



Germination ecology of three endangered river corridor plants in relation to their preferred occurrence

Katja Geissler*, Axel Gzik

Institute of Biochemistry and Biology, University of Potsdam, Maulbeerallee 2a, 14469 Potsdam, Germany

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ABSTRACT

As a contribution to conservation, we investigated germination requirements of three perennial, endangered river corridor plants of Central European lowlands coexisting in subcontinental flood meadows, but preferring particular zones of decreasing flooding frequency and duration along the elevational gradient of the banks. It was hypothesized that the species have specific germination requirements to respond successfully to open patch creation depending on their occurrence along the gradient of spring flooding in the field. This study involved controlled experiments and phenological studies.

Juncus atratus and *Gratiola officinalis*, which frequently occupy flooded, naturally disturbed sites, have an absolute light requirement for germination, typical of pioneer species. Summer-dispersed, non-dormant seeds of *J. atratus* did hardly germinate at high temperatures and lacked a gap sensitivity based on temperature fluctuation. Since the temperature amplitude decreases beneath an insulating cover of vegetation or water, seeds seem to be prepared for rapid germination at open, wet, maybe even inundated sites. Late-summer-dispersed seeds of *G. officinalis* were in a state of conditional primary dormancy. Dormancy could be completely broken by cold–wet stratification, indicating spring germination. Similar to *J. atratus*, daily temperature fluctuations did not control germination at suitable microsites. In *Cnidium dubium* that occurs at higher elevated sites, the level of primary dormancy of seeds was sufficient to prevent germination following dispersal, but the level was dependent on the year of harvest. Buried seeds showed an annual dormancy/conditional dormancy cycle. Dormancy was only partially broken by cold–wet stratification. It was completely broken by application of a high concentration of gibberellic acid. *C. dubium* had no absolute light requirement for germination, but it was stimulated by high light levels and in contrast to the other two species, seeds were stimulated by daily temperature fluctuations. Germination would therefore be maximized by gaps in early spring when the flooding water has receded. Re-entering dormancy in the late spring fails to support that germination occurs immediately after early-summer mowing – an important factor at subcontinental flood meadows.

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Introduction

A large number of endangered plant species still exist in European river valleys (Burkart, 2001). Efforts to protect some existing populations or even to establish novel populations are often hampered by limited knowledge of the basic biology of these species, especially with concern of the environmental requirements for germination (Bischoff, 2002; Hölzel and Otte, 2004a; Schütz, 1997).

In most plants, the transition from seed to seedling is a high-risk period in the life history (Harper, 1977). Species are therefore believed to depend on mechanisms for ensuring that germination occurs in conditions that are suitable for seedling recruitment

(Grime, 2001). Timing of germination is regulated both by the dormancy status of the seeds and by their germination requirements in relation to light and temperature. Riparian wetlands are naturally high dynamic ecosystems. As a result of erosion and deposition, temporary open patches may occur, which could rapidly be re-colonized by plants. In the temperate zone, habitats tend to be flooded in the cool season and the non-flood period coincides with the growing season which is often characterized by dry summers (Hölzel and Otte, 2004a). As a consequence, successful colonization of new open patches, occurring either from wetland seed banks or from the pool of water-dispersed seeds, should most probably happen in spring, after drawdown of flood waters. By then, conditions for establishment are favourable and time is sufficient to grow to a certain stage of development before the onset of winter. Traits that are known to control the timing of spring germination are primary dormancy and a need for cold–wet stratification period to break dormancy followed by increased tem-

* Corresponding author. Tel.: +49 331 9771924; fax: +49 331 9771948.

E-mail addresses: geissler.katja@hotmail.com (K. Geissler), gzik@rz.uni-potsdam.de (A. Gzik).

peratures (Baskin and Baskin, 1988). It is also believed that a requirement for daily fluctuations in the temperature may operate in this regard because decreasing spring water levels increase the daily temperature amplitude (Ekstam et al., 1999; Van Assche and Vanlerberghe, 1989). Ensuring germination at suitable microsites, it appears that both a sensitivity to fluctuating temperatures and an absolute light requirement are important factors. They can be interpreted as 'gap-detection' mechanisms by stimulating seeds to germinate in open, non-insulated patches (Thompson and Grime, 1983). Both mechanisms are characteristic for several plants of temperate wetlands, where gaps are constantly created (Thompson and Grime, 1983; Thompson et al., 1977). There is good evidence that constant disturbance may be the predominant force allowing existence of sessile species, that otherwise, as adults, would be out-competed by dominants (Keddy, 2005). Rare species often appear to be weak competitors. 'Gap-detection' mechanisms in seeds of rare river wetland plants may therefore be an important regenerative trait. This view can be expanded to include the fact that many European river wetlands have been formed and maintained by mowing or grazing over many centuries (Härdtle et al., 2006; Müller et al., 1992). Regular mowing decreases insulating vegetation cover, and it increases the availability of resources such as light, thereby possibly stimulating seedling recruitment (Rasran et al., 2007; Spačková et al., 1998). Nonetheless, at sites being submerged well into late spring natural conditions might be more important than mowing. Colonization of gaps then may not be restrained by inundation. It is known that seeds of various wetland species can readily germinate when submerged (Leck, 1996; Lorenzen et al., 2000; Morinaga, 1926). Since the temperature amplitude is small beneath an insulating cover of water (Thompson et al., 1977) those seeds are not expected to be stimulated by daily temperature fluctuations.

