available at www.sciencedirect.com
ScienceDirect
journal homepage: www.elsevier.com/locate/actoec

Original article

Effect of slug grazing on biomass production of a plant community during a short-term biodiversity experiment

Vojtěch Lanta[a,b,*]

[a]Institute of Botany, Academy of Sciences of the Czech Republic, Section of Plant Ecology, Dukelská 135, 379 82 Třeboň, Czech Republic
[b]Department of Botany, Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic

ARTICLE INFO

Article history:
Received 10 October 2005
Accepted 26 March 2007
Published online 7 May 2007

Keywords:
Biodiversity effects
Herbivore preference
Slugs
Species richness

ABSTRACT

While recent theoretical work has demonstrated several mechanisms whereby more diverse communities can exhibit greater resistance against herbivore pressure, empirical examinations have been few and the subject of much debate. The aim of this microcosm experiment was to determine how selectivity of grazing by herbivores affected relationships between plant species number and productivity within artificially created grassland communities. The influence of the slug, *Arion lusitanicus*, was assessed at four levels of plant species diversity (one, two, four and six species per aquarium). The proportion of biomass of particular species eaten by a slug was estimated on the basis of comparison of paired plots. The biomass in control (ungrazed) plots was compared with the biomass in grazed plots. A significant interaction between the number of plant species and slug grazing for aboveground biomass was found, indicating a gradual decrease in the effect of grazing pressure with increased species richness. Positive average values of the complementarity effect and overyielding index, and negative values of the selection effect, indicated niche resource partitioning between species in grazed plots. The electivity index of food selectivity suggested that food selectivity was more pronounced under higher plant species diversity.

1. Introduction

Recently, many studies have investigated biodiversity effects on ecosystem function. Some researchers give emphasis to species richness, and its relationship to ecosystem function (Hector et al., 1999; Tilman et al., 2001). Others have tested a functional group of organisms, individual types or traits (see Díaz and Cabido, 2001; Hooper et al., 2002; Díaz et al., 2003; Hooper et al., 2005). The observed response of ecosystem processes to species or functional group diversity can be generated by a combination of different effects (Tilman et al., 2002; Loreau, 1998, 2000; Loreau and Hector, 2001). Sampling effects appear when the probability of containing species in a community that are able to perform an ecosystem function increases with the number of species in the community. This effect is often observed during short-term experiments (Tilman et al., 2002). Another effect, complementarity, is manifested mainly in long-term biodiversity experiments, and occurs through niche differentiation by individual species (Loreau, 1998).

* Department of Botany, Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic. Fax: +420 385 310 366.
E-mail address: lanta@butbn.cas.cz
1146-609X/$ – see front matter © 2007 Elsevier Masson SAS. All rights reserved.
doi:10.1016/j.actao.2007.03.013

A consequence of increasing human impact on ecosystem function includes species invasions. In Central Europe, the invasive slug *Arion lusitanicus*, has gradually expanded in semi-natural meadows, where its grazing may influence the competitive ability of coexisting plant species (Grimm, 2001; Buschmann et al., 2005). Slugs and snails represent an important selection pressure (Harper, 1977) which may lead to the evolution of resistance to herbivory.

Studies that have examined the grazing effects of individual slug species have demonstrated that mollusc herbivory is important in grassland ecosystems (e.g., Pallant, 1972; Hanley et al., 1995; Grimm, 2001; Scheidel and Bruelheide, 2001). Others have focused on the grazing impacts of more than one slug species (e.g., Cates and Orians, 1975; Rees and Brown, 1992), showing that early successional perennials were more palatable than later successional plants. However, few studies have focused on the role of the herbivores in relation to vegetation diversity (Huntly, 1991; Oliveira Silva, 1992), taking into account the resistance of plant communities to mollusc herbivory (Grime, 2001; Scheidel and Bruelheide, 2005). Herbivores may remove a sizeable proportion of plant biomass and thus alter both the resource requirements of damaged plants and the availability of resources to other plant species, either of which could influence the outcome of competitive interactions (Howe and Westley, 1988; Olff and Ritchie, 1998). In other words, defoliation caused by herbivores may have the potential to mediate exploitative competition. Indirect effects of biomass removal on preemptive competition, such as increasing the number of microsites and the opportunities of colonization, may also be an important mechanism (Bullock et al., 1994).

