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Ecological significance of seed germination characteristics in flood-meadow species

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Summary

In climate chamber and outdoor experiments we analysed germination traits of 42 vascular plant species typical of flood-meadows of the alliance *Cnidion*. In Central Europe such flood-meadows and their highly endangered character species are confined to large lowland river corridors with a dry and warm climate. Due to the prevailing ecological conditions, particularly the extremely high variability in soil moisture potential, it was hypothesised that flood-meadow species exhibit specific strategies in terms of germination phenology, temperature requirements and primary dormancy to avoid constraints on seedling recruitment imposed by flooding, drought and competition from established vegetation. Furthermore, we expected that germination characteristics could be a key for the causal understanding of range size, confinement to large river corridors, recent rarification processes, seed bank persistence and establishment success in restoration projects.

PCA ordination of germination traits reflected a continuous gradient of increasing primary dormancy levels ranging from species with a high capacity for fast and almost complete germination over a wide range of temperatures to those with high and narrow temperature requirements and/or a delayed and asynchronous emergence. Many of the studied species germinated only at relatively high temperature in the year of shedding, but the primary conditional dormancy disappeared in most cases after a period of cold wet stratification. Requirements for chilling and/or high germination temperature were revealed to be the most common strategies for avoidance of harmful autumn and winter germination. The majority of the studied species tends to exploit particularly favourable regeneration niches in early spring. Surprisingly, many species with large long-term persistent soil seed banks exhibited relatively low dormancy levels in light; this was correlated with small seed size and a consequent higher probability of burial. We found no relationship between germination characteristics and river corridor confinement or Central European range size. However, there was a significant trend in endangered species towards higher temperature requirements and delayed, asynchronous germination. This is presumably disadvantageous under the environmental conditions of subcontinental flood-meadows.

Key words: Dormancy, germination temperature requirements, grassland restoration, principal component analysis, seed bank, stratification

Introduction

The temporal and spatial limitation of the “regeneration niche” (Grubb 1977) has been increasingly identified as one of the most critical constraints in the life-cycle of plant populations, and is a factor that may severely reduce diversity in plant communities (e. g. Stampfli & Zeiter 1999). Recruitment from seeds is often strongly hampered or even condemned to failure through competition by established vegetation (Rusch & Fernández-Palacios 1995; Kotorová & Lepš 1999; Touzard et al. 2002) as well as unfavourable environmental conditions such as frost and drought (Silvertown & Dickie 1980; Ryser 1993). Consequently, successful

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germination and seedling establishment in a given species will often depend on its ability to avoid or minimize such constraints. Numerous previous studies have shown that seeds of many species boast the aptitude to identify suitable conditions for seedling recruitment (Grime 2001). Narrow temperature requirements, dormancy cycles induced or broken by temperature fluctuations, warm or cold stratification, as well as other environmental factors, such as fire or nitrate concentrations, are all mechanisms that regulate the onset of germination and help in detection of favourable micro-sites with low competition (Thompson et al. 1977; Grime et al. 1981; Baskin & Baskin 2001; Hroudová & Zákravsky 2003). Such dormancy breaking mechanisms were revealed to be of particular importance in species typical of temperate wet grasslands (e.g. Milberg 1994; Schütz 1997; Knödler 2001; Jensen 2001).

Germination characteristics may play an equally important role in the formation of persistent soil seed banks. Seeds exhibiting conditional or strict dormancy (Baskin & Baskin 2001) are more likely to be buried and to establish large persistent reservoirs in the soil (Thompson et al. 1993; Grime 2001). Seed regeneration strategies are now considered as a key for the causal understanding of the decline, persistence or spread of species in changing landscapes (e. g. Schütz 2000b).

Information on germination characteristics is also particularly relevant for habitat restoration, in which species-enrichment largely depends on re-establishment by artificially introduced or naturally dispersed seeds (e. g. Bakker & Berendse 1999; Patzelt et al. 2001). By the creation of suitable regeneration niches at the right time of the year, management schemes may positively influence germination and the subsequent fate of seedlings (Olff et al. 1994; Kotorová & Lepš 1999; Schütz 2000b). If seeds of target species are introduced artificially, information on germination phenology, dormancy, response to storage and pre-treatments are essential to increase the likelihood of seeding success (Keller & Kollmann 1999; Budelsky & Galatowitsch 1999). However, knowledge on germination characteristics is still extremely scarce particularly in rare and endangered species targeted for conservation and there are a great variety of possible response types (e.g. Baskin & Baskin 2001). This also applies to declining and endangered species-rich flood-meadows of the alliance *Cnidion* that include a large number of rare plant species of Central European conservation concern (Schnittler & Günther 1999; Hölzel et al. 2002). In their Central European distribution these alluvial grasslands are strictly confined to large river corridors with dry and warm subcontinental climatic conditions (Korsch 1999; Burkart 2001). This distribution pattern is reflected by the occurrence of many highly specialised eastern species that are uncommon in Central Europe and close to the western limit of their range, such as *Allium angulosum*, *Cnidium dubium*, *Scutellaria hastifolia* and *Viola pumila* (Hultén & Fries 1988). Ecologically these flood-meadows are characterized by an extremely high variability in soil water potential (Burkart 1998; Leyer 2002). Whereas winter, spring and early summer may often bring floods summers are markedly dry and rapidly hardening clay soils are common (Dister 1980; Hölzel 1999). Thus, successful seedling recruitment may be hampered by flooding as well as by drought (Hölzel & Otte 2003a) and there is only a relatively narrow time window with favourable germination conditions.

In the present study, we investigated if there is a specific response in germination characteristics of the typical flora of flood-meadows to these particular ecological conditions. Furthermore, we attempted to assess whether germination characteristics can provide an explanation for the strict confinement of many character species to large river corridors with subcontinental climatic conditions. According to their Central European distribution pattern, it is postulated that characteristic flood-meadow species tend to have high temperature requirements for germination.