In the Central European Lowlands, certain endangered plant species, so-called river corridor plants, grow mainly or exclusively in the corridors of large rivers (Burkart, 2001). The objective of this study was to characterize basic germination requirements and seed dormancy of three of them, coexisting in subcontinental flood meadows (Burkart, 1998). However, along a gradient of decreasing flooding frequency and duration *Cnidium dubium* is mainly found on rarely flooded but regularly mown areas, whereas *Gratiola officinalis* and *Juncus atratus* occupy more frequently flooded, naturally disturbed sites and pioneer sites. We test the hypothesis that (1) *C. dubium* will equally respond to the two factors that are affected by open patch creation: light and fluctuating temperatures, whereas (2) *G. officinalis* and *J. atratus* will respond more to light than to fluctuating temperatures, and that (3) all three species possess delay mechanisms such as dormancy and specific temperature requirements that result in spring germination, although seeds are set in different time periods.

Materials and methods

Study species

The three investigated hemicryptophytic river corridor plants are endangered species in Germany (Korneck et al., 1996). *Cnidium dubium* (Schkuhr) Thell. (Apiaceae) is capable of producing several rosettes that develop from vegetative root-buds on lateral roots (Kutschera and Lichtenegger, 1992). *Gratiola officinalis* L. (Scrophulariaceae) is a dense mat-forming species comprising up to 900 shoots per individual, and *J. atratus* Krock. (Juncaceae) is a tussock-forming rush with up to 50 shoots per individual (K. Geissler, unpublished data). Important traits of life history and reproduction are shown in Table 1.

Seed sampling

Freshly matured seeds were collected from three populations per species of at least 30 individuals in the lower Havel river valley, northeast Germany (Ramsar-Site) and were mixed. Seeds of *C. dubium* were collected on 12 October 2000, seeds of *G. officinalis* on 18 September 2000, and seeds of *J. atratus* on 25 July 2002. Additional seeds from a single population of *C. dubium* were collected on 12 October 2000, 24 October 2001, 30 October 2002 and 25 October 2004. All germination studies were initiated after drying the seeds for 3 days at room temperature.

Germination experiments

Three replications of 50 seeds each were used for each test condition. Seeds were placed on a double-layer filter paper (Schleicher and Schüll, no. 595) in Petri dishes and were moistened with distilled water. All Petri dishes were wrapped with plastic film. They were placed in incubators equipped with cool white fluorescent light generating a 14 h daily photoperiod of $25 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR. The total amount of Petri dishes used in the incubator experiments was 108 per species, in *C. dubium* it was 168 per species. Germination was monitored daily for 36 days. A seed was considered to have germinated when the radicle had emerged through the seed coat.

Darkness

Germination conditions were the same as in the light, but Petri dishes were wrapped additionally with two layers of aluminium foil and the amount of Petri dishes was increased 12-fold. Starting with this high amount, every 3 days three of them were checked for germinated seeds and discharged.

Constant temperatures

Seeds germinated in incubators, which were set on constant temperatures of 10, 15, 22, and 30 °C.

Temperature fluctuation

Seeds germinated in the same incubators used for constant temperature regimes. Transfer of them from one incubator to another simulated the 12/12 h daily temperature fluctuations of 7 and 12 K at 22 °C day temperature. Thus, all but the 30 °C incubator has been used, creating two alternating temperature regimes of 22/15 °C and 22/10 °C. The 14 h daily photoperiod consisted of 2 h night temperature, with 1 h at the beginning and end of the period. The controls for this experiment were seeds that germinated at 22 °C constant temperature.

Cold stratification

Seeds were stratified at 5 °C for 12 weeks in darkness. At the end of this period, seeds were incubated in light and in darkness at all the constant and alternating temperature regimes. Germination was compared with germination of freshly matured seeds. The effect of 'time' (12 weeks) is therefore not excluded from the experimental design.

Gibberellic acid

To test the depth of physiological dormancy in *C. dubium*, freshly matured seeds collected in 2000, 2001, 2002, and 2004 were germinated at four different concentrations of gibberellic acid (GA₃) 0.01, 0.1, 1.0, and 10 mM (pH 6.0) in light. One incubator was set on 12/12 h daily thermoperiod of 22/15 °C. Similar conditions are known to be favourable for the germination of many temperate wetland species (Salisbury, 1970; Thompson and Grime, 1983; Van

Table 1

Reproductive features of populations of the three river corridor species studied.

Traits	<i>Cnidium dubium</i>	<i>Gratiola officinalis</i>	<i>Juncus atratus</i>
Life history	Polycarpic ^a	Polycarpic ^b	Polycarpic ^b
%Flowering ramets ^c	Up to 20%	Up to 95%	40–60%
Flower and seed phenology			
Main flowering period	July–August ^c	Beginning of June–August ^c	June–July (22 days) ^d
Seed ripening period ^c	September–November	End of June–October	July
Seed shedding period ^c	End of October	September	July–August
Seed dimensions			
Size ^e	2–4 mm	0.4 mm	0.2 mm
Mass ^c	0.66 mg	0.02 mg	0.01 mg
Seed viability in the soil ^e	Persistent seed bank	Persistent seed bank	Persistent seed bank
Resistance to flooding ^e	Decreasing by time	High	High

Seed mass was estimated by weighing ten samples of about hundred seeds each and then dividing the sample weight by the number of seeds. Seed size of fifty seeds was estimated using a binocular and a calliper.

