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

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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.

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-

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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 outcompeted 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 μmol m^{-2} 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 (GA_3) 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