
Experimental support for a resource-based mechanistic model of invasibility

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Abstract

Recent theory has suggested a mechanistic relationship between resource availability, competition and invasibility. In a field experiment, in which we manipulated resources and competition, we confirmed that changes in resource availability affected competition intensity, which in turn affected invasibility. We found that fluctuations in resource availability of as short as a few weeks had a large impact on plant invasion success (survival and percentage cover), including up to 1 year following the fluctuations. If resource availability is a primary mechanism controlling invasibility, it may serve as a unifying concept that can integrate earlier ideas regarding invasibility. The results emphasize the important role of history in the invasion process, particularly the occurrence of stochastic, short-lived events that temporarily reduce or suspend competition and increase invasibility. Therefore, it may be very difficult, or even impossible, to reconstruct the ecology of particular invasions after the fact.

Keywords

Biological invasions, competition, invasibility, invasions, plant invasions, resource availability, resources.

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INTRODUCTION

The ability of species to invade new communities is influenced by the traits of the invaders, the number of invaders (propagule pressure) and the susceptibility of the environment to invasion by new species (invasibility) (Lonsdale 1999). Invasibility is an emergent property of an environment, and is the outcome of several factors, including the region's climate, the environment's disturbance regime and the competitive abilities of the resident species (Lonsdale 1999). The invasibility of environments to new plant species can be quantified empirically as the probability of establishment and subsequent survival of individual plants per arriving propagule, or the increase in biomass or percentage cover of the plant species over a specified period of time given a defined propagule pressure (Davis *et al.* 2000).

Understanding the factors influencing the invasibility of environments has proven to be a challenge for ecologists, and field experiments are needed to elucidate the mechanisms of invasibility (Williamson 1999). Current hypotheses of invasibility of plant environments have emphasized the importance of disturbances (Crawley 1987), species diversity (Elton 1958; Tilman 1997), community productivity (Tilman

1993) and fluctuating resource availability (Davis *et al.* 2000). The fluctuating resource availability hypothesis of invasibility proposes that a mechanistic relationship exists between invasibility and resource availability, and that changes in invasibility are often due to changes in the competition intensity from resident vegetation, which in turn results from fluctuations in resource availability.

The purpose of the experiment described in this paper was to test the predictions of the fluctuating resource availability hypothesis. We found that both competition and invasibility were strongly affected by resource availability, and that fluctuations in resource availability of as short as a few weeks had a large impact on the invasion success of three herbaceous plant species. These brief fluctuations in resource availability not only affected initial establishment, but also patterns of vegetation cover up to 1 year later. If resource availability is a primary mechanism controlling invasibility, it may serve as a unifying concept that can integrate earlier ideas regarding invasibility.

METHODS

The study was conducted in an old field at Cedar Creek Natural History Area (CCNHA, Bethel, MN, U.S.A.), the

soils of which are well drained and low in nitrogen (Grigal *et al.* 1974). Three non-native grasses dominate the study field: *Agropyron repens* L., *Bromus inermis* L. and *Poa pratensis* L. In spring 1999, 32 plots were laid out in the old field vegetation in a split-plot design of eight replicates, each consisting of two pairs of plots (1.5 × 0.75 m) (Fig. 1). In May 1999, one plot in each pair was sprayed with a glyphosate herbicide (Roundup™). To avoid disturbing the soil and litter in these plots, the dead vegetation and litter were not removed. Subsequent light weeding kept these plots free of live resident plants during the summer of 1999, thereby eliminating all resource uptake by the resident vegetation.