^a Geissler and Gzik (2008a).

^b Rothmaler (2005).

^c Geissler (unpublished).

^d Michalski and Durka (2007).

^e Geissler and Gzik (2008b).

der Valk and Davis, 1978). The controls for this experiment are seeds, which were sown on filter paper soaked with distilled water.

Dormancy cycle of C. dubium seeds throughout the year

Approximately 1000 seeds collected on 25 October 2004 were equally placed in 30 nylon bags and were buried individually in 30 pots, which were filled with soil collected from the Havel River Valley. The pots were placed under an open roof. They were watered to field capacity daily from October to April, unless frozen, and once a week during rest of the year. On 25th of every month, seeds of three replicate pots were excavated and tested for germination in light at 22/15 °C. Retrieval of buried seeds started in November 2004 and ended in July 2005.

Response variables

We determined two parameters of each species' germination sequence: the germination onset, which is the time (in days) between the beginning of the experiment and the commencement of germination, and the final germination percentage at the end of the experiment (G). In the calculation of germination percentages, dead seeds, solely identified by their softness and changed brownish colour, were excluded. For *J. atratus* we also calculated germination rate after onset of germination ($R_{G50\%}$). Germination progress curves were plotted for each treatment. Subsequently, 50% of the final germination percentage ($G_{50\%}$), the times (t_1) taken to reach 50% of the final germination percentage, and the times of germination onset (t_2) were noted. Germination rate was calculated using the equation:

$$R_{G50\%} (\% \text{ day}^{-1}) = \frac{G_{50\%}}{(t_1 - t_2)}$$

If very few seeds germinate, an apparent structural correlation is found between germination rate and final germination percentage. For this reason, we have excluded *C. dubium* and *G. officinalis* from a comprehensive analysis of germination rate.

Germination phenology in the field

For each species, three replicates of 100 freshly matured seeds were sown in each of three 15 cm pots filled with soil collected from the natural site. The soil of the top 7 cm was sterilised by heating to >150 °C. Half of the seeds were sown on the soil surface, the other half was buried in 3 cm depth. According to Hölzel and Otte (2004b)

this depth belongs to the zone of highest seed density in temperate wetlands. Pots were placed under an open roof in water-filled trays. Trays were regularly refilled up to 2 cm water height, unless frozen, and were exposed to natural seasonal temperature. For the duration of the study, mean daily minimum and maximum air temperatures at 5 cm above soil surface were obtained from DWD (Deutscher Wetterdienst, 2007). The pots were checked weekly and if seedlings were present, they were recorded and removed. Response variable is cumulative germination.

Statistics

As treatment effects were primarily of interest within each species, three-way ANOVAs tested for the effects and interactions of light, stratification, and temperature or temperature fluctuation on germination percentage/onset. All factors were considered fixed. In many cases the three-way ANOVA was reduced to a two-way ANOVA, as no or no sufficient germination occurred in some treatments. In seeds of *C. dubium*, a two-way mixed model ANOVA was applied to test the combined effects of year of harvest and gibberellic acid concentration on final germination percentages, with year as a random factor. Bonferroni LSD test was always performed to detect differences between treatment regimes. Germination percentages were arcsine-transformed. All analyses were carried out with R 2.8.1.

Results

Light and temperature effects upon germination of freshly matured seeds

Seeds only of *C. dubium* showed germination in the dark (Table 2 and Fig. 1). The germination percentage was, however, significantly higher in light than in darkness (Tables 4 and 5). Seeds of *G. officinalis* and *J. atratus* did not germinate in complete darkness. The dark treatment was therefore omitted from the statistical analysis.

Seeds of *C. dubium* and *G. officinalis* were responsive to diurnal temperature fluctuations (Table 4): The germination percentage of fresh seeds of both species was significantly higher in the treatments with a temperature amplitude (7 and 12 K) compared to control (0 K; Fig. 1). *C. dubium* germinated significantly earlier, whereas seeds of *G. officinalis* under diurnally changing temperatures germinated significantly later than the 0 K-amplitude control (Table 3). *J. atratus* was insensitive to diurnal temperature amplitudes for both, germination percentage and germination onset

Table 2

Final germination percentages (mean \pm SD) of seeds of *C. dubium*, *G. officinalis*, and *J. atratus* at four constant temperatures (12/12 h) in light and darkness (14/8 h) either freshly matured or after a 3-month period of cold-wet stratification.

Species	Treatment								
	Age	Light				Darkness			
		10 °C	15 °C	22 °C	30 °C	10 °C	15 °C	22 °C	30 °C
<i>C. dubium</i>	Fresh	0	3 ± 2	1 ± 1	3 ± 2	0	1 ± 1	1 ± 2	1 ± 1
	Stratified	12 ± 0	5 ± 5	21 ± 12	11 ± 3	0	7 ± 4	12 ± 4	5 ± 5
<i>G. officinalis</i>	Fresh	0	10 ± 4	2 ± 1	0	0	0	0	0
	Stratified	77 ± 3	98 ± 3	91 ± 2	58 ± 3	0	0	0	0
<i>J. atratus</i>	Fresh	29 ± 9	64 ± 6	89 ± 6	1 ± 1	0	0	0	0
	Stratified	51 ± 1	75 ± 9	73 ± 4	8 ± 4	0	0	0	0

Table 3

Number of days to the onset of germination (mean \pm SD) of *C. dubium*, *G. officinalis* and *J. atratus* and germination rate after onset (% per day) of seeds of *J. atratus* at four constant and three fluctuating temperatures (12/12 h) in light (14/8 h) either freshly matured or after a 3-month period of cold-wet stratification.

