



Recruitment requirements of the rare and threatened *Juncus atratus*

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ABSTRACT

The long-term persistence of populations and species depends on the successful recruitment of individuals. The generative recruitment of plants may be limited by a lack of suitable germination and establishment conditions. Establishment limitation may especially be caused by the competitive effect of surrounding dense vegetation, which is believed to restrict the recruitment success of many plant species to small open patches ('safe sites'). We conducted experiments to clarify the roles of germination and seedling establishment as limiting processes in the recruitment of *Juncus atratus* Krock., a rare and threatened herbaceous perennial river corridor plant in Central Europe. Light intensity had a positive effect on germination. However, some seedlings emerged even in total darkness and the germination rate at 1% light intensity was more than half of that at 60% light intensity. Seedling establishment in the field after 10 weeks was 30% on bare ground, but it was close to zero in grassland. Establishment in the growth chamber after 8 weeks was close to 75% for seedlings that germinated underwater, but only about 35% for seedlings that germinated afloat. Furthermore, establishment decreased with flooding duration on bare ground, but increased with flooding duration in grassland. These data indicate that establishment, rather than germination, is a critical life stage in Central European populations of *J. atratus*. They furthermore indicate that the competition of surrounding vegetation for water limits seedling establishment under field conditions without flooding, largely restricting establishment success to bare ground habitats. In contrast, grassland is more suitable for the recruitment of *J. atratus* than bare ground under prolonged flooding. Grassland may facilitate the establishment of *J. atratus* seedlings during long-lasting floods by supplying oxygen to the soil through aerenchyma. The shift from competition to facilitation in grassland occurred after 30 days of flooding, i.e. within the ontogeny of individual plants. The specific recruitment requirements of *J. atratus* may be a main cause of its rarity in modern Central Europe. In order to prevent regional extinction of *J. atratus*, we suggest maintaining or re-establishing natural hydrodynamics in the species' habitats.

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Introduction

The generative recruitment of plants may be limited by a shortage of seeds (seed limitation) or by a lack of suitable germination and establishment conditions (establishment limitation) (Eriksson and Ehrlén, 1992; Münzbergová and Herben, 2005; Nathan and Muller-Landau, 2000; Turnbull et al., 2000). To quantify these two components of recruitment limitation, one can conduct seed addition experiments in which extra seeds are sown and the resulting increase in recruit numbers is recorded (Crawley, 1997; Hölzel, 2005; Moles and Westoby, 2002; Nathan and Muller-Landau, 2000; Turnbull et al., 2000). If a population increase is observed after seed addition, recruitment is seed-limited, whereas recruitment

is establishment-limited if no population increase occurs. In the latter case, however, the question remains as to how sensitive the different life-stage processes are that comprise establishment. Establishment limitation may be caused by germination failure, seedling mortality, or juvenile death, all of which may be caused by adverse environmental conditions. Such conditions include the competitive effect of surrounding dense vegetation, which is believed to restrict the recruitment success of many plant species to small open patches ('safe sites' sensu Burke and Grime, 1996; Donath et al., 2006; Harper, 1977; Hölzel and Otte, 2004; Yates and Ladd, 2005).

The recruitment of such competitively inferior species is often disturbance-dependent. The group of disturbance-dependent species (or ruderals; Grime, 1974) holds many rare and threatened taxa (Burkart, 2001; Holmgren and Poorter, 2007; Kirkpatrick and Gilfedder, 1998; Roschewitz et al., 2005; Smith et al., 2005). Ruderals are typically concentrated in ecosystems subject to regularly

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occurring large-scale disturbances (Ellenberg, 1996; Körner and Jeltsch, 2008; Marshall and Moonen, 2002; Roschewitz et al., 2005). In order to identify the processes that maintain and threaten biodiversity in these species-rich systems, it is thus necessary to unravel the roles of disturbance and recruitment for the life cycle of rare plants.

Here we report on a series of experiments designed to identify the recruitment requirements of the river corridor plant *Juncus atratus* Krock. *J. atratus* is a rare herbaceous perennial in Central European floodplains that has long been known to occur in disturbed habitat patches (Ascherson, 1864; Burkart, 1995; Burkart and Prasse, 1996; Taubert, 1889). Despite this affinity for ephemeral site conditions, some *J. atratus* populations have persisted for more than 100 years (Ascherson, 1864; Burkart, 1995; Plöttner, 1898). This somewhat paradox finding gives rise to questions about the persistence mechanisms and the nature of the disturbance affinity. Knowledge of the persistence mechanisms is fundamental for conservation management recommendations (Corral-Aguirre and Sanchez-Velasquez, 2006; Farnsworth, 2007). Adult *J. atratus* plants produce non-dormant seeds in large numbers that may be distributed by water during floods (K. Alsleben and M. Burkart, unpublished data). These seeds may germinate either floating on the surface or underwater after having sunk to the ground. The fate of the offspring from both germination paths must be assessed to understand the species' recruitment (Leyer, 2006; Vogt et al., 2004).

Specifically, we tested the following hypotheses: (1) germination of *J. atratus* is not restricted by reduced levels of light intensity which are typical for the soil surface in herbaceous vegetation. (2) Seedling establishment is the limiting life-stage process of Central European *J. atratus* populations under natural conditions. (3) Floodplain-specific disturbances (destruction of the vegetation cover, flooding) promote the establishment of *J. atratus*. (4) The establishment of seedlings that germinated afloat is reduced as compared to seedlings that germinated on the ground.

Based on the results of our experiments, we discuss potential causes of the rarity and the long-term persistence of *J. atratus* as well as the role of the surrounding vegetation as a potential source of competition or facilitation, and formulate guidelines for the management of its habitat and the identification of reintroduction areas.

