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The importance of disturbance for the conservation of a low-competitive herb in mesotrophic grasslands

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Abstract: For the protection or re-establishment of species-rich grasslands, the limiting factors controlling species richness have increasingly become of scientific interest. This study aims to analyze the role of disturbance for the occurrence of a low-competitive herb, Centaurium erythraea Rafn, in mesotrophic, lowland grasslands in NW Germany. We sampled a total of 38 plots with presence of C. erythraea and 24 control (random) plots in semi-natural grasslands. As a proxy for disturbance, we estimated the cover of bare ground and Ellenberg flooding indicator species and measured the distance between the plot and the nearest path. Moreover, we counted the number of C. erythraea individuals within each plot. In the GLM analyses the distance from path was the only predictor; both the presence of the species and the number of individuals decreased with the distance from path. The grasslands at the path edges had the highest disturbance intensity. Here horse riding, military-vehicle traffic and regular sod-cutting directly create bare ground. In general, disturbance creating bare ground seems to be the key factor enabling germination and growth of C. erythraea in mesotrophic grasslands and other low-competitive short-lived species. Disturbance enhances the expression of the seed bank, favours the development of the shade-avoiding and low-growing rosettes and oppresses tall-growing competitors. Therefore we suggest grazing as the best management method.

Key words: bare ground; conservation management; grazing; light germination; species-rich grassland; vegetation gap

Introduction

Land-use changes are assumed to be the major driver of global biodiversity loss (Chapin et al. 2000; Sala et al. 2000). As a man-made habitat, biodiversity of grasslands in Central Europe strongly depends on land-use intensity. In particular semi-natural grasslands harbour high numbers of plant and animal species and, thus, are of high nature conservation value (Veen et al. 2009). However, due to agricultural intensification since the 1950s, species-rich grasslands especially in the lowlands have strongly declined (van Dijk 1991; Critchley et al. 2003; Cousins & Eriksson 2008; Cousins 2009; Walker et al. 2009). Not only the direct influence of agricultural intensification but also the increasing isolation of the last semi-natural grasslands is leading to a further decline in biodiversity nowadays (Eriksson et al. 2002).

For the protection or re-establishment of speciesrich grasslands, the limiting factors controlling species richness have increasingly become of scientific interest. Seed, dispersal, microsite, habitat and recruitment limitation are seen as the driving forces controlling the establishment of species (Münzbergová & Herben 2005). With regard to grassland communities most studies fo-

According to the limitation-by-microsite hypothesis, it is conceivable that disturbance plays a more important role in the establishment of annuals and shortlived perennials that completely depend on sexual reproduction than of long-lived perennials that have the possibility to regenerate asexually to a larger degree (cf. McIntyre et al. 1995; Lavorel et al. 1997). However, colonization ability does not only depend on species traits. Besides the biology of the species, which comprises the competitive power, life form, seed production and longevity of the seed bank, site conditions play an important role. Following a productivity gradient, on extremely nutrient-poor sites species richness is limited by seed production and the intensity of abiotic stress (Tilman 1997; Zobel et al. 2000), whereas on more nutrient-rich sites with higher inter- and intraspecific competition, species richness is more strongly promoted by disturbance and the availability of gaps (Davies et al. 1999; Isselstein et al. 2002). Especially low-competitive herbs with light-germinating seeds benefit from disturbance (McIntyre et al. 1995; Grime et al. 2007).



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cus on the question whether species richness is seed-, dispersal- or microsite-limited (e.g. Hölzel 2005; Hellström et al. 2009).

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This study aims to analyze the role of disturbance and vegetation gaps for the occurrence of a low-competitive herb, Centaurium erythraea Rafn, in mesotrophic, lowland grasslands in Northwest Germany. C. erythraea is a short-lived species that reproduces entirely by seed (Grime et al. 2007) and is threatened in the North German lowland (Garve 2004; Voigtländer & Henker 2005; Ristow et al. 2006; Mierwald & Romahn 2006, LANUV 2012). Although C. erythraea can serve as an indicator for species-rich grasslands (Fleischer et al. 2010), our knowledge concerning the key factors determining the occurrence of the species is still poor. Van Rossum (2009a) showed for peri-urban forests in Belgium that population density was highest in early stages of forest succession. Moreover, connectivity between habitat patches was found to be important to allow pollen and, thus, gene flow (Van Rossum 2009b). Fleischer et al. (2010) analyzed the preferred soil conditions of C. erythraea in mesotrophic grasslands by means of Ellenberg indicator values. Based on their field observations they assume that disturbance plays an important role for the establishment of C. erythraea in these grasslands. However, hard data that could verify this assumption are missing so far.

