

Experimental support for a resource-based mechanistic model of invasibility

Mark A. Davis and Melissa Pelsor
Department of Biology,
Macalester College, Saint Paul,
MN 55105, U.S.A.
E-mail: davis@macalester.edu

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.

Ecology Letters (2001) 4: 421-428

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.

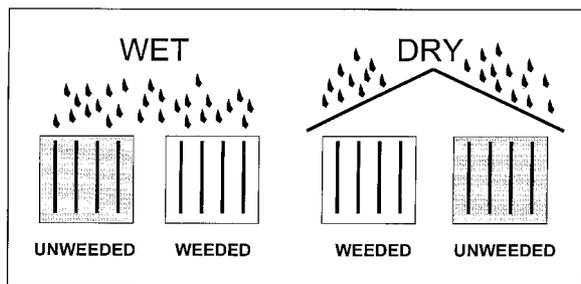


Figure 1 Layout of plots for the split-plot design used in the experiment. The experiment consisted of eight replicates, each with a whole-plot factor (water), consisting of two levels (wet and dry), and a subplot factor (disturbance), also consisting of two levels (weeded and unweeded, i.e. without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

negative index indicates facilitation by the resident vegetation and a value of zero indicates that the target species is unaffected by the presence of other vegetation. For the *D. canadense* transplants, the number of surviving plants was used instead of the percentage cover in these calculations.

The percentage volumetric soil water, θ , in all plots was measured seven times between July 13 and August 16, 1999 using a portable time domain reflectometry system (Davis *et al.* 1998). The mean value of these measurements was used as a measure of soil water availability in a plot during the experimental period. The same method was used to measure soil water in the plots on July 24, 2000. (Ten centimetres of rain had fallen during the 2 weeks prior to July 24, 2000, and 0.2 cm had fallen during the preceding 4 days.) The soil water potential, or matric potential, ψ_s , is generally regarded as a more accurate measurement of soil water availability for plants than is the percentage soil water (Thornley & Johnson 2000). The matric potential ($-Mpa$) was calculated using θ values and a soil water release curve developed at CCNHA for the soil type of the study field (Grigal *et al.* 1974): $\ln(\psi_s) = 4.84 - 3.78 \times \ln(\theta)$ ($r^2 = 0.94$, $P = 0.002$). All analyses involving soil water were conducted twice, once using θ and once using ψ_s (logarithmically transformed). In every case, the two analyses produced nearly identical results, including the same level of significance in every instance. Thus, to avoid redundancy in reporting the results, only those involving θ are presented.

The light availability (photosynthetically active radiation, PAR) at ground level was measured in August 1999 using a Licor LAI2000. Soil nitrate and ammonium levels (mg/kg soil) were measured from soil samples taken from all plots in August 1999 (Ritchie 2000), and the above-ground dry biomass of the resident vegetation was obtained from a 10 cm \times 1 m strip of vegetation harvested from each unweeded plot in August 1999. In August 1999, unweeded plots were censused and the species richness of the resident old field vegetation was recorded for the respective plots. In addition, the percentage cover of the respective resident species was estimated within a 0.25 \times 0.50 m sampling frame that was positioned in two locations in each unweeded plot, one in the eastern half and one in the western half of the plot. Species diversity in the plots was calculated using the Shannon index (Shannon 1948) and based on the percentage cover.

A split-plot analysis of variance (ANOVA) was used to analyse the combined effects of water and disturbance (weeding) on invasion success. Our primary interest was in the invasion success of the species in different environments, and not in comparisons among species. Thus a separate split-plot analysis was conducted for each species. In addition, because we were interested in the impact of these factors on the species at two very different times during their life cycles, very young seedlings (< 6 weeks old)

and 1-year-old, mature (and frequently flowering) plants, we conducted a separate split-plot analysis for 1999 (seedling) and 2000 (mature plant) results. A split-plot ANOVA was also used to analyse the combined effects of the water and disturbance factors on the flowering success (percentage cover of flowering plants) of *R. hirta* in 2000, and on resource availability in 1999 (percentage soil water, nitrate, NH_4 and light (PAR)).