Materials and methods

Study species and study sites

Juncus atratus Krock. is a hemicyptophytic monocot with short creeping rhizomes and very light seeds. It forms loose tussocks of up to 50 cm diameter that consist of a few to several hundred vertical shoots. These shoots are formed annually and reach up to 1 m in height (Buchenau, 1890; Kirschner, 2002; Snogerup, 1978). Seeds are oblong, weigh approx. 0.013 mg, ripen between mid-July and early August, are released immediately after maturity and may be dispersed by wind, water and animals. The germination rate at optimum conditions (22 °C, full light, water saturation) ranges from 70 to 100% (Geissler and Gzik, 2008; Michalski and Durka, 2007a,b; K. Alsleben and M. Burkart, unpublished data). Seeds are non-dormant and long-lived: no decline in germination rate has been observed, neither after 2 years of seed burial under natural conditions (intermittently wet and dry) nor after 1 year of dry storage at room temperature (M. Burkart, unpublished data).

In Central Europe, *J. atratus* occurs in river corridors, both on pioneer sites and in grassland communities of the alliances *Cnidion dubii* Balátová-Tuláčková 1966 and *Potentillion anserinae* R. Tx. 1947 (relevés in Burkart, 1995). However, populations have hardly been found close to river margins, but generally on the banks of backwaters, in plains and depressions, ditches and pits remote from

the river channel and even behind dikes (Burkart and Prasse, 1996; Burkart, 1995; Hejny, 1960). The habitats are exposed to full sun or are slightly shaded. They are generally flooded for 1–5 months in winter and spring. Cover and abundance of *J. atratus* declines both in shade and under tall-grass competition, but the species is flood-tolerant and able to initiate spring growth while still fully submerged (Burkart, 1995; M. Burkart, unpublished data).

The centre of the geographical range of *J. atratus* lies in the steppe zone of subcontinental western Eurasia (Hultén and Fries, 1986; Meusel et al., 1965). Currently, its northwestern range boundary is formed by several disjunct groups of populations in Germany, Poland and the Czech Republic, where it occurs mainly in river corridors (Burkart, 1995, 2001). In Central Europe, the species has always been reported as rare (Ascherson, 1864; Burkart, 1995). From a conservational viewpoint, this situation has worsened throughout the past century, when the species became extinct in southwestern Germany, Austria, and western Poland, and has been strongly declining in the remaining areas of its Central European distribution (Burkart, 1995).

For the experiments presented here, we studied the recruitment of *J. atratus* populations from the Havel floodplain (northeastern Germany). This area holds several populations of varying size, including large populations with abundant seed production. Three large populations served as seed sources for the experiments described below (Pritzerbe, 52°30'29"N, 12°25'33"E; Vehlgast, 52°48'27"N, 12°10'30"E; Havelberg, 52°49'12"N, 12°05'20"E). All these populations grow in floodplain grassland that is regularly flooded in late winter and spring. The grassland is managed by mowing (Pritzerbe, Vehlgast) or grazing (Havelberg). Besides management, there are no obvious differences between the sites. The field establishment experiment was also conducted in this region.

Experiments

We conducted three experiments to clarify the role of germination and seedling establishment as limiting processes in the recruitment of Central European populations of *J. atratus*. In a germination experiment, we tested the effect of different light intensities – as experienced by *J. atratus* seeds in their natural habitat – on their germination rate to assess the potential role of germination as a limiting process in the wild. In a field establishment experiment, we tested for the effect of vegetation structure (bare ground, low-competition grassland, and typical grassland) on the establishment of *J. atratus* seedlings. Both the effects of vegetation structure (bare ground, typical grassland) and flooding duration on seedling establishment were studied in a growth chamber experiment. Furthermore, this experiment was used to study the importance of the germination mode (on the ground vs. afloat) for establishment.

Germination

To study the effect of light intensity on the germination of *J. atratus*, we exposed 1-year-old dry stored seeds of mixed origin from the study region to four levels of solar irradiation in a greenhouse. Irradiation levels were chosen to simulate different conditions which the seeds experience in the study region (60% – open soil, 0% – subsoil, 10% and 1% – different grassland types; PPFD-values between 1.8% [36/1950 $\mu\text{mol m}^{-2} \text{s}^{-1}$] and 18.2% [360/1980 $\mu\text{mol m}^{-2} \text{s}^{-1}$] were measured in the study region at 2 July 2004 at 10:30 CEST on the soil surface in different stands with *J. atratus* in relation to values above the plant canopy [$n = 4$]). Light intensity in the greenhouse was reduced by application of one or three layers (10% and 1%, respectively) of a 2 mm \times 10 mm green mesh J56, part number 280173 (Hermann Meyer, Rellingen, Germany) or through two layers of aluminium foil (0%) to individual pots; this was in addition to the reduction due to the

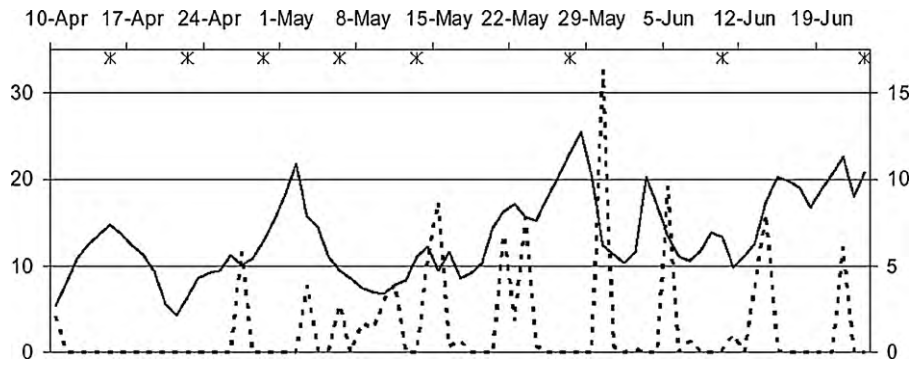


Fig. 1. Weather conditions during the field experiment in the Havel floodplain near Gülpe. Temperature (in °C, left axis, solid line) is given as day means measured 2 m above the soil surface, precipitation (in mm, right axis, dotted line) is given as day sums. Asterisks (top of diagram) mark important dates (transplanting – 15 and 22 April, mat removal – 6 May, data recording – 29 April, 13 May, 27 May, 10 June, 24 June 2005).

