1a	.
Valeriana officinalis	.	.	.	.	+	.	+	.	.	.	+	.	.	.	.	.	.

Miscellaneous species:

Aulacomnium palustre A98-06:+; Calamagrostis epigejos A98-46:+; Caltha palustris A98-22:+; Campanula patula A98-04:+, A98-08:+; Carex hirta A98-26:+, A98-47:1a; Carex leporina A98-10:+, A98-26:+; Carex pilulifera A00-12:1a; Carex vesicaria A00-24:+; Carum carvi A98-04:2b, A00-12:+; Cirsium oleraceum A00-24:1a; Cynosurus cristatus A98-04:+; Dactylorhiza incarnata A98-35:+; Danthonia decumbens A98-35:+, A98-47:+; Frangula alnus A98-35:1a; Geranium pratense A98-02:+; Glechoma hederacea A98-02:+; Hieracium umbellatum A98-46:1a, A98-10:+; Hylocomium splendens A98-06:+; Juncus conglomeratus A98-46:1a, A98-47:+; Juncus filiformis A98-46:2a, LT-8:1b; Knautia arvensis TT-7:1a; Lysimachia vulgaris A98-35:+; Mentha arvensis LT-8:+, A98-35:+; Myosotis scorpioides A98-02:+; Nardus stricta TT-7:1a; Phalaris arundinacea TT-4:+; Platanthera bifolia A98-35:+; Potentilla anserina A98-22:+, LT-10:+; Ranunculus repens A98-06:1b, A00-24:1a; Salix bicolor A98-46:1a, A98-47:1b; Salix rosmarinifolia TT-7:1a, A98-

Column no. & plot ID:

1) A98-04; 2) TT-8; 3) A98-06; 4) TT-7; 5) A98-46; 6) A98-22; 7) A00-24; 8) LT-8; 9) A98-10; 10) A98-26; 11) A98-35; 12) A00-12; 13) TT-4; 14) A98-47; 15) A98-08; 16) A98-02; 17) LT-10

Habitat parameters:

TT-7: pH: 5.0; C/N: 10.2; K (mg/kg): 43.5; N (%): 0.38; C (%): 3.9; P (mg/kg): 9.9; GW > -50: 13.2;
GW < -100: 57.2

LT-8: pH: 5.4; C/N: 10.8; K (mg/kg): 42.8; N (%): 0.39; C (%): 4.2; P (mg/kg): 32.7; GW > -50: 9.9;
GW < -100: 53.1

TT-4: pH: 4.8; C/N: 10.1; K (mg/kg): 17.5; N (%): 0.20; C (%): 2.1; P (mg/kg): 6.3; GW > -50: 0; GW < -100: 66.1

Table G.4: Festuca rubra-Deschampsia-community

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Species no.	43	31	40	39	50	35	40	37	47	38	27	32	48	51	45
Total cover (%)	100	100	100	100	100		100	100	100	100					
Graminoids (cover %)	50	70	80	90	80			90		50					
Forbs (cover %)	50	90	60	40	80			30		50					
Mosses (cover %)	30	5	30	40	70			60		10					
Anthoxanthum odoratum-group															
Anthoxanthum odoratum	+	1a	1a	+	1b	+	1b	+	1b	.	+	.	+	+	1a
Rhytidiadelphus squarrosus	2b	2a	3	3	4	4	3	.	2a	.	4	3	3	3	2b
Trifolium pratense	+	1a	.	+	3	1b	1b	1a	.	.	1a	.	1a	1a	.
Plantago lanceolata	1b	1b	1b	1b	1b	.	+	+	.	.	1b	.	.	+	.
Trifolium repens	+	.	.	.	2a	1a	+	.	+	.	1a	.	1a	+	1a
Veronica chamaedrys	2b	1a	1a	+	.	+	1a	+	.	.	+	.	1a	.	.
Hieracium lactucella	+	.	.	+	.	1b	.	+	+	.	.	.	.	.	+
Leucanthemum vulgare-group															
Cerastium holosteoides	+	+	.	+	1a	+	.	+	.	.	+	+	+	+	+
Prunella vulgaris	1a	+	+	.	3	.	+	+	1a	.	+	.	+	.	1a
Leucanthemum vulgare	.	.	.	.	2a	+	1b	1b	.	.	+	.	+	+	.
Centaurea jacea-group															
Centaurea jacea	1a	2b	2b	+	2b	1b	2a	2a	1b	1b	2b	2a	+	1a	2a
Alchemilla vulgaris agg.	2b	2a	2a	1a	3	1b	2b	2a	.	1b	2a	2b	2b	2a	1a
Achillea millefolium	+	+	+	1a	1b	1b	2a	1b	.	1a	1b	2a	1a	1a	.
Agrostis tenuis	.	1a	1a	1a	2b	1b	1a	1b	2a	.	1a	2a	1a	1b	1b
Briza media	+	+	1a	+	2a	+	+	+	1a	.	.	1a	1a	+	+
Achillea ptarmica	.	.	1a	.	2a	1a	+	1a	.	2a	1a	+	1b	1a	1a
Galium boreale	+	2a	.	.	1a	1a	1a	+	.	1a	1a	1b	1b	1a	.
Luzula campestris	+	.	1a	1a	2a	+	.	1a	1b	+	.	.	+	1a	+
Stellaria graminea	.	1a	+	+	.	+	+	+	.	+	+	.	+	+	+
Potentilla erecta	1b	2a	2a	2a	1a	1a	.	.	1b	.	.	.	1b	1b	1a
Galium mollugo	1a	2b	1b	.	+	.	1a	+	+	1a	.	.	.	+	.
Carex pallescens	+	.	.	.	1b	.	.	+	1a	2b	.	.	+	+	.
Dactylis glomerata	.	.	1a	.	+	.	1a	.	.	.	1a	1b	.	.	.
Deschampsia cespitosa-group															
Deschampsia cespitosa	3	1a	2a	2a	3	1a	2a	1b	3	2a	2a	1b	1b	1a	2a
Filipendula ulmaria	1b	2b	1a	+	2b	+	1a	1a	2b	2a	1a	1b	1b	1b	2b
Geum rivale	1a	1a	2b	1a	2b	1a	2a	1b	2a	2b	1a	1a	1b	2a	1b
Ranunculus acris	1a	1a	2a	2a	2a	1a	1b	1a	1b	1b	1a	1b	1b	1b	1b
Vicia cracca	1a	3	1a	1a	2a	1a	1a	+	1b	+	1a	1a	+	+	1a
Festuca rubra ssp. rubra	.	2a	4	5	3	4	4	4	2a	2a	4	2b	4	3	1b
Galium uliginosum	+	.	+	+	+	+	1a	+	1a	+	+	.	+	+	+
Lathyrus pratensis	+	.	+	+	1a	1a	.	+	1a	+	.	1a	1a	+	1a
Ranunculus auricomus agg.	1a	.	1a	.	2a	1a	1b	1a	1b	1a	.	+	1a	1b	1b
Rumex acetosa	+	.	1b	1b	1a	1a	1a	.	1a	1a	.	+	1a	+	+
Poa pratensis	+	1a	1a	1a	.	.	.	.	1a	+	.	1a	.	.	.
Phleum pratense-group															
Festuca pratensis	+	1a	1a	+	2a	+	2b	1a	2a	.	.	1a	1b	1b	2a
Phleum pratense	.	1a	1a	1a	2a	.	1a	+	1b	+	.	2a	+	1a	1b
Angelica sylvestris-group															
Angelica sylvestris	1b	2b	1a	+	.	.	.	.	+	+	.	+	.	.	1a
Trollius europaeus	.	1a	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex panicea-group															
Carex panicea	+	1a	1b	1b	2b	.	.	.	2a	2a	.	+	+	1a	+
Carex nigra	+	.	1a	.	+	.	.	.	1a	.	.	.	.	+	+

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Agrostis canina	.	.	.	.	1a	.	.	.	1a	.	.	.	1a	.	1a
Lychnis flos-cuculi-group															
Climacium dendroides	2b	.	.	.	1a	.	.	.	2a	2a	.	.	3	3	2b
Lychnis flos-cuculi	.	.	.	.	1b	.	+	+	1a	.	.	.	+	.	+
Calliergonella cuspidata	.	.	.	.	+	.	.	.	.	.	.	1a	1a	1a	1a
Cardamine pratensis	.	.	.	.	.	+	+	.	+	.	.	.	+	.	+
Carex disticha-group															
Juncus filiformis	1a	.	.	1a	.	.	.	.	2a	1a	.	.	1b	2a	1b
Potentilla anserina	.	.	+	+	+	.	.	.	1a	+	.	.	.	.	+
Carex disticha	.	.	.	.	.	.	.	.	.	.	.	+	1a	2a	2a
Carex cespitosa	.	.	1a	.	.	.	.	.	1a	.	.	.	.	.	.
Valeriana officinalis	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Further species															
Carex leporina	.	.	+	.	.	.	+	+	1b	.	+	.	1a	+	+
Equisetum arvense	1a	.	1a	1a	.	.	.	1a	.	1a	+	.	.	.	.
Hypericum maculatum	+	2b	1a	2b	+	+	.	.	.	.	.	.	.	.	.
Ranunculus repens	.	.	.	.	.	.	.	.	+	.	.	+	+	.	1a
Sesleria caerulea	1a	.	.	.	.	1b	.	+	.	.	.	.	1b	.	.
Viola palustris	1a	.	2a	2a	.	.	.	.	2a	.	.	.	.	.	.
Alopecurus pratensis	.	.	.	.	1a	.	1a	.	.	.	.	.	.	.	1a
Carex flava	.	.	.	+	1a	.	.	.	.	+	.	.	.	.	.
Cirsium oleraceum	.	.	.	.	.	.	.	.	.	+	.	.	+	1a	.
Geranium palustre	.	.	.	.	.	+	.	.	+	.	.	.	2a	.	.
Mentha arvensis	.	.	1a	.	.	.	.	.	1a	.	.	.	.	.	+
Platanthera bifolia	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.
Salix bicolor	.	.	.	.	+	1a	.	.	.	1a	.	.	.	.	.
Salix myrsinifolia	.	.	.	1b	.	.	.	.	.	1a	.	.	.	1a	.

Miscellaneous species

Agrostis stolonifera A98-31:1a; Alnus incana A98-32:1a; Anthriscus sylvestris A98-19:+; Betula pubescens A98-32:1a; Calamagrostis canescens A98-32:1b, TT-2:1a; Calamagrostis stricta A98-32:+, TT-10:+; Calliergon cordifolium TT-10:1a; Caltha palustris TT-10:+, TT-12:+; Campanula glomerata A00-11:+, A98-20:+; Campylium stellatum TT-2:+; Carex acuta TT-9:+; Carex canescens TT-10:+; Carex hirta A98-31:+; Carex pulicaris TT-9:+; Carex vulpina A98-31:1a, TT-10:1a; Carum carvi A00-11:+; Cerastium arvense A98-19:+; Cirriphyllum piliferum TT-6:1a; Cirsium palustre A98-30:+; Cynosurus cristatus A98-19:+; Dactylorhiza incarnata A98-30:+, A98-32:+; Danthonia decumbens A98-52:+; Drepanocladus aduncus TT-10:+, TT-12:+; Festuca ovina A98-30:2a, A00-11:3; Galium palustre A98-31:+; Glechoma hederacea TT-2:+; Helictotrichon pratense A98-19:1b; Helictotrichon pubescens A98-52:1a, A98-19:+; Hieracium pilosella A98-19:+; Juncus conglomeratus A98-50:+, A98-31:1a; Knautia arvensis A98-48:1a; Linum catharticum A00-11:1

Column no. & plot ID:

1) A98-30; 2) A98-48; 3) A98-50; 4) A98-52; 5) A00-11; 6) TT-6; 7) A98-19; 8) A98-20; 9) A98-31; 10) A98-32; 11) TT-5; 12) TT-2; 13) TT-9; 14) TT-10; 15) TT-12

Habitat parameters:

TT-9: pH: 5.0; C/N: 9′.9; K (mg/kg): 58.7; N (%): 0.41; C (%): 4.0; P (mg/kg): 9.9; GW > -50: 21.6; GW < -100: 39.4

TT-12: pH: 5.4; C/N: 10.0; K (mg/kg): 130.2; N (%): 0.49; C (%): 4.9; P (mg/kg): 36.2; GW > -50: 38.1; GW < -100: 16.8

Table G.5: Alopecurus pratensis dominated communities

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Community no.	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	5	5
Species no.	36	46	33	43	31	30	39	36	50	41	32	28	29	38	42	38	36	25	25	27	35	37	35	36	32	16	31	36	20	25	18	18	16	33	17	30	27
Total cover (%)	100	100	100	100			100	100			95			100	100	100	100	90	80	90		100				100	100	100	100								
Graminoids (cover %)	40	60	25	90			100	70			90			60	50	80	80	90	80	70		40				30	70	80	90								
Forbs (cover %)	70	40	75	50			50	70			80			60	50	80	80	40	60	70		100				80	50	50	70								
Mosses (cover %)	20	10	0	0			20	0			1			3	5	75	50	0	5	0		0				0	0	0	0								
Alopecurus pratensis-group																																					
Alopecurus pratensis	1b	1a	+	2a	1b	1b	2a	1b	1a	2a	1a	.	1a	.	1b	3	3	4	4	4	1b	+	.	.	1a	2a	2a	2a	4	4	3	3	3	2a	2b	2a	2b
Stellaria palustris	.	.	.	.	.	.	.	1a	1a	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	1a	1a	+	1a
Phleum pratense-group																																					
Phleum pratense	2a	1b	1a	2a	.	1a	2a	2a	2a	1a	1a	2a	1a	1a	1b	3	3	3	3	3	1b	1b	+	2a	2a	.	1b	2b	2b	2b	.	1a	+	.	.	1a	.
Festuca pratensis	.	.	.	2b	+	.	1b	1a	1a	2a	.	.	.	1b	1b	2a	2b	2b	2a	1b	1b	1a	.	2a	2a	.	+	2b	1a	2b	.	.	.	1a	.	+	1a
Centaurea jacea-group																																					
Achillea millefolium	2a	1b	1a	1a	1a	1b	1a	1b	1a	1b	+	1b	1a	2a	2a	2b	2b	2a	1b	1b	2a	2b	2a	2a	1b	.	+	.	.	1a	.	+	.	1a	.	.	.
Achillea ptarmica	+	1b	+	1b	.	.	1b	2a	1a	3	+	1b	1b	.	1a	2a	2a	2a	2a	1b	1a	2a	2a	1b	2a	.	+	1b	1a	+	.	1a	.	.	.	1a	+
Alchemilla vulgaris agg.	2a	1b	2a	2a	+	1a	1b	1b	.	2a	+	1a	1a	2b	1a	2b	2a	.	.	2a	2b	2b	3	2b	2b	.	.	2a	.	.	.	.	.	+	.	1a	.
Galium mollugo	2b	1a	1a	1a	1a	1a	+	+	.	.	1b	2b	1a	2a	2a	1b	2b	2a	2a	1b	1a	2a	2b	.	2a	.	.	.	.	.	.	.	1a	.	.	.	.
Galium boreale	3	.	+	.	2a	.	2b	3	2a	1b	.	.	1a	.	1a	3	2b	.	.	2a	1b	3	2a	2a	2b	.	1a	.	.	.	1b	+	.	.	.	1b	.
Carex pallescens	+	.	+	+	+	+	.	1b	+	1a	.	.	+	+	.	.	1a	+	.	.	+	.	.	1b	+	.	+	+	.	.	.	+	.	1a	.	+	.
Centaurea jacea	1b	1a	1a	1a	.	.	1a	3	2a	2a	.	.	.	2a	2a	2b	2b	2a	1b	.	2a	2b	2a	3	2a	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis tenuis	.	.	.	2a	1a	.	1b	2a	1a	.	.	.	.	3	.	2a	2b	2a	.	2b	2a	1b	+	1b	.	.	.	1b	.	.	+	.	+	.	+	.	.
Stellaria graminea	1a	+	+	+	.	.	.	+	1a	1a	.	1a	.	+	+	1a	.	+	.	.	+	1b	1b	.	1b	.	.	.	2a	+	.	.	.	.	.	.	.
Dactylis glomerata	.	+	+	.	.	.	1b	.	.	.	+	2a	.	1b	1b	3	2a	2a	1b	.	1b	2a	+	2a	1b	.	.	.	.	1b	.	.	.	.	.	.	.
Luzula campestris	.	.	.	+	+	.	1a	1a	+	.	.	.	+	+	+	.	.	.	.	.	+	1a	.	1a	.	.	.	.	.	.	.	.	.	.	.	.	.
Potentilla erecta	.	1a	.	.	.	1a	1b	2a	1a	1a	.	.	1a	.	.	.	.	.	.	.	.	1a	2a	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Briza media	.	.	.	1a	.	.	.	.	.	.	.	.	.	.	.	.	1b	+	.	.	1a	+	.	1a	.	.	.	1a	.	.	.	.	.	.	.	.	.
Anthoxanthum odoratum-group																																					
Anthoxanthum odoratum	.	1a	+	1a	.	.	1a	.	+	+	.	.	.	+	1b	1a	2b	.	.	.	+	+	.	1b	1a	2a	.	1a	.	.	.	.	.	.	.	.	.
Rhytidiadelphus squar.	2a	2a	.	.	.	2a	2b	.	1a	3	.	.	.	+	1a	4	.	.	.	.	3	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium pratense	.	.	.	1a	.	.	.	.	.	1a	.	.	.	1b	2a	2b	2b	.	.	1b	1a	1b	2a	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica chamaedrys	.	.	.	+	.	+	+	.	.	.	+	1b	.	1a	1a	1a	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.
Trifolium repens	.	+	.	1a	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	1b	1a	.	.	.	.	.	.	1a	1a	1a	.	.	.	.	.	.	.
Plantago lanceolata	+	.	.	.	.	.	.	.	.	.	.	.	.	1a	.	.	.	.	.	.	.	.	.	2a	.	.	.	.	.	.	.	.	.	.	.	.	.
Angelica sylvestris-group																																					
Angelica sylvestris	+	+	.	+	+	1a	2a	.	.	.	2a	4	.	.	+	.	1a	2a	2a	1a	+	1a	.	.	+	1a	+	.	2a	.	.	.	.	1b	.	+	.
Trollius europaeus	2b	.	.	.	.	+	.	.	.	.	2b	1b	2b	.	.	1b	2a	.	.	.	.	.	.	.	.	.	.	1a	.	.	.	.	.	.	.	.	.

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Lychnis flos-cuculi-group																																					
Lychnis flos-cuculi	+	+	+	1a	.	.	.	.	1b	1b	+	.	.	.	+	1b	1a	+	1b	1a	+	1a	.	.	.	.	+	1a	.	1a	.	.	.	1a	.	.	+
Calliergonella cuspidata	+	.	.	.	.	2a	.	.	2b	3	.	.	.	.	.	1a	3	.	1b	.	.	.	.	.	.	.	.	.	.	.	.	.	1a	1b	.	2a	.
Cardamine pratensis	.	.	.	+	+	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	1a	+	.	+	.	.	+	+	.	.
Climacium dendroides	2a	.	.	.	.	.	.	.	3	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1a	.
Deschampsia cespitosa-group																																					
Deschampsia cespitosa	2a	3	1b	2a	2b	2b	2b	3	2a	2a	3	+	3	+	1b	3	.	3	2a	3	2a	2b	1b	2a	1b	.	2b	1a	2b	1a	2b	1a	+	3	2a	3	2a
Filipendula ulmaria	1b	1a	4	1b	3	3	1a	2b	2b	2b	2b	2b	3	2a	.	.	2b	3	3	3	+	2b	2a	1b	2b	5	2a	1b	2b	2b	3	3	4	3	2b	3	3
Vicia cracca	1b	1b	1a	1a	1b	2a	1b	2a	1b	1a	1b	.	2a	1a	+	1b	2a	1b	1a	1b	1a	1b	1b	1b	1a	+	+	1a	1b	.	1b	2a	2a	2a	1a	1b	1b
Festuca rubra ssp. rubra	3	1b	1a	3	2a	2a	3	2a	2b	2a	4	2a	2b	1b	1b	3	3	2b	2b	2b	2b	1b	.	2b	2a	.	2a	2a	2a	2a	2a	1b	+	2b	.	1b	2a
Lathyrus pratensis	1b	1b	1a	1a	1b	1b	+	1a	1a	.	1b	1b	1b	1b	+	1b	2a	+	1a	1b	1a	1b	.	.	1a	1a	1a	1a	.	+	1b	1b	1b	2a	1a	1a	1b
Ranunculus acris	1b	1a	1a	2a	2a	1b	2a	2a	2a	2a	2a	1a	2a	1b	1b	2a	1a	.	1a	2a	+	2b	2a	1b	2a	.	1a	1b	1b	.	1a	1a	+	1b	.	1b	+
Ranunculus auricomus agg.	1b	1a	.	1b	1b	1b	+	2a	2a	2a	1a	1a	1b	.	1a	2a	1a	1b	1b	2b	.	1a	.	.	1a	+	1a	1b	.	2b	1a	.	+	1b	1b	1b	+
Rumex acetosa	1a	1a	+	1a	1a	1a	2a	2a	1a	2a	+	.	1a	1a	1a	2a	2a	+	.	+	+	2a	1b	1b	1b	.	.	1a	1a	.	1a	1a	.	1a	.	1a	+
Geum rivale	2a	1b	2a	1b	2a	2b	2a	2b	2a	1b	2a	.	2b	1b	1a	.	2a	1a	.	2a	1a	1a	.	2a	1a	.	2a	1b	.	.	2a	2a	.	2b	2b	1b	2b
Poa pratensis	2b	2a	1a	.	1a	1a	1b	.	+	1a	.	+	.	1a	1a	2a	.	.	.	2a	.	1a	.	.	+	.	1a	+	1a	2a	1b	1a	.	+	+	1a	1a
Galium uliginosum	.	1a	+	+	+	+	+	+	1a	1a	+	.	.	.	.	1a	.	+	.	.	.	1b	+	.	+	+	+	+	.	.	.	.	.	+	+	.	+
Caltha palustris-group																																					
Galium palustre	+	.	.	.	.	.	.	.	1a	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	.	.	+	+	.	.	+
Ranunculus repens	.	.	.	.	.	.	.	.	1b	2b	.	.	.	.	.	.	.	.	.	1a	.	.	.	.	.	.	1b	1b	2b	.	.	.	.	.	.	.	.
Caltha palustris	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1b	1a	.	.	.	.	.	.	1a	.	.
Carex disticha-group																																					
Carex cespitosa	.	+	.	.	.	.	2b	3	1a	.	1a	.	.	.	.	1b	1a	.	.	.	.	1a	.	.	.	+	1b	.	.	.	.	.	.	.	.	.	3
Valeriana officinalis	.	.	.	+	1a	.	.	.	1a	.	.	.	2a	.	.	.	.	.	.	.	.	.	.	.	.	1b	1b	1a	.	.	+	.	.	1b	1b	.	1a
Carex disticha	.	.	.	1a	.	.	.	3	4	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	1b	1a	.	.	.	.
Juncus filiformis	.	+	.	.	.	.	2b	.	1a	3	.	.	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1b	.	2b	.
Potentilla anserina	.	2a	.	1a	.	2a	.	.	1b	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.
Leucanthemum vulgare-group																																					
Cerastium holosteoides	.	.	.	+	.	.	+	.	.	+	.	.	.	+	+	1a	.	.	.	.	+	.	+	+	.	.	.	+	+	+	.	.	.	.	.	.	+
Prunella vulgaris	.	.	.	+	.	.	.	.	.	.	.	.	.	+	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Leucanthemum vulgare	.	.	.	.	.	.	.	.	.	.	.	.	.	1a	1b	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex panicea-group																																					
Carex panicea	.	+	.	+	1a	2a	2b	2b	.	1b	+	.	1a	.	.	.	.	.	.	.	.	.	+	1b	.	.	.	.	.	.	+	.	.	1b	.	2a	1b
Carex nigra	.	+	.	.	.	.	1b	1a	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	1a	+
Agrostis canina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Taraxacum officinalis-group																																					
Taraxacum officinale agg.	.	.	1a	.	.	.	.	1b	+	.	.	1b	.	1b	2a	3	2a	1b	2b	3	.	.	.	2a	.	+	+	2a	1a	3	.	.	.	.	.	.	.