The study was carried out in the framework of a large-scale restoration project aimed at the re-establishment of species-rich flood-meadows on ex-arable land by the transfer of diaspores with plant material from remnant stands (Hölzel & Harnisch 2002; Hölzel & Otte 2003). It is often claimed (e.g. Patzelt 1998; Schütz 2000b) that declining, rare and endangered species tend to have detrimental germination requirements. Thus, we expected that germination traits could be a key to detect the underlying mechanisms of successful or failing re-establishment of target species as well as for the optimisation of restoration measures.

2 Material and Methods

2.1 Study species

Seeds of 42 species were collected in bulk from autochthonous populations in flood-meadows along the northern Upper Rhine River, Germany, between the tributaries Neckar to the south and Main to the north. Seed sampling took place between May and October depending on the time of ripening and included at least 50 different plant individuals. The species studied comprise typical constituents of subcontinental flood-meadows, representing a broad variety of families, life forms and strategy types (Table 1). Besides character species, which are more or less confined to large lowland river corridors such as *Allium angulosum*, *Arabis nemorensis*, *Cnidium dubium*, *Iris spuria*, *Scutellaria hastifolia* and *Viola pumila* (Burkart 2001) we

Table 1. Traits of the studied species according to the following authors: Life form (Ellenberg et al. 1992), seed mass (Hölzel & Otte 2003/4a), river corridor area (Korsch 1999 and Burkart 2001), German Red List status (Korneck et al. 1996). Letters in bold indicate abbreviations for species names used in following tables and figures. Life forms: T = Therophyte, G = Geophyte, H = Hemicryptophyte. Confinement to river corridors: ++ strong, + weak, - none. Red List status: 1 = critically endangered, 2 = endangered, 3 = vulnerable, - = not threatened.

Species	Family	Life form	Seed mass (mg)	River corridor	Red List
Allium **angu**losum	Liliaceae	G	1.74	++	3
Alopecurus **prat**ensis	Poaceae	H	0.71	–	–
Althaea **offi**cinalis	Malvaceae	H	3.41	+	3
Arabis **nemo**rensis	Brassicaceae	H	0.06	++	2
Barbarea **stricta**	Brassicaceae	H	0.41	++	–
Cardamine **parv**iflora	Brassicaceae	T	0.07	++	3
Carex **prae**cox	Cyperaceae	H	0.16	+	3
Carex **spic**ata	Cyperaceae	H	3.34	–	–
Carex **tome**ntosa	Cyperaceae	H	1.44	–	3
Cerastium **dubi**um	Caryophyllaceae	T	0.11	++	3
Cirsium **tube**rosum	Asteraceae	H	2.27	–	3
Cnidium **dubi**um	Apiaceae	H	0.39	++	2
Elymus **repe**ns	Poaceae	H	4.50	–	–
Euphorbia **palu**stris	Euphorbiaceae	H	10.47	++	3
Festuca **arun**dinacea	Poaceae	H	3.16	–	–
Galium **bore**ale	Rubiaceae	H	0.68	–	–
Galium **wirt**genii	Rubiaceae	H	0.40	+	–
Inula **brit**annica	Asteraceae	H	0.09	++	–
Inula **sali**cina	Asteraceae	H	0.16	–	–
Iris spuria	Liliaceae	G	14.62	++	2
Lathyrus **palu**stris	Fabaceae	H	12.85	+	3
Lythrum **salic**aria	Lythraceae	H	0.06	–	–
Peucedanum **offi**cinale	Apiaceae	H	12.32	+	3
Poa angustifolia	Poaceae	H	0.21	–	–
Potentilla **rept**ans	Rosaceae	H	0.31	–	–
Pseudolysimachion **long**ifolium	Scrophulariaceae	H	0.05	++	3
Pulicaria **dyse**nterica	Asteraceae	H	0.04	–	–
Rumex **thyr**siflorus	Polygonaceae	H	0.54	+	–
Sanguisorba **offi**cinalis	Rosaceae	H	1.95	–	–
Scutellaria **hast**ifolia	Lamiaceae	H	0.68	++	2
Selinum **carv**ifolia	Apiaceae	H	1.06	–	–
Senecio **palu**dosus	Asteraceae	H	0.62	++	3
Serratula **tinctoria**	Asteraceae	H	1.26	–	3
Silaum **sila**us	Apiaceae	H	2.43	–	–
Symphytum **offi**cinale	Boraginaceae	H	3.65	–	–
Thalictrum **flav**um	Ranunculaceae	H	0.80	++	–
Valeriana **prat**ensis	Valerianaceae	H	0.62	++	–
Veronica **pere**grina	Scrophulariaceae	T	0.06	+	–
Veronica **serp**yllifolia	Scrophulariaceae	H	0.05	–	–
Viola **elat**ior	Violaceae	H	1.80	++	2
Viola **pers**icifolia	Violaceae	H	0.68	++	2
Viola **pumi**la	Violaceae	H	1.08	++	2

also studied more common and widespread components like *Festuca arundinacea*, *Potentilla reptans*, *Rumex thyrsiflorus*, *Symphytum officinale* and *Veronica serpyllifolia*. The study covers almost the entire spectrum of regionally rare and endangered target species of flood-meadows (Korneck et al. 1996). Plant nomenclature follows Wisskirchen & Haeupler (1998).

2.2 Experiment 1

After field collection seeds of the 40 species used in this experiment were stored dry in darkness at room temperature (ca. 20 °C) until further use during the following winter season. The germination experiments were performed by spreading 50 seeds of each species on a double layer of filter paper in sterile Petri dishes. In case of very large seeds only 25 seeds per dish were used. Five dishes per treatment were incubated in climate chambers at constant temperatures of 3, 7, 10, 15, 20, 25, 30, and 35 °C and in a further chamber with diurnally fluctuating temperatures 5/15 °C (8/16 hours). The latter temperature regime was also applied to seeds that received cold wet stratification at 3 °C for 8 weeks prior the incubation, which should mimic early spring germination conditions. The light regime in the climate chambers simulated long day conditions with 16 hours of light and 8 hours of darkness. The dishes were regularly watered with distilled water to optimise moisture conditions. The experiment lasted 6 weeks. Germinated seeds were counted and removed once every week. Germination was defined as the emergence of the radicule.