greenhouse glass (60%). Application of 100% irradiation was not possible because the pots had to be protected from rain, which might easily have washed out the very small *Juncus* seeds from the pots. Irradiation was measured with an LI-1400 datalogger (LI-COR-Biosciences, Lincoln, Nebr., USA) and a US-SQS/L light sensor (Heinz Walz, Effeltrich, Germany). 80 pots per light intensity treatment were randomly placed on trays that were filled with tap water up to the sand surface. In each pot, 20 seeds were placed on a thin layer of sterile sand on top of sterile soil in order to exclude any other seeds. Holes in the bottoms of the plastic pots ensured that soil and sand were constantly kept wet.

Germination was monitored over 4 weeks, with 20 pots from each treatment studied each week. Germination was counted only once for each pot, because mesh and aluminium foil had to be removed for counting, which interrupted the light treatment.

The seedlings in the 80 pots that were counted first were marked individually with wooden toothpicks, and were then kept under the same light and water conditions as before to monitor their survival in the following 4 weeks.

The experimental data were analysed with generalised linear models (GLM) with proportion of germinated seeds as the response variable and quasibinomial errors to account for overdispersion (McCullagh and Nelder, 1989). The maximal model included the factor tray (1–20), time (1–4 weeks) and light intensity (0%, 1%, 10%, 60%) as continuous explanatory variables, and all possible interactions. As in all subsequent analyses, we then obtained the minimal adequate model through stepwise backward model simplification by deleting all model terms not significant at $P < 0.05$ (Crawley, 2002). These and all other statistical analyses were conducted in R 2.6.0 (R Development Core Team, 2007).

Field establishment

To test for the effect of vegetation structure on the establishment of *J. atratus*, we conducted a field experiment in an open grassland area in the Havel floodplain near Gülpe (52°43'40"N, 12°13'00"E) where the species occurs naturally in Potentillion anserinae grasslands. In this experiment, seedlings germinated in the greenhouse were transplanted into experimental plots (0.7 m × 0.7 m). The original vegetation of these plots belonged to the association Ranunculo-Alopecuretum R. Tx. 1937, alliance Potentillion anserinae, with 10–18 plant species per 10 m², mainly *Agrostis stolonifera*, *Alopecurus pratensis*, *Eleocharis palustris*, *Elymus repens*, *Galium elongatum*, *Glechoma hederacea*, *Phalaris arundinacea*, *Poa angustifolia*, *Poa trivialis*, *Potentilla anserina*, *Ranunculus repens*, *Rorippa sylvestris*, and *Trifolium repens*, i.e. a mixture of high- and low-growing species that is typical for these sites in the region (Burkart, 1998; Burkart et al., 2003). In this system, *Phalaris arundinacea* is the tallest grass and a strong competitor, tending to become dominant

if management is reduced (Burkart et al., 2003). In the experimental plots, however, none of the species dominated the others; initial *Phalaris* cover values were between 2% and 20%; total vegetation cover was close to 100%, and mean canopy height was approx. 0.4 m in mid-June. To simulate different types of vegetation structure found in existing *J. atratus* populations, we applied three treatments to the plots: (1) complete removal of the aboveground vegetation and ca. 5 cm of the topsoil (bare ground), (2) regular aboveground removal of *Phalaris arundinacea* (low-competition grassland), and (3) no treatment (typical grassland). Plots were arranged in 10 replicate blocks each holding one plot of each treatment. The blocks were identified 600–900 m away from an existing *J. atratus* population. They were located at exactly the same elevation as the existing population to ensure comparable soil water supply. Treatments were established after the end of the flooding period in mid-April. *P. arundinacea* was removed regularly throughout the study period.

In each plot, five seedlings were planted on 15 April and an additional seven seedlings were planted on 22 April 2005 into the central 0.12 m × 0.12 m, according to seedling availability. Seedlings were taken from all origins and planted in a regular 4 cm × 4 cm grid pattern. Of the 16 possible planting spots per plot, 12 were randomly selected and assigned to the seedling origins. The pattern was kept constant within any one block, but varied between blocks. After planting, seedlings were covered with a shallow white mat permeable for light and water to reduce solar irradiation and wind, and the soil in the plots was kept constantly moist in order to prevent seedling death due to transplantation stress. Additional watering was finished at 4 May, and the mat was removed on 6 May. Survival and development of seedlings was recorded biweekly until mowing at the end of June, 10 weeks after the first planting date (Fig. 1).

Establishment rate was then calculated as the proportion of seedlings that survived until week 10 after the first planting date. Since block identity had no significant effect on seedling survival (GLM with quasibinomial error, $F_{9,140} = 0.781$, $p = 0.63$) it was excluded from subsequent analyses. Hence, the maximal GLM (with binomial error) for the field experiment included the main effects of vegetation structure, seed origin, and planting date (15 vs. 22 April) as well as all possible interactions.