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Veronica longifolia	.	.	+	.	2b	.	.	2a	1b	1a	.	2a	.	.	.	.	1a	.	1b	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Further species																																					
Anthriscus sylvestris	.	.	.	.	.	.	+	.	.	.	1b	1a	.	2a	+	2a	.	.	.	.	.	.	.	.	.	1a	.	.	+	.	.	.	.	+	.	1a	+
Campanula glomerata	+	.	.	.	.	.	.	.	.	.	.	.	.	1b	.	1b	1a	.	+	+	+	2a	1b	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Heracleum sphondylium	+	.	.	.	.	.	.	.	1a	.	+	.	.	2a	2a	3	1b	.	.	.	.	.	1a	.	.	.	.	.	.	.	.	.	1a	.	.	.	.
Viola canina ssp. montana	1a	.	+	+	+	.	.	.	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1a	.	.	1a	.	.	.	.	.	.	1a	.	.	.
Carex vulpina	.	.	.	+	.	.	.	.	.	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1b	1b	.	+	.	.	.	2a	3	.	+
Helictotrichon pratense	.	.	+	2a	+	.	.	.	.	.	+	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1a	.	.	.	.	.	.	.	+	.
Agrostis stolonifera	.	1b	1b	.	.	.	.	.	+	.	.	.	.	.	1b	.	.	.	.	.	.	.	.	.	1a	+	.	.	.	.	.	.	.	.	.	.	.
Crepis paludosa	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	+	+	1a	.	.	.	.
Mentha arvensis	.	1a	.	.	.	.	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1a	1a	2a	1a
Brachythecium mildeanum	.	.	.	.	.	.	.	.	1a	.	.	.	.	.	1a	1a	1a	.	.	.	.	.	.	1a	.	.	.	.	.	.	.	.	.	.	.	.	.
Campanula patula	.	+	.	.	.	.	.	.	.	.	.	.	.	.	2a	1a	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Equisetum arvense	.	1a	1a	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium umbellatum	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	2b	2a	2a	2a	.	.	.	.	.	.	.	.	.	.	.	.
Hypericum maculatum	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	2a	2b	+	2a	.	.	.	.	.	.	.	.	.	.	.	.
Sesleria caerulea	1a	.	.	.	+	1a	.	.	.	.	1a	.	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Thalictrum lucidum	1a	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	1a	.	.	.	.	.	.	.	.	.	.	.	1a	.	.	.	.	.	.	.
Carex acuta	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Poa palustris	.	.	.	.	.	.	.	.	1b	.	.	1b	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1b	.	.	.	.	.	.	.
Scorzonera humilis	.	.	.	.	.	.	.	2a	.	.	.	.	.	.	.	.	.	.	.	.	.	3	2a	.	1a	.	.	.	.	.	.	.	.	.	.	.	.
Thuidium philibertii	+	.	.	.	.	.	.	.	1a	.	.	.	.	1a	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.

Miscellaneous species

Betula pubescens A98-16:1a; Bromus inermis A98-17:2b; Calamagrostis epigejos A98-14:1b, A98-16:2a, A98-18:2b; Calliergon cordifolium KT-10:2b, KT-9:3; Campylium stellatum A00-15:+; Carex flava A00-07:+; Carex hartmanii A98-16:+, KT-2:+, KT-9:1b; Carex hirta A98-51:1a, LT-6:+; Carex lasiocarpa A00-22:1a; Carex leporina A98-16:+, A98-51:1b; Carex muricata A00-22:+; Carlina vulgaris ssp. longifolia A98-27:1b; Carum carvi A00-13:+, TT-3:1a, A00-16:+; Cirriphyllum piliferum A98-17:+, A98-27:1a; Cirsium heterophyllum A00-22:3, LT-6:3; Cirsium oleraceum A00-18:+; Cynosurus cristatus TT-3:+; Equisetum pratense KT-1:2b; Eurhynchium hians A98-27:1a, LT-7:+; Festuca ovina LT-6:1a, KT-2:2a; Geranium palustre A98-14:+, A00-07:1a; Geranium pratense A98-17:2a; Glechoma hederacea A98-44:1a, A00-15:1b, A98-39:+; Helictotrichon pubescens A98-18:+, LT-5:+, LT-6:+; Hierochloe odorata A98-18:1a, A98-44:+, LT-11:3; Hypericum hirsutum KT-1:1a; Juncus effusus KT-10:+; Knautia arvensis KT-1:1a, KT-2:+; Leontodon autumnalis A98-44:1b, A98-27:+; Luzula multiflora A00-22:+, KT-2:1a, A98-41:+; Lysimachia vulgaris A98-16:+, KT-1:+; Myosotis scorpioides A98-39:+, A98-41:+; Ophioglossum vulgatum LT-5:+, KT-2:1a; Phalaris arundinacea KT-1:1b, TT-3:+; Plagiothecium laetum LT-11:+; Poa trivialis A98-27:+, A98-39:+, A00-16:1b; Polygonum amphibium A98-16:+, A98-17:+; Potentilla palustris LT-16:+; Rhinanthus minor A00-09:+, A00-06:1b, KT-2:1b; Rhizomnium punctatum A00-09:1a; Salix bicolor A98-16:+, A98-18:1b, KT-9:3; Salix myrsinifolia A98-16:+, KT-5:2a, KT-3:1a; Salix rosmarinifolia KT-9:+; Scirpus sylvaticus KT-5:1b; Scutellaria hastifolia KT-10:+, A00-16:1b; Senecio paludosus LT-17:+; Succisa pratensis KT-2:+; Thalictrum aquilegiifolium A98-37:+; Trifolium medium A00-06:2b, KT-9:3; Veronica scutellata A98-16:+; Viola canina ssp. canina LT-11:+, A00-07:1b, LT-15:1a; Viola epipsila LT-11:1a, LT-7:2a; Viola palustris A98-16:+, A98-51:1a

Community types:

4) Alopecurus pratensis-Galium mollugo-community; 5) Alopecurus pratensis-Deschampsia-community

Column no. & plot ID:

1) A98-14; 2) A98-16; 3) A98-18; 4) A98-44; 5) LT-5; 6) LT-11; 7) A98-51; 8) A00-07; 9) KT-10; 10) KT-5; 11) A00-22; 12) KT-1; 13) LT-6; 14) A98-17; 15) A98-27; 16) A00-09; 17) A00-13; 18) A00-14; 19) A00-15; 20) A00-18; 21) TT-3; 22) A00-06; 23) KT-2; 24) KT-9; 25) KT-3; 26) A98-37; 27) A98-39; 28) A98-41; 29) A98-45; 30) A00-16; 31) LT-4; 32) LT-3; 33) LT-2; 34) LT-16; 35) LT-17; 36) LT-7; 37) LT-15

Habitat parameters:

LT-6: pH: 5.5; C/N: 10.5; K (mg/kg): 24.0; N (%): 0.49; C (%): 5.2; P (mg/kg): 16.9; GW > -50: 7.2; GW < -100: 82.2

KT-2: pH: 5.1; C/N: 11.0; K (mg/kg): 24.0; N (%): 0.22; C (%): 2.4; P (mg/kg): 16.9; GW > -50: 0; GW < -100: 75.1

KT-3: pH: 5.2; C/N: 10.0; K (mg/kg): 14.9; N (%): 0.33; C (%): 3.3; P (mg/kg): 13.4; GW > -50: 0.3; GW < -100: 80.7

LT-3: pH: 5.5; C/N: 9.9; K (mg/kg): 21.8; N (%): 0.43; C (%): 4.2; P (mg/kg): 32.7; GW > -50: 7.9; GW < -100: 82.2

LT-17: GW > -50: 23.0; GW < -100: 44.2

Table G.6: Molinion communities

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Community no.	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	7
Species no.	43	43	41	40	40	31	42	37	44	33	43	40	37	47	36	35	53	30	36	44	31	41	39	38	24	22	23	39	28	11
Total cover (%)	100	95	100	95	100						100	100	100	100			100					100						100		
Graminoids (cover %)	30	40	80	70	70						90	80	80	75			50					70						80		
Forbs (cover %)	70	60	80	70	80						50	80	70	75			75					80						90		
Mosses (cover %)	40	20	70	5	30						80	60	80	80			70					50						1		
Selinum carvifolia-group																														
Scorzonera humilis	2b	2a	.	3	3	3	3	1a	3	1a	.	3	3	2a	2b	1b	.	2b	+	.	3	2a	+	+	1a	+	1a	.	2a	.
Selinum carvifolia	.	2a	1b	1a	1a	+	1a	+	2a	2a	+	2a	2a	.	+	3	.	.	1b	.	2a	2b	2b	1b	1b	1a	.	1a	2b	.
Thuidium philibertii	+	+	1a	1a	3	3	2b	.	1a	3	1a	2b	4	.	.	3	3	2b	4	4	.	3	3	1a	1a	.	.	.	1a	.
Succisa pratensis	2b	+	2b	1a	1a	2a	2a	1b	1a	1b	1b	2a	2a	2a	1b	1a	+	.	.	.	.	.	2b	1a	.	.	.	+	.	.
Viola canina ssp. montana	.	2a	.	+	.	1a	+	+	+	.	.	.	+	2a	.	1b	1a	1a	.	.	+	+	1b	1b	.	.	+	1b	1a	.
Campylium stellatum	.	.	.	1a	1a	.	1a	.	1a	.	.	.	+	.	.	.	+	+	.	.	.	.	1a	.	.	.	.	.	.	.
Iris sibirica	.	.	.	1a	1a	.	1a	.	+	.	.	.	.	+	.	.	.	3	.	.	.	.	.	.	.	.	2a	1a	.	.
Geranium palustre-group																														
Melampyrum nemorosum	.	.	.	.	.	.	.	.	.	.	.	.	.	2b	.	2b	.	.	.	.	.	3	3	3	4	3	2a	3	3	4
Geranium palustre	.	.	.	.	1b	.	.	.	.	.	.	.	.	.	.	2b	.	.	3	.	1a	+	2a	1b	.	.	.	2b	4	.
Thalictrum lucidum	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	1a	1b	1b	2a	1b	1b	+	1b	.
Trifolium medium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2a	1b	1a	.	.	2a	.	.	.
Sesleria caerulea-group																														
Sesleria caerulea	2b	2b	4	4	4	3	2b	3	2b	2a	4	4	4	4	3	1a	+	+	.	.	.	.	2a	+	.	.	.	.	.	.
Festuca ovina	1b	.	3	2a	1a	2a	+	+	2a	1a	3	3	2a	1a	.	.	2a	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex pulicaris	.	.	.	.	1a	.	+	.	.	.	1b	1b	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Calamagrostis epigejos-group																														
Calamagrostis epigejos	.	1b	.	.	3	+	2a	+	2a	2a	2a	.	.	.	2b	.	.	2a	3	2a	1b	.	.	.	.	.	.	.	.	.
Carex flava	.	.	+	1a	+	1a	+	1a	1b	2a	.	1a	.	+	+	.	.	.	.	1a	.	.	.	.	.	.	.	1a	.	.
Equisetum palustre	.	.	1a	.	+	+	+	.	.	.	.	1a	.	+	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.
Centaurea jacea-group																														
Galium boreale	1a	2b	3	1b	2a	2a	1a	2a	1b	2a	2a	2a	1b	1b	1b	2a	3	1b	1a	1b	2a	2b	2a	2a	2a	1a	1b	2b	3	1b
Centaurea jacea	2a	2b	1b	1a	2b	1b	2a	1b	2a	2b	2b	1b	2a	1b	.	1a	2b	2a	2a	2a	1a	1a	1a	+	1b	.	.	+	+	.
Potentilla erecta	2a	2a	2a	2a	2a	2a	1b	2a	2a	2a	2a	2b	2a	2a	1b	1a	+	1b	.	1b	2a	1a	1a	.	1a	.	.	2b	1a	.
Alchemilla vulgaris agg.	2a	2a	2a	.	2a	2b	1b	1a	+	2a	2b	2a	+	2b	.	1b	1b	2a	.	.	.	3	2b	1b	.	.	.	1a	.	.
Achillea ptarmica	+	.	+	+	+	1a	1a	+	1a	1a	.	.	+	+	+	.	+	.	.	+	1a	.	.	.	.	.	.	+	.	.
Briza media	.	.	1a	1a	+	1a	1b	+	1b	1a	1a	2a	1a	+	.	.	1b	.	.	+	.	+	+	.	.	.	.	.	.	.
Agrostis tenuis	.	+	1a	+	1a	.	.	.	.	.	.	1a	.	1a	.	+	1a	.	.	.	.	1a	+	.	+	.	+	1a	+	.
Galium mollugo	.	1a	.	.	+	.	.	+	.	.	.	.	1a	+	.	.	+	.	2a	.	.	1a	1a	2a	.	1b	1b	+	.	1b

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Luzula campestris	+	1a	.	.	+	+	+	.	+	+	1a	1a	+	.	.	.	+	+	.	.	.	.	+	.	.	.	.	.	.	.
Achillea millefolium	1b	1a	.	.	.	.	+	+	.	.	1a	.	+	+	.	.	+	.	.	.	.	.	+	.	.	.	+	+	.	.
Carex pallescens	1a	1b	1a	.	.	.	.	.	.	.	+	1a	.	+	.	.	+	.	+	+	.	+	.	.	.	.	.	.	.	.
Stellaria graminea	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	+	.	1a	.	+	.	.
Dactylis glomerata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	2a	.	1b	.	.	1b	.	.	2a
Deschampsia cespitosa-group																														
Deschampsia cespitosa	1b	1a	3	3	1a	2b	1a	2b	1b	3	1a	2b	+	1a	2a	3	2b	1b	1b	3	1b	2a	2a	4	1a	3	1b	2b	2a	1a
Filipendula ulmaria	1b	1b	2a	2b	3	1a	2b	+	2b	1b	+	1a	+	+	1b	.	2b	2b	3	.	3	+	+	1a	4	1b	1b	2b	2a	2a
Ranunculus acris	2a	1b	2a	2a	1b	1b	1b	1b	1b	2a	1b	1b	+	1a	1a	1b	1b	2a	1b	2a	2b	1b	1b	2a	.	.	.	1a	1a	.
Ranunculus auricomus agg.	2a	1a	2a	1b	1a	1a	1a	1b	1a	1b	1a	1a	+	1a	1b	.	1a	1a	1a	1b	1b	1a	1a	.	1a	1a	.	1a	+	.
Geum rivale	+	2a	1a	1a	2a	1b	1a	1a	1b	1b	1a	1a	+	.	1a	1b	3	2a	2a	1a	1b	1a	1a	1b	1a	.	.	1a	.	.
Vicia cracca	1a	+	+	1a	1a	1a	1a	1b	1b	1a	1b	1a	+	1a	1a	.	+	1b	1a	1b	2a	+	.	.	.	+	.	.	.	.
Rumex acetosa	+	+	+	+	+	.	+	.	+	.	.	+	.	+	.	+	.	1a	1a	1a	.	1a	1a	1a	1a	2a	1a	1a	1a	.
Festuca rubra ssp. rubra	1b	2a	1a	.	.	1a	+	+	1a	+	.	.	.	.	+	3	.	1a	1a	1a	.	3	3	2a	.	2b	2a	1a	+	.
Poa pratensis	+	1a	.	.	1a	.	+	+	1a	.	.	.	.	1a	1a	1a	.	.	+	1b	.	1a	2a	1b	2b	2b	2a	+	1b	.
Lathyrus pratensis	+	1a	1a	+	+	1a	+	+	+	+	.	.	.	1a	+	.	+	1a	+	1a	+	.	.	.	.	.	.	.	.	.
Galium uliginosum	.	.	.	.	+	+	+	+	+	+	+	.	.	+	.	+	.	.	+	+	.	.	.	.	.	.	.	+	.	.
Angelica sylvestris-group																														
Angelica sylvestris	.	1b	2a	1a	.	1a	+	.	1a	2a	1a	2a	+	+	.	2b	1b	2a	1a	2a	.	+	1a	1b	1b	1b	1b	2b	2a	+
Trollius europaeus	.	.	.	.	.	.	+	.	+	.	2a	2a	+	1a	.	+	+	.	1a	2b	.	2b	2a	1a	.	2b	2a	2a	.	.
Lychnis flos-cuculi-group																														
Calliergonella cuspidata	+	+	1a	1b	1a	3	2b	.	+	.	1a	2b	1a	.	2a	3	.	.	+	1a	1a	1a	.	3	1a	.	.	1a	.	.
Climacium dendroides	3	2b	4	1a	.	3	.	.	.	3	.	.	1a	.	2a	3	3	.	2a	1a	.	1a	3	1a	.	.	.	.	1a	.
Lychnis flos-cuculi	+	+	+	+	.	.	.	.	.	+	.	.	.	.	1a	1a	+	.	+	1a	+	.	.	+	.	.	.	+	1b	.
Cardamine pratensis	.	.	+	.	.	.	+	+	+	+	.	.	.	.	1a	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.
Carex panicea-group																														
Carex panicea	+	.	2a	2a	+	2a	2a	1a	1b	2a	1a	2a	+	.	1b	.	1b	+	.	.	.	.	+	+	.	.	.	+	.	.
Carex nigra	+	+	.	.	.	.	.	.	.	.	.	+	+	1a	.	1a	.	.	.	.	.	2a	.	.	.	.	.	1a	1a	.
Agrostis canina	.	.	1a	.	.	.	.	.	.	.	.	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Carex disticha-group																														
Carex cespitosa	1a	.	.	1a	1a	.	.	.	.	.	.	.	.	.	.	2a	.	1b	1b	2a	1a	2a	.	.	4	3	4	.	2a	.
Valeriana officinalis	+	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	+	1b	+	1a	2a	.	1a	1b	1a	+	.	.	.	.
Carex disticha	.	.	.	2a	.	.	.	.	.	.	.	.	.	.	.	1b	.	.	.	2a	2a	.	.	1b	1b	.	.	4	4	.
Potentilla anserina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Further species:																														
Phleum pratense	.	.	+	1a	.	.	.	.	.	.	.	.	.	.	.	.	+	.	1a	1b	1b	+	.	.	.	+	1b	1a	.	.
Festuca pratensis	.	.	.	+	.	.	.	.	.	1a	.	+	.	.	1a	.	.	.	.	2a	1a	+	.	.	.	+	.	.	.	.
Prunella vulgaris	.	.	.	.	+	.	+	+	+	.	.	+	.	.	+	.	.	.	+	1a	.	.	.	.	.	.	.	.	.	.

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Rhytidiadelphus squarrosus	.	.	1a	.	.	.	.	.	.	.	3	2b	.	3	.	.	.	.	.	1a	.	3	3	1a	.	.	.	.	.	.
Anthoxanthum odoratum	.	+	+	.	.	.	.	.	.	.	+	1a	.	.	.	2a	+	.	.	1a	.	.	.	.	.	.	.	.	.	.
Drepanocladus aduncus	.	.	1a	1a	.	.	.	.	1a	.	.	.	+	.	+	1a	.	.	.	.	.	.	.	.	1a	.	.	.	.	.
Taraxacum officinale agg.	1b	1a	.	.	.	.	.	1a	.	.	1a	.	.	.	1a	.	.	.	+	.	1b	.	.	.	.	.	.	.	.	.
Viola canina ssp. canina	.	.	1b	.	1a	.	.	.	.	+	2a	1b	.	.	.	.	.	.	1a	.	.	.	.	.	+	.	.	.	.	.
Campanula glomerata	.	.	.	.	.	.	.	.	.	.	1b	.	1a	+	.	.	+	.	.	.	.	+	1b	.	.	.	.	.	.	.
Cerastium holosteoides	.	.	+	.	.	.	+	.	.	.	.	+	.	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.
Galium palustre	.	.	.	+	+	.	.	.	+	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.
Lysimachia vulgaris	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	1a	.	.	+	1a	.	.	.	+	.
Phragmites australis	.	.	.	+	.	.	.	+	.	.	+	.	+	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.
Trifolium pratense	+	+	+	.	.	.	.	.	.	.	1a	1a	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Fissidens adianthoides	+	.	.	.	.	.	1a	.	.	.	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.
Veronica chamaedrys	.	.	.	.	.	.	.	.	.	.	.	.	.	1a	.	.	+	.	.	.	.	1a	1a	.	.	.	.	1b	.	.
Calamagrostis canescens	.	.	.	.	.	.	.	+	.	.	.	.	.	.	1a	.	.	.	.	2a	2b	.	.	.	.	.	.	.	.	.
Carex acuta	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1a	.	.	.	.	.	2a	1a	.	.	.	.	1a	.
Geranium pratense	+	.	.	.	.	.	1b	.	1a	.	.	.	.	.	.	.	.	1b	.	.	.	.	.	.	.	.	.	.	.	.
Inula salicina	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	1a	.	.	.	.	.	.	1b	.	+	.	.	.	.	.
Luzula multiflora	.	.	1a	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1a	.	.	.	.	.	.	.	.	.	.
Melampyrum cristatum	.	.	.	.	1a	.	+	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Trifolium montanum	.	1b	.	.	.	.	.	.	.	.	.	.	.	2b	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.

