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Original article

Sudden changes in environmental conditions do not increase invasion risk in grassland

Eszter Ruprecht [a,b,*], Annamária Fenesi [a], Ivan Nijs [b]

[a] Hungarian Department of Biology and Ecology, Babeş-Bolyai University, Republicii Street 42, RO-400015 Cluj Napoca, Romania
[b] Research Group Plant and Vegetation Ecology, Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Wilrijk, Belgium

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ABSTRACT

After direct habitat transformation, biological invasions are considered to be the second most important threat to biodiversity. A better understanding of the factors affecting invasion success in new areas is crucial, and may provide insight into potential control actions. We hypothesized that invasion risk increases in habitats undergoing a sudden change in the disturbance regime or environmental conditions. For testing this assumption we initiated a seed sowing experiment while introducing two novel treatments, mowing twice and fertilizer application, in two grassland sites (one dryer and one mesic) in Romania. The seeds of two invasive species, *Solidago canadensis* and *Rudbeckia laciniata*, and two resident natives of similar seed sizes, life-forms and strategies were sowed in treated and control plots, and seed germination, seedling establishment and growth were followed during four months. Contrary to our expectations, there was no difference in the treatment effects on seed germination and seedling establishment between species, while there was on seedling vigour of the larger seeded species in the dryer grassland site, where the native had a higher performance especially in increased nutrient conditions. Indifferently from applied treatments, invasive species had greater cumulative germination in the mesic site, while natives were far more successful in seedling establishment in the drier site. At the same time, seed size was found to be a very important factor explaining germination and establishment success, with large seeded species outperforming small seeded species in any circumstances. Our results call the attention upon management interventions in mesic, productive grassland sites opening colonization windows for the recruitment of those invasive species of which ecological requirements correspond to local environmental conditions.

1. Introduction

The introduction and spread of non-native species have become a global ecological and conservation crisis as alien invasive organisms are increasingly altering terrestrial and aquatic communities worldwide (Parker et al., 1999; Byers et al., 2002; Mack et al., 2000; Gurevitch and Padilla, 2004). Thus, biological invasions are stated to be a serious threat to biodiversity (Vitousek et al., 1997). In this context, assessing the effects of invasive nonindigeneous species on native species and ecosystems has become one of the world's most serious conservation issues (Byers et al., 2002).

Invasion success is known to be influenced by two main factors: the tendency of the new species to invade, i.e. invasiveness, and the susceptibility of the environment to invasion by new species, i.e. invasibility (e.g. Lonsdale, 1999; Sakai et al., 2001). The search for species characteristics that promote invasiveness constitutes one of the most challenging tasks in invasion ecology, however, only a few traits have been proved to be generally associated with invasiveness (Pyšek and Richardson, 2007). Therefore, it is increasingly considered that the role of plant traits in the invasion process is to a very large extent context dependent (Mack et al., 2000; Pyšek and Richardson, 2007).

Concerning invasibility of plant communities, several factors have been identified to influence this process with topography, soil type, land use, land cover, disturbance, resource availability, biotic interactions and microclimate operating at smaller, e.g. local, spatial scales (sensu Milbau et al., 2009). For example, it has been shown that a high supply of nutrients (high productivity) and disturbances are particularly responsible for promoting invasion (Burke and Grime, 1996; Daehler, 2003; Gross et al., 2005). Even so, invasion success may not be a temporally stable property of

* Corresponding author. Hungarian Department of Biology and Ecology, Babeş-Bolyai University, Republicii Street 42, RO-400015 Cluj Napoca, Romania. Tel.: +40 748032687; fax: +40 264431858.
E-mail address: eszter.ruprecht@ubbcluj.ro (E. Ruprecht).

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the invader/invaded system because of possible influences of ecosystem alteration over time (e.g. climate warming, land-use change or resource fluctuations such as eutrophication) (Davis et al., 2000; Weltzin et al., 2003).

The majority of plant invasions seem to occur in areas where environmental conditions such as the disturbance regime or resource availability have recently changed (e.g. Hobbs and Huenneke, 1992; Davis et al., 2000; Facon et al., 2006; Seastedt and Pyšek, 2011). In accordance to this, the new conditions would be less suitable for the resident species, since these were adapted to the former conditions, but might represent new, empty niches to species coming from outside the system, e.g. invasive species ready to colonize. In case the propagules of an invasive species are present, of which the ecological attributes or demands match the altered environmental conditions, it will successfully colonize. This approach, which is combining two well known hypotheses formulated to explain the success of exotic species in their recipient communities: the 'empty niche hypothesis' and the 'disturbance hypothesis' (reviewed by Hierro et al., 2005), was used by Moles et al. (2008) for predicting traits that are likely to confer invasion success. However, this approach can also present a useful methodology for predicting invasions that result from changes in environmental conditions.