Growth chamber establishment

To examine the joint effect of vegetation structure (bare soil vs. typical grassland), flooding duration, and germination mode (germination on the ground vs. afloat) on *J. atratus* establishment, we conducted an additional establishment experiment in two growth chambers. The use of growth chambers enabled us to control the duration of flooding, which is difficult to regulate in

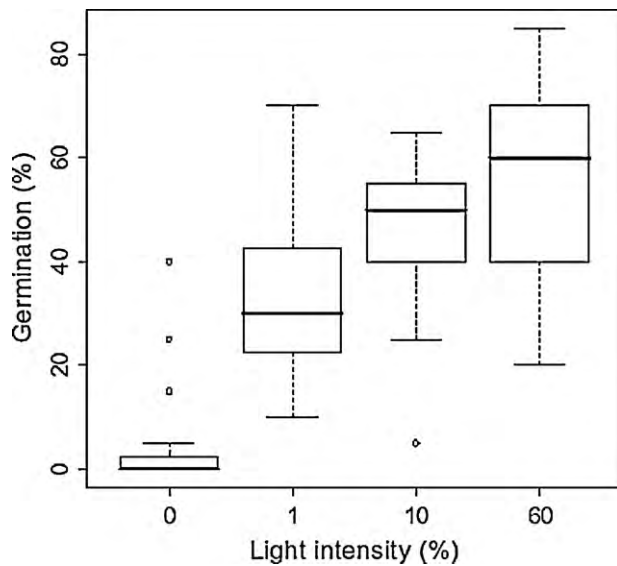


Fig. 2. Germination of *Juncus atratus* under different light intensities. The box-whisker plot shows the distribution of germination percentages per pot. Bold central lines indicate the median, boxes span the interquartile range, whiskers encompass values less than 1.5 box lengths away from the box, and points show outliers.

the field. The chambers were set to 12 h full light and a 24 °C/12 °C 12 + 12 h diurnal temperature regime. Six-month-old seeds from Pritzerbe and Vehlgest were germinated in water tanks, either afloat or on the ground. 50 seedlings per pot were transferred individually into small pots. The small pots were either filled with mineral soil from the Havel floodplain to simulate bare ground or filled with small grassland divots from the same area to simulate a flood meadow, and placed 63 cm below the lamps (PPFD 325–425 $\mu\text{mol m}^{-2} \text{s}^{-1}$ [$n=5$]). Pots were either kept constantly wet up to the soil surface in the same manner as in the germination experiment (see above), or they were inundated with 6 cm of water above soil surface for 1, 3, 10, 20, or 42 days after transplanting. Each individual combination of treatments, seed origins and germination modes was replicated five times. Seedling survival was monitored twice per week up to 56 days after transplanting.

To account for random effects of growth chamber and tray, the proportion of seedlings surviving up to 56 days was arcsin-transformed and analysed using linear mixed-effects models (Pinheiro and Bates, 2000). The maximal model for this analysis contained vegetation structure, germination mode, and seed origin as fixed factors, flooding duration as a fixed covariate as well as all two-way interactions between these variables.

Results

Germination and seedling survival

Light intensity had a positive effect on the germination of *J. atratus* (Fig. 2; $F_{1,317} = 76.826$, $p < 0.001$): the mean germination rate after 4 weeks increased from 4.5% in darkness to 53.7% at 60% light. It is, however, noteworthy that some seedlings emerged even in total darkness and that the germination rate at 1% light intensity was more than half of that at 60% light intensity. Germination rates increased continuously over the 4 weeks of the experiment ($F_{1,317} = 12.984$, $p < 0.001$). Seedlings that germinated in the first week had a high survival over the following 4 weeks, with mean survivorship ranging from 80% to 100% in all light treatments, including total darkness (Fig. 3).

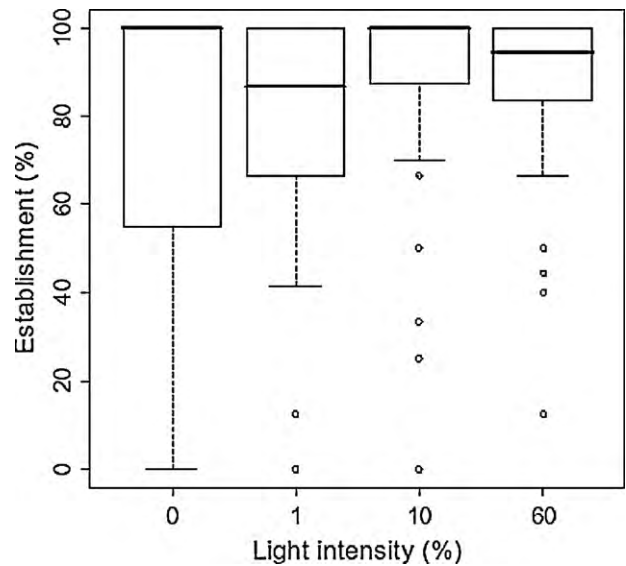


Fig. 3. Seedling survival after 4 weeks under different light intensities. The box-whisker plot shows the distribution of survivorship per pot for seedlings that germinated in the first week of the germination experiment. See Fig. 1 for interpretation of the box-whisker plots.

Field establishment

Establishment in the field experiment depended on vegetation structure (Fig. 4): of the seedlings planted on bare ground, 30% survived for 10 weeks, whereas the equivalent rate was close to zero on the typical and low-competition grassland.

Seedling mortality in the typical and low-competition plots (but not in the bare ground plots) increased after 4 weeks (Fig. 4), i.e. under ambient weather conditions after the end of additional watering and the removal of the mat (Fig. 1).

The interaction between vegetation structure and seed origin had a significant effect on field establishment ($\chi^2_4 = 11.016$, $P < 0.05$): in the low-competition treatment, seedlings from the Vehlgest population survived longer than those from Pritzerbe.