Table G.6 continued …

Miscellaneous species:

Agrostis stolonifera A98-11:+; Alnus incana A98-34:1b, MT-8:4; Alopecurus pratensis A98-11:+; Anemone nemorosa A98-12:2a; Anthriscus sylvestris MT-4:1a, MT-7:2a; Aulacomnium palustre A00-29:3, A00-32:1a; Betonica officinalis A00-32:1a, MT-4:1b; Betula pubescens A98-11:+; Brachythecium mildeanum A00-32:1a, MT-1:1a; Caltha palustris A00-19:+, MH1T-8:1a; Campanula patula MT-2:1a, A98-34:+, MT-6:+; Carex acutiformis MH2T-3:+; Carex elata A98-12:+; Carex hartmanii A98-34:+; Carex riparia A98-11:+; Carex vaginata MH2T-5:1a; Carex vesicaria A98-11:+, A00-19:1a; Cerastium arvense A98-12:+; Cirriphyllum piliferum A00-01:1a, A00-32:1a; Cirsium heterophyllum A98-12:1b, A98-34:+; Cirsium oleraceum A00-05:1b, MH2T-5:1a, MH1T-8:1b; Cirsium palustre MH1T-8:+; Crepis paludosa MH1T-5:+; Dactylorhiza incarnata MH1T-5:+, A98-34:+; Danthonia decumbens A00-20:+, A00-29:+; Equisetum arvense A98-34:+; Equisetum pratense A98-12:+; Frangula alnus A00-01:+, A00-29:+, A98-34:1a; Glechoma hederacea MH1T-8:1a, MT-7:+; Heracleum sphondylium A98-34:+, MT-4:1a, MT-8:1a; Hieracium pilosella A00-29:+, A98-34:+; Hieracium umbellatum A98-12:+, A00-27:+; Hierochloe odorata MT-1:1a; Hylocomium splendens A00-01:3, A00-05:2b, A00-29:3; Juniperus communis ssp. communis A00-01:+; Leucanthemum vulgare A00-29:+, A98-34:+; Linum catharticum A00-01:1a, A00-05:1a, A00-20:+; Lythrum salicaria MH1T-2:+; Mentha arvensis A98-34:+; Molinia caerulea A00-29:1a; Myosotis scorpioides A98-11:+; Nardus stricta A00-29:+; Ophioglossum vulgatum MH1T-3:+, A00-01:1b; Phalaris arundinacea MH2T-2:2a, MT-8:2a; Plagiomnium elatum MT-2:1a, A98-34:+; Plantago lanceolata A98-34:1a; Platanthera bifolia A98-34:+; Poa palustris MH1T-2:1a, MH1T-8:1a, A00-31:+; Poa trivialis A98-12:+; Polygala amarella A00-01:1a; Populus tremula A98-11:+, A00-29:+; Rhamnus catharticus MH2T-7:+; Rhizomnium punctatum A00-03:1a, MH2T-7:1a; Salix pentandra A00-19:+; Salix starkeana A00-29:3; Sanionia uncinata A00-01:+; Stachys palustris MT-7:1a, MT-8:1a; Taraxacum palustre agg. MH1T-4:+, MH1T-3:+, MH1T-2:1a; Trifolium repens MH1T-3:+, MH2T-7:+, A00-01:+; Veronica longifolia MH1T-2:2a, MH2T-3:+, MH2T-2:1a; Viola epipsila A98-11:+, MH2T-7:1b; Viola palustris A98-11:2a, MH1T-8:+; Viola persicifolia A00-03:1b, MH1T-2:+, MH2T-2:1a; Viola uliginosa MH1T-2:+

Community type:

1) Sesleria caerulea-Deschampsia-community; 7) Melampyrum nemorosum-Deschampsia-community

Column no. & plot ID:

1) A98-11; 2) A98-12; 3) A00-03; 4) A00-19; 5) A00-27; 6) MH1T-4; 7) MH2T-6; 8) MH1T-3; 9) MH2T-7; 10) MH1T-5; 11) A00-01; 12) A00-05; 13) A00-20; 14) A00-29; 15) MH1T-2; 16) MT-2; 17) A98-34; 18) MH2T-5; 19) MH2T-3; 20) MH1T-8; 21) MH2T-2; ; 22) A00-32; 23) MT-3; 24) MT-4; 25) MT-5; 26) MT-6; 27) MT-7; 28) A00-31; 29) MT-1; 30) MT-8

Habitat parameters:

MH1T-4: pH: 5.6; C/N: 10.8; K (mg/kg): 26.7; N (%): 0.62; C (%): 6.7; P (mg/kg): 25.7; GW > -50: 22.5; GW < -100: 38.9

MH2T-6: pH: 5.5; C/N: 10.7; K (mg/kg): 18.7; N (%): 0.66; C (%): 7.1; P (mg/kg): 11.6; GW > -50: 30.3; GW < -100: 31.0

MT-3: pH: 5.3; C/N: 10.9; K (mg/kg): 59.5; N (%): 0.44; C (%): 4.8; P (mg/kg): 39.7; GW > -50: 25.9; GW < -100: 0

MT-5: pH: 5.2; C/N: 10.1; K (mg/kg): 80.1; N (%): 0.63; C (%): 6.3; P (mg/kg): 46.8; GW > -50: 15.7; GW < -100: 27.9

MT-7: pH: 5.5; C/N: 10.4; K (mg/kg): 26.6; N (%): 0.45; C (%): 4.7; P (mg/kg): 13.4; GW > -50: 4.8; GW < -100: 55.1

Table G.7: Carex cespitosa-Deschampsia-community

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Species no.	34	26	39	31	33	22	23	22	40	21	18	51	58	23	14	12	32	32
Total cover (%)	90			90				100				100	100		100		100	100
Graminoids (cover %)	45			80				40				80	100		80		50	50
Forbs (cover %)	45			80				70				80	80		60		50	50
Mosses (cover %)	3			1				0				2	50		0		10	0
Carex disticha-group																		
Carex cespitosa	2b	2a	1a	2b	3	3	3	2b	+	3	4	2a	3	1a	3	4	2a	2a
Carex disticha	.	2a	1a	2b	.	.	2a	2b	2b	2b	2b	4	3	3	.	.	.	2a
Valeriana officinalis	+	1b	1a	+	1a	.	.	.	.	.	+	2a	+	1a	1a	1a	.	+
Juncus filiformis	.	.	.	.	.	.	.	.	1b	.	.	.	3	.	.	.	+	.
Caltha palustris-group																		
Galium palustre	+	+	+	+	+	+	.	.	.	+	+	+	+	.	.	.	.	.
Caltha palustris	.	.	+	.	1b	1a	.	.	2a	.	2a	2a	2b	.	1a	.	.	.
Ranunculus repens	.	.	.	.	1a	+	.	.	.	.	.	.	2a	.	1a	.	.	.
Alopecurus pratensis-group																		
Stellaria palustris	.	.	+	.	.	.	.	+	+	.	.	.	.	.	.	.	+	+
Alopecurus pratensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2b	2a	1b	2a
Calamagrostis canescens-group																		
Calamagrostis canescens	.	2a	3	3	3	1a	2a	.	2a	2a	.	3	.	.	.	.	.	.
Carex vesicaria	.	.	+	+	+	.	1a	.	.	1a	+	+	.	.	.	.	.	+
Viola uliginosa	.	.	.	2b	.	.	3	.	1b	2b	2a	2a	.	.	.	.	.	.
Lychnis flos-cuculi-group																		
Lychnis flos-cuculi	+	+	1a	.	+	.	.	.	.	+	.	1a	1a	2a	.	.	1a	1a
Calliergonella cuspidata	1a	.	.	+	.	2a	.	.	3	1a	.	+	2b	.	.	.	+	.
Climacium dendroides	1a	.	1b	.	1b	.	.	.	1a	.	.	+	2b	.	.	.	+	.
Cardamine pratensis	.	.	+	+	.	.	.	.	+	.	.	.	+	.	.	.	.	.
Deschampsia cespitosa-group																		
Filipendula ulmaria	2a	4	2b	4	3	2b	3	4	2a	4	3	2b	3	+	2b	3	2a	3
Lathyrus pratensis	1a	+	1a	1a	1a	1a	1a	+	1b	1a	1b	1b	1b	.	1b	1a	2a	1a
Ranunculus acris	2b	2a	2a	.	1b	2a	1b	+	2a	1a	1a	2a	1b	1a	.	+	2a	1b
Geum rivale	+	2a	2a	2a	1b	2b	2a	1a	.	2a	+	2a	2a	.	1a	.	2b	2b
Ranunculus auricomus agg.	2a	1b	1b	1a	1b	1b	1b	.	1b	1a	1b	2a	1b	.	+	.	2a	1a
Deschampsia cespitosa	2b	2a	3	2b	2b	4	.	.	3	1a	1a	3	3	1a	.	.	2a	2a
Vicia cracca	+	1a	1a	+	1a	.	1a	+	1b	1a	.	1b	1b	.	.	.	2a	1a
Festuca rubra ssp. rubra	1a	.	1b	+	1a	1a	+	.	1a	+	.	2a	3	.	.	.	3	2a
Poa pratensis	.	+	1a	+	.	.	+	.	+	.	.	1a	2a	+	.	.	1a	1b
Galium uliginosum	.	.	+	+	+	.	+	.	+	.	.	1a	+	.	.	.	+	.
Rumex acetosa	+	.	1a	.	.	.	1a	.	.	+	.	1b	+	.	.	.	1b	1a
Calamagrostis epigejos-group																		
Calamagrostis epigejos	1b	3	2b	2a	2b	1b	2a	1b	.	.	1b	.	+	.	.	.	.	.
Equisetum palustre	.	+	+	+	+	.	.	.	+	.	.	+	.	.	.	.	.	.
Carex flava	.	.	.	.	.	+	.	.	2a	.	.	.	+	1a	.	.	.	.
Angelica sylvestris-group																		
Angelica sylvestris	.	1a	2b	+	1a	2a	1a	1b	2a	1a	.	2a	2a	1a	.	.	1a	+
Trollius europaeus	.	.	1a	.	1a	.	.	2b	.	.	.	3	.	1b	.	.	.	.
Selinum carvifolia-group																		
Iris sibirica	1a	.	.	+	.	.	1a	.	.	.	+	+	.	.	.	.	+	+
Selinum carvifolia	2a	1b	.	+	.	.	1b	.	.	.	.	.	2a	1a	.	.	.	+
Succisa pratensis	+	.	.	.	.	1a	.	.	.	.	.	1b	1b	.	.	.	.	.
Campylium stellatum	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Thuidium philibertii	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Viola canina ssp. montana	.	.	.	.	.	.	.	.	.	.	.	.	1a	.	.	.	.	2a
Centaurea jacea-group																		

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Potentilla erecta	2a	+	1a	1a	.	1a	1b	1a	.	1b	.	1a	2a	.	.	.	.	1b
Galium boreale	.	1a	.	+	.	.	1b	2a	+	.	.	.	1b	2b	.	.	2a	+
Centaurea jacea	.	.	1a	.	.	.	.	+	2a	.	.	2b	2a	.	.	.	.	.
Achillea ptarmica	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	2a	1a
Carex pallescens	+	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	+	.
Luzula campestris	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	1a	+
Briza media	.	.	.	.	.	.	.	.	+	.	.	1a	+	.	.	.	.	.
Agrostis tenuis	.	.	.	.	.	.	.	.	.	.	.	1a	1a	.	.	.	.	.
Alchemilla vulgaris agg.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	2a
Dactylis glomerata	.	.	.	.	.	.	.	.	.	.	.	.	+	1a	.	.	.	.
Galium mollugo	.	.	.	.	.	.	.	+	.	.	.	1a	.	.	.	.	.	.
<u>Carex panicea-group</u>																		
Carex panicea	.	.	1b	+	.	2a	.	.	2a	.	.	1a	2a	.	.	.	.	.
Carex nigra	+	.	.	.	.	.	.	.	+	.	.	.	1a	.	.	.	.	+
Agrostis canina	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.
<u>Taraxacum officinale-group</u>																		
Taraxacum officinale agg.	+	+	+	.	+	.	.	.	.	.	.	+	.	.	+	.	2a	.
Veronica longifolia	1b	1a	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	1a
<u>Phleum pratense-group</u>																		
Phleum pratense	.	.	+	.	1a	.	.	.	+	.	.	2a	+	.	.	.	1a	1b
Festuca pratensis	.	.	.	.	.	.	.	.	1a	.	.	1b	+	.	.	.	.	.
<u>Further species:</u>																		
Myosotis scorpioides	.	1a	.	+	.	+	.	.	.	.	+	.	.	.	.	.	.	+
Carex vulpina	.	.	.	.	.	.	.	1a	.	.	.	.	.	.	1b	2a	1a	.
Cirsium oleraceum	.	.	2a	.	2a	.	.	.	.	.	.	2a	+	.	.	.	.	.
Glechoma hederacea	.	.	1b	.	+	.	.	.	.	.	.	2a	.	.	.	.	.	+
Prunella vulgaris	.	.	+	.	.	.	.	.	1a	.	.	1a	+	.	.	.	.	.
Rhizomnium punctatum	.	.	.	.	.	.	.	.	+	.	.	+	1a	+	.	.	.	.
Thalictrum flavum	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	1a	.	.
Viola epipsila	.	.	+	.	1a	.	.	.	.	.	.	1b	2a	.	.	.	.	.
Agrostis stolonifera	.	.	.	.	.	1a	.	.	2a	.	.	.	.	.	.	.	1a	.
Anthoxanthum odoratum	.	.	.	.	.	.	.	.	.	.	.	1a	.	2a	.	.	.	1a
Brachythecium mildeanum	.	.	.	.	1a	.	.	.	3	.	.	.	.	2b	.	.	.	.
Geranium palustre	.	.	.	.	.	.	.	2b	.	2a	.	.	.	4	.	.	.	.
Luzula multiflora	.	.	+	.	.	.	.	.	.	.	.	1a	1a	.	.	.	.	.
Mentha arvensis	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	+	.
Plagiomnium elatum	.	.	.	+	.	.	.	.	.	.	.	.	1a	.	.	.	1a	.
Poa palustris	.	.	.	.	.	.	.	1a	.	.	.	1a	.	.	1b	.	.	.

<u>Miscellaneous species:</u>

Calamagrostis stricta MH1T-10:1a, A00-21:2b; Campanula glomerata A98-03:+; Carex acuta LT-12:1a; Carex diandra A00-21:2a; Carex leporina MH1T-7:1a; Cerastium holosteoides A00-02:+, A00-21:+; Cirsium palustre MH1T-10:+, MH1T-7:+; Crepis paludosa MH2T-4:+, MH1T-9:+; Drepanocladus aduncus MT-0:+; Drepanocladus vernicosus A98-03:+; Equisetum fluviatile A00-21:1a; Equisetum sylvaticum A00-21:1a; Festuca ovina MH1T-7:+; Geranium pratense MH2T-10:1a; Glyceria fluitans A98-07:+; Hieracium lactucella A00-02:1a; Hierochloe odorata LT-12:3; Hypericum maculatum A98-28:+; Iris pseudacorus MH1T-10:+, MH1T-6:+; Juncus effusus MH1T-7:+, A00-21:+; Leontodon autumnalis A98-03:+; Lysimachia vulgaris A98-03:+, A00-26:1a; Lythrum salicaria MH2T-9:+; Melampyrum cristatum MH2T-4:+; Melampyrum nemorosum MT-0:4; Phalaris arundinacea MH1T-9:1a, MH1T-10:1a; Phragmites australis MH1T-7:+, MH2T-11:+; Plagiomnium affine MT-0:+; Poa trivialis MH1T-10:+, A98-28:1a; Rhytidiadelphus squarrosus A98-07:2a; Salix cinerea A98-28:1a, A00-21:+; Salix myrsinifolia MH2T-10:+; Senecio paludosus A98-28:+; Sesleria caerulea A98-03:2b, A00-21:+; Symphytum officinale A98-38:2b, LT-12:1a; Thalictrum aquilegiifolium A98-38:+; Thalictrum lucidum MT-0:1a; Veronica scutellata A98-03:+; Viola canina ssp. canina MH2T-4:+, A00-02:1b; Viola palustris A00-21:2a, LT-12:1a; Viola persicifolia A98-03:2b

Table G.7 continued …

Column no. & plot ID:

1) A98-03; 2) MH2T-4; 3) MH1T-9; 4) A00-26; 5) MH1T-10; 6) MH1T-6; 7) MH2T-10; 8) A98-28; 9) MH1T-7; 10) MH2T-11; 11) MH2T-9; 12) A00-02; 13) A00-21; 14) MT-0; 15) A98-38; 16) LT-12; 17) A98-07; 18) A98-13

Habitat parameters:

MH2T-4: pH: 5.6; C/N: 10.1; K (mg/kg): 70.1; N (%): 0.98; C (%): 9.9; P (mg/kg): 55.6; GW > -50: 37.4; GW < -100: 23.1
MH1T-9: pH: 5.3; C/N: 10.3; K (mg/kg): 50.4; N (%): 0.71; C (%): 7.32; P (mg/kg): 22.2; GW > -50: 31.4; GW < -100: 32.9
MH1T-6: pH: 5.2; C/N: 10.6; K (mg/kg): 49.4; N (%): 0.63; C (%): 6.6; P (mg/kg): 27.4; GW > -50: 37.5; GW < -100: 28.2
MH2T-10: pH: 5.1; C/N: 11.1; K (mg/kg): 88.5; N (%): 0.72; C (%): 7.94; P (mg/kg): 36.2; GW > -50: 45.2; GW < -100: 14.6
MT-0: pH: 5.2; C/N: 10.8; K (mg/kg): 62.4; N (%): 0.56; C (%): 6.0; P (mg/kg): 18.7; GW > -50: 27.9; GW < -100: 27.2
LT-12: pH: 5.4; C/N: 10.1; K (mg/kg): 78.3; N (%): 0.76; C (%): 7.7; P (mg/kg): 48.5; GW > -50: 25.7; GW < -100: 16.4

Table G.8: Communities dominated by Carex disticha

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Community no.	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	10	10	10	11	11	11	11	11	11	11	11	11	11
Species no.	20	28	41	28	23	27	17	32	30	30	20	21	18	17	4	51	30	13	20	13	24	23	27	19	27	27	21	27	32	40
Total cover (%)	100	100	100	100	98	100	100									95	98	80			90		95	90	85	95				95
Graminoids (cover %)	75	90	50	90	80	80	90									75	90	60			50		80	85	50	80				80
Forbs (cover %)	40	30	60	60	60	40	60									80	60	20			50		70	3	35	20				60
Mosses (cover %)	0	0	5	0	0	0	0									30	50	0			70		5	3	40	0				80
Carex disticha-group																														
Carex disticha	3	4	3	5	4	4	4	5	5	4	5	5	5	5	5	2a	5	1b	1a	2b	.	2b	.	4	3	5	4	4	4	4
Carex cespitosa	.	1b	+	1a	.	3	.	.	1b	.	.	.	.	1b	.	4	3	.	.	.	+	3	2a	2b	1b	3	1a	2a	1b	1a
Juncus filiformis	.	1a	1a	.	.	1b	3	2b	2b	2a	3	4	4	.	.	2b	1a	2a	4	2b	.	.	.	.	.	1a	.	.	2a	2a
Potentilla anserina	.	.	.	1a	.	.	.	.	.	+	.	.	.	.	.	.	.	1a	+	1a	.	.	.	.	.	.	.	.	+	.
Valeriana officinalis	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ranunculus flammula	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2a	2a	1a	.	.	.	.	.	.	.	.	.	.
Potentilla palustris-group																														
Potentilla palustris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1a	.	2a	4	2a	+	+	2a	2a	1a	1a	+
Calliergon cordifolium	.	.	.	.	.	.	.	.	1a	.	.	.	4	.	.	.	.	.	.	2a	3	.	1a	1a	.	.	.	1a	.	1a
Calamagrostis stricta	.	.	.	.	.	.	.	.	.	.	.	.	.	2a	.	2a	.	.	.	.	2a	1a	.	.	.	.	.	.	+	1b
Caltha palustris-group																														
Caltha palustris	.	1b	1a	2a	.	1b	2a	.	.	2b	.	.	1a	.	1b	2b	+	1b	1b	.	2a	1b	.	2a	1a	2a	1a	2a	2a	1a
Galium palustre	.	.	.	+	+	.	1a	+	.	+	1b	1a	2a	1b	.	+	+	2a	1a	.	1b	+	+	.	.	+	+	+	+	.
Ranunculus repens	1a	.	.	3	2b	2a	1b	4	2b	.	3	2b	2b	1b	.	1a	.	+	1b	.	2a	.	2b	2a	2b	1b	.	1a	.	.
Carex panicea-group																														
Carex panicea	.	.	.	.	.	.	.	.	1a	+	+	1a	.	.	.	2a	1a	.	+	1b	+	2a	1a	.	1b	+	1a	.	+	2a
Carex nigra	.	.	.	.	1b	.	.	.	.	.	.	1a	.	+	.	2a	+	.	1a	1a	3	1a	.	+	1a	.	+	.	.	+
Agrostis canina	.	.	.	.	.	.	.	.	.	1a	.	.	.	.	.	2a	+	1a	2a	1b	.	1a	.	.	1a	.	.	1a	.	1b
Alopecurus pratensis-group																														
Alopecurus pratensis	1b	1b	1a	2a	2b	1a	1b	1b	1b	.	2a	.	.	+	.	.	.	.	+	1a	+	.	1a	.	1a	+	.	1b	1b	.
Stellaria palustris	1b	.	+	1a	.	.	2a	2a	1b	.	2a	+	1b	.	.	.	.	.	.	.	+	.	.	.	.	+	.	+	.	.
Phleum pratense-group																														
Phleum pratense	1a	1a	1a	1a	2a	1a	.	1a	.	1a	1b	.	.	.	.	1a	.	.	+	.	.	.	.	.	.	+	.	.	.	.
Festuca pratensis	.	1a	1a	+	2a	1a	.	1b	.	1b	1b	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1a	.
Calamagrostis canescens-group																														
Calamagrostis canescens	.	.	.	.	.	.	.	.	1a	.	.	2a	.	.	2a	.	1a	.	.	.	.	3	4	.	.	.	.	.	.	.