Species	Age	Constant temperature				Temperature fluctuation		
		10 °C	15 °C	22 °C	30 °C	0K	7K	15 K
Days to germination onset								
<i>C. dubium</i>	Fresh	∞	10 ± 2	15 ± 9	13 ± 1	15 ± 9	7 ± 1	12 ± 2
	Stratified	18 ± 2	12 ± 1	4 ± 1	5 ± 3	4 ± 1	6 ± 1	5 ± 1
<i>G. officinalis</i>	Fresh	∞	26 ± 5	7 ± 2	∞	7 ± 2	18 ± 1	14 ± 1
	Stratified	8 ± 1	4 ± 1	1 ± 1	1 ± 1	1 ± 1	2 ± 1	13 ± 1
<i>J. atratus</i>	Fresh	12 ± 1	5 ± 1	3 ± 1	16 ± 2	3 ± 1	4 ± 1	4 ± 1
	Stratified	10 ± 1	3 ± 1	4 ± 1	23 ± 1	4 ± 1	4 ± 1	4 ± 1
Germination rate after onset								
<i>J. atratus</i>	Fresh	3 ± 1	6 ± 2	7 ± 1	1 ± 1	7 ± 1	9 ± 1	6 ± 1
	Stratified	4 ± 1	6 ± 1	2 ± 1	1 ± 1	2 ± 1	5 ± 1	4 ± 1

(Table 4 and Fig. 1). Only the germination rate increased at 22/15 °C (Tables 3 and 4).

In fresh seeds of two species, germination differed significantly between constant temperature treatments (Table 5). *G. officinalis*

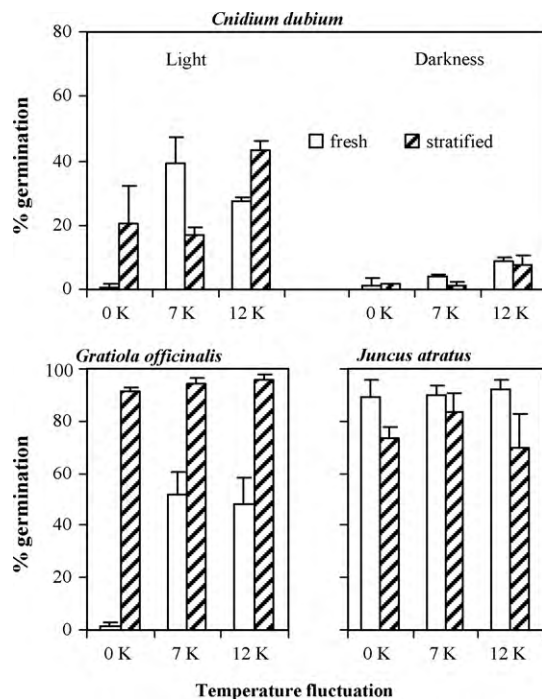


Fig. 1. Mean final germination percentages ($n=3$) of seeds of *C. dubium*, *G. officinalis* and *J. atratus* at three fluctuating temperatures (12/12 h) based on 22 °C day temperature in light (14/8 h) and darkness (14/8 h) either freshly matured or after a 3-month period of cold-wet stratification.

did not germinate at either 30 or 10 °C (Table 2). Similar results were obtained for *J. atratus*. Here, almost no germination had occurred at highest temperature of 30 °C and only 29% at lowest temperature of 10 °C. At both temperatures even the onset of germination was late and the germination rate was low compared to the other temperatures (Table 3). The third species *C. dubium* did hardly germinate at any constant temperature (Table 2).

Across most temperature treatments and in contrast to the other two species, fresh seeds of *J. atratus* germinated to a very high extent (Table 2 and Fig. 1). Peak germination was between 89–92% at 22 °C day temperature; it was independent of night temperature. The peak germination of *G. officinalis* and *C. dubium* was only

Table 4

The effects of temperature fluctuation (F), stratification (S), and light (L) on final germination percentage (arcsin transformed), germination onset and germination rate of seeds of *C. dubium*, *G. officinalis*, and *J. atratus* with their level of significance.

	Main effects			Interactions			
	F	S	L	F \times S	F \times L	S \times L	F \times S \times L
Germination percentage							
<i>C. dubium</i>	***	**	***	***	***	***	***
<i>G. officinalis</i>	***	***		***			
<i>J. atratus</i>	ns	***		ns			
Days to germination onset							
<i>C. dubium</i> ^a	ns	***		*			
<i>G. officinalis</i>	***	***		***			
<i>J. atratus</i>	ns	ns		ns			
Germination rate after onset							
<i>J. atratus</i>	***	***		***			

^a Data were ln transformed; and due to inhomogeneous variances the real level of significance is twice as high as the level chosen (Lindquist, 1953).

ns: not significant.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

Table 5

The effects of constant temperature (*T*), stratification (*S*), and light (*L*) on final germination percentage (arcsin transformed), germination onset and germination rate of seeds of *C. dubium*, *G. officinalis*, and *J. atratus* with their level of significance.