Three species (*Desmodium canadense* L. (Fabaceae), *Dalea purpurea* Vent. (Fabaceae) and *Rudbeckia hirta* L. (Asteraceae)) were sown (1.5 g of seed mixed with 700 cm³ of soil) into every plot on July 1, 1999, each species in its own 10 × 75 cm planting strip. In addition, on July 2, 1999, 12 3-week-old *D. canadense* seedlings were transplanted into their own planting strip in every plot. Seeds were obtained from a local seed source and the three species were selected because they are adapted to sandy low-nutrient soils such as those at Cedar Creek. All three species are perennials (*R. hirta* sometimes exhibits a biennial life cycle) and are native to North America. Thus, the experiment consisted of native species invading a novel environment (an old field) that was dominated by non-native grasses. Although this may seem to be a paradoxical system in which to study invasibility, the processes and mechanisms governing invasions by non-native species are believed to be the same as those governing colonization events by native species (Davis & Thompson 2000). Also, the experimental system essentially represents a European invasion experiment, that is, a European grassland being invaded by North American species.

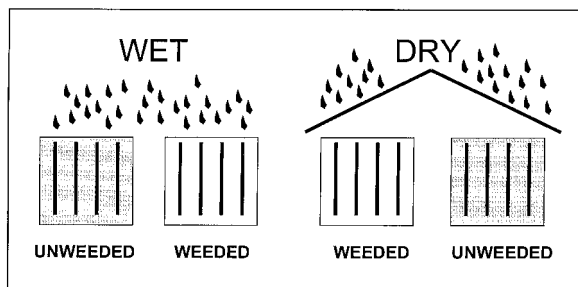


Figure 1 Layout of plots for the split-plot design used in the experiment. The experiment consisted of eight replicates, each with a whole-plot factor (water), consisting of two levels (wet and dry), and a subplot factor (disturbance), also consisting of two levels (weeded and unweeded, i.e. without competitors and with competitors).

A water treatment (wet or dry) was applied to each pair of plots in a replicate. Thus, there were four experimental environments in each replicate (wet weeded, wet unweeded, dry weeded and dry unweeded), with the whole-plot factor being water and the subplot factor being disturbance (weeding). Each of the four experimental plots in a replicate contained four planting strips, one for each of the three species introduced by seed, plus one strip of the *D. canadense* transplants (Fig. 1). All treatment levels and planting strip assignments were randomly assigned. Following the species introductions, all plots were watered using sprinklers every other day (1 cm of water) for 2 weeks to promote the germination of the seeds and the initial establishment of the *D. canadense* transplants. Then, a 32-day drought or wet spell was imposed on the respective pairs of plots (July 16–August 17) which represented the fluctuating resource availability. During this time, the wet plots continued to receive 1 cm every other day plus ambient rainfall. The dry plots were managed with rain tarps that were placed over the dry plots prior to a rain event and removed immediately afterwards (Davis *et al.* 1998). During the 1-month treatment period, the wet plots received 29 cm of water input, while the dry plots received 3 cm, the latter due to a few surprise rain events. No subsequent water or disturbance (weeding) treatments were imposed on the plots after August 17, 1999.

Because propagule pressure was the same in all plots, and the same three species were introduced into all plots, differences in invasion success among plots can be attributed to differences in invasibility among the plots. Invasion success (and hence invasibility) was measured as the percentage cover of species introduced by seed (all three species) and as the number of survivors for the *D. canadense* transplants. The percentage cover was estimated using a 10 × 75 cm wooden frame, divided with string into 100 equal-sized squares, which was positioned above each planting strip. The percentage cover, defined as the number of squares overlaying some portion of the introduced plants, was measured on August 17, 1999 and July 19, 2000. For the *D. canadense* transplants, the number of surviving plants was used as a measure of invasion success. The percentage cover of flowering plants was estimated in the same way in 2000 for *R. hirta*, which was the only species to flower in the majority of plots in that year.

For each species in each undisturbed plot, competition intensity from the resident vegetation in 1999 was calculated as the percentage cover of the introduced species in the disturbed (weeded) plot minus the percentage cover of the introduced species in the paired undisturbed plot, with the difference divided by the largest of the two cover values (Markham & Chanway 1996). This calculation yields an index of competition intensity ranging from -1 to +1. A positive index indicates the presence of competition, a

