GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 22 (2017) 20–27
Basic and Applied Ecology
www.elsevier.com/locate/baae

Suppression of an invasive legume by a native grass — High impact of priority effects

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Received 23 December 2016; accepted 23 June 2017
Available online 11 July 2017

Abstract

Nitrogen-limited ecosystems are threatened by extensive spread of broom (*Cytisus scoparius* (L.) Link), a European leguminous shrub that is invasive in several countries. The establishment of invading species may, however, be suppressed by competition from native vegetation. The neighbor impact of the grass *Festuca rubra* subsp. *commutata* Gaudin on the performance of *C. scoparius* was studied in a greenhouse experiment with different arrival order, under low and high nitrogen supply, and with or without inoculation of nitrogen-fixing bacteria. Aboveground biomass of both species was measured after a six-months establishment period, and after a five-months regrowth period. In both periods, presence of *F. rubra* reduced the performance of *C. scoparius* as indicated by negative neighbor-effect intensity indices ($NInt_A$).

During the establishment period the competitive impact of *F. rubra* was highest, when planted before *C. scoparius*, followed by synchronous and late planting. Inoculation with rhizobia and low fertilization decreased the competitive impact of *F. rubra*. After cutting and regrowth priority effects of *F. rubra* were still visible. Interaction between the two study species was not affected anymore by inoculation, but strongly by fertilization, with highest competitive impact of *F. rubra* on *C. scoparius* under high nitrogen fertilization. In both study periods biomass of *C. scoparius* was negatively correlated with biomass of *F. rubra*. Our study provides knowledge about competition processes, which help to improve conservation and restoration measures regarding the spread of *C. scoparius*. Early sowing of a native grass can help to suppress the invasive species at an early stage. Competitive impact of the grass might be strengthened by high nitrogen availability.

Keywords: Competition; Fertilization; Grass; Priority-effect; Restoration; Rhizobia

Introduction

Alien N-fixing species have a marked impact on nutrient-poor ecosystems, causing changes both to abiotic and biotic ecological conditions (Vitousek & Walker 1989). The strategy of symbiotic N-fixation is, however, costly in terms of carbon, and draws on resources that could be allocated to

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http://dx.doi.org/10.1016/j.baae.2017.06.005

other functions. There is a trade-off between investment in N-fixation and other functions that may affect the performance of N-fixing species as the availability of soil nitrogen increases and hence the plants' ability to compete with other species. Competition is a key aspect shaping plant communities and ecosystem dynamics (Grace 1995). Invasive alien species may at least under certain environmental conditions and biotic interactions, be more competitive than native ones (Vilá & Weiner 2004) but results are not conclusive (e.g. Shelby et al. 2016). The invader's performance is modulated by environmental conditions like vegetation matrix and resource availability. On the other hand, competition by native species can decrease the performance and success of an invader (Levine, Adler, & Yelenik 2004) contributing as biotic resistance to invasion.

Little is known about the way abiotic and biotic factors influence the establishment process of N-fixing species and how they may be suppressed by native vegetation. While some studies found that establishment of species like *Cytisus scoparius* can be reduced by dense vegetation (Bellingham & Coomes 2003; Harrington 2011), others showed adverse effects (Hosking, Smith, & Sheppard 1998). Priority effects are of particular importance in such competitive relationships. Early arriving species can occupy space and gain bigger reserve pools resulting in higher biomass and stronger competitive ability towards later arriving species (Körner, Stöcklin, Reuther-Thiébaud, & Pelaez-Riedl 2008; Von Gillhaussen et al. 2014; Young, Stuble, Balachowski, & Werner 2016). Not only alien but also native plants can benefit from early arrival, as shown in a mesocosm experiment for old-field plant species (Stuble & Souza 2016). Initial differences in arrival time can result in continuous priority effects (grassland species in Körner et al. 2008). However, this depends on the relative setback of the interacting species and their adaption to frequent disturbance, e.g. mowing, grazing or fire. In a long-term view, timing of species arrival can alter vegetation composition and may lead to communities either dominated by native or alien plant species (Martin & Wilsey 2012).

Beside priority effects, resources play a major role for competitive interactions (Vilá & Weiner 2004). The competitive advantage of N-fixing species under low N availability is expected to diminish as availability of soil N increases. Competing species like grasses benefit from a fibrous root systems that extract soil nutrients more efficiently than the tap roots of legumes (Kutschera & Lichtenegger 1992; Lambers, Chapin, & Pons 1998). There are indications that N-fixing species (at least in the short term) benefit from nitrogen fixation under increased competition for soil resources (Werner, Vinuesa-Fleischmann, Scheidemann, Wetzel, & Redecker 1998; Valladares et al. 2002).

Scotch broom *C. scoparius* (L.) Link (Fabaceae) is a perennial shrub native to sandy soils in heathlands and acidic grasslands in western and central Europe. This species has become a serious weed throughout USA, New Zealand, Australia and India, and further expansion is expected (Potter, Kriticos, Watt, & Leriche 2009). There is also a range expansion of non-native genotypes observed in North-western Europe. In Denmark introduced genomes of *C. scoparius* were shown to invade the native ones (Rostgaard Nielsen, Brandes, Dahl Kjær, & Fjellheim 2016). These cryptic invasions can not only threat the native gene pool (Skou, Toneatto, & Kollmann 2012), but may also alter the local vegetation composition. Symbiosis with N-fixing rhizobia enables it to invade nutrient-poor environments and increasingly change the natural vegetation of pastures, dunes and shrubland (Shaben & Myers 2009; Simberloff 2011).

We tested the impact of arrival order, nitrogen fertilization and inoculation on the interaction between an alien and native species, and how this is affected by disturbance in terms of cutting. We investigated these three factors and their two-way interactions in a controlled greenhouse experiment with the native grass *Festuca rubra* subsp. *commutata* as neighbor and the alien legume *C. scoparius* as N-fixing target species

We addressed the following hypotheses:

I Interaction between *F. rubra* and *C. scoparius* is subject to arrival time and N-fertilization.
II Inoculation with rhizobia favors *C. scoparius* in its interaction with *F. rubra*, especially under low N availability.
III Cutting and regrowth of *C. scoparius* and *F. rubra* will mitigate possible priority effects and increase effects of N-fertilization and inoculation of rhizobia.

Materials and methods

Study species and plant material

As part of a larger project studying *C. scoparius* (L.) Link (Fabaceae) range expansion in Norway, seeds of this species were collected at the southwest coast of Norway between Mandal and Stavanger during 2011–2013. The species is potentially a native species there, but the sampled populations are assumed to be non-native or mixed with native ones (pers. Comm. Siri Fjellheim, Norwegian University of Life Science). To give our study a broader base, seeds from several populations, including several seed families per population, were used (mean seed mass 9.0 mg). The area of seed origin has moderate maritime climate (Köppen type Cfb) with fairly mild winters and summers (average temperature 7.8 °C, www.climatedata.eu, Stavanger), and precipitation all year round (average annual precipitation 1180 mm, www.climatedata.eu, Stavanger). Chewing's fescue *F. rubra* subsp. *commutata* Gaudin (Poaceae) is a perennial bunchgras found worldwide in a broad range of climates and habitats, co-occuring with *C. scoparius* in many habitats, such as road verges. Seeds of *F. rubra* were derived from a Norwegian seed company (Felleskjøpet, seed mass 1.2 mg).