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Carex vesicaria	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	1a	.	.	.	.	.	+	.	.	.	1b	.	.	+	.
Viola uliginosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	1b	.	.	.	.	.	.	.	2b
Lychnis flos-cuculi-group																														
Lychnis flos-cuculi	.	+	+	+	+	+	.	1b	1a	+	1a	1a	.	1b	.	2a	.	.	.	.	+	.	.	.	1b	+	1a	1b	1a	1a
Calliergonella cuspidata	.	.	1a	.	.	.	.	.	5	2a	.	2a	1a	1a	.	3	2b	.	.	.	3	2a	1b	.	2b	.	3	1b	1a	4
Climacium dendroides	.	.	+	.	.	.	.	1a	1a	2a	.	2a	.	.	.	1a	1a	.	.	.	.	.	.	.	2b	.	.	1a	1b	2a
Cardamine pratensis	.	.	.	.	.	+	.	1a	+	+	.	.	+	1a	.	+	.	.	.	.	.	.	.	.	.	.	.	+	1a	.
Deschampsia cespitosa-group																														
Deschampsia cespitosa	2a	1a	1b	1b	2b	1b	3	2a	2a	1a	2a	2a	1a	+	.	3	+	1a	1b	1a	1b	2b	2a	1a	1a	1a	1b	.	1a	2b
Filipendula ulmaria	2b	2b	2a	1b	3	2b	3	1b	4	2b	2b	2b	2b	2a	2b	2b	2b	.	.	.	2a	2a	3	+	2b	2a	3	2b	2b	1b
Ranunculus auricomus agg.	1a	1a	1a	1a	1b	1a	1b	1b	.	1a	2a	+	1a	+	.	2a	1a	.	.	.	1b	+	1b	+	2a	.	1a	1a	+	1a
Lathyrus pratensis	1b	1a	+	1a	1b	+	1b	.	2a	1a	.	+	1a	.	.	1a	1a	.	+	.	+	.	+	.	1a	+	+	1a	1a	+
Ranunculus acris	1a	1a	1a	1a	1b	1a	.	1b	.	1b	1b	+	.	.	.	2a	1a	.	.	.	1a	.	1a	.	2a	+	1a	2a	1a	1a
Galium uliginosum	+	+	+	+	+	1a	.	1a	1b	+	.	.	.	.	.	+	+	.	.	.	1a	.	.	+	2a	+	+	+	+	+
Festuca rubra ssp. rubra	1b	.	2b	2a	1b	.	+	2b	1b	.	1b	.	.	1a	.	2b	+	.	.	.	+	.	1a	+	.	.	1b	1a	1b	1a
Geum rivale	1a	1a	1b	.	.	1b	1b	.	2b	2a	1a	.	2a	.	.	2a	+	.	+	.	1b	.	2a	.	1a	+	.	+	1a	.
Poa pratensis	.	.	+	1a	2a	1a	.	.	.	1a	.	1a	.	.	.	1a	.	1a	.	.	1a	.	1a	.	.	.	.	1b	1a	1a
Rumex acetosa	.	+	+	.	+	1a	.	1b	1a	.	.	.	.	.	.	2a	1a	.	.	.	.	.	.	.	+	.	+	.	1a	+
Vicia cracca	1a	1a	+	+	.	+	.	1a	1a	1a	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	+	.
Further species																														
Poa palustris	1b	1a	1a	1a	.	.	+	.	1a	.	.	.	+	1a	.	.	.	.	.	.	.	.	.	.	.	1a	.	.	+	.
Carex acuta	3	.	.	.	.	+	1a	.	+	.	.	1b	2a	.	.	.	.	1a	.	.	.	.	.	+	.	+	.	.	.	.
Carex vulpina	1a	.	1a	1b	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1a	1a	.	+	+	+	.	.	.	.	.
Angelica sylvestris	.	+	2a	.	.	1a	.	1a	.	.	.	.	.	.	.	2a	2a	.	.	.	.	.	.	.	+	.	2b	.	.	.
Galium boreale	+	1a	2b	.	1a	1a	.	2a	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Achillea ptarmica	.	.	1b	.	.	.	.	1b	1a	.	2a	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
Myosotis scorpioides	.	+	+	.	.	+	.	.	.	.	.	.	.	+	.	+	.	.	+	.	.	.	.	.	.	.	.	+	.	.
Salix bicolor	.	.	.	.	.	.	.	2a	.	+	2b	.	.	.	.	.	.	.	1a	.	.	.	.	1a	.	.	.	.	.	1a
Agrostis tenuis	1a	.	1a	.	1b	.	.	.	.	1a	.	.	.	.	.	.	.	.	.	.	.	1a	.	.	.	.	.	.	.	.
Centaurea jacea	.	.	+	.	.	.	.	1b	+	1a	.	.	.	.	.	2a	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Drepanocladus aduncus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2a	.	.	+	+	1a	.	.	.	.	+
Poa trivialis	.	.	.	1a	2a	1a	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Potentilla erecta	.	.	.	.	.	.	.	.	1a	.	1b	.	.	.	.	2a	1a	.	.	.	.	.	.	.	.	.	.	.	.	2a
Rhytidiadelphus squarrosus	.	.	1a	.	.	.	.	1a	.	.	.	.	1a	.	.	1a	1a	.	.	.	.	.	.	.	.	.	.	.	.	.
Anthoxanthum odoratum	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.
Briza media	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1a	.	.	.	.	.	.	.	.	1a	.	.	.	.	+
Luzula multiflora	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Salix myrsinifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1a	.	.	.	2b	.	.	+	.	.	.	.	.	.	1a

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Succisa pratensis	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	2a	+	.	.	.	.	.	.	.	.	.	.	.	.	+
Veronica longifolia	.	1a	+	.	.	.	1a	.	1a	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica scutellata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	+	.	+	.	.

Miscellaneous species:

Achillea millefolium A98-25:1b, KT-4:+; Agrostis stolonifera A98-43:1b, KT-4:+, TT-14:+; Alchemilla vulgaris agg. KT-4:1a; Anthriscus sylvestris A98-23:+, A98-25:+, A00-17:1a; Aulacomnium palustre A00-04:1a, A00-30:2b; Campanula patula A98-21:+; Carex appropinquata A00-04:1a, A98-01:+; Carex canescens A98-33:+, A98-05:1b; Carex diandra MH2T-12:3; Carex dioica A00-28:+; Carex elata A98-01:+; Carex flava A00-04:1a, A00-28:+; Carex pallescens KT-4:+; Carex paniculata A00-25:1a; Carex pulicaris A00-28:+; Cirsium palustre A00-04:1b; Crepis paludosa A98-43:1a; Dactylis glomerata A98-23:+; Dactylorhiza incarnata A00-04:+; Daucus carota A98-25:1b; Epilobium palustre A00-30:+; Equisetum palustre A00-04:+, MH2T-12:1a, A00-28:+; Festuca ovina A00-04:1a; Galium mollugo A98-25:+, KT-11:1a; Geranium palustre A98-25:+, MT--1:+; Glechoma hederacea A98-43:+; Glyceria fluitans TT-13:+; Helictotrichon pubescens A98-25:+; Hierochloe odorata A98-23:+, A98-24:+; Iris pseudacorus A00-08:+, MH2T-12:1a; Iris sibirica A00-30:+, A98-09:+, A98-24:+; Juncus effusus KT-7:+, A00-04:1a, A00-25:+; Linum catharticum A00-28:+; Luzula campestris A98-23:+, A98-05:1a; Lysimachia vulgaris A00-04:+, A00-30:2a, A98-24:+; Lythrum salicaria MH2T-12:1a, A00-25:+; Melampyrum nemorosum MT--1:3; Mentha arvensis A00-28:+; Phragmites australis MH2T-12:+; Plagiomnium elatum A98-25:+, A00-04:1a, TT-15:+; Polygonum amphibium A98-23:1a, A98-24:1b; Prunella vulgaris A00-04:+; Rhizomnium punctatum KT-11:+, KT-6:+, A00-28:1a; Rumex obtusifolius TT-17:1b; Sanionia uncinata A00-30:+; Scutellaria galericulata A00-25:+; Selinum carvifolia A00-04:+, MH2T-12:1b; Senecio paludosus A98-05:+, TT-15:+; Sesleria caerulea A00-28:1a; Stachys palustris MT--1:1a; Taraxacum officinale agg. A00-17:2b, A98-21:+, TT-16:1a; Thalictrum aquilegiifolium A00-25:+; Thalictrum flavum A98-25:+; Thalictrum lucidum A98-15:+; Thuidium philibertii A00-04:1a, A00-28:2a; Trifolium pratense TT-14:1a; Trifolium repens A98-43:+; Trollius europaeus A98-23:1a; Viola epipsila A00-04:+, A00-30:+, A00-25:1a

Column no. & plot ID:

1) A98-15; 2) A98-23; 3) A98-25; 4) A98-43; 5) A00-17; 6) A98-21; 7) A00-08; 8) KT-4; 9) KT-11; 10) TT-14; 11) KT-7; 12) KT-6; 13) KT-8; 14) TT-17; 15) TT-20; 16) A00-04; 17) A00-30; 18) A98-33; 19) TT-13; 20) TT-11; 21) A98-09; 22) MH2T-12; 23) A00-25; 24) A98-01; 25) A98-05; 26) A98-24; 27) MT--1; 28) TT-16; 29) TT-15; 30) A00-28

Habitat parameters:

KT-11: pH: 5.1; C/N: 10.4; K (mg/kg): 33.0; N (%): 0.61; C (%): 6.4; P (mg/kg): 9.9; GW > -50: 33.2; GW < -100: 18.9
KT-7: pH: 5.1; C/N: 11.0; K (mg/kg): 48.8; N (%): 0.38; C (%): 4.16; P (mg/kg): 36.2; GW > -50: 33.2; GW < -100: 19.6
MH2T-12: pH: 5.0; C/N: 11.5; K (mg/kg): 19.9; N (%): 1.02; C (%): 11.7; P (mg/kg): 11.5; GW > -50: 56.8; GW < -100: 0
TT-16: pH: 5.2; C/N: 10.7; K (mg/kg): 61.7; N (%): 1.01; C (%): 10.8; P (mg/kg): 64.4; GW > -50: 49.8; GW < -100: 4.4

Table G.9: Magnocaricion and reed communities

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Community no.	12	12	12	12	12	12	12	12	12	13	13	14	14	14	14	14	15	15
Species no.	16	6	5	7	3	15	8	5	12	4	4	5	8	6	22	11	6	8
Total cover (%)	100	95	95	95	90	85	100	100	90	95	90	95	100	85	90	100	90	90
Graminoids (cover %)	90								85									
Forbs (cover %)	60								5									
Mosses (cover %)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
Carex acuta	5	5	5	5	5	4	5	3	3	.	.	.	.	.	.	.	3	3
Carex elata	.	.	.	.	.	.	.	.	.	5	5	.	.	.	.	.	.	.
Schoenoplectus lacustris	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	1b	2a
<u>Phalaris arundinacea-group</u>																		
Phalaris arundinacea	.	.	.	.	1a	1b	2b	3	.	.	.	5	4	3	1a	4	3	.
Phragmites australis	.	.	.	.	.	1b	.	.	.	.	.	.	4	3	3	+	.	3
<u>Caltha palustris-group</u>																		
Galium palustre	2a	.	+	.	.	+	.	.	.	.	.	.	.	.	1a	.	.	.
Caltha palustris	2b	1a	1a	1a	.	1a	1a	1b	.	.	.	+	.	.	1a	.	.	.
Ranunculus repens	2b	.	.	.	.	+	+	.	.	.	.	.	2a	.	.	.	.	.
<u>Calamagrostis canescens-group</u>																		
Calamagrostis canescens	.	.	.	1a	.	.	.	.	2a	.	+	.	.	.	.	.	.	.
Carex vesicaria	.	1a	+	1b	1a	.	.	.	1a	.	.	.	.	.	.	.	.	.
<u>Further species:</u>																		
Filipendula ulmaria	2b	1a	1b	.	.	1a	.	3	+	2b	.	2a	.	.	2b	1a	.	.
Lysimachia vulgaris	.	+	.	1a	.	.	.	.	+	1a	.	.	.	.	1a	+	.	.
Veronica longifolia	.	.	.	.	.	+	+	.	.	.	.	.	1a	.	2b	.	.	.
Alopecurus pratensis	1a	.	.	.	.	.	.	2a	.	.	1a	.	.	.	.	.	.	.
Angelica sylvestris	.	.	.	.	.	.	1a	.	.	.	.	.	.	.	2a	1b	.	.
Anthriscus sylvestris	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	1b	.	.
Lathyrus pratensis	+	.	.	.	.	.	.	.	.	.	.	.	.	.	1a	2b	.	.
Polygonum amphibium	1b	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.
Urtica dioica	.	.	.	.	.	.	.	.	.	.	.	2a	.	1b	.	3	.	.

<u>Miscellaneous species:</u>

Alnus incana LT-0:3; Amblystegium serpens KT-0:1b; Cardamine pratensis A98-42:1a, MH2T-1:+; Carex disticha A98-29:3; Carex lasiocarpa A98-29:1a; Carex rostrata KT-12:+; Carex vulpina A98-42:2b, LT-19:1a; Centaurea jacea MH2T-1:+; Dactylis glomerata KT-0:1a; Deschampsia cespitosa A98-42:1b, KT-0:+; Equisetum arvense KT-0:2a; Galium uliginosum KT-12:+; Glechoma hederacea TT-1:+, MH2T-0:+; Heracleum sphondylium LT-1:1a; Hydrocharis morsus-ranae TT-0:+, MH2T-0:+; Hypericum hirsutum KT-0:+; Iris pseudacorus TT-0:1a; Iris sibirica A98-29:+; Juncus filiformis A98-42:2a; Lychnis flos-cuculi MH2T-1:+, KT-0:1a; Lythrum salicaria MH2T-1:1a, MH1T-1:1a; Mentha arvensis A98-42:+; Menyanthes trifoliata MH2T-0:1a; Myosotis scorpioides A98-42:1a, MT-9:2a; Nuphar lutea MH2T-0:1a; Phleum pratense KT-0:1a; Poa palustris A98-42:1a, KT-0:2a; Poa pratensis TT-18:+; Potentilla anserina MT-9:+; Potentilla palustris A98-29:1b; Ranunculus acris KT-0:1a; Ranunculus auricomus agg. LT-1:+; Scrophularia nodosa MT-9:1b, KT-0:1a; Sedum maximum KT-0:+; Sium latifolium TT-0:1b, MH2T-0:1a; Stachys palustris TT-19:+; Stellaria graminea A98-29:+; Stellaria palustris A98-42:1b, A98-29:+; Taraxacum officinale agg. MH2T-1:+; Thalictrum flavum MT-9:+; Valeriana officinalis MH2T-1:1b, KT-0:1b; Vicia cracca LT-0:1b, LT-1:1a

<u>Community types:</u>

12) Carex acuta-community; 13) Carex elata-community; 14) Phalaris-Phragmites-community; 15) Carex acuta-Schoenoplectus lacustris-community

<u>Column no. & plot ID:</u>

1) A98-42; 2) LT-19; 3) LT-13; 4) KT-12; 5) LT-14; 6) MH2T-1; 7) MH1T-1; 8) LT-18; 9) A98-29; 10) TT-19; 11) TT-18; 12) TT-1; 13) MT-9; 14) LT-0; 15) KT-0; 16) LT-1; 17) TT-0; 18) MH2T-0

Table G.9 continued …

Habitat parameters:

KT-12: pH: 5.2; C/N: 12.0; K (mg/kg): 46.0; N (%): 0.90; C (%): 10.8; P (mg/kg): 60.8; GW > -50: 84.4; GW < -100: 0
MH2T-1: pH: 5.7; C/N: 10.9; K (mg/kg): 20.4; N (%): 0.73; C (%): 8.0; P (mg/kg): 39.7; GW > -50: 88.7; GW < -100: 0
MH1T-1: pH: 5.7; C/N: 11.3; K (mg/kg): 34.4; N (%): 0.64; C (%): 7.2; P (mg/kg): 4.6; GW > -50: 43.2; GW < -100: 1.4
MT-9: pH: 6.5; C/N: 13.2; K (mg/kg): 59.1; N (%): 0.37; C (%): 4.9; P (mg/kg): 53.8; GW > -50: 17.7; GW < -100: 14.3

Table G.10: Raw data of the Käära seed traps (SR = seed rain) and vegetation samples (EV = established vegetation), listing species occurring only in the seed rain, only in the established vegetation and in both.

	K1		K2		K3		K4		K5		K6		K7		K8		K9		frequency		total seed number
	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	
species number	18	17	21	24	20	23	23	17	14	17	11	12	26	21	26	21	7	7			
total seed number	299		850		575		478		4438		12311		1070		601		7295				27917
Sørensen similarity	0.588		0.682		0.698		0.600		0.516		0.522		0.638		0.553		0.571				
Bray-Curtis dissimilarity	0.845		0.676		0.660		0.838		0.634		0.665		0.781		0.908		0.938				
1. present only in SR																					
Alnus incana	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	0	1	1
Anthriscus sylvestris	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	1	3
Betula pubescens	–	8	–	29	–	34	–	38	–	21	–	19	–	21	–	25	–	34	0	9	229
Carex leporina	–	–	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	0	1	8
Carex rostrata	–	–	–	–	–	–	–	–	–	12	–	–	–	–	–	–	–	–	0	1	12
Cerastium holosteoides	–	–	–	7	–	6	–	–	–	–	–	–	–	–	–	–	–	–	0	2	13
Epilobium hirsutum	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	0	2	2
Phragmites australis	–	–	–	1	–	–	–	–	–	–	–	–	–	4	–	7	–	4	0	4	16
Selinum carvifolia	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	0	1	3
Valeriana officinalis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	0	1	2
Veronica spec	–	3	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	2	4
2. present only in EV																					
Achillea ptarmica	–	–	2a	–	2a	–	1b	–	1a	–	–	–	–	–	1a	–	–	–	5	0	0
Angelica sylvestris	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0	0
Campanula glomerata	–	–	–	–	–	–	–	–	–	–	–	–	1a	–	–	–	–	–	1	0	0
Cardamine pratensis	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	–	–	–	2	0	0
Crepis paludosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	1	0	0
Dactylis glomerata	2a	–	+	–	–	–	+	–	–	–	–	–	2a	–	–	–	–	–	4	0	0
Festuca ovina	–	–	–	–	–	–	–	–	–	–	–	–	1b	–	–	–	–	–	1	0	0
Galium boreale	–	–	2a	–	2b	–	2a	–	–	–	–	–	–	–	1a	–	–	–	4	0	0
Galium palustre	–	–	–	–	–	–	–	–	1a	–	2a	–	–	–	1a	–	1a	–	4	0	0
Galium uliginosum	–	–	–	–	+	–	1a	–	1a	–	1a	–	–	–	–	–	–	–	4	0	0
Heracleum sibiricum	1a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0	0
Lathyrus pratensis	1b	–	–	–	–	–	+	–	–	–	–	–	1a	–	2a	–	–	–	4	0	0
Plantago lanceolata	–	–	–	–	–	–	–	–	–	–	–	–	2a	–	–	–	–	–	1	0	0