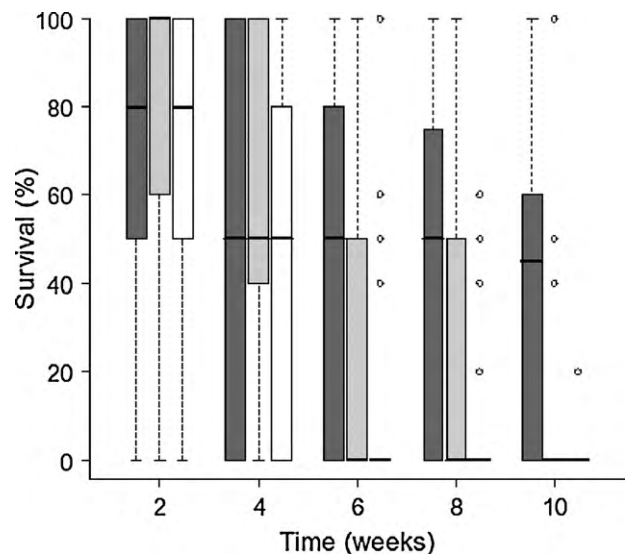


Fig. 4. Seedling survival in the field experiment as a function of vegetation structure and time after seedling transplantation. The box-whisker plot shows the distribution of survivorship per plot. Dark grey boxes represent bare ground treatments, light grey boxes show low-competition grassland treatments, white boxes represent typical grassland treatments. See Fig. 1 for interpretation of the box-whisker plots.

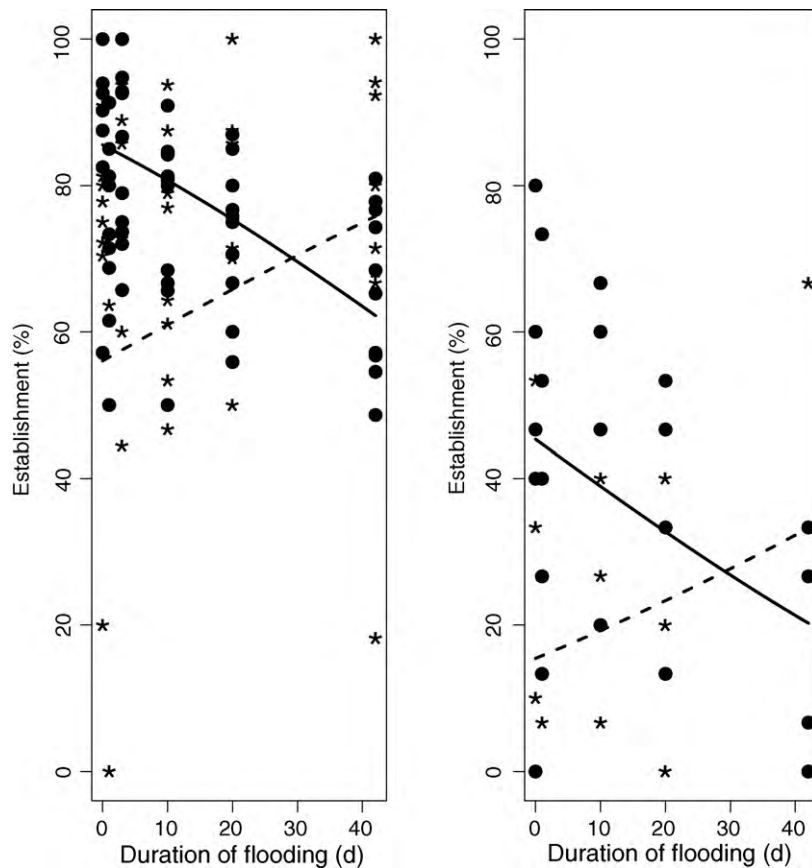


Fig. 5. Seedling establishment after 56 days in the growth chamber experiment as a function of germination mode, vegetation structure and flooding duration. Points and asterisks depict observed survival rates, and lines illustrate model predictions. The subplots show the survival of seedlings that germinated on the ground (A, left) and afloat (B, right), respectively. Point and line types indicate vegetation structure (points and lines: bare ground; asterisks and dashed lines: typical grassland).

On 6 June 2006 (i. e. more than 13 months after transplanting), four plants (two from Vehlgest and two from Pritzerbe) out of the initial 360 were still alive (1.1%). All of these survivors grew on bare ground plots, and three of them co-occurred in the same plot.

Growth chamber establishment

Establishment differed significantly between the two germination modes ($\chi^2_1 = 59.801$, $p < 0.001$): it was close to 75% for seedlings that germinated submerged on the ground (Fig. 5A), but only about 35% for seedlings that germinated afloat (Fig. 5B). Furthermore, there was a strong interaction between vegetation structure (bare ground vs. typical grassland) and flooding duration ($\chi^2_1 = 13.091$, $p < 0.001$): establishment decreased with the duration of flooding on bare ground, but increased with the duration of flooding in grassland (Fig. 5). Due to this interaction, establishment was higher on bare ground when flooding was short (0–20 days), whereas it was higher in grassland when pots were flooded for 42 days (Fig. 5).

Discussion

Germination

The results of the germination experiment show that high light intensities promote the germination of *J. atratus* (Fig. 2). However, the reduced light intensities (1–10%) likely to prevail on the soil surface in typical grasslands still result in germination rates of more than half the maximum germination rate (Fig. 2). This implies that seeds deposited in grassland vegetation can germinate at a moderate level, given that other conditions (mainly water

and temperature; Geissler and Gzik, 2008) are suitable for germination.

It therefore seems unlikely that germination has a strong limiting effect on *J. atratus* establishment in grassland vegetation in the study area if warmth and water supply are sufficient, as is often the case there in spring during and after floods (Burkart et al., 2003; Geissler and Gzik, 2008; Itzerott and Kaden, 2003). Rather, *J. atratus* seeds in grassland should germinate at moderate to high rates, similar to those on bare soil, during wet and moist periods in the warm season.