	Main effects			Interactions			
	<i>T</i>	<i>S</i>	<i>L</i>	<i>T</i> × <i>S</i>	<i>T</i> × <i>L</i>	<i>S</i> × <i>L</i>	<i>T</i> × <i>S</i> × <i>L</i>
Germination percentage							
<i>C. dubium</i> ^a	ns	***	***	*	ns	**	*
<i>G. officinalis</i>	***	***	***	***			
<i>J. atratus</i>	***	ns	***	**			
Days to germination onset							
<i>C. dubium</i> ^{a,b}	ns	*	***	ns			
<i>G. officinalis</i> ^c	***	***	***	***			
<i>J. atratus</i>	***	ns	***	***			
Germination rate after onset							
<i>J. atratus</i>	***	ns	***	***			

ns: not significant.

^a Without data of the 10 °C treatment.

^b Due to inhomogeneous variances the real level of significance is three times higher than the level chosen.

^c Without 10 and 30 °C.

* *P* < 0.05.

** *P* < 0.01.

*** *P* < 0.001.

52% and 39%, respectively, and occurred at 22/15 °C (7 K amplitude, Fig. 1).

Light and temperature effects upon germination after 12 weeks of cold stratification

Stratification did not change the absolute light requirement for germination of seeds of *G. officinalis* and *J. atratus* (Table 2 and Fig. 1). In seeds of *C. dubium* the positive light effect was more pronounced (significant *S* × *L* interaction; Tables 4 and 5), although, there was still germination in complete darkness.

Stratification substitutes the temperature-fluctuation requirement for germination in *G. officinalis*; it weakens this requirement in *C. dubium* (significant *F* × *S* interaction for germination and its onset; Table 4): seeds of *G. officinalis* germinated more than 90% with and without temperature fluctuation (Fig. 1). Those of *C. dubium* still germinated better at high temperature amplitude (12 K: 43%) compared with medium amplitude (7 K: 21%) and control (17%). *Juncus atratus* remained insensitive to diurnal temperature amplitudes for both, germination percentage and germination onset (no significant *F* × *S* interaction; Table 4). The increase of germination rate due to diurnal temperature fluctuation was, however, more pronounced in stratified seeds than in fresh seeds (significant *F* × *S* interaction; Tables 3 and 4).

Stratification significantly increased the temperature range of germination in seeds of *G. officinalis* and *J. atratus* (*T* × *S* interaction; Table 5). In seeds of *G. officinalis* this was true for both, the lowest (10 °C) and highest (30 °C) experimental temperature (Table 2). In *J. atratus* germination percentage nearly doubled at 10 °C; it only slightly increased at 30 °C. Stratification even significantly postponed germination onset at this high temperature (Tables 3 and 5).

Although stratification significantly decreased both, germination percentage and rate of germination of *J. atratus* in the fluctuation experiment (Fig. 1, Tables 3 and 4), peak germination percentage remained generally high. The low germination percentages observed in fresh seeds of *G. officinalis* and *C. dubium* were, however, significantly increased by stratification across all temperature treatments (Tables 2 and 5). In *G. officinalis* this was remarkable, with more than 90% of all seeds germinating at 15 and 22 °C. In *C. dubium* the effect was more pronounced at 22 °C in light compared with the other tested constant temperatures (significant *T* × *S* interaction; Table 5), although in contrast to *G. officinalis* the

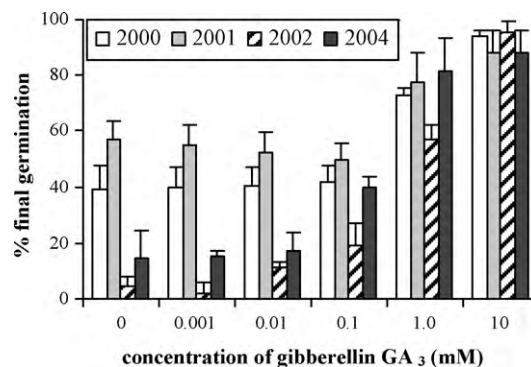


Fig. 2. Mean final germination percentages (*n* = 3) of freshly matured seeds of *C. dubium* harvested in different years: 2000, 2001, 2002, and 2004 after incubation at different concentrations of gibberellic acid.

Table 6

ANOVA of the effects of year of harvest and concentration of gibberellic GA₃ on final germination percentage of seeds of *C. dubium*.

Source	d.f.	<i>F</i>	<i>P</i>
Concentration	5	22.4***	***
Year	3	76.7	***
Concentration × Year	15	8.6	***
Error	48		

Degrees of freedom (d.f.) and *F*-values are given with their level of significance:

*** *P* < 0.001.

maximum germination that was reached was only 21%. Stratified seeds of both species germinated significantly earlier than the fresh seeds (Tables 3 and 5).

Effect of gibberellic acid on low germinating *C. dubium* seeds

Mean germination percentage of freshly matured seeds was dependent on the year of harvest (Fig. 2 and Table 6). It was lowest in the 2002 and 2004 seed cohorts. Both cohorts were, however, more sensitive to gibberellic acid than the 2000 and 2001 seed cohorts (significant concentration × year interaction). They increased germination already at 0.01 and 0.1 mM GA₃. These differences in germination level between the four different seed cohorts were maintained until a concentration of 1.0 mM was reached. Germination for all cohorts increased with increasing concentration of gibberellic acid, eventually reaching more than 90%. Hence, seeds showed physiological dormancy.