Accordingly, we analyzed the distribution of the species in mesotrophic grasslands in relation to disturbance. As a proxy for disturbance we used the distance from path, the cover of Ellenberg flooding indicator species and the cover of bare ground. Specifically we addressed the following questions: (i) What role does disturbance play for the occurrence and reproduction of *C. erythraea*? (ii) How should grasslands be managed to promote *C. erythraea* and other threatened species?

Material and methods

Study species

Centaurium erythraea Rafn (Gentianaceae) is a winterannual or biennial, semi-rosette herb (Rosenbauer 1996; Grime et al. 2007). Seeds germinate in autumn or spring. Biennial plants overwinter as a small rosette. Flowering occurs from July to October (Rosenbauer 1996; Grime et al. 2007) and C. erythraea reproduces entirely by minute seeds that have no particular dispersal mechanism (Grime et al. 2007). Pollen is mostly transferred by self-pollination but also by insects (Ubsdell 1979; Rosenbauer 1996). Seeds can form a persistent seed bank in the soil (Brown & Oosterhuis 1981; Dutoit & Alard 1995; Davies & Waite 1998; Reiné et al. 2006). Centaurium erythraea colonizes a range of open unproductive habitats, particularly on calcareous soils (Grime et al. 2007). Characteristic habitats in Central Europe are calcareous grasslands, wastelands, clear-felled areas (Rosenbauer 1996) and forest edges (Van Rossum 2009a). Moreover, the species occurs in mesotrophic and inundation grassland (Fleischer et al. 2010). Centaurium erythraea is distributed from western and southern Europe to southern Scandinavia and to south-west Asia (Rosenbauer 1996).

Study area

The study was carried out on the military training area *Handorf Ost*, located in NW Germany 10 km north-east of

the city center of Münster (federal state of North Rhine-Westphalia; $51^{\circ}59'45''$ N, $07^{\circ}44'00''$ E). The study area of about 320 ha is a plain (~ 55 m a.s.l) dominated by silty sands (Fleischer et al. 2010). The climate is suboceanic with humid winters and moderate warm summers (mean annual temperature 9.2 °C, annual precipitation about 760 mm; Deutscher Wetterdienst pers. comm). Since World War II most of the study area has been used as pasture, and in the 1980s fertilization has been prohibited. Since then, the majority of the grasslands have regularly been grazed by sheep and some have been mown. Today, the grasslands are mostly managed by sheep paddock grazing (March to November); in the remaining parts low-intensity management takes place (short-term paddock grazing, mowing once a year, biennial mulching) or they are unmanaged (Standortverwaltung Münster 2005).

Due to differences in land use and soil moisture, the study area is characterized by a patchwork of different nutrient-poor and mesotrophic habitat types such as semi-dry, fresh and wet grassland (Fleischer et al. 2010). The grasslands are unfenced and are crossed by a net of gravel and some asphalt paths. The predominant grassland types are mesic pastures belonging to the *Lolio-Cynosuretum* Tx. 1937 where *C. erythraea* mainly occurs (Fleischer et al. 2010). The habitats of *C. erythraea* can be classified as fresh to moderately humid with water level fluctuations, moderately nutrient-rich and moderately acidic (Fleischer et al. 2010).

Experimental design

To represent the full range of environmental conditions under which C. erythraea occurs, we randomly selected 38 plots within the distribution area of the study species (presence plots) as well as 24 random plots with absence of C. erythraea (control plots). All presence plots belonged to the mesic grasslands of the Lolio-Cynosuretum or the inundation grasslands of the Potentillion anserinae Tx. 1947 (Fleischer et al. 2010). We sampled vegetation on 3×3 m plots in July and August 2008 and recorded the cover-abundance data of all higher plants according to the method of Braun-Blanquet (Dierschke 1994) using the modified Wilmanns scale (Wilmanns 1998).

As a proxy for disturbance, we estimated the cover of bare ground and measured the distance between the plot and the nearest path by use of a geographic information system (ArcGiS 10.0). Moreover, we counted the number of C. erythraea individuals on 1×1 m with the highest abundance of the species within each plot.

Data analysis

We calculated the cover-abundance of plants defined as flooding indicators by Ellenberg et al. (2001) by transforming the cover-abundance-scale data to mean cover percentages (cf. Dierschke 1994) and summing up the values for each plot.