Seedling survival and establishment

Fig. 3 shows that seedlings were able to survive at high rates for several weeks under virtually all light regimes, including even total darkness, given that the soil is wet. Their mean survival rates were more than 80% after 4 weeks for all light intensity treatments. In the field experiment, however, the mean survival rates of seedlings were between 40% and 60% after the same time period (Fig. 4). The divergence between these results is a strong hint that we should look for factors other than competition for light as causes of natural mortality in the seedling stage.

During the first 4 weeks of the field experiment, seedlings survived at a rate of 40–60% in all vegetation structure treatments (Fig. 4). After exposure to ambient weather conditions on 6 May and the subsequent period of increasingly warm and dry weather until the end of May, (Fig. 1), seedling numbers dropped substantially in the two meadow treatments (low-competition and typical grassland), but decreased only moderately in the bare ground treatment (Fig. 4, transition week 4 → 6). The divergence between the

treatments suggests that seedling mortality was not directly caused by the warm and dry weather, but was rather due to the combined effects of ambient weather conditions and competition for water from the surrounding established vegetation.

An adverse competitive effect of dense vegetation on seedling establishment is a common result of recruitment studies (e. g., Doménech and Vilá, 2006; Issestein et al., 2002; Jeschke and Kiehl, 2008) and was actually a main background of the regeneration niche concept (Grubb, 1977). In most recruitment studies, however, there is no specification as to which mechanism of competition might cause the competitive effect. In our study, the combination of factors strongly suggests that the mechanism is competition for water in the seedling rhizosphere, i.e. in the uppermost soil layer. Alternative explanations for the striking increase in seedling mortality in the grassland treatments after 4 weeks seem less likely: seedling predation was virtually absent, and it is unlikely that competition for light caused substantial seedling mortality at a time when ambient solar irradiation increased from low to high levels. Furthermore, the greenhouse germination experiment shows that *J. atratus* seedlings are able to survive for several weeks at very low levels of light intensity (Fig. 3).

In a striking contrast to this negative effect of established grassland vegetation on *J. atratus* seedling survival under non-flooding conditions, grassland vegetation was more suitable for the recruitment of *J. atratus* than bare ground under prolonged flooding (Fig. 5). This correlates with the notion that *J. atratus* is strongly restricted to periodically flooded habitats in nature (Burkart, 1995; Hejný, 1960), including both grasslands and pioneer sites. A potential explanation for this is that prolonged flooding reduces the competitive strength of established grassland vegetation, thereby promoting the establishment of *J. atratus*, which – in contrast to many other grassland species – is capable of growing submerged (Burkart, 1995). Additionally, the established vegetation may even facilitate the establishment of *J. atratus* seedlings during long-lasting floods, for instance by supplying oxygen through the aerenchyma of plants that project above the water surface (Colmer, 2003; Jackson and Armstrong, 1999; Stottmeister et al., 2003). Such a facilitative mechanism may explain why establishment rates of *J. atratus* increase with flooding duration in grassland while they simultaneously decrease on bare soil (Fig. 5).

Shifts from competition to facilitation along stress gradients have been observed in many different environments (Brooker et al., 2006; Holzapfel et al., 2006; Maestre et al., 2005; Malkinson and Kadmon, 2007; Van Wesenbeeck et al., 2007; see Brooker et al., 2008, for a recent review), where facilitation commonly occurred in the more stressful parts of the gradients and competition in the more modest parts. Of course, increasing duration of flooding may be seen as a stress gradient. In our experiment, however, individual *J. atratus* target plants first experienced competition by the surrounding vegetation, which shifted to facilitation after 30 days of flooding, whereas in the stress gradients that were tested in the studies mentioned, different target plants that were placed along the gradients experienced either competition or facilitation, respectively, during the whole study period. There exist only a few other studies that demonstrated such a shift from competition to facilitation within the ontogeny of individual organisms (Holzapfel and Mahall, 1999; Kawai and Tokeshi, 2007; Kikvidze et al., 2006; Reisman-Berman, 2007; Schifffers and Tielbörger, 2006; Stultz et al., 2007).

Rarity, persistence, and conservation

Taken together, the data presented here indicate that establishment is a critical life stage in Central European populations of *J. atratus*, as in many other plant taxa (Eriksson and Ehrlén,

1992; Münzbergová and Herben, 2005). Since our results show that seeds of the rare *J. atratus* readily germinate under various light intensities, it seems unlikely that germination limits recruitment in grassland vegetation. In contrast, establishment seems to be a critical life stage for recruitment: it depends on disturbance, be it prolonged flooding or the creation of bare ground patches, both of which may occur naturally in floodplains, although nowadays the latter is more likely to occur as a consequence of human activities (Cooper et al., 2003; Leyer, 2005; Naiman et al., 1993).

These specific recruitment requirements may be a main cause of the rarity of *J. atratus* in modern Central Europe, because natural disturbances have substantially decreased both in spatial extent and frequency in contemporary river corridors due to human activities (Dynesius and Nilsson, 1994; Leyer, 2006). Anthropogenic disturbances, on the other hand, are probably too infrequent and spatially too restricted to fully counterbalance the decrease of natural disturbances in these areas. From this perspective, it is not so surprising that vigorous *J. atratus* populations have persisted in the river corridor of the lower Havel, which forms main parts of the Naturpark Westhavelland, one of the the largest semi-natural wetland areas of Central European lowland.

In order to prevent extinction of *J. atratus* in Central Europe, we suggest maintaining or re-establishing natural hydrodynamics in those parts of floodplains where the species is still present. Declining populations may additionally be supported by artificial soil disturbance in their direct vicinity. Optimal areas for the reintroduction of *J. atratus* are bare ground sites that are regularly flooded.