2.3 Experiment 2

Results obtained in climate chambers are often strongly divergent from those set up in outdoor germination experiments, and certain species may even completely fail to germinate under laboratory treatments (e. g. Grime et al. 1981; Patzelt 1998). Thus, we combined both approaches in order to investigate germination phenology under more natural conditions.

A total of 800 seeds of each species were sown in February into two Styrofoam basins (18 cm × 28 cm) filled with sterile garden soil and exposed at an experimental field near Giessen, Germany. During dry periods the basins were watered daily. Emerging seedlings were counted and removed at least every two weeks. The outdoor study was continued for 24 months.

2.4 Experiment 3

To investigate primary dormancy levels (Baskin & Baskin 2001) and the timing of germination under near natural conditions, seeds from a subset of 20 species were collected at the time of shedding in the field and exposed about 2 weeks later under outdoor conditions. The mode of exposure and counting was principally the same as in experiment 2. In contrast to natural field conditions the 800 sown seeds were watered regularly during dry periods.

2.5 Characterisation of germination

For each laboratory and outdoor treatment, the percentage of seeds that had germinated after the end of the observation period was determined. To correlate temporal patterns of outdoor germination with thermal conditions we used meteorological data from the nearby (ca. 500 m) climate research station Linden. Starting on the last day with a daily average temperature below 1 °C we calculated the number of days with daily averages above 5 °C as well as total temperature sums of daily averages until the onset and the first pronounced peak in outdoor germination, respectively. Both temperature traits revealed to be highly correlated ($r^2 = 0.98$), thus we used only the number of days with averages above 5 °C for further numerical analyses.

To describe germination characteristics for each species the following values were calculated:

LOPT, the optimal temperature for germination, was calculated as weighted average of germination rates over all constant temperatures in the climate chamber experiment, according to the mode described by Olff et al. (1994): $[(3\,P_3 + 7\,P_7 + 10\,P_{10} + 15\,P_{15} + 20\,P_{20} + 25\,P_{25} + 30\,P_{30} + 35\,P_{35})/(P_3 + P_7 + P_{10} + P_{15} + P_{20} + P_{25} + P_{30} + P_{35})]$ in which P_3 was percentage germination at 3 °C, P_7 percentage germination at 7 °C, and so on.

LMAX, the maximum germination rate, was defined as the highest percentage of germination in one of the climate chamber treatments after six weeks.

GFAS was the maximum germination rate at constant temperature after 7 days in the climate chamber.

TFAS was the temperature at which *GFAS* was reached.

LOW was the lowest constant temperature with at least 5% germination.

HIGH was the highest constant temperature with at least 5% germination.

AMP was the range in degrees Kelvin between *HIGH* and *LOW*.

ALT was the difference in germination rate at fluctuating temperatures of 5/15 °C in comparison to the constant temperature of 15 °C.

STRAT, the effect of cold wet stratification, was the difference in germination rate in comparison with *ALT*.

FMAX was the maximum germination rate under outdoor conditions.

ONSET was the date of outdoor germination begin in days with daily averages above 5 °C counted from the last day with a daily average below 1 °C.

FOPT was the date of the first germination peak under outdoor conditions (measured as for *ONSET*).

PEAK1 was the maximum germination during one single count as a percentage of total final outdoor germination.

PEAK4 was the maximum germination during the four following weeks, measured as for *PEAK1*.

SPAN was the period in days between the first and last count, in which at least 5% of total final outdoor germination occurred.

2.6 Data analysis

The correlation structure of germination traits was investigated by principal component analysis (PCA) on a data matrix with z-transformed standardised variable values (Legendre & Legendre 1998). The traits *LOPT*, *TFAS*, *HIGH* and *LOW* were not included in the analysis because their calculation requires germination under constant temperatures in the climate chamber, which did not occur in a number of species. As PCA does not accept missing values, the inclusion of these traits would have lowered the number of analysed species. Correlations between single germination traits and PCA-axis scores, on the one hand, and species attributes such as seed mass (Hölzel & Otte 2003/4a), seed longevity, threat status, range size and type on the other hand were examined by nonparametric Spearman rank correlation coefficients. As a measure of seed longevity we applied the seed accumulation index (SAI) given in Hölzel & Otte (2003/4 a) for 36 of the stu-

Table 2. Germination traits (for abbreviations see chapter 2.5) of 42 flood-meadow species (for abbreviations see Table 1): (s) = as temperature sum, (d) = in days, n.m. = not measured.