Comparisons among means in split-plot analyses in which there was a significant interaction between the whole-plot factor (water) and the split-plot factor (disturbance) were conducted using the appropriate standard error for the respective comparisons: comparisons among subplot means at a fixed level of the whole-plot factor = $(2 \times MSE(\text{subplot})/ra)^{1/2}$ with d.f. = $a(r-1)(b-1)$; comparisons among whole-plot means at a fixed level of the subplot factor = $(2 \times MSE(\text{whole-plot}) + (b-1) \times MSE(\text{subplot})/rb)^{1/2}$ with d.f. = $(r-1)(a-1)$. a is the number of levels in the whole-plot factor, b is the number of levels in the subplot factor and r is the number of replicates. With two levels each in the water and disturbance factors, four pairwise comparisons of means were made in these analyses. To ensure a 0.05 Type I error for the set of four comparisons, the Bonferroni correction was used and 0.0125 (0.05/4) was employed as the significance level for a Type I error for individual comparisons.

A paired t -test was used instead of the split-plot ANOVA for those analyses confined only to the unweeded plots. Simple regression analysis was used to examine the relationship between invasion success and neighbour biomass, neighbour species richness and resource availability (water, nitrogen and light), and between competition intensity and the same environmental variables. Simple regression analysis was also used to examine the relationship between invasion success measured in 1999 and that measured in 2000, and between the percentage volumetric soil water measured in 1999 and 2000.

RESULTS

The water and disturbance treatments affected resource availability. Soil water was affected by an interaction between the two treatments ($F = 16.29$, $P = 0.001$). In the wet environment, the percentage soil water did not differ between weeded and unweeded plots ($t = 1.35$, $P > 0.50$); however, the percentage soil water differed between weeded and unweeded plots in the dry environments ($t = 4.33$, $P < 0.005$, Table 1). Soil nitrate levels were affected by water ($F = 6.27$, $P < 0.05$), with dry plots having higher levels than wet plots, and by weeding ($F = 11.51$, $P = 0.004$), with weeded plots having higher levels than unweeded plots (Table 1). Ammonium levels were affected by weeding ($F = 7.58$, $P = 0.02$), with weeded

Table 1 Mean resource measurements and standard errors in the four experimental environments. Two of the dry weeded plots had very high nitrate levels (5.3 and 7.8 mg/kg soil), levels that were confirmed by an additional and separate soil analysis. If these two plots are deleted from the soil nitrate calculations, the mean nitrate level in the dry weeded plots is 1.69 ± 0.30 mg/kg soil. The result of the split-plot analysis of nitrate reported in the text is not changed if these two plots are deleted from the analysis, i.e. the water factor is still significant ($F = 9.44$, $P < 0.25$), as is the disturbance factor ($F = 30.46$, $P < 0.0001$)

Plot	Soil water (%)	Soil nitrate (mg/kg soil)	Soil NH ₄ (mg/kg soil)	Light (PAR) ($\mu\text{mol photons/m}^2/\text{s}$)
Dry unweeded	6.58 \pm 0.005	0.51 \pm 0.037	0.44 \pm 0.045	625 \pm 86.7
Dry weeded	8.82 \pm 0.008	2.91 \pm 0.865	0.68 \pm 0.086	1224 \pm 3.8
Wet unweeded	12.57 \pm 0.004	0.42 \pm 0.074	0.46 \pm 0.069	191 \pm 26.3
Wet weeded	11.87 \pm 0.005	1.02 \pm 0.171	0.58 \pm 0.052	1222 \pm 4.5

plots having higher levels than unweeded plots, but were not affected by water ($F = 0.82$, $P > 0.25$) (Table 1). Light was affected by an interaction between water and disturbance ($F = 21.75$, $P < 0.001$). In the unweeded environments, light levels at the soil surface were higher in the dry plots ($t = 7.41$, $P < 0.001$), whereas light levels in the weeded environments were uniformly high in both wet and dry plots ($t = 0.03$, $P > 0.50$, Table 1).