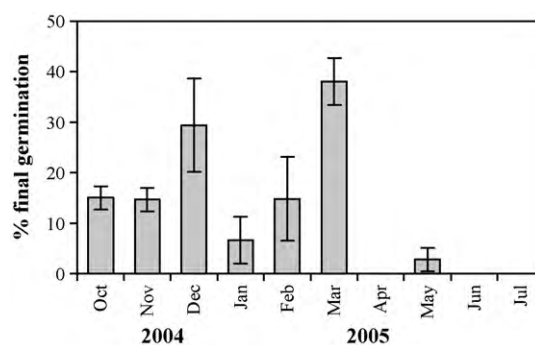


Fig. 3. Mean final germination percentages (\pm SD, *n* = 3) of *C. dubium* seeds incubated for 30 days in light at 22/15 °C following 0–9 months of burial in soil.

Dormancy cycle of *C. dubium* seeds throughout the year

Freshly matured *C. dubium* seeds germinated to a total of 15%, in light at 22/15 °C (Fig. 3). A first germination peak was attained in December. Low stratifying winter temperatures favoured subsequent germination, since a second peak of 38% was reached in March. Germination ceased later in spring and summer.

Phenology of seed germination in the field

Seeds of *G. officinalis* and *C. dubium*, which were surface-sown in autumn 2000, commenced germination in the next spring on 12 and 17 April 2001, when mean weekly maximum and minimum temperatures were 13 and 1 °C, respectively (Fig. 4a). Surface-sown seeds of *C. dubium*, which were harvested two years later in autumn 2002, also postponed germination to the next spring (Fig. 4b). They germinated on 11 April 2003 at relatively low mean weekly maximum and minimum temperatures of 6 and –6 °C, respectively. There was, however, a preceding 3-week warmer period of approximately 13/–1 °C. For summer-dispersed seeds of *J. atratus*, which were surface-sown on 2 August 2002, germination began only 11 days after sowing at mean weekly maximum and minimum temperatures of 22 and 11 °C, respectively (Fig. 4b).

The germination period in *C. dubium* lasted until the end of May. Another 1% of the year-2000-seed cohort germinated, however, in spring 2002. Germination in *G. officinalis* lasted almost until the end of July. For *J. atratus*, the phase of germination was very short. It continued until mid-September. A small number of seeds germinated until mid-October.

The year of seed maturation remarkably affected the germinability of *C. dubium*. Only 3% of the seeds, originating from the year 2000 germinated, contrary to 48% of the seeds, which were harvested in 2002. Yet, the germination percentages were low compared with 71% of *G. officinalis* and with 72% of *J. atratus*.

Buried seeds of *C. dubium* may not germinate till the second, or some subsequent, season after maturation. The first seedling from seeds which had been buried on 3 November 2000 emerged on 3 June 2002. Total germination was 3%. A total of 8% of those seeds,

which had been buried on 3 November 2002, germinated, and the first percent was observed on 11 May 2004. The emergence period lasted until mid-July. Of buried seeds of *G. officinalis* and *J. atratus* 2% and 4% germinated, respectively.

Discussion

Light requirement in general

Gratiola officinalis and *Juncus atratus* which occupy more frequently flooded, naturally disturbed sites and pioneer sites showed an absolute light requirement for germination. This property along with small seed size is considered to be a common response pattern controlling establishment in open spaces (Baskin and Baskin, 2002; Eriksson, 2005; Grime et al., 1981). It has been found in small-seeded, early-successional temperate species (Jensen and Gutekunst, 2003) and in wetland species including many Juncaceae (Baskin et al., 1989; Grime et al., 1981). However, it is notable, that very small seeds are typical for all temperate *Juncus* and *Gratiola* species and that in the field experiment, some seeds of *G. officinalis* and *J. atratus* emerged in spite of burial. The absence of elongated hypocotyls or epicotyls indicates that seeds may have simply moved to the soil surface due to animal activity. But also Burkart et al. (in press) were unable to find an absolute light requirement for germination in *J. atratus*, even though germination was stimulated by high light intensities. Factors such as pH or nitrate might account for the lack of such absolute response pattern, since soil soaked with tap-water was used in both studies. In either case, however, a stimulation of germination by high light intensities can equally be seen as a function to support colonization of gaps (Burkart et al., in press; Grime, 2001). *C. dubium* was the only species in this study that clearly emerged when kept in darkness, although germination was also stimulated by high light levels. It has large seeds compared with *G. officinalis* and *J. atratus*, providing simply the opportunity for gap establishment from shallow buried seeds (Harper and Obeid, 1967; Pearson et al., 2002). Most of the seeds should have been incorporated into the soil by bioturbation when disturbance by early-summer mowing occurs, an important factor at sites of *C.*