In the present study we hypothesize that invasion risk increases with a sudden change in the disturbance regime and resource availability. In addition, since the relative performance of invasive species compared to natives is known to be different depending on the specific combination of water, nutrient and light availability (see for e.g. Daehler, 2003), invasion success of the same species is expected to depend strongly on site abiotic conditions. To this end, we followed and compared early establishment after sowing of native and invasive plant species in two experimental grassland sites, one dryer and one mesic. Based on our hypothesis we were interested in whether, by introducing repeated mowing and fertilizer application to simulate intensified land-use, suddenly altered environmental conditions negatively influence recruitment success of resident species adapted to the former conditions, and will promote establishment of the invasive species. Our experiment refers to the very early stages of plant establishment, germination and seedling recruitment (the initial colonization phase of the invasion process sensu Jongejans et al., 2007). The success of these processes is known to be primarily influenced by environmental factors but also by the interplay between environmental factors and the quantity of seed reserves (Moles and Westoby, 2004, 2006; Eckstein and Donath, 2005; Ruprecht et al., 2010b). Thus, seed size is expected to shape considerably the establishment success of species under different scenarios (with or without mowing and fertilizer application, higher or lower water availability).

Field experiments conducted in semi-natural habitats are indispensable in order to assess the real contamination risk of high nature value habitats and the real conservation threats posed by the spreading of invasive species. Thus, we selected hardly disturbed semi-natural sites having different abiotic conditions, induced sudden changes in environmental conditions by experimental manipulations to the resident communities and tested the initial colonization phase of two invasive species that were absent from the sites compared to resident natives. The manipulations were chosen in a way as to imitate realistic land use interventions. Being aware of the risks of this study, we applied all measures assuring the ecological value of the grassland sites during and after the experiment. In addition, in order to find out the ecological requirements of the invasive species involved and to unravel potential mechanisms responsible for invasion success under different manipulations and site conditions, we complemented our field study with a controlled pot experiment involving the germination of the two invasive species under different levels of three environmental factors (light, nutrient and water availability). With our field experiment, we tested in a broader context whether invasive species are recruited more successfully when the environmental conditions are altered experimentally, as opposed to natives being more successful in unchanged environments.

2. Material and methods

2.1. Field experimental design and data collection

A factorial field experiment was performed in two meadow sites in Romania (Corneşti and Sic), which had not been managed (mowed or grazed) for a longer time. One of the sites (Corneşti) was dryer (average depth of ground water table during March–May 2011 was 43 cm) than the other (Sic, 20 cm), they had slightly different soil properties, especially in terms of pH (soil samples analysed by the Belgian Soil Service: Corneşti 522 mg total N, 3 mg P, 23 mg K in 100 g soil, $pH_{KCl} = 4.6$; Sic 384 mg total N, 3 mg P, 18 mg K in 100 g soil, $pH_{KCl} = 7.3$), and harboured different plant communities. The experimental site at Corneşti was a meso-xeric grassland dominated by *Festuca pratensis* and *Festuca rupicola* which was very rich in dicotyledonous species, while that at Sic was a mesic grassland dominated by *Carex hirta* and *Agrostis stolonifera* with a high representation of *Ranunculus acris*, *Lysimachia nummularia* and *Cirsium canum*.

Four resident native (two in both sites) and two invasive species were selected for the seed sowing experiment. The two invasive forbs, *Solidago canadensis* and *Rudbeckia laciniata*, were both introduced in Central-Eastern Europe from North-America. These species are widespread in Romania, but not occurring in the experimental grassland sites or their surroundings. Lack of the two invasive species in the study sites and their surroundings can be explained rather by dispersal limitation and not by unsuitable environmental conditions, since they occur in other regions of the country with similar climate, and have small, isolated populations in the study region (Cluj county) as well (especially *S. canadensis*). The resident natives were abundant in the grassland plant communities, sharing similar seed sizes, life-forms and strategies with the invasive species. Seeds of the resident natives were collected in the experimental grassland sites (Table 1), while that of the invasives from one population each near Cluj-Napoca (*S. canadensis*) and Praid (*R. laciniata*), Romania, during August and September 2010. For all six species used in the experiments, seed collection included at least 12 different individuals per species. Seeds (in fact seeds or fruits) cleaned from appendages were subsequently dry-stored in darkness at room temperature (*c.* 20 °C) until sowing.

Two experimental treatments were applied in 3 m × 3 m main plots in both sites. We selected management interventions that plant communities in the two grassland sites had not experienced for a long time, which were (i) mowing twice and (ii) mowing twice combined with fertilizer application. These treatments simulate a potential management of the grasslands as intensive hayfields. As well, we had main plots with biomass left intact and without fertilizer application as a control. In treated plots, mowing was performed at the beginning of the experiment, in November 2010, and in mid June 2011. Mowing comprised removal of clippings, and at first mowing litter was also removed by raking. Nutrient addition amounted to 10 g m^{-2} $year^{-1}$ N-fertilizer, which was delivered in two items to decrease leaching losses and to avoid scorching. Half of the total fertilizer quantity was added in March, before the beginning of the vegetation period, and half at the end of May 2011.

Within the main plots 25 cm × 25 cm subplots (seed sowing plots) were set out. Fifty seeds of the two invasives and two