The invasion success of *R. hirta* (sown) was significantly affected by water treatment ($F = 24.01$, $P < 0.0025$), with invasion success being higher in wet plots, but was not affected by weeding ($F = 0.39$, $P > 0.50$, Fig. 2). The invasion success of *Dalea purpurea* (sown), *D. canadense* (sown) and *D. canadense* (transplanted) was affected by a significant interaction between water treatment and disturbance (*Dalea purpurea*: $F = 4.84$, $P = 0.045$; *D. canadense* (sown): $F = 42.02$, $P < 0.0001$; *D. canadense* (transplanted): $F = 11.74$, $P = 0.004$). Although disturbance usually increased invasion

success in dry conditions for these species, it did not increase invasion success in wet conditions (Fig. 2).

The results showed that species introduced into wet environments experienced significantly less competition from the resident vegetation than those introduced into dry environments (*D. canadense* (transplanted), wet: -0.064 ± 0.114 ; dry: 0.85 ± 0.105 ; two-tailed paired $t = 5.40$, $P = 0.001$; *D. canadense* (sown), wet: -0.45 ± 0.065 ; dry: 0.66 ± 0.155 ; paired $t = 7.65$, $P < 0.0001$; *R. hirta* (sown), wet: -0.05 ± 0.217 ; dry: 0.75 ± 0.164 ; paired $t = 4.46$, $P = 0.003$; *Dalea purpurea* (sown), wet: 0.31 ± 0.118 ; dry: 0.79 ± 0.058 ; paired $t = 6.11$, $P = 0.005$; standard error (SE) provided for these and other results reported). These results showed that disturbance usually increased invasibility when gross resource supply was low (dry plots). Under these conditions, disturbance eliminated resource uptake by resident vegetation, thereby increasing soil water availability for the

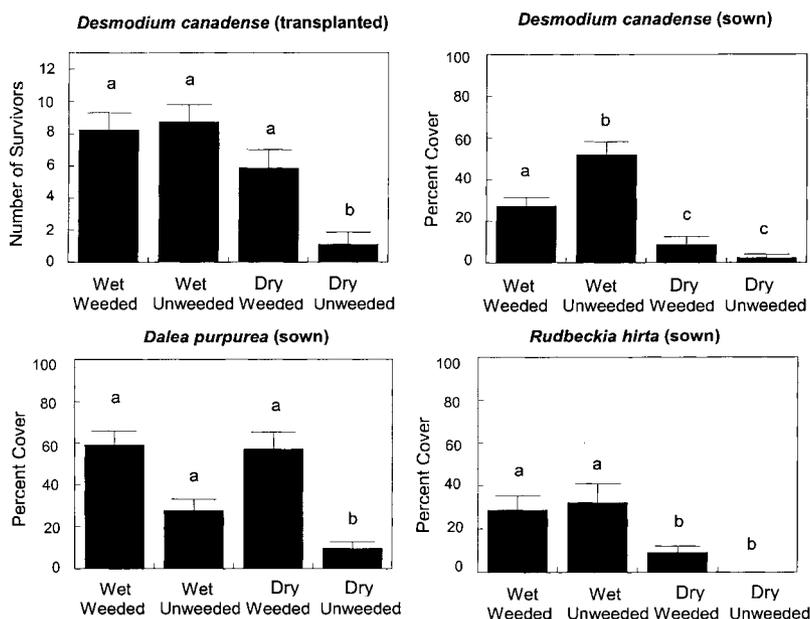


Figure 2 First-year invasion success (percentage cover or seedling survival) of the introduced species in each of the four experimental environments. Standard errors shown. Columns with different letters indicate a significant difference ($P < 0.05$) in invasion success among the respective experimental environments.

introduced species (Table 1). In wet environments, disturbance did not increase invasibility because soil water levels were high in both disturbed and undisturbed plots (Table 1), and thus competition from resident vegetation was effectively eliminated in wet plots.