	Species	*OPT*	*LMAX*	*TFAS*	*GFAS*	*AMP*	*LOW*	*HIGH*	*ALT*	*STRAT*	*FMAX*	*ONSET(s)*	*ONSET(d)*	*FOPT(s)*	*FOPT(d)*	*PEAK1*	PEAK4	SPAN
A	Cera dubi	10.6	100	15	75	17	3	20	3	0	78	81	8	81	8	96	100	0
	Alop prat	11.2	16	25	2	8	7	15	10	–6	36	142	15	142	15	55	99	28
	Card parv	13.8	98	10	65	27	3	30	46	–1	96	81	8	81	8	75	98	14
	Gali wirt	14.4	82	15	28	27	7	30	–2	–40	88	81	9	137	15	41	91	18
	Vero serp	15.1	100	20	92	22	3	25	0	–1	93	200	17	200	17	78	99	16
	Rume thyr	15.3	95	10	90	27	3	30	2	–16	81	107	9	187	17	31	66	28
	Fest arun	16.3	97	20	88	27	3	30	–2	–20	95	142	15	181	19	70	98	14
	Vero pere	18.3	98	20	73	18	7	25	–21	60	59	181	19	194	19	28	95	38
	Valer prat	18.8	69	25	53	27	3	30	14	–16	64	197	21	197	21	46	95	21
B	Gali bore	20.1	38	20	1	20	10	30	–19	21	71	197	21	313	35	47	78	48
	Pseu long	21.9	91	25	46	28	7	35	17	32	65	197	21	197	21	35	61	48
	Arab nemo	22.6	84	30	82	20	10	30	12	32	87	197	21	197	21	93	99	48
	Care spic	22.9	28	–	0	5	20	25	–2	16	84	329	35	533	56	39	88	28
	Cirs tube	23.0	66	25	51	23	7	30	35	14	46	157	16	197	21	34	81	32
	Sang offi	25.4	93	30	36	20	15	35	3	74	63	194	21	286	32	34	84	28
	Alli angu	25.8	30	25	16	10	20	30	4	22	94	157	16	197	21	50	94	18
	Serr tinc	26.5	36	35	3	20	15	35	–2	28	35	197	21	197	21	77	97	18
	Lyth sali	26.6	100	25	93	15	20	35	10	88	54	234	21	234	21	34	86	35
	Puli dys	28.3	52	30	8	5	25	30	2	33	48	181	19	181	19	53	90	38
	Inul brit	28.8	58	25	47	15	20	35	12	25	66	252	28	269	30	39	88	35
	Inul sali	29.1	75	35	73	15	20	35	0	0	17	316	34	501	49	33	74	22
	Barb stri	29.9	99	30	98	10	25	35	0	0	75	200	17	200	17	93	100	9
	Alth offi	30.5	15	30	10	10	25	35	0	0	39	828	80	828	80	31	62	90
	Thal flav	27.6	15	–	0	0	30	30	0	14	70	414	39	520	47	13	48	111
C	Cnid dubi	–	12	–	0	0	–	–	2	11	8	197	21	313	35	37	51	84
	Sila sila	–	42	–	0	0	–	–	5	37	25	197	21	197	21	84	97	18
	Peuc offi	–	38	–	0	0	–	–	0	38	48	157	16	197	21	65	95	18
	Euph palu	–	23	–	0	0	–	–	0	22	76	157	16	181	19	16	39	149
	Symp offi	–	31	–	0	0	–	–	5	26	38	181	19	181	19	25	61	45
	Sene palu	–	21	–	0	0	–	–	0	21	74	200	17	234	21	45	71	44
D	Viol pers	–	5	–	0	0	–	–	0	0	18	337	36	337	36	46	63	388
	Viol elat	–	2	–	0	0	–	–	0	2	59	295	33	342	37	21	59	77
	Viol pumi	–	2	–	0	0	–	–	0	2	66	295	33	342	37	25	92	35
	Care prae	–	0	–	0	0	–	–	0	0	24	280	28	466	49	38	82	42
	Care tome	–	0	–	0	0	–	–	0	0	54	490	56	828	80	29	38	381
	Iris spuria	–	1	–	0	0	–	–	1	–2	76	157	16	2156	164	48	84	35
	Pote rept	–	6	–	0	0	–	–	0	6	68	280	28	466	49	28	75	42
	Scut hast	–	0	–	0	0	–	–	0	0	62	466	49	882	80	19	53	88
	Elym repe	–	3	–	0	0	–	–	2	0	67	181	19	181	19	51	91	24
	Poa angu	–	2	–	0	0	–	–	2	–1	32	181	19	235	24	21	86	45
	Lath palu	n.m	n.m	n.m	n.m	n.m	n.m	n.m	n.m	n.m	35	101	11	235	24	28	30	724
	Seli carv	n.m	n.m	n.m	n.m	n.m	n.m	n.m	n.m	n.m	55	295	33	383	43	56	92	33

died species. To describe range size on a Central European scale we used grid frequency data from the German flora mapping project provided by the electronic resource Floraweb (BfN 2003). Threat status was assessed by a simple ordinal scale ranging from 0 (unthreatened) to 2 (strongly threatened) based on the list of Korneck et al. (1996). In the same way river corridor confinement was allocated from the specifications of Korsch (1999) and Burkart (2001). Differences between groups were tested using a non-parametric Mann-Whitney U-test. All calculations were carried out with STATISTICA 6.0.

3 Results

3.1 Patterns of single germination traits

Under laboratory conditions only a limited proportion of the studied species (Group A, Table 2) germinated with high rates over a wide range of constant temperatures (*AMP*) or showed a clear preference for low germination temperatures (*OPT*, *LOW*). In contrast, many species reached maximum germination rates only at relatively high constant temperatures (*OPT*) above 20 °C (Group B, Table 2). However, in all of these species except *Althaea officinalis* and *Barbarea stricta* germination rates increased considerably after 8 weeks of cold wet stratification (*STRAT*) and following low fluctuating temperatures (5/15 °C), most strikingly in *Lythrum salicaria* and *Sanguisorba officinalis*. Positive effects of fluctuating temperatures (*ALT*) alone without stratification were less pronounced and restricted to a few species such as *Cardamine parviflora* and *Cirsium tuberosum*. In some other species they even caused a decline in germination rate. In Apiaceae and some other species (Group C, Table 2) germination under laboratory conditions was confined to the stratification treatment (*STRAT*).

A surprisingly high number of species (Group D, Table 2) almost completely failed to germinate under all laboratory treatments, showing maximum germination rates below 5%. Under outdoor conditions in all of these species (except *Cnidium dubium*) the germination rates (*FMAX*) increased considerably and were usually well above 20%.

In the outdoor treatment about half of the species had an initial pronounced germination peak (*FOPT*) after around 20 days with daily averages above 5 °C, which is equal to a temperature sum of ca. 200 °C. Most species with a highly positive response to the cold wet stratification treatment under laboratory conditions (*STRAT*) were found within this group. *Galium boreale*, *Cnidium dubium*, *Sanguisorba officinalis*, *Selinum carvifolia* and all *Viola* species showed slightly higher temperature requirements (*FOPT*) with peak germination about two weeks later (around 30 days with averages > 5 °C, temperature sum > 300 °C).

However, there were also some species with explicitly deviating behaviour indicating significantly lower or higher temperature requirements. In *Cerastium dubium* and *Cardamine parviflora* outdoor germination started considerably earlier (< 10 days with averages > 5 °C, temperature sum < 100 °C). In contrast, *Althaea officinalis*, all *Carex* species, *Inula britannica*, *I. salicina*, *Potentilla reptans*, *Scutellaria hastifolia* and *Thalictrum flavum* showed a much higher temperature requirement with a first germination peak occurring only after 50 days with averages > 5 °C and a temperature sum > 500 °C. In both response groups these results largely coincided with the germination temperature requirements found in the laboratory experiment.

