GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 10 (2009) 61–69
Basic and Applied Ecology
www.elsevier.de/baae

Negative effects of habitat degradation and fragmentation on the declining grassland plant *Trifolium montanum*

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Received 24 April 2007; accepted 1 December 2007

Abstract

Changes in land use have resulted in a strong decline in the plant diversity of nutrient-poor grasslands, but little is known about the combined effects of habitat degradation and fragmentation on populations of individual species. We studied these effects on stage structure, recruitment, reproduction and offspring fitness in populations of the declining perennial grassland plant *Trifolium montanum* in central Germany. Density and survival probability of juvenile plants decreased with light competition, measured as leaf area index (LAI) above *T. montanum* plants, resulting in aged populations with few juvenile plants at unmanaged sites with higher LAI. Reproduction of *T. montanum* was not related to LAI, but increased strongly with local density, suggesting pollinator limitation in fragmented populations with a low density of flowering plants. In the common garden, the survival of sown offspring increased with mean seed size, whereas seed production of offspring decreased with isolation, and in strong contrast to previous studies, also decreased with size and density of the population of origin. This could be due to increased inbreeding because of pollination between closely related neighbouring plants in dense and large populations. Our results indicate that both habitat degradation and fragmentation have negative effects on populations of *T. montanum*, but affect different phases of the life cycle. In the short term, the effects of habitat degradation are more important than those of fragmentation, and populations of *T. montanum* are primarily threatened by an increase in light competition in unmanaged sites, which rapidly affects the dynamics of the populations. The observed opposite effects of habitat fragmentation on reproduction and offspring fitness indicate that the effects of population size, density and isolation on plant fitness and population viability may be complex.

Zusammenfassung

Eine veränderte Landnutzung hat während der letzten Jahrzehnte zu einem starken Rückgang der Pflanzenvielfalt des Grünlandes geführt. Über die Auswirkungen von verminderter Qualität und zunehmender Fragmentierung der Habitate für die Populationen selten gewordener Pflanzenarten ist allerdings wenig bekannt. Wir untersuchten Stadienstruktur, Rekrutierung, Reproduktion und Fitness der Nachkommen in verschiedenen Populationen der seltenen ausdauernden Kleeart *Trifolium montanum* in Kalkmagerrasen in Nordhessen und Südniedersachsen. Die Dichte und Überlebenswahrscheinlichkeit von jungen Pflanzen nahm mit zunehmender Lichtkonkurrenz, gemessen als Blattflächenindex (LAI) oberhalb von *T. montanum*, ab. Dies führte zur Bildung von überalterten Populationen mit sehr wenigen Jungpflanzen an Orten ohne regelmäßige Nutzung. Reproduktion im Gelände war unabhängig vom LAI,

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doi:10.1016/j.baae.2007.12.002

nahm aber mit der lokalen Dichte blühender Pflanzen zu, wahrscheinlich bedingt durch eine verringerte Bestäubung in Populationen geringer Blühdichte. In einem Anzuchtexperiment im Botanischen Garten nahm die Überlebenswahrscheinlichkeit der angesäten Pflanzen mit der mittleren Masse der Samen zu, während die Samenproduktion der Nachkommen mit der Isolation und im Gegensatz zu früheren Studien auch mit der Größe und Dichte der Ursprungspopulation abnahm. Dies war wahrscheinlich die Folge von Inzuchteffekten aufgrund häufigerer Bestäubung zwischen benachbarten und nahe verwandten Individuen in großen und dichten Populationen von *T. montanum*. Unsere Ergebnisse zeigen, dass die Verminderung der Habitatqualität und die Fragmentierung negative Auswirkungen auf die Populationen von *T. montanum* haben können, aber unterschiedliche Phasen des Lebenszyklus betreffen. Kurzfristig sind die Effekte der verminderten Habitatqualität wichtiger als die der Fragmentierung, und Populationen von *T. montanum* sind vor allem durch die erhöhte Lichtkonkurrenz an Orten ohne Management gefährdet, die unmittelbar die Populationsdynamik beeinflusst. Allerdings zeigen die beobachteten gegensätzlichen Effekte der Habitatfragmentierung auf Reproduktion und Fitness der Nachkommen, dass die Effekte von Größe, Dichte und Isolation der Populationen auf die Fitness von Pflanzen und das Überleben von Populationen sehr komplex sein können.

Keywords: Light competition; Local density; Management; Offspring fitness; Perennial plant; Population isolation; Population size; Recruitment; Reproduction; Stage structure

Introduction

Many formerly common plants of nutrient-poor grasslands have strongly declined in central Europe in recent decades (Korneck, Schnittler, & Vollmer 1996). The main driving force for their decline is a change in land use and subsequent habitat loss and degradation (Hodgson, Grime, Wilson, Thompson, & Band 2005; Poschlod, Bakker, & Kahmen 2005). In the remnant grasslands, cessation of traditional management like grazing or mowing has resulted in changes in the composition of the vegetation (Poschlod et al. 2005). While populations of short-lived species become quickly extinct when habitat quality decreases (Fischer & Stöcklin 1997; Matthies, Brauer, Maibom, & Tscharntke 2004), established perennial plants can survive for a long time (Ehrlén & Lehtilä 2002). However, reduced recruitment of long-lived plants in degraded habitats, often caused by increased light competition (Lepš 1999), may result in the formation of aged populations with few juvenile plants, which are doomed to become extinct in the long term (Colling, Matthies, & Reckinger 2002; Oostermeijer, van't Veer, & Den Nijs 1994).

The negative effects of habitat degradation may be exacerbated by the effects of habitat fragmentation that result in increased isolation and reduced size and density of plant populations (Lienert & Fischer 2003). Because of their greater sensitivity to environmental and demographic stochasticity, small populations face an increased risk of extinction (Matthies et al. 2004). Moreover, small and isolated populations may suffer from genetic erosion (Young, Boyle, & Brown 1996), and reduced genetic diversity has been found to reduce offspring fitness (Leimu, Mutikainen, Koricheva, & Fischer 2006) and population viability (Frankham 2005). However, plant fitness and population viability are not always affected by a reduction of genetic diversity, in particular during early phases of the genetic erosion process (Ouborg & van Treuren 1995). In addition, small and low-density populations may be less attractive to pollinators and experience pollinator limitation (Kunin 1997).

Fragmentation of nutrient-poor grasslands has strongly reduced the probability of colonization of new sites, and today the regional survival of long-lived grassland plants mainly depends on the survival of the remaining populations (Herben et al. 2006; Soons, Messelink, Jongejans, & Heil 2005). However, few studies have investigated different demographic processes in a large number of remnant populations to unravel the effects of habitat degradation and fragmentation on the declining long-lived grassland species (but see Vergeer, Rengelink, Copal, & Ouborg 2003). We studied habitat conditions and stage structure of 23 populations of the declining perennial grassland plant *Trifolium montanum* L. in central Germany and analysed establishment, seedling survival and reproduction in the field in a subset of these populations, and offspring performance in a common garden experiment. We addressed the following questions: (1) Do habitat quality and fragmentation affect population structure, establishment and seedling survival of *T. montanum*? (2) Are reproduction in the field populations and the performance of offspring in the common garden affected by habitat quality and fragmentation of *T. montanum* populations?

Materials and methods

Study species

Trifolium montanum is a long-lived herbaceous perennial of calcareous grasslands, which has strongly