The invasion success of all species was *negatively* correlated with light availability, the invasion success of *D. canadense* (transplanted) and *R. hirta* (sown) was significantly *positively* correlated with the biomass of resident vegetation, the competition intensity for all species was significantly *negatively* correlated with biomass, and the competition intensity for *D. canadense* (transplanted) and *D. canadense* (sown) was *positively* correlated with light availability (Table 2). These findings are due to the increased success of introduced plants in wet plots. Although watering doubled the productivity (above-ground biomass) of resident vegetation (wet: $97.5 \pm 17.2 \text{ g/m}^2$; dry: $46.8 \pm 9.9 \text{ g/m}^2$; two-tailed paired $t = 2.16$, $P = 0.068$) and reduced light availability in the unweeded plots by more than half (wet: $191 \pm 26.3 \text{ } \mu\text{mol photons/m}^2/\text{s}$; dry: $625 \pm 86.7 \text{ } \mu\text{mol photons/m}^2/\text{s}$; two-tailed paired $t = 6.17$, $P = 0.0005$), the increase in water supply exceeded any increase in water uptake, resulting in a doubling of water availability for the introduced species in the wet unweeded compared to the dry unweeded plots (wet: $12.6 \pm 0.38\%$; dry: $6.6 \pm 0.48\%$; $t = 9.67$, $P < 0.001$).

The competition intensity was inversely correlated with water availability for all species (Table 2). Overall, invasibility was strongly and consistently positively correlated with water availability for all species (Table 2, Fig. 3). The reduction in competition intensity and the increase in invasion success, in the face of increasing neighbour biomass, is predicted by the net resource supply theory of competition (Davis *et al.* 1998), which holds that competition intensity is best predicted by net resource supply, not gross resource supply or resource uptake by competitors.

The species richness of the resident vegetation in the unweeded plots ranged from two to seven species and was greater in wet plots (wet: 4.88 ± 0.61 species; dry: 3.88 ± 0.58 species; paired $t = 2.37$, $P = 0.05$). Neither invasion success nor competition intensity was correlated with the species richness of the resident vegetation (Table 2). The same lack of significant correlation was found when invasion success and competition intensity were compared with species richness separately for wet and dry plots ($P > 0.10$ for all species in both sets of plots). Species diversity, measured using the Shannon index, ranged from 0.10 to 1.07, and did not differ between wet and dry plots (wet: 0.64 ± 0.08 ; dry: 0.51 ± 0.14 ; paired $t = 0.76$, $P = 0.47$). Neither invasion success nor competition intensity was correlated with species diversity of the resident vegetation ($P > 0.25$ in both cases for all species).

During the summer of 2000, 1 year following ‘‘the invasion’’, all three species grew vigorously, with cover of the seeded species increasing in 52 of the 96 plots compared to 1999 values. In addition, all species flowered in some of the plots. The 2000 flowering success of *R. hirta* (the only species that flowered in the majority of the plots) was affected by the 1999 water treatment ($F = 7.29$, $P < 0.05$), with the cover of flowering plants being greater in the wet than dry plots, and by the 1999 disturbance treatment ($F = 86.9$, $P < 0.0001$), with more plants flowering in weeded than unweeded plots (Fig. 4). All flowering of the other two species occurred in weeded plots (*D. canadense* (transplanted): flowered in two weeded wet plots and two weeded dry plots; *D. canadense* (sown): flowered in one weeded wet plot and one weeded dry plot; *Dalea purpurea* (sown): flowered in one weeded wet plot and two weeded dry plots).

The invasion success measured on July 19, 2000 was highly correlated with the invasion success measured on

Table 2 Coefficients of determination (r^2 values) from regression analyses of the invasion success of the species and the environmental variables shown (top half of table) and of the competition intensity experienced by the species and the same variables (bottom half of the table). Asterisks indicate significance levels (* $P = 0.05$, ** $P = 0.01$, *** $P = 0.001$). The plus and minus signs indicate whether a significant regression relationship is positive or negative. The measurements and regressions involving light, species richness and above-ground biomass are based on the unweeded plots only