In 60% of the studied species more than 80% of the final outdoor germination took place within four weeks. In some, such as *Arabis nemorensis*, *Cerastium dubium*, *Serratula tinctoria*, *Silaum silaus* and *Veronica serpyllifolia* such rates were even reached during a single count. This particularly synchronous germination behaviour is contrasted by other species that emerged over a long period with low but constant rates. This was most obvious in *Carex tomentosa*, *Euphorbia palustris*, *Scutellaria hastifolia* and *Thalictrum flavum*.

3.2 Multivariate analysis of germination traits

The principal-component analysis (PCA) revealed the correlation structure of the germination traits (Table 3, Fig. 1). The first factor axis, which explained the bulk of the variance (40.99%), reflected a continuous gradient from species with high, rapid and strongly synchronised germination over a wide range of temperatures (left side of Fig. 2) to those with high temperature requirements and a delayed germination over a relatively long period (right side of Fig. 2). Factor axis 2 largely coincided with the variation of *AMP*, *SPAN* on the one hand and *PEAK4* on the other hand. Factor axes 3 and 4 predominantly represented the variance in *STRAT* and *ALT*, respectively (Table 3, Fig. 1 and 2).

3.3 Timing of germination after natural seed shedding

In experiment 3, in which the timing of germination after natural seed release was investigated the following major response types appeared (Fig. 3):

I) Potential for complete germination within the season of shedding: Among the species used in this experiment only the therophytes *Cardamine parviflora* and *Cerastium dubium* belong to this response type. Seeds of these species reached 100% of the final germination

Table 3. Correlation between factor axes of PCA ordination and germination traits. High correlations are given in bold (for abbreviations of germination traits see chapter 2.5).

	Factor 1	Factor 2	Factor 3	Factor 4
Eigenvalue	4.51	1.34	1.19	0.96
Variance (%)	40.99	12.16	10.81	8.71
LMAX	**–0.89**	–0.26	0.26	–0.15
GFAS	**–0.81**	–0.38	0.14	–0.16
AMP	**–0.76**	**–0.50**	0.06	–0.05
PEAK1	**–0.64**	0,26	–0.25	0.04
PEAK4	**–0.73**	**0.47**	–0.22	–0.06
ALT	–0.35	–0.24	0.05	**–0.78**
STRAT	–0.08	0,29	**0.81**	–0.25
FMAX	**–0.51**	–0.28	–0.42	–0.29
ONSET	**0.65**	–0.36	0.08	–0.18
FOPT	**0.59**	–0.20	–0.34	–0.30
SPAN	**0.62**	**–0.43**	0.14	0.12

rate within two months after shedding in late May. Whereas germination started directly after sowing in *Cardamine parviflora* the onset of germination in *Cerastium dubium* was about 4 weeks later.

II) Potential for partial germination directly after shedding in late summer with a second peak in March/April of the following year: All species belonging to this response group germinated to a certain degree directly after shedding. However, germination stopped abruptly by the end of September at the latest, when daily averages were usually still well above 10 °C. Spring germination, in contrast, started at the earliest in late February, with a significant peak in March at temperatures considerably lower than those in early autumn when germination stopped. Only in *Inula salicina* did germination start as late as April, indicating significantly higher temperature requirements.

III) No germination in the year of shedding, but almost complete and rapid germination in March/April of the following year: Most species of this group comprise Apiaceae with relatively late seed release (September), but species with a much earlier shedding are also represented, such as *Galium boreale*. Early spring germination occurred very abruptly and was highly synchronised. Only *Cnidium dubium* showed a slightly extended germination period towards summer.

IV) Delayed, slow germination over an extended period, starting in the first summer after shedding: In most species of this response type significant germination started no earlier than late April or May and continued over the whole summer season. In *Carex tomentosa* peak germination occurred only in the second, and in *Lathyrus palustris* even in the third and fourth year (data not shown) after shedding.

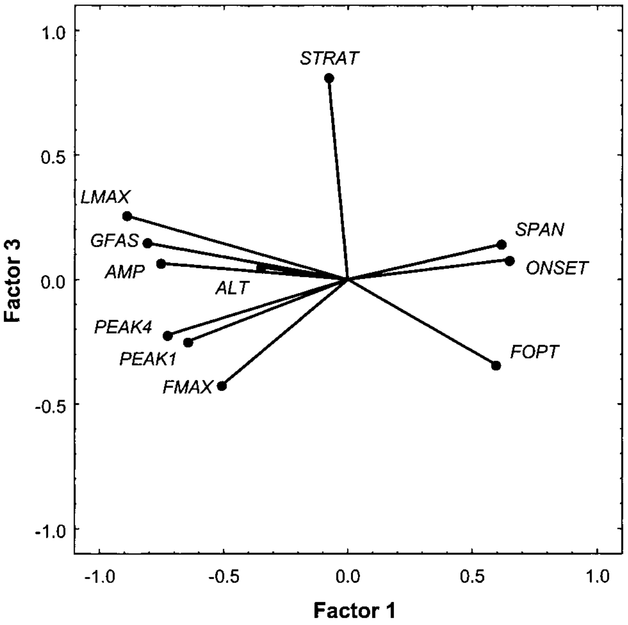

Fig. 1. Biplot displaying correlation structure of germination traits along factor axis 1 and 3 in PCA-ordination (for abbreviations of germination traits see chapter 2.5).

3.4 Correlation between germination characteristics and other species traits

According to Spearman rank correlation species with small seed mass tended to germinate faster (*GFAS*) ($r = -0.51$, $p < 0.001$) and had a higher temperature amplitude (*AMP*) ($r = -0.38$, $p < 0.05$) and maximum germination rate (*LMAX*) ($r = -0.44$, $p < 0.01$) under laboratory conditions. No further correlations between seed weight and germination characteristics were found.