	K1		K2		K3		K4		K5		K6		K7		K8		K9		frequency		total seed number
	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	
Salix phylicifolia	–	–	–	–	–	–	–	–	2a	–	–	–	–	–	–	–	–	–	1	0	0
Scorzonera humilis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1a	–	–	–	1	0	0
Taraxacum sect. Ruderalia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	1	0	0
Vicia cracca	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1a	–	–	–	1	0	0
3. present in SR & EV																					
Achillea millefolium	1b	2	2a	6	1b	14	+	3	–	1	–	–	2a	–	–	–	–	–	5	5	26
Agrostis capillaris	+	9	+	2	–	–	+	1	–	1	1a	–	1b	4	1a	4	–	–	6	6	21
Alchemilla vulgaris agg.	1a	1	3	18	2b	3	–	–	–	–	–	–	2b	–	–	–	–	–	4	3	22
Alopecurus pratensis	–	–	–	–	1a	1	1b	–	–	–	–	–	–	–	1b	–	–	–	3	1	1
Anthoxanthum odoratum	–	18	–	4	1a	7	+	39	–	–	–	–	1b	24	–	–	–	–	3	5	92
Briza media	–	–	+	1	–	–	–	–	–	–	–	–	1a	–	–	–	–	–	2	1	1
Calamagrostis canescens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1a	18	1	3	19
Carex acuta	–	–	–	–	–	–	–	–	–	–	2a	–	–	–	–	11	1a	–	2	2	11
Carex cespitosa	–	–	–	–	–	–	–	–	1a	57	–	–	–	1	–	–	–	–	1	2	58
Carex disticha	–	–	–	–	–	–	5	–	5	27	5	105	–	–	5	1	5	14	5	5	147
Carex pallescens	–	–	–	2	+	3	–	–	–	–	–	–	1b	14	–	–	–	–	2	3	19
Carex panicea	–	–	+	–	–	–	–	–	–	–	–	–	1b	13	–	–	–	–	2	1	13
Carex vesicaria	–	–	–	–	–	–	–	–	–	6	+	2	–	–	–	–	–	–	1	2	8
Centaurea jacea	–	–	1a	19	2a	16	1b	34	–	–	–	1	3	58	+	3	–	–	5	6	131
Deschampsia cespitosa	+	27	1b	22	–	1	2a	42	2a	31	–	8	2a	42	2a	9	–	1	6	9	183
Festuca pratensis	–	–	–	–	2a	13	1b	3	1a	1	–	1	2a	8	1a	4	–	–	5	6	30
Festuca rubra	2a	1	2a	–	2a	–	2b	–	–	–	–	–	2b	1	1b	–	–	–	6	2	2
Filipendula ulmaria	–	18	2a	3	2b	25	1b	3	2b	97	2b	1	1b	13	4	–	4	28	8	9	188
Galium mollugo	–	–	2b	–	–	2	+	–	–	–	–	–	1a	–	–	–	–	–	3	1	2
Geum rivale	–	–	–	–	1a	–	1b	–	–	–	–	–	–	–	2b	1	–	–	3	1	1
Hieracium umbellatum	–	10	+	299	+	30	–	24	–	–	–	1	–	6	–	–	–	–	2	6	370
Hypericum maculatum	1a	–	2b	213	–	5	+	172	–	1	–	–	+	790	–	–	–	–	4	5	1181
Juncus filiformis	–	–	–	–	–	–	–	–	4	4116	4	12168	–	15	–	10	2a	7192	3	6	23501
Leontodon autumnalis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	1	–	–	1	1	1
Luzula campestris	–	–	1a	18	–	1	–	2	–	–	–	–	1a	8	–	–	–	–	2	4	29
Lychnis flos-cuculi	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1a	408	–	–	1	2	409
Phleum pratense	2a	15	–	1	2a	29	1a	1	–	–	–	–	–	–	2a	2	–	–	4	5	48
Poa palustris	1b	2	–	–	–	–	–	–	–	–	+	3	–	–	–	9	–	–	2	3	14

	K1		K2		K3		K4		K5		K6		K7		K8		K9		frequency		total seed number
	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	
Poa pratensis	+	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	1	1
Potentilla erecta	–	–	–	8	–	–	–	–	–	–	–	–	1a	–	–	–	–	–	1	1	8
Ranunculus acris	1a	121	2a	80	2a	84	1b	69	+	21	–	–	1b	20	1b	27	–	–	7	7	422
Ranunculus auricomus agg.	–	2	–	3	1a	92	–	17	+	43	1a	1	1b	13	1b	67	–	–	5	8	238
Rhinanthus minor	–	–	1b	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	4
Rumex acetosa	1b	9	1b	81	1b	51	1b	24	1a	–	–	–	1b	7	1a	–	–	–	7	5	172
Stellaria graminea	1a	–	1b	2	1b	145	1a	5	–	–	–	–	–	–	–	–	–	–	4	3	152
Stellaria palustris	–	–	–	–	–	–	–	–	+	–	–	–	–	1	1b	6	1a	–	3	3	7
Trifolium pratense	2a	–	2a	26	1a	2	1a	–	–	–	–	–	2a	–	–	–	–	–	5	2	28
Trollius europaeus	1b	50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	50
Veronica longifolia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1a	1	–	–	1	1	1
Viola canina	–	–	–	–	–	–	–	–	–	–	–	–	1a	7	–	2	–	–	1	2	9

Table G.11: Raw data of the Läti seed traps (SR = seed rain) and vegetation samples (EV = established vegetation), listing species occurring only in the seed rain, only in the established vegetation and in both.

	L1		L2		L3		L4		L5		L6		L7		L8		L9		L10		frequency		total seed number
	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	
species number	11	15	7	9	14	18	9	11	16	16	16	17	18	14	24	20	11	14	10	11			
total seed number	1001		368		203		173		428		471		329		911		603		194				4681
Sørensen similarity	0.538		0.375		0.625		0.500		0.563		0.688		0.438		0.727		0.500		0.600				
Bray-Curtis dissimilarity	0.711		0.406		0.744		0.589		0.360		0.715		0.798		0.629		0.554		0.405				
1. present only in SR																							
Alnus incana	–	113	–	54	–	85	–	16	–	12	–	2	–	2	–	–	–	–	–	–	0	7	284
Betula pubescens	–	4	–	2	–	2	–	5	–	1	–	–	–	–	–	4	–	1	–	–	0	7	19
Epilobium hirsutum	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0	2	2
Hypericum maculatum	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	2	2
Lychnis flos-cuculi	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	15	–	–	–	–	0	1	15
Rumex thyrsiflorus	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	0	1	1
Salix phylicifolia	–	–	–	–	–	2	–	–	–	–	–	2	–	–	–	–	–	–	–	–	0	2	4
Selinum carvifolia	–	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	1	5
2. present only in EV																							
Anthoxanthum odoratum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1a	–	–	–	1	0	0
Briza media	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	1	0	0
Bromus inermis	1a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0	0
Calamagrostis canescens	–	–	–	–	1a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0	0
Calamagrostis sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1a	–	1a	–	2	0	0
Cardamine pratensis	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0	0
Festuca rubra	–	–	–	–	–	–	2a	–	2a	–	–	–	2a	–	2b	–	–	–	–	–	4	0	0
Galium boreale	+	–	–	–	+	–	1b	–	1a	–	–	–	2a	–	–	–	–	–	–	–	5	0	0
Lathyrus pratensis	2a	–	1b	–	1b	–	–	–	1b	–	–	–	1a	–	1b	–	1a	–	2a	–	8	0	0
Mentha arvensis	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	1	0	0
Potentilla anserina	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	–	–	2	0	0
Stellaria palustris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1a	–	1	0	0
Viola palustris	–	–	–	–	–	–	–	–	–	–	1a	–	–	–	–	–	–	–	–	–	1	0	0
3. present in SR & EV																							
Achillea millefolium	–	–	–	–	–	–	–	–	–	–	–	–	1b	–	1b	2	–	–	–	–	2	1	2
Achillea ptarmica	–	–	–	–	1a	14	–	–	–	–	1b	–	–	–	2a	–	–	–	–	–	3	1	14

	L1		L2		L3		L4		L5		L6		L7		L8		L9		L10		frequency		total seed number
	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	
Agrostis capillaris	–	–	–	–	–	1	–	–	1a	–	–	–	–	2	1a	–	–	–	–	–	2	2	3
Alchemilla vulgaris agg.	–	–	–	–	–	–	–	–	1a	–	–	–	2a	–	1a	2	–	–	–	–	3	1	2
Alopecurus pratensis	3	17	3	22	3	14	3	1	–	–	–	–	–	–	1a	10	–	2	2a	9	6	7	75
Anthriscus sylvestris	1b	24	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	24
Carex acuta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1a	1	–	6	1	2	7
Carex disticha	–	–	1a	–	1b	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	2	2	2
Carex flava	–	–	–	–	–	–	–	–	–	–	1a	1	–	–	–	–	–	–	–	–	1	1	1
Carex leporina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	19	–	–	–	–	1	1	19
Carex pallescens	–	–	–	–	–	–	–	–	–	1	–	6	1a	38	1a	34	–	–	–	–	2	4	79
Carex panicea	–	–	–	–	–	–	–	–	–	–	1b	18	2a	2	–	1	–	–	–	–	2	3	21
Carex vulpina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2a	22	1	2	24
Centaurea jacea	–	–	–	–	–	–	–	–	1a	7	–	–	–	–	–	–	–	–	–	–	1	1	7
Deschampsia cespitosa	–	1	–	–	–	1	2b	26	2b	138	2b	20	2b	202	2b	285	–	6	3	12	6	9	691
Festuca ovina	–	–	–	–	–	–	–	–	–	–	2b	–	–	43	1b	–	–	–	–	–	2	1	43
Festuca pratensis	–	–	–	–	1a	1	–	–	–	–	–	–	–	6	–	–	–	–	–	2	1	3	9
Filipendula ulmaria	2b	232	4	282	3	17	3	33	3	119	–	3	2a	2	2b	34	3	436	3	69	9	10	1227
Geum rivale	–	–	–	–	2a	2	2a	–	2a	–	1b	2	–	13	2a	8	2a	–	2b	58	7	5	83
Heracleum sibiricum	1a	–	1a	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	1
Hierochloe odorata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	9	–	–	1	1	9
Juncus filiformis	–	2	–	1	–	1	–	–	–	–	1b	191	–	–	–	3	1a	80	–	–	2	6	278
Luzula campestris	–	–	–	–	–	–	–	–	–	–	+	2	–	5	+	–	–	–	–	–	2	2	7
Phleum pratense	–	–	–	–	1a	3	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	2	4
Phragmites australis	+	15	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	1	3	18
Poa pratensis	–	–	–	–	1a	4	1b	10	1a	2	–	–	–	–	1a	3	–	–	–	–	4	4	19
Potentilla erecta	–	–	–	–	–	–	–	–	–	1	2a	77	–	1	2a	301	–	1	–	–	2	5	381
Ranunculus acris	–	–	–	–	1a	20	–	–	1b	49	1b	48	2a	2	1b	41	–	1	–	–	5	6	161
Ranunculus auricomus agg.	+	1	+	–	1a	5	–	10	1b	3	1b	65	1b	8	1b	107	1a	57	1b	1	9	9	257
Rumex acetosa	–	–	–	–	–	1	–	–	1a	8	1a	7	1b	3	1a	26	–	2	–	2	4	7	49
Sesleria caerulea	–	–	–	–	–	–	–	–	+	2	4	25	3	–	–	–	–	–	–	–	3	2	27
Trollius europaeus	–	–	–	–	–	–	–	–	2b	54	–	–	–	–	+	5	–	–	–	–	2	2	59
Urtica dioica	3	61	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	61
Valeriana officinalis	–	5	–	–	–	–	–	–	–	25	–	–	–	–	1a	8	–	–	–	12	1	4	50

	L1		L2		L3		L4		L5		L6		L7		L8		L9		L10		frequency		total seed number
	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	
Veronica chamaedrys	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	3	–	–	–	–	2	1	3
Veronica longifolia	1a	519	–	4	–	29	1b	69	–	4	–	1	–	–	–	–	–	–	–	–	2	6	626
Vicia cracca	–	–	2a	–	2a	–	–	1	1b	–	2a	–	2a	–	2b	–	1a	–	2a	–	8	1	1
Viola canina	–	–	–	–	–	–	–	–	–	2	–	–	1a	–	–	–	–	–	–	–	1	1	2
Viola epipsila	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1a	3	–	–	1	1	3

Table G.12: Raw data of the Mulgi Heinamaa seed traps (SR = seed rain) and vegetation samples (EV = established vegetation), listing species occurring only in the seed rain, only in the established vegetation and in both.

	MH1		MH2		MH3		MH4		MH5		MH6		MH7		MH8		MH9		frequency		total seed number
	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	
species number	4	8	21	17	21	13	18	10	20	11	25	18	24	18	13	6	16	16			
total seed number	30		98		93		43		83		197		912		41		312				1809
Sørensen similarity	0.364		0.316		0.303		0.357		0.387		0.488		0.476		0.421		0.621				
Bray-Curtis dissimilarity	0.406		0.789		0.928		0.806		0.704		0.794		0.814		0.624		0.702				
1. present only in SR																					
Agrostis canina	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	0	2	5
Alnus incana	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	0	1	2
Alopecurus pratensis	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	1	1
Betula pubescens	–	8	–	7	–	3	–	8	–	9	–	12	–	8	–	12	–	28	0	9	95
Carex canescens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	0	1	4
Carex pallescens	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	0	1	3
Carex pulicaris	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	0	1	3
Cerastium holosteoides	–	–	–	–	–	1	–	–	–	–	–	13	–	–	–	–	–	–	0	2	14
Epilobium hirsutum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	0	1	3
Hieracium pilosella	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	0	1	1
Hypericum maculatum	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0	3	3
Juncus filiformis	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	0	1	4
Viola uliginosa	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–	1	0	2	5
2. present only in EV																					
Achillea ptarmica	–	–	–	–	1a	–	–	–	–	–	–	–	1a	–	–	–	–	–	2	0	0
Angelica sylvestris	–	–	–	–	–	–	–	–	–	–	–	–	1a	–	–	–	–	–	1	0	0
Briza media	–	–	–	–	–	–	–	–	–	–	1b	–	–	–	–	–	–	–	1	0	0
Cardamine pratensis	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	1	0	0
Carex nigra	–	–	–	–	–	–	–	–	–	–	1a	–	–	–	–	–	1a	–	2	0	0
Centaurea jacea	–	–	–	–	2a	–	–	–	2a	–	2a	–	2a	–	–	–	–	–	4	0	0
Comarum palustre	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	1	0	0
Equisetum palustre	–	–	–	–	+	–	–	–	–	–	+	–	–	–	–	–	1a	–	3	0	0
Festuca pratensis	–	–	1a	–	–	–	–	–	1a	–	–	–	–	–	–	–	–	–	2	0	0
Festuca rubra	–	–	–	–	–	–	–	–	–	–	+	–	1a	–	–	–	–	–	2	0	0
Galium boreale	–	–	2a	–	–	–	1a	–	1b	–	1a	–	1b	–	1b	–	–	–	6	0	0

	MH1		MH2		MH3		MH4		MH5		MH6		MH7		MH8		MH9		frequency		total seed number
	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	
Galium mollugo	–	–	–	–	2a	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0	0
Galium palustre	–	–	–	–	+	–	+	–	–	–	–	–	–	–	–	–	+	–	3	0	0
Galium uliginosum	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	–	–	–	2	0	0
Geranium pratense	–	–	–	–	3	–	–	–	1b	–	–	–	–	–	–	–	–	–	2	0	0
Lathyrus pratensis	–	–	+	–	+	–	+	–	1a	–	–	–	–	–	1a	–	–	–	5	0	0
Lysimachia thyrsiflora	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	1	0	0
Lysimachia vulgaris	–	–	1a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0	0
Lythrum salicaria	1a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0	0
Phalaris arundinacea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	1	0	0
Phleum pratense	–	–	1b	–	–	–	–	–	–	–	1a	–	–	–	–	–	–	–	2	0	0
Succisa pratensis	–	–	–	–	–	–	–	–	2a	–	2a	–	–	–	–	–	–	–	2	0	0
Vicia cracca	–	–	2a	–	1a	–	1a	–	1b	–	1a	–	1a	–	1a	–	–	–	7	0	0
Viola epipsila	–	–	–	–	–	–	–	–	–	–	–	–	1a	–	3	–	–	–	2	0	0
Viola persicifolia	–	–	1a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0	0
3. present in SR & EV																					
Alchemilla vulgaris agg.	–	–	–	1	–	–	–	–	2a	–	1b	20	–	–	–	–	–	–	2	2	21
Calamagrostis canescens	–	–	2b	–	–	–	2a	–	–	–	–	–	–	–	–	–	3	2	3	1	2
Calamagrostis epigejos	–	–	–	2	3	–	3	–	2a	1	2a	–	2a	–	2a	–	–	–	6	2	3
Calamagrostis stricta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1a	20	1	1	20
Caltha palustris	1a	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1b	4	2	2	5
Carex acuta	4	15	–	9	–	–	–	–	–	12	–	52	–	695	–	3	–	–	1	6	786
Carex appropinquata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	166	1	1	166
Carex cespitosa	–	–	1a	–	1b	–	2a	1	1b	–	1b	11	4	106	–	–	3	–	7	3	118
Carex disticha	–	–	–	–	–	–	2a	–	–	–	–	–	2b	4	2a	1	2b	4	4	3	9
Carex flava	–	–	–	–	–	–	–	–	–	–	+	3	–	7	–	–	–	–	1	2	10
Carex panicea	–	–	–	–	–	–	–	–	–	1	2a	–	1b	12	–	–	2a	4	3	3	17
Carex vesicaria	–	–	–	1	–	–	–	–	–	–	–	–	+	10	1a	–	–	–	2	2	11
Cirsium heterophyllum	–	1	–	–	–	–	–	–	1a	–	–	–	–	–	–	–	–	–	1	1	1
Deschampsia cespitosa	–	1	1b	–	1b	–	2a	–	–	–	1a	–	1b	–	–	–	2b	65	6	2	66
Filipendula ulmaria	–	–	3	2	3	–	4	3	2b	38	2b	11	2b	1	3	12	–	–	7	6	67
Geum rivale	–	–	1b	1	2a	2	2a	6	–	–	1a	3	1a	1	–	–	–	–	5	5	13
Iris sibirica	–	–	–	–	–	–	–	–	3	10	–	–	+	–	–	–	–	–	2	1	10
Luzula campestris	–	–	–	3	–	4	–	–	–	–	+	3	–	–	–	–	–	–	1	3	10

	MH1		MH2		MH3		MH4		MH5		MH6		MH7		MH8		MH9		frequency		total seed number
	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	EV	SR	
Lychnis flos-cuculi	–	–	–	3	+	–	–	7	–	–	1a	–	1a	21	–	–	–	–	3	3	31
Phragmites australis	1b	2	+	7	–	2	–	–	–	1	–	–	–	–	–	–	+	2	3	5	14
Poa pratensis	–	–	–	–	+	–	+	–	+	4	–	–	–	2	–	–	–	–	3	2	6
Potentilla erecta	–	–	2a	3	1a	–	–	–	1b	5	–	32	2a	22	1b	1	–	–	5	5	63
Ranunculus acris	–	–	2b	22	1b	8	–	4	2a	–	–	–	1a	2	–	–	–	–	4	4	36
Ranunculus auricomus agg.	–	–	–	18	–	11	1b	8	–	–	1a	10	1a	13	1b	12	+	3	5	7	75
Rumex acetosa	–	–	–	1	1a	16	–	–	1a	1	–	5	–	–	–	–	–	–	2	4	23
Scorzonera humilis	–	–	3	–	–	–	–	–	2b	–	3	1	2a	–	–	–	–	–	4	1	1
Selinum carvifolia	–	–	2a	–	1b	–	1b	–	–	–	–	1	2a	–	1b	–	1b	–	6	1	1
Sesleria caerulea	–	–	–	–	–	–	–	–	–	–	2b	10	2a	–	–	–	–	–	2	1	10
Taraxacum sect. Ruderalia	–	–	1b	–	–	–	+	–	–	1	–	–	–	–	–	–	–	1	2	2	2
Trollius europaeus	–	–	–	–	1a	31	–	1	–	–	+	6	–	1	–	–	–	–	2	4	39
Valeriana officinalis	–	1	2a	16	+	10	1b	1	1b	–	–	–	–	–	–	–	–	–	4	4	28
Veronica longifolia	–	–	1a	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1
Viola canina	–	–	+	–	–	1	1a	–	1a	–	1a	–	1a	–	–	–	–	–	5	1	1

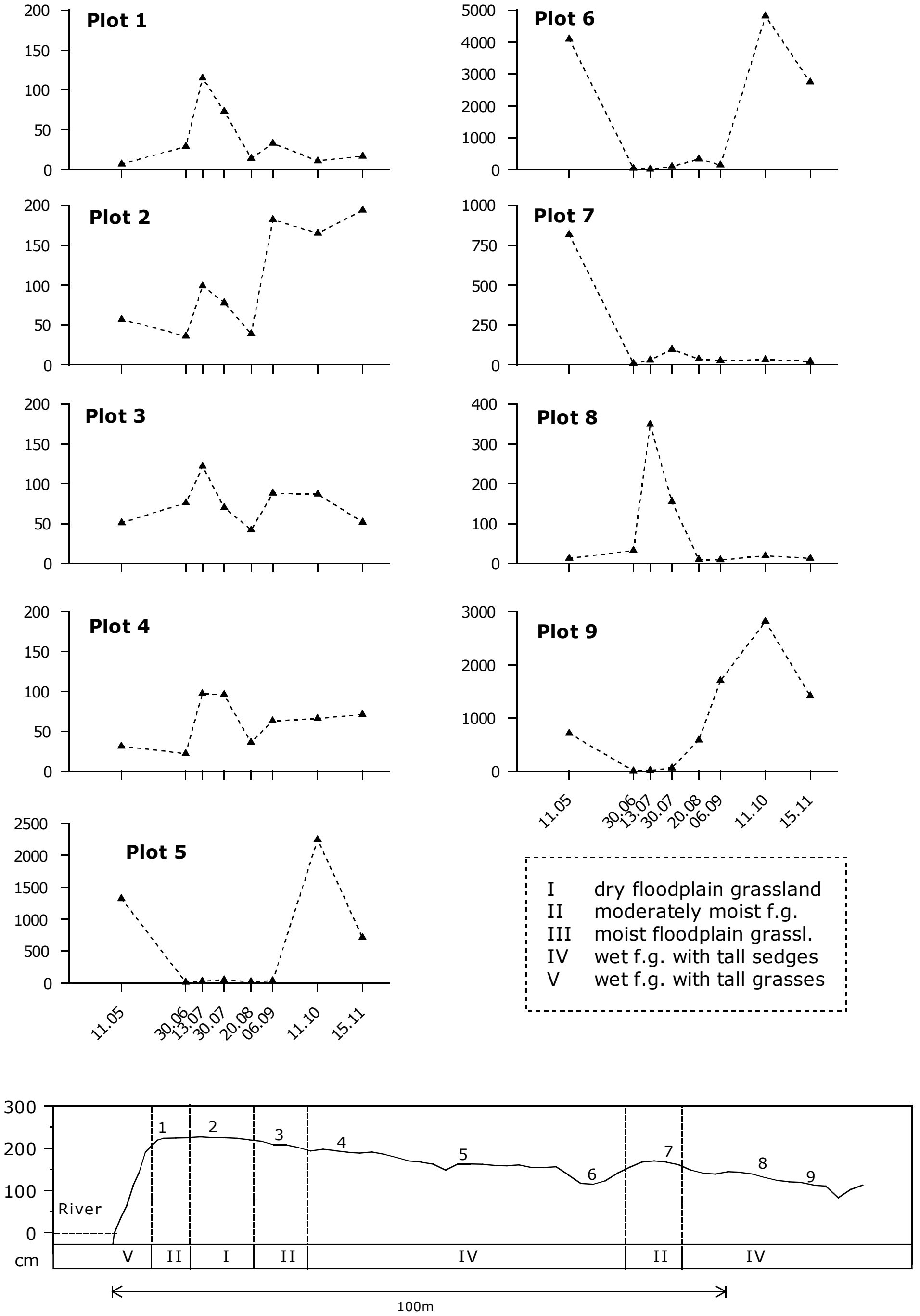


Fig. G.10: Temporal variation of seed rain in the Käära transect, absolute seed number for each seed trap and sketch of transect with location of seed traps and vegetation types.