Species	Soil water	Light	Nitrate	NH ₄	Species richness	Above-ground biomass
Invasion success						
<i>D. canadense</i> (transplanted)	0.61***+	0.59***-	0.01	0.04	0.15	0.33*+
<i>D. canadense</i> (sown)	0.46***+	0.65***-	0.07	0.00	0.09	0.08
<i>R. hirta</i> (sown)	0.36***+	0.44**-	0.02	0.05	0.06	0.26*+
<i>Dalea purpurea</i> (sown)	0.15*+	0.44**-	0.04	0.04	0.17	0.14
Competition intensity						
<i>D. canadense</i> (transplanted)	0.65***-	0.52**+	0.02	0.01	0.08	0.32*-
<i>D. canadense</i> (sown)	0.60***-	0.30*+	0.07	0.00	0.12	0.28*-
<i>R. hirta</i> (sown)	0.46**-	0.19	0.07	0.01	0.02	0.37*-
<i>Dalea purpurea</i> (sown)	0.46**-	0.21	0.08	0.05	0.13	0.34*-

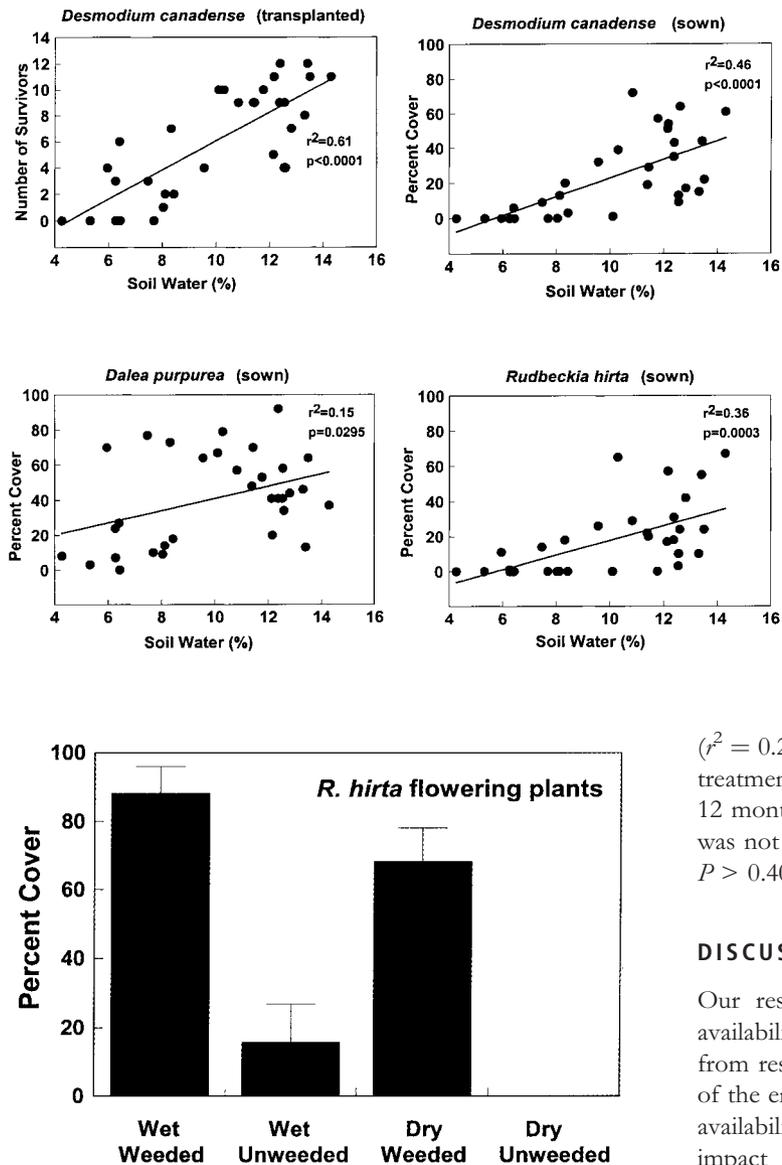


Figure 4 Percentage cover of *R. hirta* flowering plants in 2000 in the four experimental environments. Standard errors shown.