Significant differences between presence and control plots were detected using the Mann-Whitney U Test in SPSS 16.0. For detection of ecological gradients that distinguish the presence and control plots we performed a Detrended Correspondence Analysis (DCA) by using the distance from the nearest path, the summed abundances of flooding indicator plants and the percentage of bare ground as environmental data. Species abundance data were square-root transformed, and rare species were down-weighted. The detrending was conducted by the use of segments. We carried out the analysis with Canoco 4.5.

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We applied two generalized linear models (GLM) to ascertain the relationship between environmental variables and the presence of C. erythraea (quasi-binomial error-structure) and the number of C. erythraea individuals (quasi-Poisson error-structure) on 1 m², respectively. In all models we used all environmental data. We excluded non-significant predictors (P>0.05) from the final model by stepwise-backward selection using likelihood-ratio tests. The models were calculated with R 2.12.2 (R Development Core Team 2010).

Results

The number of C. erythraea individuals ranged from 1 to 90 with a mean of 11.7 (\pm 18.3 SE) at the presence plots. Centaurium erythraea occurred in close proximity to paths (Fig. 1a); in 13 of the 38 presence plots directly at path edges. Distance from paths was significantly lower for presence plots than for control plots (Fig. 1a). Cover of flooding indicators was significantly higher at presence than at control plots (Fig. 1b). The cover of bare ground was also higher at presense plots, however, the difference was slightly not significant (Fig. 1c).

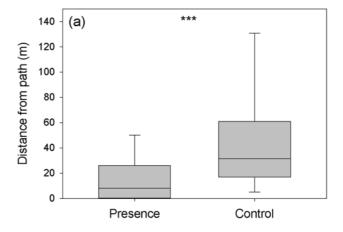
Species composition of the plots was evaluated by means of DCA (length of gradient of the first axis: 2.70 SD). The first axis mainly represented a disturbance gradient (Fig. 2, Table 1). Hence, the presence plots were positively correlated with bare ground and the cover of flooding indicator species, while the correlation with the distance from path was negative.

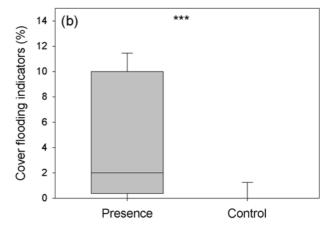
The only factor explaining the presence and the number of *C. erythraea* individuals in the GLM analyses was the distance from path (Table 2). Both presence of the species and the number of individuals were negatively correlated with the distance to path.

Discussion

Based on the results of this study disturbance creating patches with bare ground has been identified as an important factor determining the occurrence and abundance of *C. erythraea* in mesotrophic grasslands. In the GLM analyses the distance from path was the only predictor; both the presence of the species and the number of individuals decreased with the distance from path.

The grasslands at the path edges had the highest disturbance intensity. Here horse riding, military-vehicle traffic and regular sod-cutting directly create bare ground (own. obs.) and here *C. erythraea* predominantly occurs. Van Rossum (2009a) also observed along a successional gradient in forests that the species depends on early successional stages with patches of bare ground in the herbaceous vegetation. Flooding is another disturbance type that can also produce microsites with bare ground (Van Uytvanck et al. 2010). Consequently, presence plots had a significantly higher cover of flooding indicators than control plots. The flood swards of the study area are not restricted to path edges and are mostly inundated in late winter and dry up in spring (Fleischer et al. 2010). Due to the long inunda-





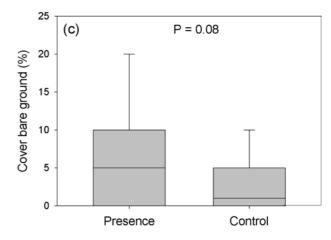


Fig. 1. Box-plots of (a) distance from path, (b) cover of flooding indicators and (c) cover of bare ground at presence and control plots of Centaurium erythraea. Box-plots show 10th and 90th percentile (whiskers), 25th and 75th percentile (boundary of box) and median (line). Comparison of the two groups by Mann-Whitney U test. *** $P \leq 0.001$. For further explanations, see the section "Material and Methods".

tion period parts of the original vegetation die off and bare ground occurs. In addition, inundation, especially on the sandy soils of the study area, might be beneficial for the species for another reason. *C. erythraea* has a late-summer flowering period and, thus, depends on sufficient moisture to complete the life cycle (Grime et al. 2007).

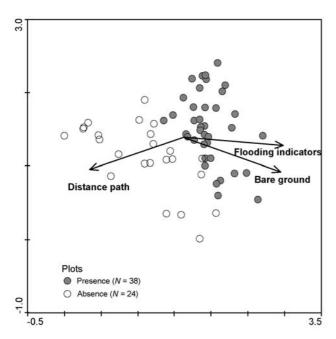


Fig. 2. DCA ordination of the *Centaurium erythraea* plots with all environmental data.