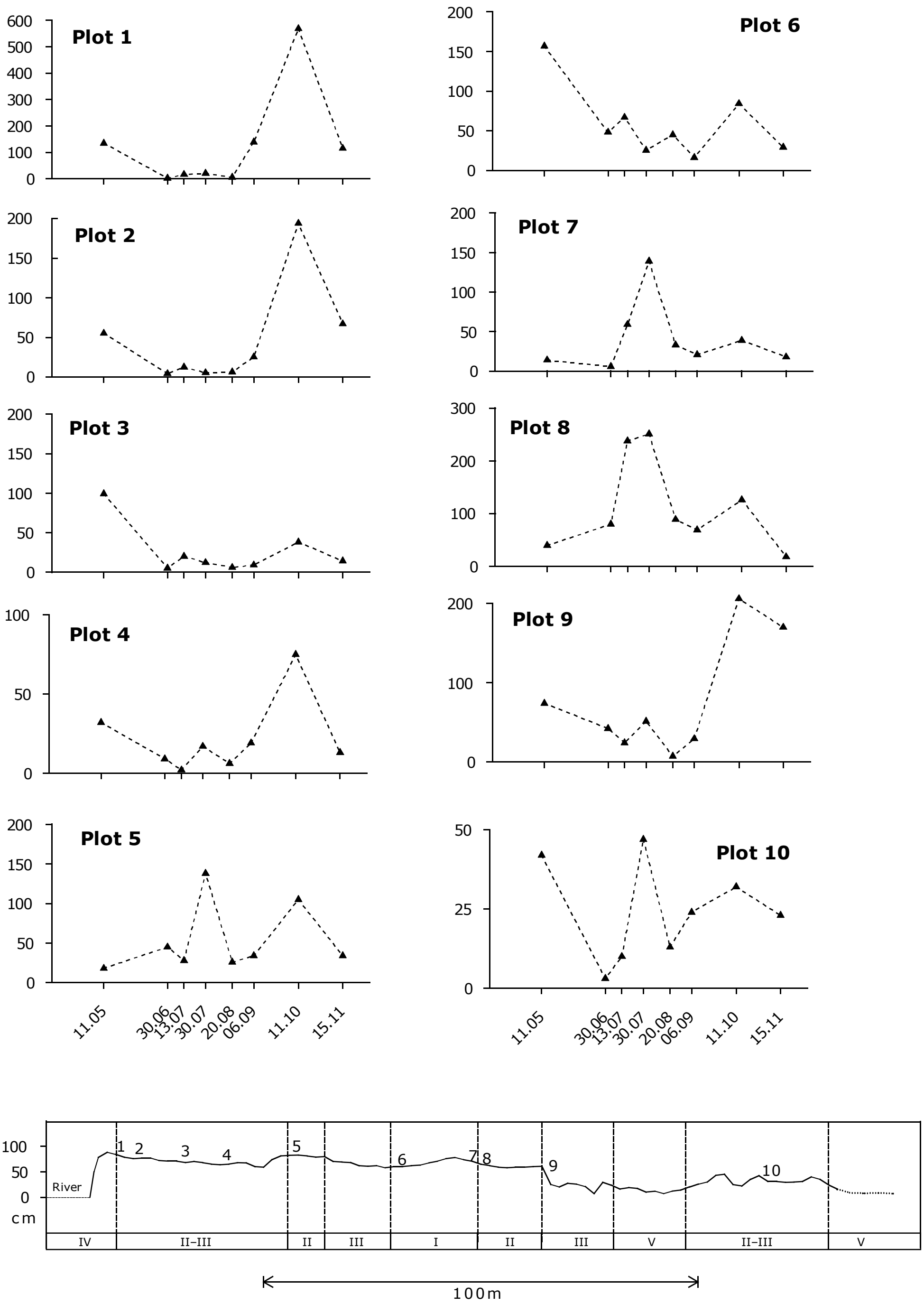


Fig. G.11: Temporal variation of seed rain in the Läti transect, absolute seed number for each seed trap and sketch of transect with location of seed traps and vegetation types.

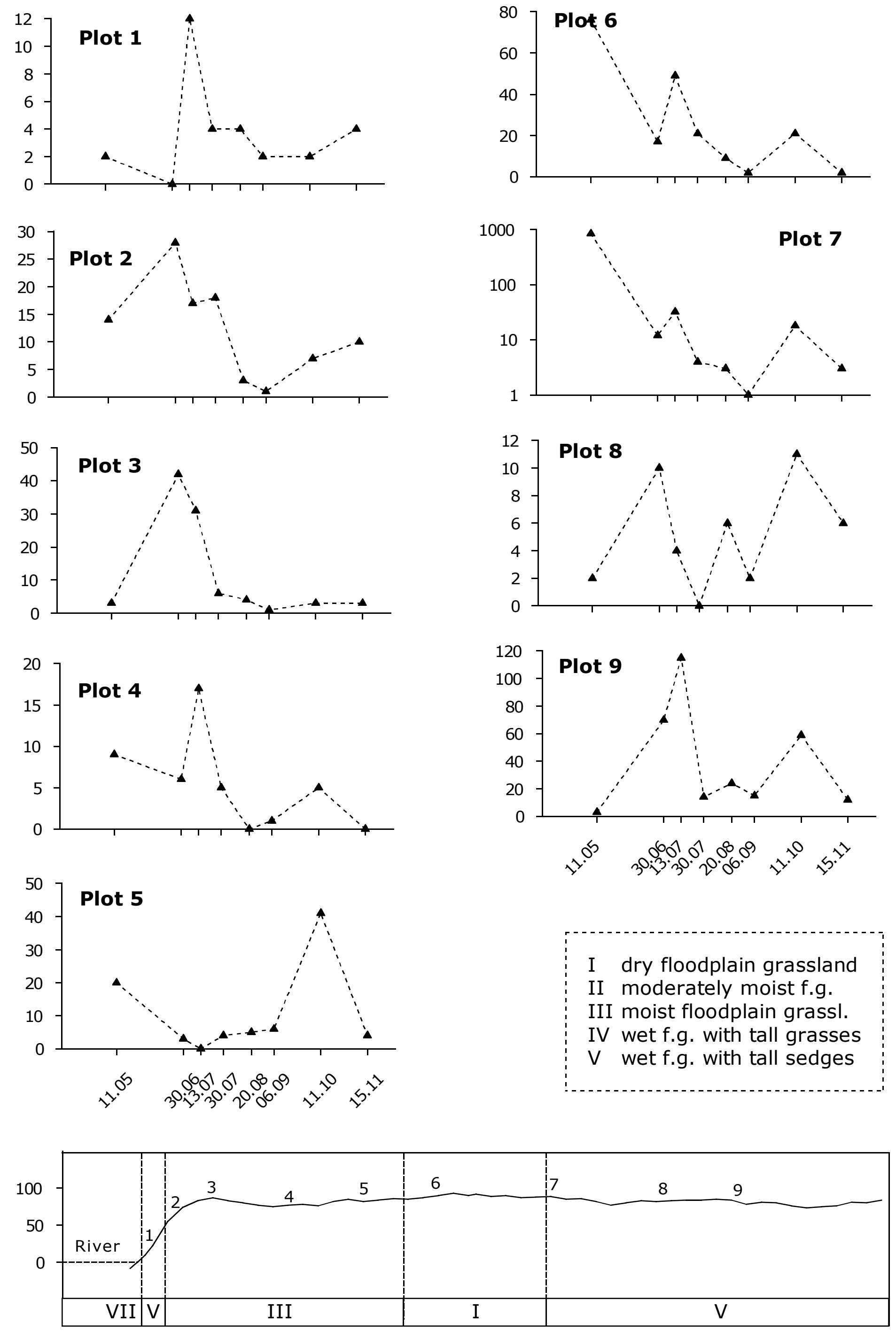


Fig. G.12: Temporal variation of seed rain in the Mulgi Heinamaa transect, absolute seed number for each seed trap and sketch of transect with location of seed traps and vegetation types.

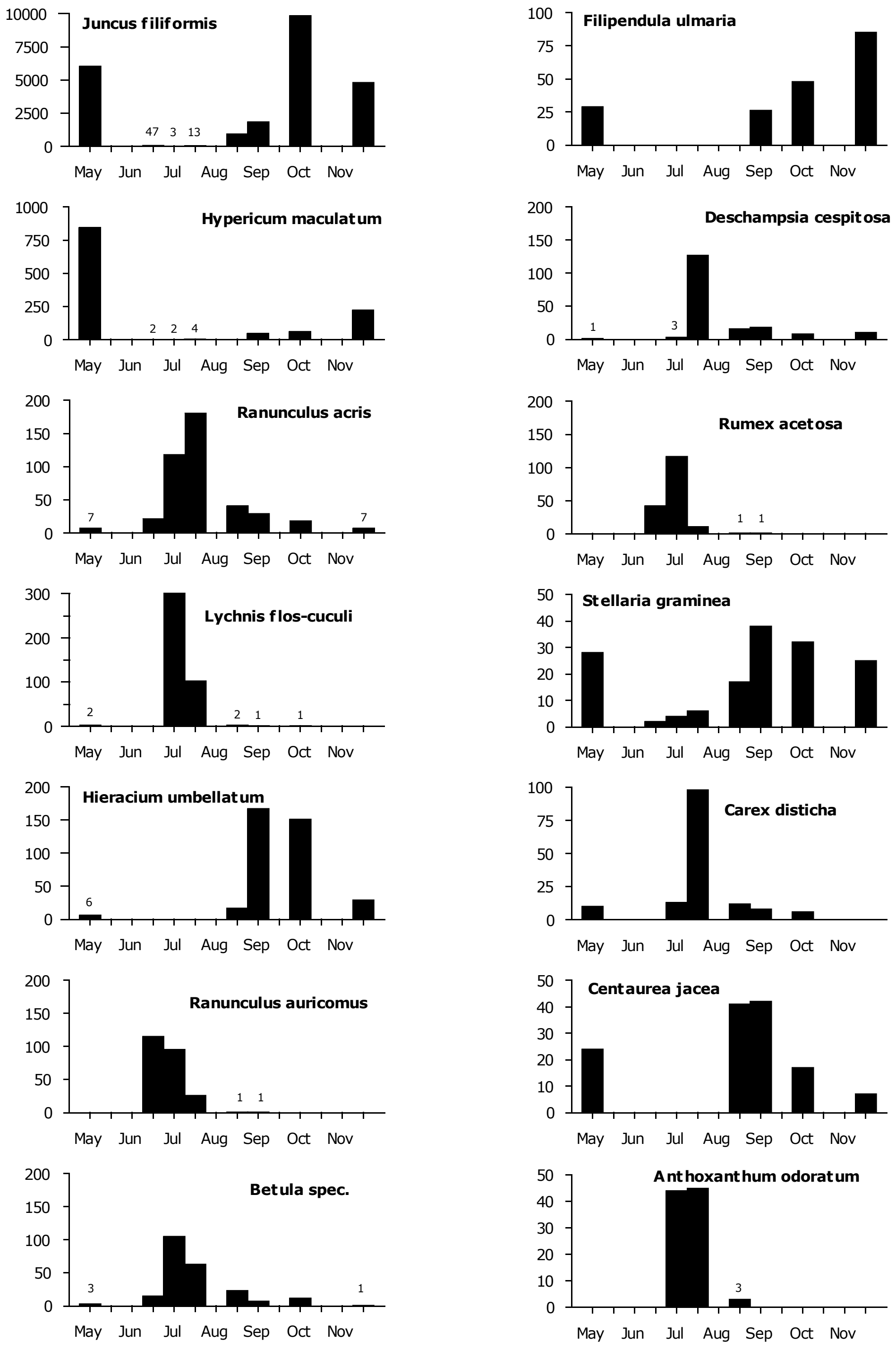


Fig. G.13: Temporal variation of the seed rain of the fourteen most abundant species in Käära transect

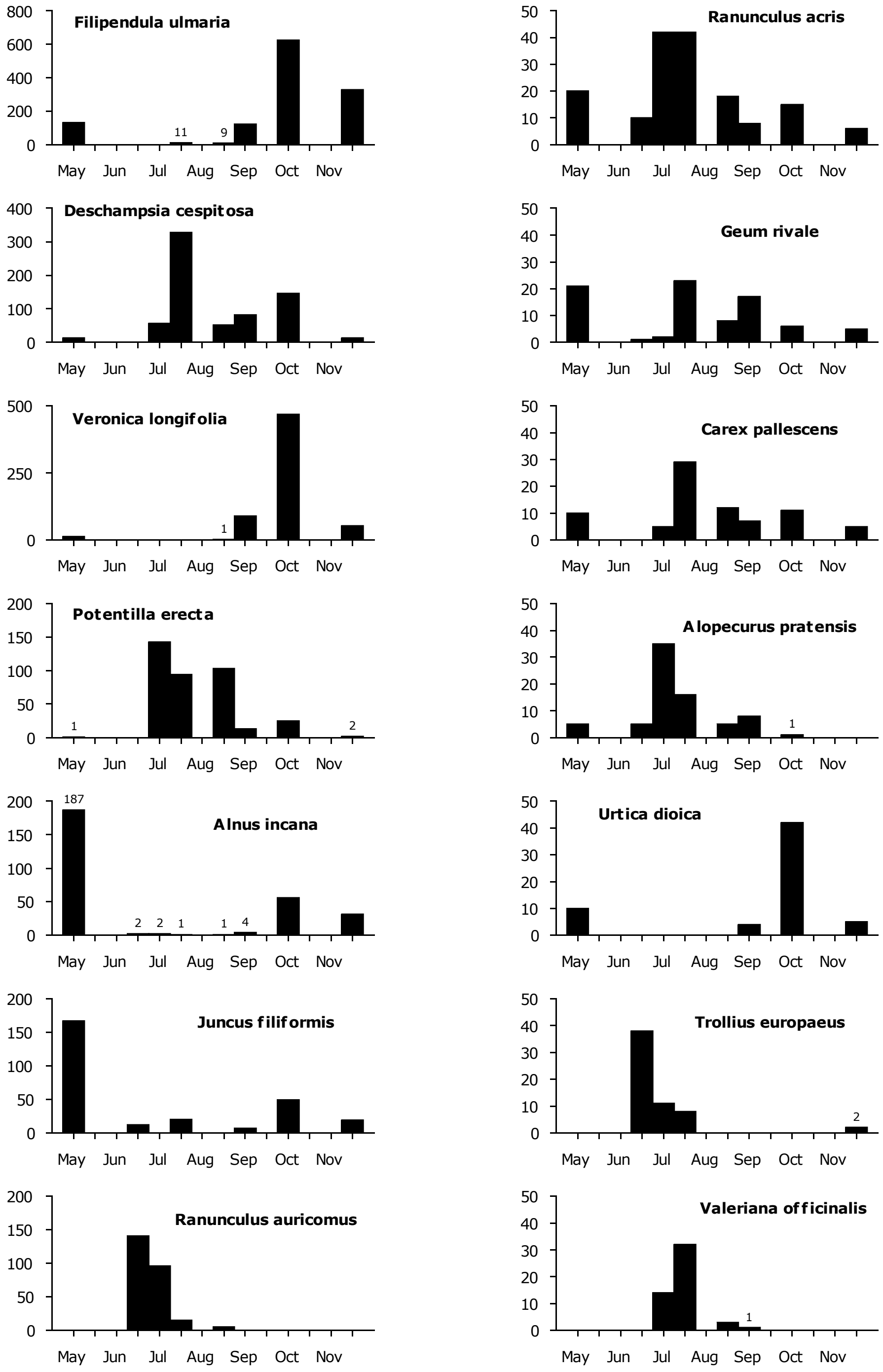


Fig. G.14: Temporal variation of the seed rain of the fourteen most abundant species in Läti transect

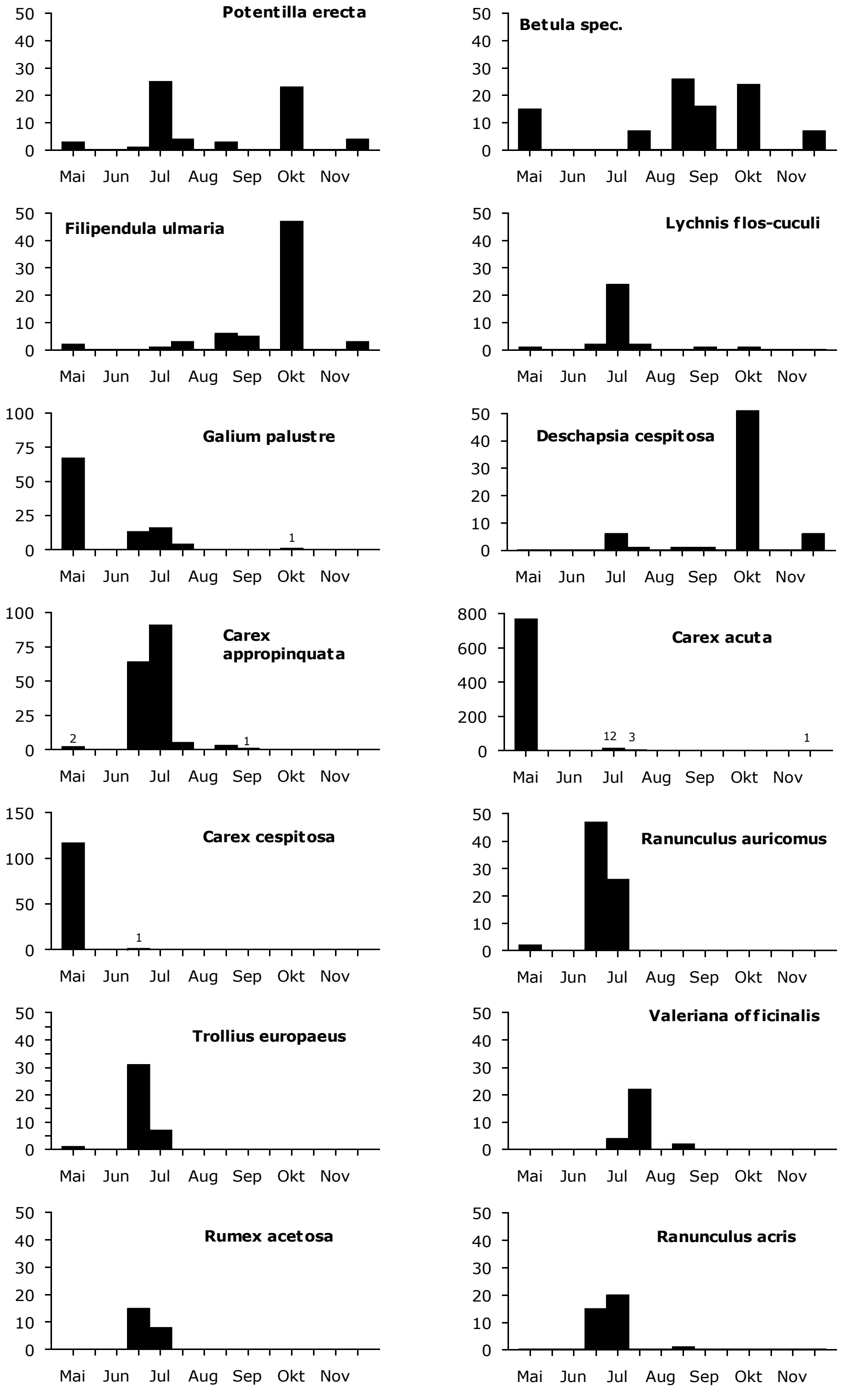


Fig. G.15: Temporal variation of the seed rain of the fourteen most abundant species in Mulgi Heinamaa transect

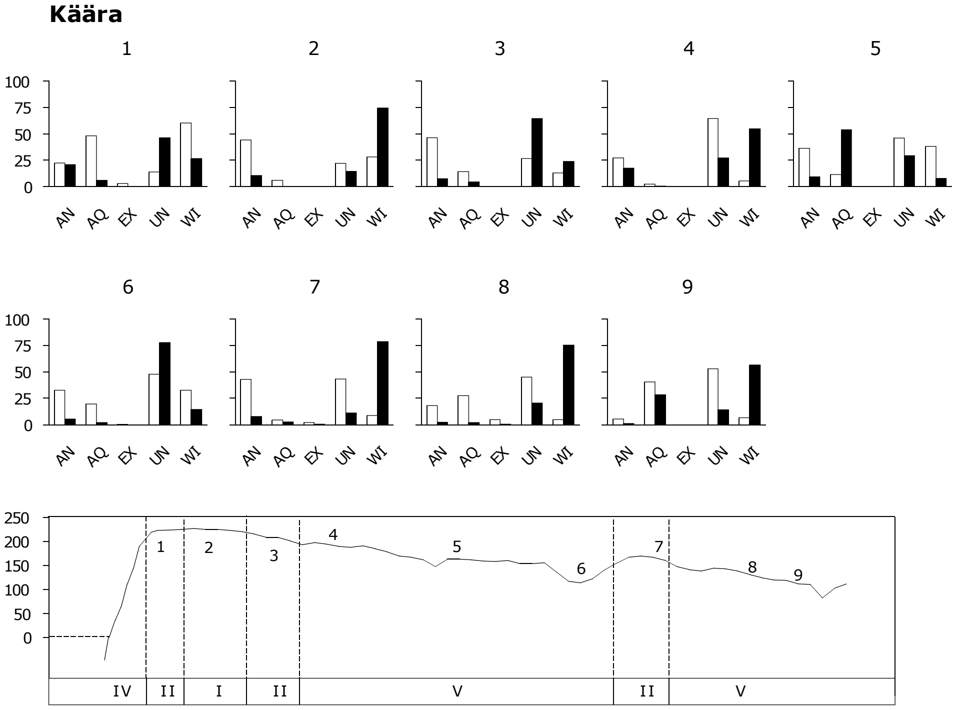


Fig. G.16: Spectra of dispersal vectors on Käära transect for the established vegetation (open bars) and the seed rain (filled bars)