August 17, 1999 (*R. hirta* (sown): $r^2 = 0.48$, $P < 0.0001$; *Dalea purpurea* (sown): $r^2 = 0.44$, $P < 0.0001$; *D. canadense* (sown): $r^2 = 0.55$, $P < 0.0001$; *D. canadense* (transplanted), $r^2 = 0.51$, $P < 0.0001$), demonstrating that the initial establishment patterns (success or failure) persisted long after the original conditions favouring or inhibiting the original establishment had passed. Although the percentage soil water measured in the plots in 2000 was not correlated with the 1999 soil water ($r^2 = 0.07$, $P = 0.1315$), the invasion success calculated with the 2000 data was still significantly correlated with the 1999 soil water data for *R. hirta* (sown) ($r^2 = 0.26$, $P = 0.003$), *D. canadense* (sown) ($r^2 = 0.16$, $P = 0.025$) and *D. canadense* (transplanted)

Figure 3 First-year invasion success (percentage cover or seedling survival) of the introduced species shown as a function of the percentage volumetric soil water. Regressions of invasion success vs. soil water availability measured as soil water potential (matric potential) produced virtually identical results (*D. canadense* (transplanted): $r^2 = 0.60$, $P < 0.0001$; *D. canadense* (sown): $r^2 = 0.45$, $P < 0.0001$; *R. hirta* (sown): $r^2 = 0.33$, $P = 0.0005$; *Dalea purpurea* (sown): $r^2 = 0.18$, $P = 0.0168$).

($r^2 = 0.23$, $P = 0.006$), despite the fact that the 1999 water treatment period lasted only 1 month and occurred 12 months earlier. The invasion success of *Dalea purpurea* was not correlated with the 1999 soil water data ($r^2 = 0.02$, $P > 0.40$).

DISCUSSION

Our results show that short-term increases in resource availability can temporarily reduce or suspend competition from resident vegetation, thereby increasing the invasibility of the environment. This short-term fluctuation in resource availability was shown to have a legacy effect, with the impact of high or low resource availability during the establishment phase still evident 12 months later. The primary reason for the legacy effect of the wet or dry spells is their pronounced impact on the survival of the germinating seedlings. In most cases, the majority of seedlings died in the dry plots, leaving few, if any, seedlings to contribute to the cover of the species in the plot the following year, whereas the seedling survival was high in the wet plots, leaving many plants to contribute to the cover in the second year.

The results also show that a disturbance that kills or debilitates the resident vegetation can enhance a positive legacy effect produced by a short-term pulse in resource availability, or ameliorate a negative effect produced by a short-term decrease in resource availability. For example, although the 1999 cover of *R. hirta* was lower in dry weeded plots than in wet unweeded plots, those seedlings that

survived the 32-day drought in the weeded plots exhibited a higher subsequent growth rate than those in the wet unweeded plots, as evidenced by the much higher rate of flowering in the weeded plots (Fig. 4). Those few seedlings that survived the 32-day drought in the unweeded plots continued to experience competition from the resident vegetation, did not enjoy the increased growth rate afforded by weeding and none of these plants flowered in 2000.

Similarly, the high establishment success of the seedlings in the wet weeded plots in 2000 was enhanced by increased subsequent growth, and these plants flowered at a much higher rate than those in the wet unweeded plots (Fig. 4), even though plants in both groups enjoyed similar initial establishment success in 1999 due to the comparable wet environments (Table 1, Fig. 2). Thus, the important impact of a short-term fluctuation in resource availability (water) on invasion success is the effect on initial seedling survival via changes in competition intensity. A disturbance that killed the resident vegetation generally enhanced the initial seedling establishment when gross resource supply (water) was low, and produced a longer term impact by enhancing the subsequent growth of surviving seedlings. Although the old field resident vegetation was re-establishing itself into the weeded plots in 2000, these plots still contained less cover of the resident vegetation than the unweeded plots in 2000. Thus, the mechanism by which disturbance increased survival and growth in this study is probably via the increase in light and soil resources (water, nitrate, NH_4) that resulted from the initial elimination of resource uptake (Table 1) and, over a longer time span, the comparatively reduced resource uptake by the re-establishing old field vegetation.