This study investigated the impact of slug grazing by using aquariums as microcosms. These microcosms lack the variability of natural habitats, and consequently restrict (in comparison with field conditions) the possibility of niche differentiation. However, the aquarium experiment can be more replicated than field experiments (which is very important, particularly as there is need the monocultures of all of the constituent species), and better control of environmental conditions.

I performed an outdoor aquarium experiment to test the effect of slug herbivory on ecosystem functioning. The following questions were addressed: (i) Are species-rich communities more resistant to slug grazing than species-poor communities? (ii) Are there biodiversity effects? If so, what is the nature of these effects? (iii) Is there any relationship between increased plant diversity and herbivore preference?

To test these questions, I manipulated species richness and grazing of slugs by using perennial grassland species planted in four biodiversity treatments. As an experimental herbivore I chose the slug *A. lusitanicus* Mabille, a common agricultural pest in Central Europe (Grimm, 2001; Frank, 1998). The design of the experiment allowed me to investigate how slugs influence plant diversity effects in experimental mixtures.

2. Methods

The microcosm study was conducted in June–September 2003 at experimental garden (Academy of Sciences, České Budějovice, Czech Republic; 390 m a.s.l.), where the mean annual precipitation is 600–650 mm, mean annual temperature is 7.8°C.

2.1. Selected plants

For the experiment I selected plant species occurring commonly and representing major components of the European grasslands. Thus, the experimental mixtures are likely to occur and be able to coexist under natural conditions. I selected six perennial plant species for the slug herbivory experiment: two grasses *Holcus lanatus* and *Alopecurus pratensis*; two rosette hemicryptophytes *Lychnis flos-cuculi* and *Hypochaeris radicata* and two other forbs *Plantago lanceolata* and *Achillea millefolium*. All species are polycarpic perennials (annuals are rare and unimportant in wet meadows; Lepš, 2004) occurring in a wide range of grasslands in the Czech Republic. *Holcus* and *Alopecurus* (*Poaceae*) dominate most of the grasslands. *Alopecurus* is a weak competitive species, occurring most frequently within wet areas of the meadow. *Lychnis* (*Caryophyllaceae*) and *Hypochaeris* (*Asteraceae*) are both long-lived rosette plants, these produce a single shoot bearing reproductive organs. *Plantago* (*Plantaginaceae*) and *Achillea* (*Asteraceae*) are common herbs, occurring mainly within the drier parts of the meadow.

2.2. Experimental design

I used two paired plots (grazed and ungrazed by slugs) in complete randomized design. On the 12th of July 2003, each microcosm, measuring $38 \times 58 \times 38$ cm in diameter, was divided by glass partition into two plots. The first one was held under slug grazing activity and second one was the control (without slug grazing). The slug, *A. lusitanicus* Mabille (Mollusca: Pulmonata), was collected from the surroundings of greenhouses at the Academy of Sciences in České Budějovice, Czech Republic. Individual slugs were added into one plot of each aquarium four times during the experiment. Slugs were introduced to aquariums for 2 days on the 12th August, the 2nd and the 10th of September. The last introduction was conducted on the 17th of September, when slugs were left in aquariums for 5 days. After the last census, aboveground plant biomass was clipped (separately in grazed and control plots), sorted into species and dried for six hours at temperature of 105°C.

Sand and sterile peat mix (in 2:1 ratio) was used as the soil substrate. The following plant assemblages were used in the experiment: monocultures (two replicates of each species), all 15 combinations of two-species mixtures (individual combinations were not replicated), all 15 combinations of four-species mixtures (combinations not replicated) and six-species mixtures (all species included, five replicates). Plant assemblages were sown in a replacement series design in both plots of the aquarium at the same density of 800 seeds. Aquaria were completely randomized at the experimental site.

2.3. Data analysis

I used the Loreau and Hector (2001) equation to separate selection and complementarity effects. The term ''selection effect'' is used instead of the term ''sampling effect'' because it is more general. It does not require complete dominance of the performing species, with extreme trait values selection