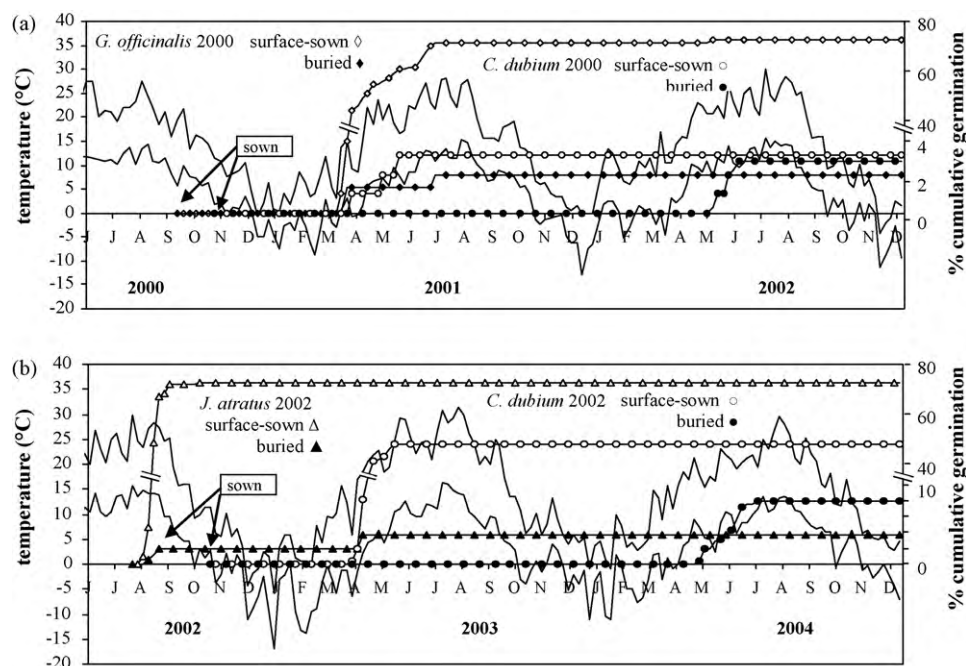


Fig. 4. Biweekly maximum and minimum temperatures (solid lines without symbols) and cumulative percentage of emergence in seeds of (a) *C. dubium* + *G. officinalis* harvested 2000; (b) *C. dubium* + *J. atratus* harvested 2002. Open symbols: emergence when sown on the soil surface; solid symbols: emergence when buried at 3 cm depth.

dubium (Burkart, 2001; Geissler and Gzik, 2008a; Härdtle et al., 2006). However, the seasonal dormancy pattern detected and the germination in the field experiment fail to support that germination of *C. dubium* is beneficial at that time of the season.

Freshly matured seeds

Most plants adapted to exploit natural disturbances by regeneration in gaps are stimulated to germinate by a combination of two factors: high light levels and fluctuating temperatures (Grime et al., 1981). The responsiveness to temperature fluctuations provides the seed a 'gap- or depth-sensing' mechanism, because the temperature amplitude is small beneath an insulating cover of water, vegetation, or soil (Thompson et al., 1977).

Freshly matured seeds of both *G. officinalis* and *C. dubium* were strongly responsive to temperature in addition to light. Dependence on the two factors is a common trait of species that occur on moist, frequently disturbed soils and of wetland species (Ekstam et al., 1999; Schütz, 1999; Thompson and Grime, 1983; Thompson et al., 1977). Freshly matured seeds of *J. atratus*, in contrast, lack any considerable 'gap sensitivity' based on temperature fluctuation. Seedling recruitment of this species should therefore not be restrained by inundation or location under a canopy, as Burkart et al. (in press) have recently shown. Immediate recruitment is only dependent on a position sufficiently close to the soil surface, based on the light requirement. However, interpreting the ecological benefits of traits, measured in the laboratory, requires an important decision: whether traits are relevant in nature or not. Seeds of *J. atratus* are already dispersed in mid-July, and in the field experiment they germinated shortly after. Here, it seems reasonable to test if insulating but shady vegetation and a summer inundation, the latter with additional oxygen depletion, would impose effects on germination. Results of the germination phenology of both *C. dubium* and *G. officinalis* indicated that the level of primary dormancy was sufficient to prevent germination following dispersal, irrespective of their responsiveness to temperature fluctuations. Seed release of *C. dubium* does not begin until the autumn, when the temperature is too low for germination. And even if seeds of *G. officinalis* would be released at the end of August, as occurring in certain years, a stimulative effect of temperature fluctuations may be not of great importance. It must be doubted whether seedlings germinating at this time would reach a size that would be sufficient to survive the cold winter conditions.

Dormancy in general optimizes the distribution of germination over time. Non-dormant seeds germinate over the full range of environmental conditions possible for a species, dormant seeds do not germinate under any condition, whereas conditionally dormant seeds germinate under influence of a limited set of conditions (Baskin and Baskin, 2004). It seems that all the three investigated species were conditionally dormant at maturity. Their hampered germination at low and high temperatures can prevent germination in hot summers and in autumn. The latter is especially important for plants in river floodplains with harsh but predictable winter flooding (Voeselek and Blom, 1992). Along with a light requirement, which is the most consistent attribute in species that form persistent soil seed banks, seed dormancy enhances the chances for the species to become incorporated into the local seed pool (Grime et al., 1981; Thompson et al., 2003). That is, all three species have the potential to form persistent soil seed banks for which evidence is available from Geissler and Gzik (2008b).