Although the resource manipulated in this study was water, other studies have shown that the addition of nitrogen also facilitates invasion (Hobbs & Atkins 1988; Maron & Connors 1996). We believe that it is the temporary elimination or substantial reduction of competition, due to an increase in resource availability, that is the primary mechanism responsible for an increase in invasibility in a plant community. This proposal may help to unify previous ideas regarding invasibility. The reason that disturbances often facilitate invasions (Crawley 1987) may be due to an increase in resource availability caused by a reduction in resource uptake by the resident vegetation killed or debilitated by the disturbance (Grime 1977), or by a pulse of new resources, e.g. nutrients from a flood (Day *et al.* 1988).

The proposed mechanisms affecting invasibility — fluctuating resources and competition — are believed to operate at a small scale, e.g. the plant neighbourhood during the establishment phase of new plants. Thus, the reason why field experiments often show that species richness reduces invasibility (Tilman 1997; Naeem *et al.* 2000) may be due to

the fact that resources do not fluctuate much over the small spatial and temporal scales of the experiments, and thus competition in the species-rich plots and neighbourhoods may remain consistently high due to the ability of the resident plants to consistently sequester most of the resources. However, over larger spatial and temporal scales, resource availability, and hence competition, probably does fluctuate, resulting in periodic increases in the invasibility of the environment. This increase in invasibility may occur temporarily throughout the entire environment due to large-scale disturbances or resource pulses, or it may occur more or less continually in the environment, in a sort of shifting mosaic of invasibility, due to ongoing small disturbances that increase resource availability at the neighbourhood scale, e.g. the soil mounds produced by burrowing animals. This may explain why some resource-rich natural communities with a high diversity of native species also contain a high number of introduced species (Stohlgren *et al.* 1999). That is, the same processes that permit or promote high species richness of the resident community in the first place probably play an important role in facilitating invasions by novel species.

Species richness was greater in the wet than in the dry plots in this study. Given that the water treatment was imposed for just 32 days and that species richness was measured only a few weeks following the treatment, it is doubtful that the difference in species richness can be attributed to the water treatment; it is more likely a random sampling effect. In any case, invasion success was not correlated with species richness or species diversity (Shannon index) for any species. Thus, there was no evidence that an increase in species richness or diversity reduced invasibility at the temporal and spatial scale of the experiment. In fact, invasion success (and hence invasibility) was greater in the more species-rich wet plots than in the dry plots. It should be noted that one or two grass species accounted for more than 55% of the vegetation cover in each of the unweeded plots, and for more than 70% cover in all but one of the unweeded plots. Thus, the species diversity of the plant neighbourhoods for the introduced species (*sensu* Naeem *et al.* 2000) would have been low in most of the plots. Under these conditions, one might not expect to see much of a negative relationship between invasibility and plot species richness. It is conceivable that more diverse vegetation might reduce soil water, and hence invasibility, under very stable conditions. However, the fluctuations in water availability (dry and wet) in this experiment overwhelmed any existing diversity effect. Because the magnitude of these fluctuations are within the bounds of natural variation over a 1-month period in mid-summer, the results show that fluctuating resource availability can temporarily override any existing diversity effect on invasibility in this environment.

Because propagule pressure was intentionally controlled in this study, we could not measure the impact of this factor on invasion success. Other studies have shown that propagule pressure is a major determinant of invasion success (Williamson 1996; Levine 2000). We believe that it is probable that plant invasions most commonly occur when high propagule pressure from the introduced species coincides with a period of high invasibility in the host environment, the latter due to an increase in resource availability that reduces competition from the resident vegetation. Factors that would increase invasibility are those that would increase resource availability, either by increasing gross resource supply faster than the resident vegetation can capture it (e.g. via increased precipitation or eutrophication) or by decreasing resource uptake by resident vegetation (e.g. via mortality or debilitation of resident vegetation caused by disturbances, herbivory or disease).

In conclusion, the results emphasize the important role that history may play in the invasion process, particularly the occurrence of stochastic, short-lived events that temporarily reduce or suspend competition and increase invasibility. This indicates that it may be very difficult, or even impossible, to reconstruct the ecology of particular invasions after the fact.