Surprisingly, the tendency in species to build up long-term persistent soil seed banks was positively correlated with fast germination under laboratory conditions (*GFAS*) ($r = 0.40$ $p = 0.02$) and a high outdoor germination rate (*FMAX*) ($r = 0.35$ $p = 0.04$).

Spearman rank correlation also revealed a significant but relatively weak correlation ($r = 0.36$ $p = 0.02$) between the first factor axis in PCA ordination and Red List status. A similar relationship was found between Red List status and single germination traits such as *LMAX* ($r = -0.43$ $p = 0.006$), *GFAS* ($r = -0.32$ $p = 0.04$), *FOPT* (0.43 $p = 0.03$) and *SPAN* ($r = 0.37$ $p = 0.02$), indicating a trend towards higher dormancy levels, increased temperature requirements and asynchronous germination in endangered species. In contrast, there was no relationship at all between germination traits and river corridor

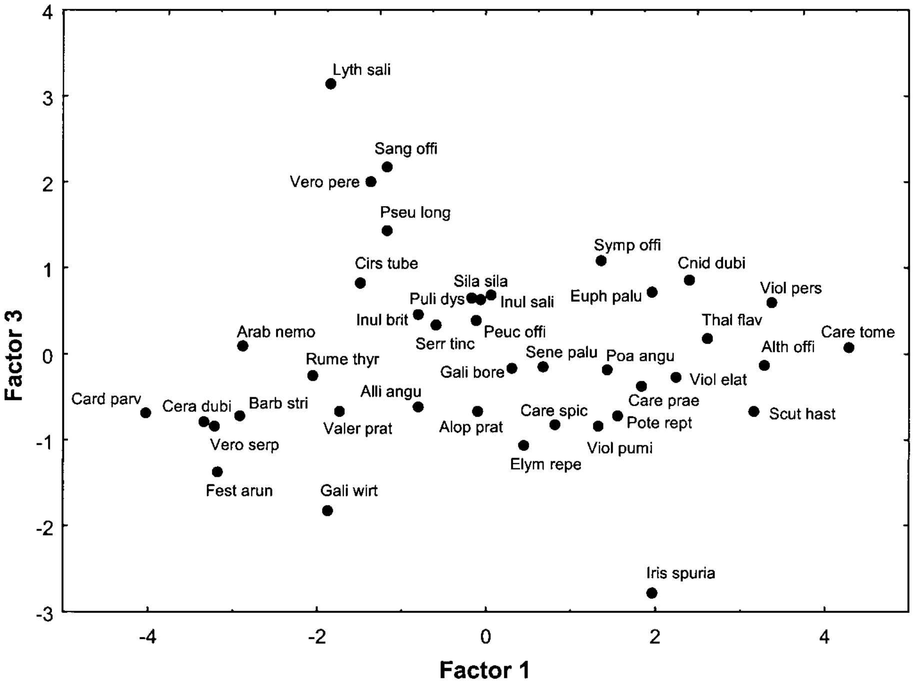

Fig. 2. Distribution of species in PCA ordination space along factor axes 1 and 3 (for abbreviations of species names see Table 1).

confinement or Central European range size. Identical results (not shown) were obtained in group comparisons by the Mann-Whitney U-test.

4 Discussion

4.1 Germination strategies in flood-meadows

In flood-meadows of the studied type the survival of insufficiently developed seedlings will often be severely hampered by frost damage and prolonged flooding during the winter season (e. g. Voesenek & Blom 1992). Equally, open patches with poor competition are more likely to occur in spring after the retreat of flood water, which often creates gaps in established vegetation. Consequently, it makes ecological sense that many of the flood-meadow species studied exhibited various levels of conditional or even strict dormancy in the year of shedding, while there were fewer species that germinated spontaneously at high rates over a wide temperature range including lower temperatures.

The existing diversity of germination response types in flood-meadow species was clearly visible in PCA-ordination, which reflected a continuous gradient of increasing dormancy levels along the first factor axis (Fig. 1) with *Cardamine parvifolia* (non dormant) and *Carex tomentosa* (highly dormant) as the most extreme points of the spectrum (Fig. 2). An almost identical main gradient in germination traits was found by Olff et al. (1994) in the flora of Dutch wet meadows.

A high capacity for spontaneous germination directly after shedding is typical of many dominant Poaceae in temperate grasslands (Thompson & Grime 1979), which could be confirmed in our study for *Festuca arundinacea*. The relatively low total germination rates compared to other studies (Grime et al. 1981) achieved in some dominant grasses of flood-meadows, such as *Alopecurus pratensis*, *Elymus repens* and *Poa angustifolia*, are probably partly due to heavy mildew infestation within the climate chamber treatments and/or low quality of the seeds used.

According to Grime (2001) two major strategies can be distinguished that enable seeds to delay germination until the following spring and summer season: i) high temperature requirements for germination, which are usually not fulfilled during the autumn season, ii) a requirement for chilling to break dormancy. In accordance with Washitani & Masuda (1990), who studied germination characteristics in a moist tall grassland community in Japan, both strategy types could be found. However, our study clearly established that some species may combine both principal strategies for the avoidance of harmful late autumn and winter germination. Within the year of shedding many of the studied species such as *Allium angulosum*, *Arabis nemorenis*, *Cirsium tuberosum*, *Pseudolysimachion longifolium* and others showed relatively high temperature requirements to reach significant germination rates, but came out of pri-