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References

- Ascherson, P., 1864. Flora der Provinz Brandenburg, der Altmark und des Herzogthums Magdeburg. Hirschwald, Berlin.
- Brooker, R.W., Scott, D., Palmer, S.C.F., Swaine, E., 2006. Transient facilitative effects of heather on Scots pine along a grazing disturbance gradient in Scottish moorland. *J. Ecol.* 94, 637–645.
- Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., et al. (24 authors), 2008. Facilitation in plant communities: the past, the present, and the future. *J. Ecol.* 96, 18–34.
- Buchenau, F., 1890. Monographia Juncacearum. *Bot. Jahrb. Systematik* 12, 1–495.
- Burkart, M., 1995. *Juncus atratus* in Nordostdeutschland. *Verh. Bot. Vereins Berlin Brandenburg* 128, 83–107.
- Burkart, M., 1998. Die Grünlandvegetation der unteren Havelaue in synökologischer und syntaxonomischer Sicht. In: *Arch. naturwiss. Diss.*, vol. 7. M. Galunder, Wühl.
- Burkart, M., 2001. River corridor plants (Stromtalpflanzen) in Central European lowland: a review of a poorly understood plant distribution pattern. *Global Ecol. Biogeogr.* 10, 449–468.
- Burkart, M., Prasse, R., 1996. Zur pflanzlichen Besiedlung wechsellasser Pionierstandorte im Elbhavelwinkel. *Untere Havel Naturk. Ber.* 5, 38–50.
- Burkart, M., Wattenbach, M., Wichmann, M.C., Pötsch, J., 2003. Die Vegetation der unteren Havelaue: Stand der Forschung und Perspektiven. *Brandenburg. Umwelt Berichte* 13, 53–71.
- Burke, M.W., Grime, J., 1996. An experimental study of plant community invasibility. *Ecology* 77, 776–790.
- Colmer, T., 2003. Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant Cell Environ.* 26, 17–36.