ACKNOWLEDGEMENTS

We thank Claudia Curran, Andy Miller, Andrea Tietmeyer and David Bosanko for their help in the field, Oliver Schabenberger for guidance on the split-plot analyses and Phil Grime, Ken Thompson, Anne-Helene Prieur-Richard, Marcel Rejmanek, Shahid Naeem and an anonymous reviewer for their thoughtful comments on the manuscript. This research was supported by the National Science Foundation grant DEB-9873673 (M.A.D.).

REFERENCES

- Crawley, M.J. (1987). What makes a community invulnerable?. In: *Colonization, Succession, and Stability*, ed. Gray, A.J., Crawley, M.J. & Edwards, P.J. London: Blackwell Scientific, pp. 429–453.
- Davis, M.A., Grime, J.P. & Thompson, K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.*, 88, 528–534.
- Davis, M.A. & Thompson, K. (2000). Eight ways to be a colonizer; two ways to be an invader: a proposed nomenclature scheme for invasion ecology. *Bull. Ecol. Soc. Am.*, 81, 226–230.
- Davis, M.A., Wrage, K.J. & Reich, P.B. (1998). Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. *J. Ecol.*, 86, 652–661.
- Day, R.T., Keddy, P.A., McNeil, J. & Carleton, T. (1988). Fertility and disturbance gradients: a summary model for riverine marsh vegetation. *Ecology*, 69, 1044–1054.
- Elton, C.S. (1958). *The Ecology of Invasions by Animals and Plants*. London: Methuen.
- Grigal, D.F., Chamberlain, L.M., Finney, H.R., Wroblewski, D.V. & Gross, E.R. (1974). *Soils of the Cedar Creek Natural History Area. Miscellaneous Report 123*. St. Paul, MN: University of Minnesota Agricultural Experiment Station.
- Grime, J.P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Naturalist*, 111, 1169–1194.
- Hobbs, R.J. & Atkins, L. (1988). Effects of disturbances and nutrient addition on native and introduced annuals in plant communities in the Western Australia wheatbelt. *Aust. J. Ecol.*, 13, 171–179.
- Levine, J.M. (2000). Species diversity and biological invasions: relating local process to community pattern. *Science*, 288, 852–854.
- Lonsdale, W.M. (1999). Global patterns of plant invasions and the concept of invasibility. *Ecology*, 80, 1522–1536.
- Markham, J.H. & Chanway, C.P. (1996). Measuring plant neighbor effects. *Funct. Ecol.*, 10, 548–549.
- Maron, J.L. & Connors, P.G. (1996). A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia*, 105, 302–312.
- Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T. & Gale, S. (2000). Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos*, 91, 97–108.
- Ritchie, M.E. (2000). Nitrogen limitation and trophic vs abiotic influences on insect herbivores in a temperate grassland. *Ecology*, 81, 1601–1612.
- Shannon, C.E. (1948). The mathematical theory of communication. In: *The Mathematical Theory of Communication*, ed. Shannon, C.E. & Weaver, W. Urbana: University of Illinois Press, pp. 3–91.
- Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. (1999). Exotic plant species invade hot spots of native plant diversity. *Ecol. Monogr.*, 69, 25–46.
- Thornley, J.H.M. & Johnson, I.R. (2000). *Plant and Crop Modelling*. Caldwell, NJ: The Blackburn Press.
- Tilman, D. (1993). Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology*, 74, 2179–2191.
- Tilman, D. (1997). Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, 78, 81–92.
- Williamson, M. (1996). *Biological Invasions*. London: Chapman & Hall.
- Williamson, M. (1999). Invasions. *Ecography*, 22, 5–12.

BIOSKETCH

Mark Davis's research interests include plant invasions, plant competition along resource gradients, tree–grass interactions in semiarid environments and how these phenomena may be affected by changes in precipitation, nitrogen deposition and atmospheric levels of carbon dioxide.

Editor, M. Rejmanek

Manuscript received 14 March 2001

First decision made 10 April 2001

Second decision made 11 May 2001

Manuscript accepted 23 May 2001