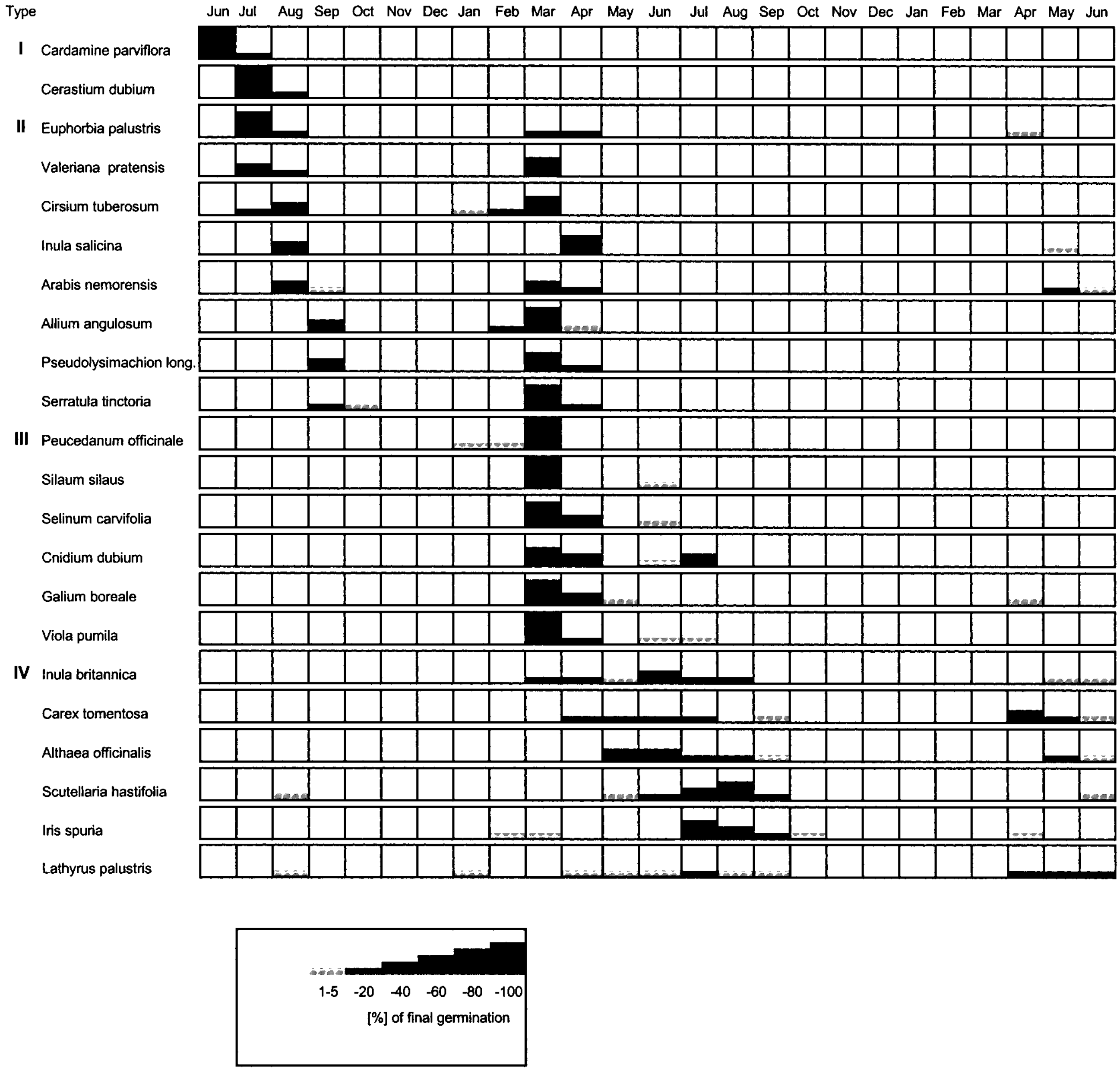

Fig. 3. Timing in germination of freshly shed seeds under outdoor conditions.

mary conditional dormancy (Baskin & Baskin 2001) after a period of cold wet stratification. This phenomenon could be observed in the climate chamber treatments as well as under outdoor conditions. Ecologically this means that germination will stop well before the onset of the cool season while the same species are able to exploit gaps at relatively low temperatures in early spring.

Under natural habitat conditions in flood-meadows dormancy after shedding will often also be enforced by environmental constraints such as drought or shading through established vegetation. Additionally, in some species with high temperature requirements such as *Arabis nemorensis*, *Inula britannica* and *Sanguisorba officinalis* autumn germination is simply avoided by a strongly delayed seed release.

Besides conditional dormancy enforced by high temperature requirements prior to chilling, hardening of seed shells due to dry and warm weather conditions (or dry storage prior to laboratory experiments) may also be responsible for poor germination in the year of shedding (e. g. Otte 1996, Jensen 2001). This applies in particular to species that lack a response to the stratification treatment in the climate chamber but have high early spring germination rates such as *Barbarea stricta*, *Viola elatior* and *V. pumila* or those with strongly increased outdoor germination rates such as *Allium angulosum*, *Euphorbia palustris* and *Galium boreale*. All these species exhibit relatively hard and compact seed shells that obviously require softening in the course of prolonged outdoor stratification. In particular, *Euphorbia palustris* showed a high initial germination rate only in seeds sown directly after shedding. When seeds were dry stored and sown in winter germination extended over a much longer period. This phenomenon may be referred to as secondary induced physical dormancy (Baskin & Baskin 2001).

As in other studies (Grime et al. 1981; Patzelt 1998) Apiaceae proved to exhibit a strict chilling requirement due to morphophysiological dormancy caused by an underdeveloped embryo (Stokes 1952; Baskin & Baskin 2001), which necessarily delays germination until the spring season.

In accordance with Milberg & Andersson (1998) we found that differences in conditional dormancy were largely compensated by cold stratification under outdoor conditions resulting in a highly synchronised germination peak in March and early April. However, there was also a group of species in which high temperature requirements did not disappear after chilling. *Althaea officinalis*, *Potentilla reptans*, *Thalictrum flavum* and *Scutellaria hastifolia* and the *Carex*-species obviously require an obligatory extended period of warm moist incubation under outdoor conditions to come out of dormancy. This confers with results reported by other authors (Baskin & Baskin 2001; Patzelt 1998; Schütz 1997, 2000a; Ziron 2002). In most of these species, high temperature requirements go hand in hand with a strongly delayed and asynchronous germination over the whole summer period. Conspicuously, species with the most delayed and asynchronous germination have relatively large and compact seeds with features of physical dormancy such as water-impermeable testa (*Lathyrus palustris*) or particularly thick and hard seed coats (*Carex tomentosa*, *Iris spuria*). After the breaking of physical dormancy, at least *Lathyrus palustris* and *Iris spuria* exhibited no particular temperature requirements for germination, as has been found in other studies for species of the same genera (Baskin & Baskin 2001; Grime et al. 1981).