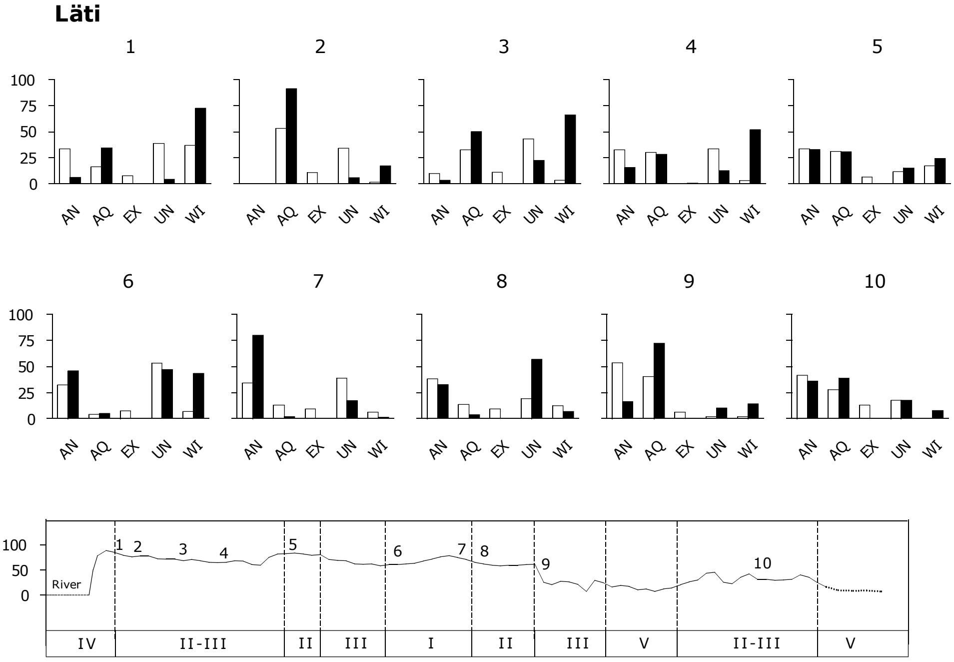


Fig. G.17: Spectra of dispersal vectors on Läti transect for the established vegetation (open bars) and the seed rain (filled bars)

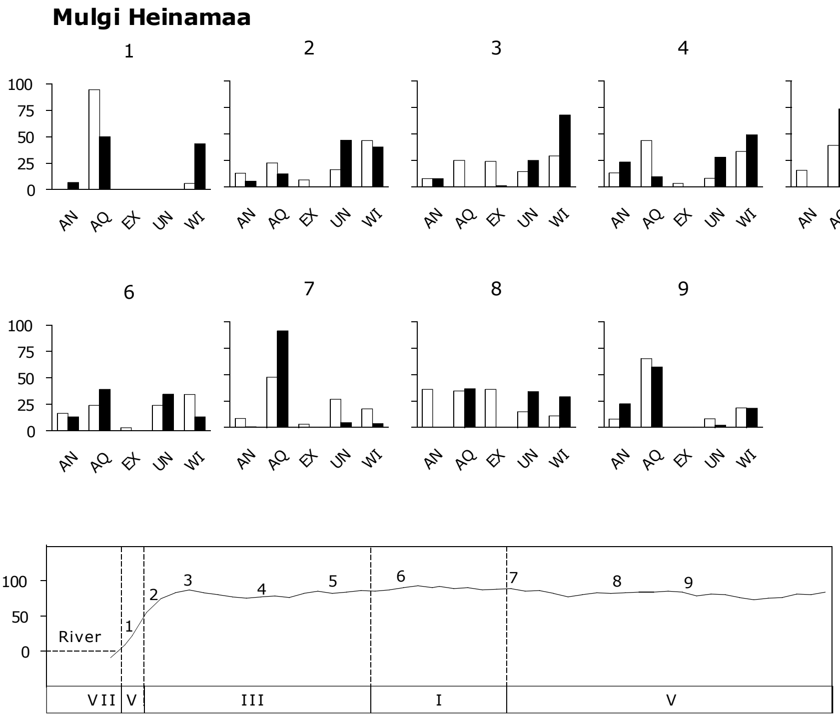


Fig. G.18: Spectra of dispersal vectors on Mulgi Heinamaa transect for the established vegetation (open bars) and the seed rain (filled bars)

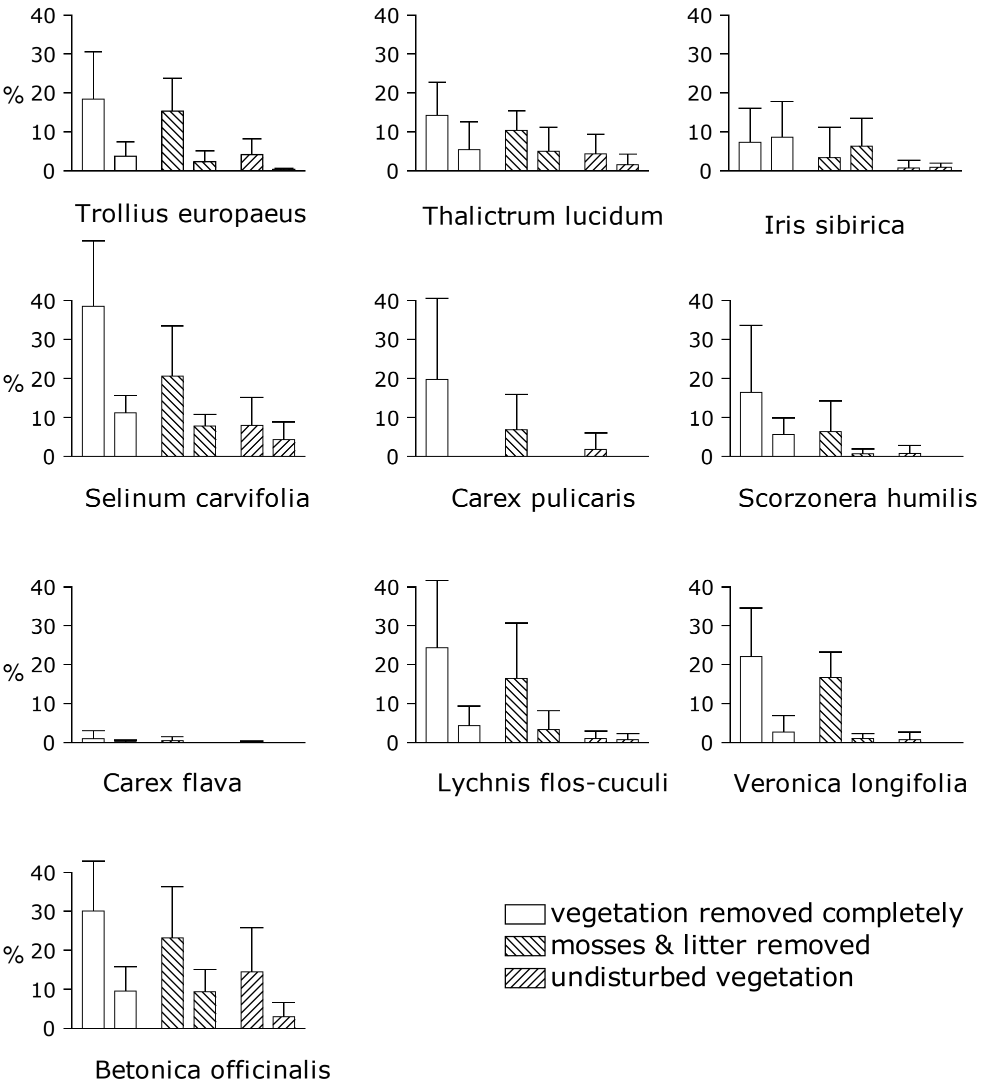


Fig. G.19: Results of seed sowing experiment: percentage recruitment after one year (left bar) and after three years (right bar); whiskers denote one SD.

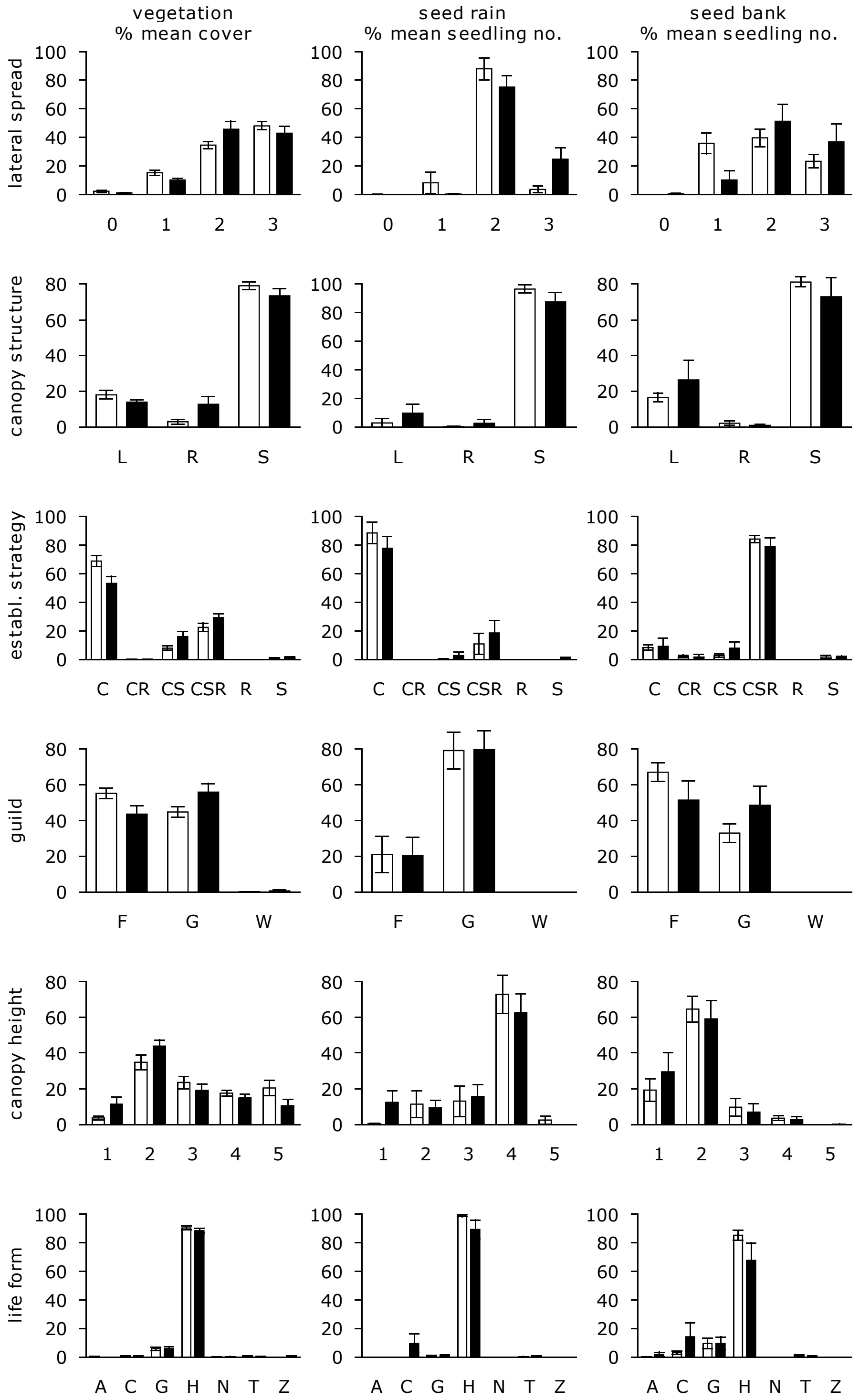
Table G.13: Composition of established vegetation and of experimental seedling assemblages established from different sources separately for moist and dry sites: percentage mean cover (MC), frequency (FR), mean seedling number (MSN) and total seedling number (TSN).

	established vegetation				seed rain				seed rain & bank				seed bank				total
	moist (n=10)		dry (n=10)		moist (n=10)		dry (n=10)		moist (n=10)		dry (n=10)		moist (n=9)		dry (n=9)		
	mean cover	frequ.	mean cover	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.	freq u.	seedl. no.
1. present only in vegetation																	
Achillea millefolium	2.6	8	4.2	8	–	–	–	–	–	–	–	–	–	–	–	–	–
Achillea ptarmica	3.4	8	3.4	5	–	–	–	–	–	–	–	–	–	–	–	–	–
Anthriscus sylvestris	2.2	3	0.5	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Calamagrostis canescens	4.0	1	2.0	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Calamagrostis stricta	1.3	2	1.0	3	–	–	–	–	–	–	–	–	–	–	–	–	–
Caltha palustris	3.8	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Carex disticha	4.0	1	2.0	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Carex hartmanii	0.5	1	0.5	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Carex leporina	1.0	3	0.5	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Centaurea jacea	9.6	4	7.6	4	–	–	–	–	–	–	–	–	–	–	–	–	–
Cirsium oleraceum	3.0	6	3.8	3	–	–	–	–	–	–	–	–	–	–	–	–	–
Comarum palustre	4.0	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Equisetum arvense	0.5	1	0.5	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Festuca pratensis	5.4	2	0.5	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Galium boreale	5.5	5	5.5	5	–	–	–	–	–	–	–	–	–	–	–	–	–
Galium mollugo	5.4	4	3.4	5	–	–	–	–	–	–	–	–	–	–	–	–	–
Geranium palustre	18.8	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Glyceria fluitans	0.5	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hierochloe odorata	1.6	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hypericum maculatum	–	–	3.0	2	–	–	–	–	–	–	–	–	–	–	–	–	–
Juncus effusus	0.5	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Juncus filiformis	3.1	5	2.3	2	–	–	–	–	–	–	–	–	–	–	–	–	–
Nardus stricta	0.5	2	18.5	5	–	–	–	–	–	–	–	–	–	–	–	–	–
Phalaris arundinacea	0.5	1	0.5	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Phleum pratense	3.8	6	2.0	2	–	–	–	–	–	–	–	–	–	–	–	–	–
Plantago lanceolata	–	–	0.5	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Poa trivialis	0.5	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

	established vegetation				seed rain				seed rain & bank				seed bank				total
	moist (n=10)		dry (n=10)		moist (n=10)		dry (n=10)		moist (n=10)		dry (n=10)		moist (n=9)		dry (n=9)		
	mean cover	frequ.	mean cover	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.
Polygonum amphibium	0.5	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Potentilla anserina	2.1	4	1.3	4	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhinanthus serotinus	–	–	0.5	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Salix cinerea	0.5	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Salix myrsinifolia	0.5	1	1.3	2	–	–	–	–	–	–	–	–	–	–	–	–	–
Salix phylicifolia	0.5	1	0.5	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Stellaria graminea	0.5	2	1.0	3	–	–	–	–	–	–	–	–	–	–	–	–	–
Stellaria palustris	1.0	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Trollius europaeus	4.5	10	2.5	7	–	–	–	–	–	–	–	–	–	–	–	–	–
Vaccinium vitis-idaea	–	–	4.0	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Valeriana officinalis	2.2	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Vicia cracca	3.6	9	3.6	9	–	–	–	–	–	–	–	–	–	–	–	–	–
Viola palustris	0.5	1	2.0	1	–	–	–	–	–	–	–	–	–	–	–	–	–
2. present only in seedling plots																	
Barbarea sp.	–	–	–	–	–	–	–	–	–	–	1	1	–	–	3	1	4
Cardamine pratensis	–	–	–	–	–	–	–	–	–	–	–	–	4	1	–	–	4
Crepis paludosa	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	1
Euphrasia sp.	–	–	–	–	1	1	–	–	–	–	6	1	–	–	–	–	7
Peplis portula	–	–	–	–	–	–	–	–	2	1	–	–	–	–	–	–	2
Plantago major	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	1
Viola uliginosa	–	–	–	–	–	–	–	–	–	–	–	–	8	1	–	–	8
3. present in vegetation and seedling plots																	
Agrostis canina	0.5	1	0.5	1	–	–	–	–	2	2	1	1	–	–	1	1	5
Agrostis tenuis	4.0	1	3.8	6	3	1	2	3	12	2	2	4	–	–	100	1	140
Alchemilla vulgaris agg.	4.2	7	7.3	9	–	–	–	–	3	7	10	4	4	1	26	2	117
Alopecurus pratensis	9.1	6	4.0	3	4	1	–	–	–	–	–	–	–	–	–	–	4
Angelica sylvestris	4.2	7	2.2	6	–	–	–	–	–	–	1	1	–	–	1	1	2
Anthoxanthum odoratum	4.3	3	1.5	3	–	–	1	1	2	4	2	6	2	4	4	1	33
Briza media	2.0	2	2.5	4	–	–	–	–	1	1	1	1	–	–	–	–	2

	established vegetation				seed rain				seed rain & bank				seed bank				total
	moist (n=10)		dry (n=10)		moist (n=10)		dry (n=10)		moist (n=10)		dry (n=10)		moist (n=9)		dry (n=9)		
	mean cover	frequ.	mean cover	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.
Campanula glomerata	1.3	2	0.9	4	–	–	–	–	1	1	–	–	–	–	–	–	1
Carex acuta	2.0	1	2.0	1	–	–	–	–	3	2	1	1	–	–	–	–	6
Carex cespitosa	5.5	5	2.0	2	–	–	–	–	–	–	2	1	–	–	–	–	2
Carex flava	1.4	5	2.1	5	1	1	–	–	11	4	5	5	7	5	118	1	221
Carex hirta	2.0	1	0.5	2	–	–	–	–	10	1	–	–	–	–	–	–	10
Carex nigra	1.9	7	2.7	6	–	–	1	1	6	7	5	6	8	3	1	3	100
Carex pallescens	1.4	7	1.1	8	–	–	1	1	7	8	8	7	4	6	5	7	170
Carex panicea	4.1	9	5.4	10	1	1	–	–	17	8	7	9	9	8	4	7	300
Carex pulicaris	–	–	0.5	1	–	–	–	–	4	1	–	–	–	–	–	–	4
Carex vesicaria	1.0	3	–	–	–	–	–	–	–	–	3	1	–	–	–	–	3
Carex vulpina	2.1	4	1.3	2	–	–	–	–	1	1	–	–	5	1	–	–	6
Cerastium holosteoides	0.5	1	0.5	4	–	–	–	–	2	9	9	3	3	4	2	3	59
Cirsium heterophyllum	6.6	3	3.0	2	–	–	–	–	–	–	–	–	–	–	1	1	1
Dactylis glomerata	2.1	5	2.2	3	–	–	–	–	1	1	–	–	–	–	–	–	1
Danthonia decumbens	–	–	0.5	1	–	–	–	–	–	–	1	1	6	1	17	2	40
Deschampsia cespitosa	25.2	10	4.5	10	15	10	19	9	23	9	22	8	3	7	3	4	734
Festuca ovina	7.6	3	42.2	8	–	–	–	–	1	1	1	1	–	–	2	1	4
Festuca rubra	24.5	9	20.5	9	4	1	10	3	–	–	11	6	1	2	–	–	101
Filipendula ulmaria	26.3	10	12.7	7	–	–	–	–	1	1	–	–	–	–	–	–	1
Galium palustre	0.5	2	–	–	–	–	–	–	–	–	1	1	1	2	–	–	3
Galium uliginosum	0.8	6	0.8	6	–	–	–	–	6	6	2	3	6	7	–	–	82
Geum rivale	13.7	10	2.5	9	–	–	–	–	–	–	–	–	1	1	–	–	1
Glechoma hederacea	4.0	1	0.5	2	–	–	–	–	–	–	1	1	–	–	–	–	1
Helictotrichon pratensis	–	–	4.0	2	–	–	1	1	–	–	–	–	–	–	–	–	1
Helictotrichon pubescens	0.5	6	0.8	5	1	1	–	–	2	1	–	–	–	–	–	–	3
Hieracium lactucella	–	–	1.0	3	–	–	1	1	–	–	1	1	–	–	7	1	9
Lathyrus pratensis	2.3	9	1.8	5	–	–	–	–	2	1	–	–	1	1	–	–	3
Luzula campestris s.l.	0.8	5	1.0	10	1	1	3	3	2	9	7	6	2	8	2	6	97
Lychnis flos-cuculi	2.1	8	1.3	2	–	–	–	–	10	8	20	2	9	7	6	4	202
Mentha arvensis	0.5	2	0.5	2	1	1	–	–	1	4	–	–	5	2	1	1	16
Poa palustris	2.0	2	–	–	–	–	–	–	3	1	–	–	2	1	–	–	5

	established vegetation				seed rain				seed rain & bank				seed bank				total
	moist (n=10)		dry (n=10)		moist (n=10)		dry (n=10)		moist (n=10)		dry (n=10)		moist (n=9)		dry (n=9)		
	mean cover	frequ.	mean cover	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.	frequ.	seedl. no.
Poa pratensis	1.8	6	2.0	2	–	–	–	–	2	4	1	1	–	–	1	1	11
Potentilla erecta	6.9	6	7.0	8	–	–	–	–	10	4	4	6	9	4	6	4	120
Prunella vulgaris	–	–	0.5	1	–	–	–	–	1	3	5	2	2	2	3	1	20
Ranunculus acris	5.7	10	6.4	10	–	–	–	–	4	7	2	5	4	5	8	2	78
Ranunculus auricomus	4.4	10	3.3	9	26	3	–	–	31	10	5	8	34	8	4	5	717
Ranunculus repens	–	–	2.0	1	–	–	–	–	17	8	11	3	9	5	13	1	226
Rumex acetosa	2.1	9	2.8	9	4	5	3	5	7	5	4	7	2	2	–	–	103
Sesleria caerulea	13.2	3	22.7	7	1	1	3	1	5	7	1	6	5	4	1	2	65
Thalictrum flavum	0.5	1	–	–	–	–	–	–	–	–	–	–	1	1	–	–	1
Trifolium pratense	2.0	1	2.0	2	–	–	–	–	–	–	1	1	1	1	2	3	9
Trifolium repens	0.5	1	–	–	–	–	–	–	2	5	3	6	2	4	3	4	48
Veronica chamaedrys	0.9	7	0.7	7	–	–	3	2	–	–	7	2	–	–	40	1	60
Viola canina s.l.	2.1	4	1.9	6	–	–	–	–	10	7	7	7	4	6	12	6	212
4. dubious species																	
Agrostis sp.	–	–	–	–	–	–	–	–	3	1	–	–	6	1	–	–	9
Carex flava/vulpina	–	–	–	–	–	–	–	–	8	2	1	3	3	1	16	1	38
Carex nigra/acuta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	2
Carex pulicaris/dioica	–	–	–	–	–	–	–	–	5	2	3	1	8	3	–	–	37
Carex sect. Phacocystis	–	–	–	–	1	1	–	–	5	2	–	–	2	3	7	1	24
Carex sp.	–	–	–	–	–	–	–	–	4	1	–	–	–	–	–	–	4
C. vesicaria/acutiformis	–	–	–	–	–	–	–	–	9	1	–	–	1	1	3	2	15
Cirsium sp.	0.5	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Juncus sp.	–	–	–	–	–	–	–	–	1	3	2	2	–	–	2	4	14
Ranunculus sp.	–	–	–	–	–	–	–	–	–	–	5	1	–	–	–	–	5
Salix sp.	0.5	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Stellaria sp.	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	1
Vaccinium sp.	–	–	–	–	–	–	–	–	–	–	2	3	–	–	–	–	7
Viola sp.	–	–	–	–	–	–	–	–	4	2	1	1	4	3	–	–	20
total species	83		75		14		12		48		44		38		35		


vegetation
% mean cover
seed rain
% mean seedling no.
seed bank
% mean seedling no.
lateral spread
0 1 2 3
canopy structure
L R S
establ. strategy
C CR CS CSR R S
guild
F G W
canopy height
1 2 3 4 5
life form
A C G H N T Z
0 20 40 60 80 100