Table 1. Output values of the DCA: Eigenvalues of the first two axes, correlation coefficients of the environmental parameters with these axes. Proportion of variance explained by means of the environmental parameters = 8%.

| Axis | 1 | 2 | |
|---------------------------------------------------------------|----------------------------|------------------------------|--|
| Eigenvalue Bare ground Distance from path Flooding indicators | 0.31 0.27 -0.25 0.28 | 0.22 -0.11 -0.09 -0.03 | |

In this study we found indirect, but no direct evidence for the dependence on bare soil of *C. erythraea* in mesotrophic grasslands. The lack of difference between the cover of bare soil in presence and control plots is very likely to be explained by the sampling period. Conditions in summer, when vegetation was recorded, did not reflect the vegetation structure during the time of germination. The moderate nutrient-rich soil conditions in the study area (Fleischer et al. 2010) lead to a rapid

closure of vegetation gaps during the growing season (cf. Davies et al. 1999; Isselstein et al. 2002).

In general, disturbance creating bare ground seems to be the key factor enabling germination and growth of *C. erythraea* in mesotrophic grasslands (cf. Bullock et al. 1994; Grime et al. 2007; Van Rossum 2009a) and other low-competitive short-lived species (McIntyre et al. 1995). Disturbance enhances the expression of the seed bank, favours the development of the shadeavoiding and low-growing rosettes and oppresses tallgrowing competitors (cf. Grime et al. 2007).

Implications for conservation

Due to large-scale eutrophication throughout Europe, conservation should mainly focus on the maintenace of unfertilized oligo- and mesotrophic grasslands (cf. Bobbink et al. 1998; Chytrý et al. 2009). Within grasslands in the North-West German lowland C. eruthraea can serve as a target species as it is associated with speciesrich stands, threatened and represents the dominating grassland life forms (hemicryptophypte, therophyte) (Fleischer et al. 2010). To enhance the establishment of light-germinating and low-growing species adapted to nutrient-poor conditions the removal of biomass and litter and hence management or disturbance is necessary (Bakker 1989; Rosenthal 2010). Occurrence of C. erythraea in grasslands depends on management without use of fertilizers. Grazing seems to be a more suitable management strategy than moving as gaps are created by the former (McIntyre et al. 1995; Trimble & Mendel 1995; Bullock et al. 2001). The creation of gaps within the sward is necessary for the expression of the soil seed bank (Grime et al. 2007; Van Rossum 2009a) and to favor germination of wind-dispersed species (McIntyre et al. 1995). However, Grime et al. (2007) postulates that the hemi-rosette plant C. erythraea avoids pastures due to the vulnerability of its erect flowering stems to grazing. Although the plant stem is within the grazing zone, grazing animals should avoid C. erythraea as it has a high content of bitterns (3%) (Düll & Kutzelnigg 2005). The frequent occurrence of *C. erythraea* in the sheep pastures of our study area and own observations from low-intensity horse and cattle pastures corroborate this assumption. The irregular and very intensive disturbance by the small-scale sod-cutting as practised at the path edges is another way that seems to be very ben-

Table 2. Statistics of Generalized Linear Models (GLM). The cover of bare ground, the distance to a path and the cover of flooding indicator species were included in the models as predictor variables. Non-significant predictors (P > 0.05) were excluded from the final models by likelihood-ratio tests and stepwise backward selection.

| | Family | Estimate | SE | t value | P | Pseudo \mathbb{R}^2 |
|--------------------------------------------|----------------|----------|---------|---------|-----|-----------------------|
| Presence $(N = 38)$ vs. Control $(N = 24)$ | quasi-binomial | | | | | 0.16 |
| Intercept | | 1.46942 | 0.43542 | 3.375 | | |
| Distance from path (m) | | -0.0367 | 0.01281 | -2.865 | *** | |
| Number of individuals $(N = 35^{\dagger})$ | quasi-Poisson | | | | | 0.21 |
| Intercept | | 2.30704 | 0.18617 | 12.392 | | |
| Distance from path (m) | | -0.02699 | 0.01082 | -2.494 | ** | |

 $[\]dagger$ 3 outliers deleted (number of individuals = 50, 59, 90)

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eficial for the establishment of *C. erythraea* and other threatened low-competitive species like the annual *Centaurium pulchellum* (own obs.).

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