- Cooper, D., Andersen, D., Chimner, R., 2003. Multiple pathways for woody plant establishment on floodplains at local to regional scales. *J. Ecol.* 91, 182–196.
- Corral-Aguirre, J., Sanchez-Velasquez, L.R., 2006. Seed ecology and germination treatments in *Magnolia dealbata*: an endangered species. *Flora* 201, 227–232.
- Crawley, M.J. (Ed.), 1997. *Plant Ecology*, 2nd ed. Blackwell Science, Malden-Oxford-Carlton.
- Crawley, M.J., 2002. *Statistical Computing: An Introduction to Data Analysis using S-Plus*. John Wiley & Sons, Hoboken.
- Doménech, R., Vilá, M., 2006. The role of successional stage, vegetation type and soil disturbance in the invasion of the alien grass *Cortaderia selloana*. *J. Veg. Sci.* 17, 591–598.
- Donath, T., Hölzel, N., Otte, A., 2006. Influence of competition by sown grass, disturbance and litter on recruitment of rare flood-meadow species. *Biol. Conserv.* 130, 315–323.
- Dynesius, M., Nilsson, C., 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* 266, 753–762.
- Ellenberg, H., 1996. *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht*. 5th ed., Ulmer, Stuttgart.
- Eriksson, O., Ehrlén, J., 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia* 91, 360–364.
- Farnsworth, E.J., 2007. Plant life history traits of rare versus frequent plant taxa of sandplains: implications for research and management trials. *Biol. Conserv.* 136, 44–52.
- Geissler, K., Gzik, A., 2008. The impact of flooding and drought on seeds of *Cnidium dubium*, *Gratiola officinalis*, and *Juncus atratus*, three endangered perennial river corridor plants of Central European lowlands. *Aquat. Bot.* 89, 283–291.
- Grime, J., 1974. Vegetation classification by reference to strategies. *Nature* 250, 26–31.
- Grubb, P., 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev. Cambridge Philos. Soc.* 52, 107–145.
- Harper, J.L., 1977. *Population Biology of Plants*. Academic Press, London.
- Hejný, S., 1960. *Ökologische Charakteristik der Wasser- und Sumpfpflanzen in den slowakischen Tiefebene (Donau- und Theissgebiet)*. Verlag slowak. Akad. Wissensch., Bratislava.
- Holmgren, M., Poorter, L., 2007. Does a ruderal strategy dominate the endemic flora of the West African forests? *J. Biogeogr.* 34, 1100–1111.
- Holzappel, C., Mahall, B.E., 1999. Bi-directional facilitation and interference between shrubs and associated annuals in the Mojave desert. *Ecology* 80, 1747–1761.
- Holzappel, C., Tielbörger, K., Parag, H.A., Kigel, J., Sternberg, M., 2006. Annual plant–shrub interactions along an aridity gradient. *Basic Appl. Ecol.* 7, 268–279.
- Hölzel, N., 2005. Seedling recruitment in flood-meadow species: the effects of gaps, litter and vegetation matrix. *Appl. Veg. Sci.* 8, 115–124.
- Hölzel, N., Otte, A., 2004. Ecological significance of seed germination characteristics in flood-meadow species. *Flora* 199, 12–24.
- Hultén, E., Fries, M., 1986. *Atlas of North European Vascular Plants*. Koeltz, Königstein.
- Isselstein, J., Tallowin, J.B., Smith, R.N., 2002. Factors affecting seed germination and seedling establishment of fen-meadow species. *Restor. Ecol.* 10, 173–184.
- Itzerott, S., Kaden, K., 2003. Die hydrologischen Verhältnisse in der Unteren Havelniederung. Brandenburg. *Umwelt Berichte* 13, 27–52.
- Jackson, M.B., Armstrong, W., 1999. Formation of aerenchyma and the processes of plant ventilation in relation to soil flooding and submergence. *Plant Biol.* 1, 274–287.
- Jeschke, M., Kiehl, K., 2008. Effects of a dense moss layer on germination and establishment of vascular plants in newly created calcareous grasslands. *Flora* 203, 557–566.
- Kawai, T., Tokeshi, M., 2007. Testing the facilitation-competition paradigm under the stress-gradient hypothesis: decoupling multiple stress factors. *Proc. Roy. Soc. B: Biol. Sci.* 274, 2503–2508.
- Kikvidze, Z., Khetsuriani, L., Kikodze, D., Callaway, R.M., 2006. Seasonal shifts in competition and facilitation in subalpine plant communities of the central Caucasus. *J. Veg. Sci.* 17, 77–82.
- Kirkpatrick, J.B., Gilfedder, L., 1998. Conserving weedy natives: two Tasmanian endangered herbs in the Brassicaceae. *Aust. J. Ecol.* 23, 466–473.
- Kirschner, J., 2002. *Juncaceae 2: Juncus subg. Juncus*. *Species Plantarum: Flora of the World Part 7*. Australian Biological Resources Study, Canberra.
- Körner, K., Jeltsch, F., 2008. Detecting general plant functional type responses in fragmented landscapes using spatially-explicit simulations. *Ecol. Model.* 210, 287–300.
- Leyer, I., 2005. Predicting plant species' responses to river regulation: the role of water level fluctuations. *J. Appl. Ecol.* 42, 239–250.
- Leyer, I., 2006. Dispersal, diversity and distribution patterns in pioneer vegetation: the role of river floodplain connectivity. *J. Veg. Sci.* 17, 407–416.
- Maestre, F.T., Valladares, F., Reynolds, J.F., 2005. Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *J. Ecol.* 93, 748–757.
- Malkinson, D., Kadmon, R., 2007. Vegetation dynamics along a disturbance gradient: spatial and temporal perspectives. *J. Arid Environ.* 69, 127–143.
- Marshall, E.J.R., Moonen, A.C., 2002. Field margins in northern Europe: their functions and interactions with agriculture. *Agricult. Ecosyst. Environ.* 89, 5–21.
- McCullagh, P., Nelder, J.A., 1989. *Generalized Linear Models*. Chapman & Hall, London.
- Meusel, H., Jäger, E., Weinert, E., 1965. *Vergleichende Chorologie der zentral-europäischen Flora*. Bd. 1. G. Fischer, Jena.
- Michalski, S., Durka, W., 2007a. High selfing and high inbreeding depression in peripheral populations of *Juncus atratus*. *Mol. Ecol.* 16, 4715–4727.
- Michalski, S., Durka, W., 2007b. Synchronous pulsed flowering: analysis of the flowering phenology in *Juncus* (Juncaceae). *Ann. Bot.* 100, 1271–1285.
- Moles, A.T., Westoby, M., 2002. Seed addition experiments are more likely to increase recruitment in larger-seeded species. *Oikos* 99, 241–248.
- Münzbergová, Z., Herben, T., 2005. Seed, dispersal, microsite, habitat and recruitment limitation: identification of terms and concepts in studies of limitations. *Oecologia* 145, 1–8.
- Naiman, R.J., Decamps, H., Pollock, M., 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecol. Appl.* 3, 209–212.
- Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* 15, 278–285.
- Pinheiro, J.C., Bates, D.M., 2000. *Mixed-effects Models in S and S-plus*. Springer, New York.
- Plöttner, T., 1898. Verzeichnis von Fundorten seltener und weniger verbreiteter Gefäßpflanzen der Umgegend von Rathenow. *Verh. Bot. Vereins Prov. Brandenburg* 40, XL–XIV.
- R Development Core Team, 2007. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Reisman-Berman, O., 2007. Age-related change in canopy traits shifts conspecific facilitation to interference in a semi-arid shrubland. *Ecography* 30, 459–470.
- Roschewitz, I., Gabriel, D., Tschamtker, T., Thies, C., 2005. The effects of landscape complexity on arable weed species diversity in organic and conventional farming. *J. Appl. Ecol.* 42, 873–882.
- Schiffers, K., Tielbörger, K., 2006. Ontogenetic shifts in interactions among annual plants. *J. Ecol.* 94, 336–341.
- Smith, M., Caswell, H., Mettler-Cherry, P., 2005. Stochastic flood and precipitation regimes and the population dynamics of a threatened floodplain plant. *Ecol. Appl.* 15, 1036–1052.
- Snogerup, S., 1978. A revision of the *Juncus atratus* group. *Bot. Not.* 131, 189–196.
- Stultz, C.M., Gehring, C.A., Whitham, T.G., 2007. Shifts from competition to facilitation between a foundation tree and a pioneer shrub across spatial and temporal scales in a semiarid woodland. *New Phytol.* 173, 135–145.
- Stottmeister, U., Wiessner, A., Kusch, P., Kappelmeyer, U., Kästner, M., Bederski, O., Müller, R., Moormann, H., 2003. Effects of plants and microorganisms in constructed wetlands for wastewater treatment. *Biotechnol. Adv.* 22, 93–117.
- Taubert, P., 1889. Beitrag zur Flora der Neumark und des Oderthales. *Verh. Bot. Ver. Prov. Brandenburg* 30, 310–321.
- Turnbull, L., Crawley, M., Rees, M., 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88, 225–238.
- Van Wesenbeeck, B.K., Crain, C.M., Altieri, A.H., Bertness, M.D., 2007. Distinct habitat types arise along a continuous hydrodynamic stress gradient due to interplay of competition and facilitation. *Marine Ecol. Progr. Ser.* 349, 63–71.
- Vogt, K., Rasran, L., Jensen, K., 2004. Water-borne seed transport and seed deposition during flooding in a small river-valley in Northern Germany. *Flora* 199, 377–388.
- Yates, C.J., Ladd, P., 2005. Relative importance of reproductive biology and establishment ecology for persistence of a rare shrub in a fragmented landscape. *Conserv. Biol.* 19, 239–249.