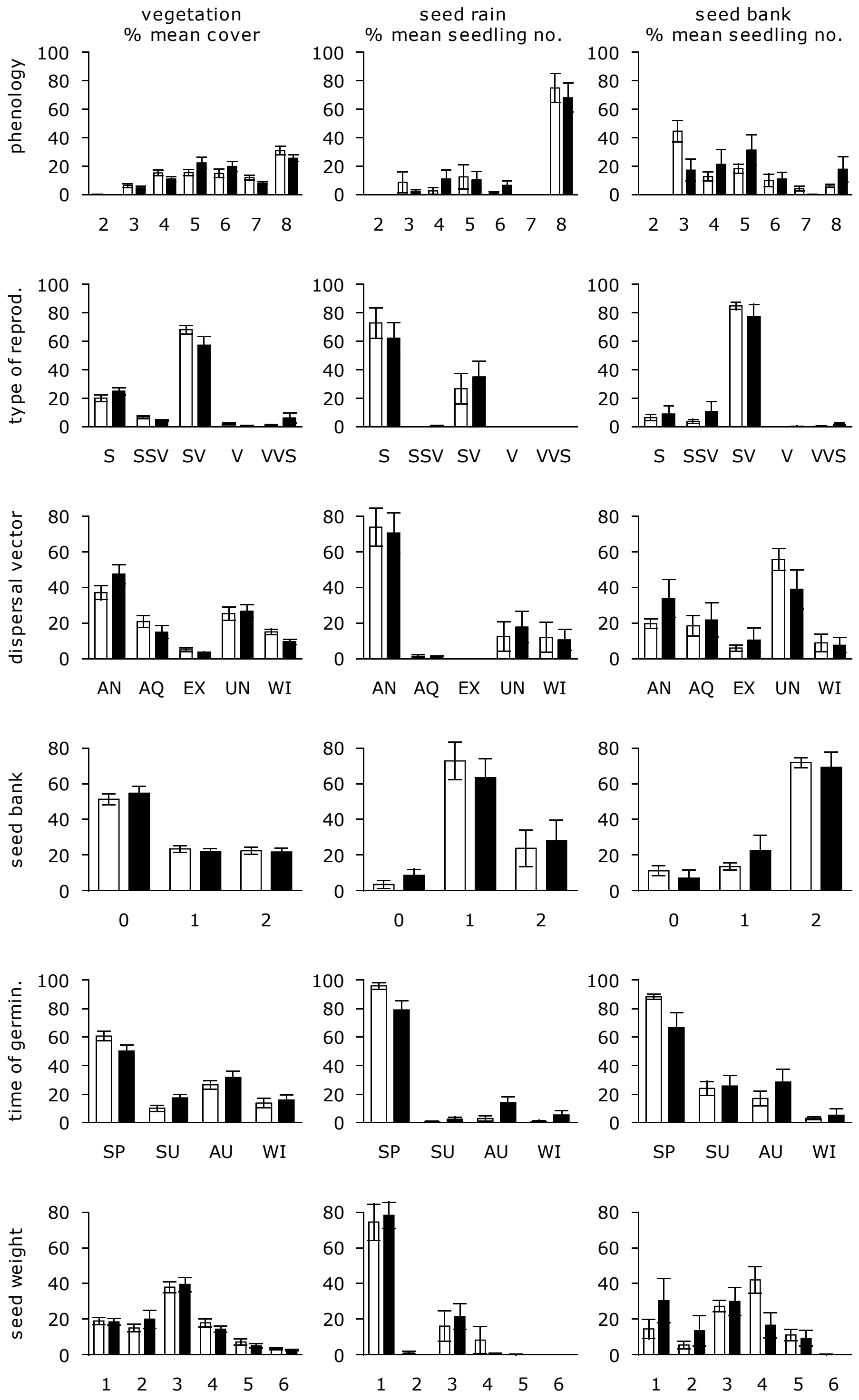


Fig. G.20: Distribution of twelve traits in the established vegetation and in seedling assemblages of different origin (seed rain and seed bank). Open bars show data for moist, filled bars for dry sites, percentage mean cover and percentage mean seedling number ± one standard-error. For detailed explanation of traits see Table D.2.

Table G.14: List of 135 species of the Soomaa floodplain meadows with plant traits used for multivariate analysis in Chapter D. 3.4 and membership in functional groups (PFG) as defined in Table D.19. For abbreviations of traits see end of this table and Table D.2.

	PFG	LIF	LFO	GLD	CLO	HEI	STR	ROS	REP	PHE	GER	SEN	SEW	SEB	DIS
Achillea millefolium	1	P	H	F	3	2	C	S	SV	7	AS	2	1	2	WIw
Achillea ptarmica	8	P	H	F	3	2	CS	L	SV	8	S	2	1	0	WIw
Agrostis canina	3	P	H	G	3	2	CSR	S	SV	7	AS	1	1	2	ANa
Agrostis capillaris	3	P	H	G	3	2	CSR	S	SV	8	AS	1	1	2	UN
Agrostis stolonifera	3	P	H	G	3	3	CSR	S	SV	7	S	1	1	2	UN
Alchemilla vulgaris agg.	2	P	H	F	2	2	CSR	S	SV	5		1	3	0	ANa
Alnus incana		P	P	W	1	5	C	L	SV	1		3	2	2	AQ/WIw
Alopecurus pratensis	3	P	H	G	2	5	C	L	SV	4		1	3	0	UNag
Angelica sylvestris	9	S	H	F	0	5	C	S	V	8	S	2	4	0	AQ/WIw
Anthoxanthum odoratum	3	P	H	G	2	2	CSR	S	SV	4		1	3	1	ANa
Anthriscus sylvestris	9	S	H	F	1	5	C	S	SSV	5	SW	1	5	0	UN
Betonica officinalis	4	P	H	F	2	3	C	L	SV	8	S	2	4	1	UN
Betula pubescens		P	P	W	0	5	CS	L	S	3		3	1	2	WIw
Briza media	3	P	H	G	3	2	CSR	S	SV	7	AU	1	3	0	UN
Calamagrostis canescens	8	P	H	G	3	5	CS	S	SV	8		2	1	2	WIp
Calamagrostis epigejos	8	P	G	G	3	5	C	S	SV	8		2	1	1	WIp
Calamagrostis stricta	8	P	H	G	3	3	CS	S	SV	8		2	1		WIp
Caltha palustris	3	P	H	F	1	2	CSR	S	SV	3	S	1	3	0	AQ
Campanula glomerata	1	P	H	F	1	3	CSR	S	SV	7		2	1		WIc
Campanula patula	1	S	H	F	1	3	CSR	S	S	6	A	2	1	2	WIc
Cardamine pratensis	3	P	H	F	1	2	CSR	S	VVS	3	S	1	3	2	EX
Carex acuta	3	P	G	G	3	4	CS	S	SV		S	1	3	2	AQ
Carex cespitosa	3	P	H	G	2	2	CS	S	SV	3	S	1	3		AQ
Carex disticha	3	P	G	G	3	3	CSR	L	SV	4	U	1	3	0	UN
Carex elata	3	P	H	G	2	4	CS	S	SV	4	U	1	3	2	AQ
Carex flava	3	P	H	G	2	2	CSR	S	SV	5	S	1	2	2	AQ
Carex hirta	3	P	G	G	3	2	C	S	SV	4	U	1	5	0	ANa
Carex leporina	3	P	H	G	2	2	CSR	S	SV	6	S	1	2	2	UN
Carex nigra	3	P	G	G	3	2	S	S	SV	4	S	1	3	1	AQ
Carex pallescens	3	P	H	G	2	2	CSR	S	SV	5	S	1	3	1	UN
Carex panicea	3	P	G	G	3	2	CSR	S	SV	4	SU	1	5	2	AQ

	PFG	LIF	LFO	GLD	CLO	HEI	STR	ROS	REP	PHE	GER	SEN	SEW	SEB	DIS
Carex pulicaris	3	P	H	G	2	1	CSR	S	SV	3	S	1	4	0	UN
Carex vesicaria	3	P	A,H	G	3	3	CS	S	SV	4	A	1	5	2	AQ
Carex vulpina	3	P	H	G	2	3	CSR	S	SV	4	S	1	4		UN
Centaurea jacea	2	P	H	F	1	3	C	S	S	8		1	4	1	UN
Cerastium holosteoides		P	C	F	2	1	CR	L	SV	4	ASU	2	1	2	UNc
Cirsium heterophyllum	1	P	H	F	3	5	C	S	SV	7		2	5	0	WIp
Cirsium oleraceum	1	P	H	F	2	5	C	S	SV	8		2	5	0	WIp
Cirsium palustre	9	S	H	F	0	5	C	S	S	7	S	2	5	2	WIp
Comarum palustre	4	P	C	F	3	2	CS	L	SV	6	SU		4	2	AQ
Dactylis glomerata	7	P	H	G	2	4	C	S	SSV		S	2	3	1	UNag
Deschampsia cespitosa	7	P	H	G	2	4	C	S	S	8	S	2	1	1	ANa
Festuca ovina	2	P	H	G	2	2	CSR	S	S	6	U	1	2	0	ANa
Festuca pratensis	7	P	H	G	2	4	C	S	S	7	A	1	4	0	UN
Festuca rubra	3	P	H	G	3	3	C	S	SV	6	AW	1	3	0	ANa
Filipendula ulmaria	4	P	H	F	3	5	C	S	SV	8	S	2	2	0	AQ
Galium boreale	3	P	H	F	3	2	CSR	L	SV	7		1	3	0	ANa
Galium mollugo	4	P	H	F	3	3	C	L	SV			1	3	1	UN
Galium palustre	6	P	H	F	3	1	CSR	L	SV	6	S	1	3	2	AQ
Galium uliginosum	3	P	H	F	3	2	CSR	L	SV	7	S	1	3	0	UN
Geranium palustre	5	P	H	F	2	3	C	S	SV	5		1	5	0	EX
Geranium pratense	5	P	H	F	2	3	C	S	SV	7	SW	1	5	1	EX
Geum rivale	3	P	H	F	3	2	C	S	SV	4		1	4	0	ANa
Gladiolus imbricatus	1	P	G	F	1	3	CSR	L	SV			1			WI
Glechoma hederacea	6	P	G,H	F	3	1	CSR	L	SV	3	SU	1	3	2	UN
Glyceria fluitans	4	P	A,H	G	3	4	CS	L	SV	6		2	4	1	UN
Helictotrichon pratensis	7	P	H	G	1	4	CS	S	SSV	6	A	1	4	0	ANa
Helictotrichon pubescens	3	P	H	G	3	3	C	S	SV	6	A	1	4	0	ANa
Heracleum sibiricum	9	P	H	F	1	5	C	S	SSV	6	SW	1	5	0	WIw
Hieracium lactucella	6	P	H	F	3	1	CSR	R	SV	6		1	1	0	WIp
Hieracium pilosella	6	P	H	F	3	1	CSR	R	SV	6	ASU	1	1	2	WIp
Hieracium umbellatum	1	P	H	F	1	3	CS	S	SV	8	S	2	2	0	WIp
Hierochloe odorata	3	P	G,H	G	3	3	CS	S	SV	4		1	2		ANa
Hypericum maculatum	8	P	H	F	3	3	CSR	L	SV	8	S	3	1	2	WIc

	PFG	LIF	LFO	GLD	CLO	HEI	STR	ROS	REP	PHE	GER	SEN	SEW	SEB	DIS
Inula salicina	8	P	H	F	3	3	CS	L	SV	8		2	1	0	WIp
Iris pseudacorus	5	P	G,H	F	2	3	CS	S	SV	6	SW	1	5	0	AQ
Iris sibirica	5	P	G,H	F	2	3	CS	S	SV	6		1	5	0	AQ
Juncus conglomeratus	8	P	H	G	2	4	C			7		3	1	2	ANm/WIm
Juncus effusus	8	P	H	G	2	4	C	L	SV	6	S	3	1	2	ANm/WIm
Juncus filiformis	8	P	G	G	3	2	CSR	L	VVS	6		3	1	2	ANm/WIm
Knautia arvensis	2	P	H	F	1	3	C	S	S	7	S	1	5	2	ANa
Lathyrus pratensis	5	P	H	F	3	3	C	L	SSV	7	AS	1	6	2	EX
Leontodon autumnalis	1	P	H	F	1	2	CSR	R		6	AS	1	3	1	WIp
Leucanthemum vulgare	1	P	H	F	2	3	C	S	SV		AS	2	2	2	UNag
Linum catharticum	9	S	T	F	0	1	SR	S	S	6	S	1	1	2	UN
Luzula campestris	6	P	H	G	3	1	CSR	S	SV	3	U	1	3	2	ANe
Luzula multiflora	3	P	H	G	2	2	CSR	S	SV	5	U	1	2	2	ANe
Lychnis flos-cuculi	1	P	H	F	2	3	CSR	S	SV	6	AS	2	1	2	WIc
Lysimachia vulgaris	4	P	H	F	3	5	CS	L	SV	8	S	2	2	1	AQc
Lythrum salicaria	8	P	H	F	1	4	CS	L	SSV	8	SU	3	1	2	AQ
Melampyrum nemorosum	2	S	T	F	0	2		L	S	7		1	5	0	ANe
Mentha arvensis	4	P	G,H	F	3	2	C	L	SV	8	S		2	2	AQ
Molinia caerulea	7	P	H	G	3	4	CS	R	SSV	8	SU		3	1	UN
Myosotis scorpioides	3	P	H	F	3	2	CSR	S	SV	6	S	1	2	0	UN
Nardus stricta	7	P	H	G	2	1	CS	R	VVS	5		1	2	0	ANa
Peucedanum palustre	9	S	H	F	1	5	CS	S	SSV	8	SU	2	5	0	WIw/AQ
Phalaris arundinacea	4	P	G,H	G	3	5	C	L	SV	8	S	2	3	2	AQ
Phleum pratense	7	P	H	G	1	4	C	S	SSV	7	AS	1	3	2	ANa
Phragmites australis	8	P	A,G	G	3	5	CS	L	VVS	9	S	3	1	0	WIp
Plantago lanceolata	2	P	H	F	0	2	CSR	R	SSV	4	ASW	1	4	2	ANm
Poa palustris	3	P	H	G	3	4	CS	S	SV	7	A	1	1	0	UNag
Poa pratensis	3	P	H	G	3	2	C	S	SV	6	AS	1	2	2	UNag
Polygala amarella	2	P	H,C	F	1	1	CSR	S	S	5		1	3	0	ANe
Polygonum amphibium	5	P	A,G	F	3	3	CS	L	VVS	6		1	3	0	AQ
Potentilla anserina	3	P	H	F	3	2	CSR	R	SV	5	U	1	3	1	UN
Potentilla erecta	6	P	H	F	2	1	CSR	L	SV	5	SU	1	3	2	UN
Prunella vulgaris	6	P	H	F	3	1	CSR	L	SV	8	S	1	3	2	ANm

	PFG	LIF	LFO	GLD	CLO	HEI	STR	ROS	REP	PHE	GER	SEN	SEW	SEB	DIS
Ranunculus acris	2	P	H	F	1	2	C	S	S	5	ASW	1	4	1	UN
Ranunculus auricomus	3	P	H	F	1	2	CSR	S	SV	3	S	1	4	2	UN
Ranunculus flammula	3	P	H	F	3	2	CSR			5	S	1	2	2	AQ
Ranunculus repens	3	P	H	F	3	2	CSR	S	SV	5	SU	1	5	2	AQ/AN
Rhinanthus minor	9	S	T	F	0	2	SR	L	S	6	S	1	4	1	WIcw
Rhinanthus serotinus	9	S	T	F	0	2		L	S	6	S	1		0	WIcw
Rumex acetosa	1	P	H	F	2	3	C	S	SV	5	S	1	3	2	WIw
Salix cinerea		P	N	W	2	5	C	L	S	2		3	1	0	WIp
Salix myrsinifolia		P	N	W	2	5	C	L	S			3	1	0	WIp
Salix phylicifolia		P	N	W	2	5	C	L	S			3	1	0	WIp
Schoenopl. lacustris	8	P	A,G	G	2	5	CS	L	SV	8	SU	3		0	ANa
Scorzonera humilis	2	P	H	F	1	2	CSR	S	S	6	U	1	5	0	WIp
Selinum carvifolia	1	P	H	F	1	4	CS	S	S	7	S	2	3	0	WIw
Sesleria caerulea	7	P	H	G	2	2	CS	R			A	1	3	0	UN
Stachys palustris	4	P	G	F	3	3	C	L	SV	8	U	2	3	2	AQ
Stellaria graminea	4	P	H	F	3	2	CS	L	SV	6	S	2	2	2	UNc
Stellaria palustris	4	P	H	F	3	2	CSR	L	SV	6	A	2	2	2	UNc
Succisa pratensis	2	P	H	F	1	3	CSR	S	SSV	8	ASUW	1	4	1	ANa
Symphytum officinale	2	P	H	F	1	4	C	S	SSV	5		1	3	0	AQ/ANe
Taraxacum sect. Palustria	1	P	H	F	1	1	CSR	R	S	3			3		WIp
Taraxacum sect. Ruderalia	1	P	H	F	1	2	CSR	R		3	S	2	3	2	WIp
Thalictrum lucidum	1	P	H	F	1	5	CS	S	SV	7		2	3		UN
Trifolium medium	5	P	H	F	3	1	C	L	SV	7	A	1	5	0	ANa
Trifolium montanum	2	P	H	F	0	2	CSR	S	S	7		1	4	0	ANa
Trifolium pratense	2	P	H	F	0	2	C	S	S	6	A	1	4	2	ANa
Trifolium repens	6	P	H	F	3	1	CSR	S	SV	6	U	1	2	2	ANa
Trollius europaeus	1	P	H	F	1	3	C	S	SV	5	S	2	3	0	WIc
Urtica dioica	8	P	H	F	3	4	C	L	SV	7	S	3	1	2	WI/ANa
Valeriana officinalis	1	P	H	F	1	5	C	S	SV	7	SU	1	3	0	WIpw
Veronica chamaedrys	6	P	C,H	F	3	1	CSR	L	SV	4		1	1	2	UNcw
Veronica longifolia	8	P	H	F	1	4	C	L	SV	8		3	1		WIc
Vicia cracca	5	P	H	F	3	4	C	L	SSV	7	AS	1	6	2	EX
Viola canina ssp. canina	6	P	H	F	2	1	CSR	L	SSV	3	SU	1	3	2	EX/ANe

	PFG	LIF	LFO	GLD	CLO	HEI	STR	ROS	REP	PHE	GER	SEN	SEW	SEB	DIS
Viola canina ssp. montana	6	P	H	F	2	1	CSR	L	SV	3	SU	1	3	2	EX/ANe
Viola epipsila	6	P	H	F	3	1	CSR	R	SV			1	3		EX/ANe
Viola palustris	6	P	H	F	3	1	S	R	VVS	3	SU	1	3	0	EX/ANe
Viola persicifolia	6	P	H	F	2	1	CSR	L	SV	6		1	3		EX/ANe
Viola uliginosa	6	P	H	F		1	CSR	R	VVS			1	3		

LIF: life cycle, LFO: Raunkiaer life form, GLD: guild, CLO: lateral spread, HEI: plant height, STR: CSR-strategy type, ROS: canopy structure, REP: reproductive mode, PHE: time of flowering, GER: time of germination, SEN: seed number, SEW: seed weight, SEB: seed bank type, DIS: dispersal vector; see Table D.2 for a complete list of traits and trait states.