Asynchronous germination can be seen as a strategy to minimise the risk of total failure of seed regeneration due to regularly occurring disruptive environmental constraints such as drought, which is particularly relevant in species with a delayed germination during summer. Equally, this strategy seems to be a benefit in amphibious habitats with strongly fluctuating moisture conditions. Consequently, in our study high temperature requirements and/or delayed and asynchronous germination were most common in perennial species with a clear preference for the dampest parts of flood-meadows such as *Euphorbia palustris*, *Lathyrus palustris*, *Scutellaria hastifolia*, *Thalictrum flavum* and *Viola persicifolia*. According to Grime et al. (1981) and Baskin & Baskin (2001) high temperature requirements and dormancy levels are a common feature in temperate wetland species.

4.2 Germination characteristics and seed bank persistence

In previous studies (Hölzel & Otte 2001; 2003/4a) species, such as *Arabis nemorensis*, *Cardamine parviflora*, *Cerastium dubium*, *Lythrum salicaria*, *Pseudolysimachium longifolium*, *Potentilla reptans*, *Veronica peregrina*, *V. serpyllifolia* were revealed to build up large long-term persistent seed banks. Surprisingly, with the exception of *Potentilla reptans*, all these species exhibited relatively low dormancy levels and a high potential for fast germination in light. Thus, the formation of a long-term persistent soil seed bank is obviously completely due to dark dormancy. Typically, all these species have very small seeds, which according to Grime (2001) almost generally show an obligatory light requirement for germination. There seems to be an interesting link between the higher probability of burial in small seeds (Thompson et al. 1993; Bekker et al. 1998) and their capacity for fast and almost complete germination in light. Species with regeneration strategies involving a large persistent soil seed bank typically exploit gaps in established vegetation caused by stochastic, largely unpredictable disturbances (Thompson & Grime 1979; Grime 2001). Thus, the ability of spontaneous and rapid germination after exposure to light is an essential prerequisite for the successful exploitation of such temporary gaps. This strategy is of particular importance in ephemeral annuals of flood-meadows like *Cardamine parviflora*, *Cerastium dubium* and *Veronica peregrina*. However, even among these annuals significant differences could be found in the main period of germination. *Cerastium dubium* exhibited a delayed germination directly after shedding obviously due to a requirement for warm stratification to come out of dormancy at high temperatures, which is typical of facultative winter annuals (e. g. Baskin & Baskin 1983a). In seed bank experiments (Hölzel & Otte 2001) this species showed a pronounced germination peak in late summer and early autumn. Equally, mass occurrence of *Cerastium dubium* in the field coincides with years of low winter flooding intensity (Hölzel 1999). In contrast, *Veronica peregrina* is preferably a summer annual due to its strong response to cold wet stratification, which was also found by Baskin & Baskin (1983b).

Some species exhibiting particularly high dormancy levels such as *Carex tomentosa* and *Viola persicifolia* were also found to create long-term persistent soil seed banks (Hölzel & Otte 2003/4a). However, their densities were usually much lower than in small seeded species, which may be caused by a lower probability of burial as well as a higher potential for germination in darkness (Grime 2001). Our results suggest that only in relatively large seeded species dormancy levels established in germination experiments are a good predictor for the capacity of a certain species to build up persistent seed banks.

4.3 Germination characteristics and rarification

We did not find any single germination trait or a multivariate response type that corresponded with the confinement of species to large river corridors. There appears to be nothing really particular in the germination behaviour of river corridor plants that could explain their conspicuous habitat and range restriction in Central Europe. A comparable set with similar variability in germination traits has been found in other temperate wet grassland communities (Washitani & Masuda 1990; Olff et al. 1994; Patzelt 1998; Jensen 2001).

Equally, there were no significant differences in germination characteristics between species with small or large Central European range. Comparable results were obtained by Thompson et al. (1999) who found no relationship between germination traits and range size of vascular plants in the British flora. Although there was a significant albeit weak trend for higher dormancy levels in endangered species, we found little evidence for the assumption made by Schütz (2000b) that germination traits may play a prominent role in the causal understanding of rarity and decline. Regeneration characteristics are obviously outweighed by other species traits such as habitat specialism and the respective life strategy in the established phase, which have proved to be much better predictors of rarification processes in the Western and Central European flora (Korneck et al. 1998; Thompson et al. 1999; Grime 2001).

4.4 Conclusions for restoration management

In species with high temperature requirements causing delayed and asynchronous summer germination, recruitment in flood-meadows will often fail due to drought and competition through established vegetation. The frequent failure of regeneration by seeds does not usually diminish the viability of existing populations, since most of the relevant species are long-lived and exhibit extensive clonal growth. In contrast, this could become a serious problem in habitat restoration, in which species re-establishment crucially depends on regeneration by introduced seeds (e. g. Patzelt 1998). In a plant material transfer experiment aimed at recreation of a species-rich flood-meadow (Hölzel & Otte 2003), we found poor establishment success after four years in a number of species with delayed and asynchronous germination behaviour, such as *Lathyrus palustris*, *Scutellaria hastifolia*, *Thalictrum flavum* and almost all *Carex* species. Especially in *Carex* species the very specific and narrow germination requirements are obviously a major constraint and may explain their notoriously low colonisation capacity (Grime et al. 1988; Budelsky & Galatowitsch 1999; Schütz 2000a). In most species with high germination temperature requirements, successful regeneration by seeds is probably confined to certain years with particularly favourable moisture conditions and low competition by established vegetation, as may occur in the course of prolonged early summer flooding and following drawdown (Jutila 2001; Hölzel & Otte 2003, 2003/4b).

As demonstrated in this study the majority of flood-meadow species are able to exploit the particular favourable recruitment conditions (constant moisture supply, open vegetation structure) prevailing in early spring (March/early April). Management schemes that support the creation of open vegetation structures and patches of bare soil at this time of the year – such as mowing and removal of plant litter, aftermath pasture or scarring of the sward – may actively enhance regeneration by seeds (e.g. Kotorová & Lepš 1999).

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