Primary dormancy

A period of cold stratification simulating natural winter conditions can break primary dormancy in many temperate plants (Baskin and Baskin, 1988; Schütz and Rave, 1999). This was true

for both late-dispersing species *C. dubium* and *G. officinalis*. An increased number of seeds gained the ability to germinate at low temperature of 10 °C. As a consequence, seeds of both species can germinate in early spring when conditions are favourable for seedling survival and growth, confirming the observed germination phenology in the field. But in contrast to *C. dubium*, there is evidence that in *G. officinalis* decreasing water levels are no factor controlling the timing of spring germination (Ekstam et al., 1999; Van Assche and Vanlerberghe, 1989), since stratification did fully substitute the temperature-fluctuation requirement for germination. *G. officinalis* may have the potential to germinate even when submerged, similar to *J. atratus* (Burkart et al., in press). This may be an important trait for weak competitors. The hypothesis that inundation does not interfere still needs to be tested. There is no doubt, however, that germination of *G. officinalis* in the subsequent spring will be supported by a stable, well-lighted substrate.

In *C. dubium* further evidence for the temporal effect of cold stratification on germination was obtained from the investigation of its annual dormancy cycle. Seeds showed maximum germination in March. But in contrast to *G. officinalis*, a large proportion of cold stratified seeds rarely germinated. The low overall germination values confirm the results obtained for this species by Hölzel and Otte (2004a). It might either emphasize the importance of vegetative relative to generative reproduction (see Table 1) or it may be an expression of germination polymorphism. Silvertown et al. (1993) proposed that the latter has been selected to reduce the risk of high mortality caused by synchronous seed emergence from the seed pool. Dormancy of seeds of *C. dubium* was, however, completely broken by gibberellic acid. The hormone can substitute the stratification requirement for dormancy break in various species (Pinfield and Stobart, 1972; Timson, 1966). Both, the primary level of dormancy of freshly matured seeds of *C. dubium* and the sensitivity of these seeds to gibberellic acid or natural winter conditions were dependent on the year of harvest. Certainly something must be varying among years to produce a specific dormancy status of the seed cohort set. An effect of the maternal environment on seed dormancy has been shown in many studies (Guterman, 1992; Hayes and Klein, 1974; Langens-Gerrits et al., 2001; Van der Sman et al., 1993). Dormancy level of the 2002 seed cohort of *C. dubium*, for example, might have been modified by an extraordinary summer flood. We suspect that complex preconditioning, i.e. specific effects of the environment on perhaps different dormancy types, would account for the contrasting results regarding primary level of dormancy and sensitivity to dormancy breaking agents. A combination of morphological dormancy, like an undeveloped embryo, and physiological dormancy is found in many species of the Apiaceae (Grushvitzky, 1967). With concern to environmental constraints on reproduction, the investigated annual dormancy cycle of *C. dubium* elucidates that seeds avoided germination in light at high summer temperatures by re-entering dormancy in the late spring. This is a typical finding for temperate spring germinators (Jensen, 2004; Schütz, 1997). Contrary to other wetland plants, no requirement for high summer temperatures was given to induce this so-called secondary dormancy (Baskin et al., 1989, 1993, 1996). Our findings taken together indicate that germination of *C. dubium* would be maximized by open vegetation structures in early spring when the flooding water has receded.

In contrast to *C. dubium* and *G. officinalis*, stratified seeds of *J. atratus* seemed to remain in a conditional dormant state. First, they were still to some extent unable to germinate at high temperatures. Secondly, they neither enhanced germination rate nor decreased time to germination onset. Long lag phases accompanied by low germination rates are considered to show a high degree of dormancy (Baskin and Baskin, 1983; Courtney, 1968; Schütz, 2000). Hence, missing changes in both onset and rate may reflect missing changes in the degree of dormancy and vice versa. Thus, there is

evidence that mature seeds of *J. atratus* were rather non-dormant, yet they had species-specific temperature requirements for germination (Baskin and Baskin, 2004; Bouwmeester and Karssen, 1993), with an upper temperature limit. In our field experiment, *J. atratus* reached immediately a high amount of germinated seedlings in late summer. Obviously, no dormancy effect was operating. This picture fits well with the comparative study of Grime et al. (1981). They found a high initial germinability and a low response to cold–wet stratification in many taxa of *Juncus*. Baskin and Baskin (1988) argued that such trait is important at sites with frequent fluctuations in water level. It was already stated that frequently open sites are advantageous for *J. atratus*. On the other hand, open sites may show high soil temperatures in summer (Balisky and Burton, 1993; Morecroft et al., 1998), for which *J. atratus* has obviously a strong avoidance mechanism. We suggest, therefore, that soil temperature at favourable sites must never be too high. At very wet sites, for instance, high soil–water content decreases the temperature by increasing soil heat flux. The refined implication of these results is that germination of *J. atratus* in the field would be maximized by a stable, wet, well-lighted substrate, at any time of the year, provided that temperature exceeds 10 °C.

In conclusion, these three endangered river corridor plants show different germination patterns in response to temperature and light. Methods such as mowing that support the creation of long-standing open patches (Kotorová and Lepš, 1999) may actively enhance regeneration of *C. dubium* by seeds. It is not clear if *J. atratus* and *G. officinalis* benefit equally from these management schemes because their germination is confined to the soil surface. Here, it appears that both the proximity to the water and the flooding regime with its marked winter/spring floods are more relevant for creating suitable patches available for germination. In this context it is important to clarify if germination of *G. officinalis* can occur also at low oxygen levels and if seeds of both species are buoyant, because the ability of seeds to float and sink to the bottom after a period of time (Coops and van der Velde, 1995) may play an important role in directing seeds toward soil surface in spring.

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