

Plant colonization windows in a mesic old field succession

Bartha, Sándor^{1*}; Meiners, Scott J.²; Pickett, Steward T.A.³ & Cadenasso, Mary L.³

¹*Institute of Ecology and Botany, Hungarian Academy of Sciences, Vácrátót, Hungary;*

²*Department of Biological Sciences, Eastern Illinois University, Charleston, IL, USA; E-mail cfsjm2@eiu.edu;*

³*Institute of Ecosystem Studies, Millbrook, NY, USA; E-mail picketts@ecostudies.org; cadenassom@ecostudies.org;*

**Corresponding author; E-mail sanyi@botanika.hu*

Abstract. Closed canopy vegetation often prevents the colonization of plant species. Therefore the majority of plant species are expected to appear at the initial phase of post-agricultural succession in mesic forest environment with moderate levels of resources. This hypothesis was tested with data from the Buell-Small Successional Study, NJ, USA, one of the longest continuous fine-scale studies of old-field succession. The study started in 1958, including old fields with different agricultural histories, landscape contexts, and times of abandonment. In each year of the study, the cover values of plant species were recorded in 48 permanent plots of 1 m² in each field. We analysed the temporal patterns of colonization at plot scale and related these to precipitation data and other community characteristics. The number of colonizing species decreased significantly after ca. 5 yr, coinciding with the development of a continuous canopy of perennial species. However, species turnover remained high throughout the whole successional sequence. The most remarkable phenomenon is the high inter-annual variation of all studied characteristics. We found considerable temporal collapses of vegetation cover that were synchronized among fields despite their different developmental stages and distinctive species compositions. Declines of total cover were correlated with drought events. These events were associated with peaks of local species extinctions and were followed by increased colonization rates. The transitions of major successional stages were often connected to these events. We suggest that plant colonization windows opened by extreme weather events during succession offer optimum periods for intervention in restoration practice.

Keywords: Community dynamics; Local colonization; Local extinction; Long-term study; New Jersey; Permanent plot; Spatial synchrony; Species turnover; Time series; Vegetation dynamics.

Nomenclature: Gleason & Cronquist (1991).

Abbreviation: BSS = Buell-Small Succession Study.

Introduction

Restoration management often starts on bare surfaces where the simultaneous re-establishment of vegetation cover and diversity is necessary. In many applications, ensuring the fast return of vegetation cover often has priority for preventing soil erosion. The reconstruction of prior species composition and vegetation structure needs longer time, typically decades (Luken 1990; Prach et al. 1999; Schulz & Wiegand 2000; van Diggelen et al. 2001). Community re-assembly, and consequently the success of restoration, depends on the interactions between colonizing (or invasive) species and the established vegetation matrix (Crawley 1987; Rejmánek 1989). Inverse relationships between colonization success and the biomass or total cover of the resident community have been reported from various plant communities (Brenner et al. 1984; Biondini & Redente 1986; Peart 1989; van der Putten et al. 2000; Foster 2001; Verheyen & Hermy 2001). Similarly, experiments have shown that removing biomass increases colonization rates, species turnover and diversity (Iverson & Wali 1987; Gibson & Brown 1991; Chytrý et al. 2001), while fertilizer treatments have the opposite effect (Biondini & Redente 1986; Tilman 1993; Wilson & Tilman 2002). These data indicate that increasing vegetation cover and diversity are conflicting goals for restoration ecology because the successful establishment of continuous plant cover may prevent the colonization of new species.

The term 'regeneration window' (Gross 1980) or 'plant invasion window' (Johnstone 1986) was coined to characterize the interactions of colonizing species and resident vegetation and the conditions that offer special opportunities for species to enter into community. Most studies (e.g. Gross 1980; Rankin & Pickett 1989; Kollmann 1995; Eriksson & Fröberg 1996; Burke & Grime 1996) analysed the specific life-history characteristic of particular species; mainly the safe-site requirements of their seedlings (*sensu* Harper 1967) or in a broader sense their regeneration niches (Grubb 1977). A more holistic meaning of the term was used by Johnstone (1986) for characterizing the overall invasibility of communities. In this

paper we are interested in community level patterns of colonizations, and therefore, we use Johnstone's definition. To avoid confusion with studies focusing on exotic species invasions, we will use 'colonization window' instead of 'invasion window'.

Understanding succession provides a valuable knowledge base for restoration (Luken 1990; Prach et al. 1999, 2001). The current paradigm within successional literature emphasizes the importance of spatio-temporal dynamics, i.e. the role of specific site histories, landscape contexts, and episodic events (Pickett et al. 1992, 2001). However, spatio-temporal contingencies are typically lacking from generalizations gained from chronosequence studies (e.g. Peet 1981; Inoyue et al. 1987; Peet & Christensen 1988; Burrows 1990; Osbornová et al. 1990). These generalizations report simple, predictable trends in succession. In contrast, continuous permanent plot records show considerable temporal variation of the same characteristics (Austin 1981; Pickett 1982; Bornkamm 1988; Prach & Pyšek 2001).

In this paper we will examine data from the Buell-Small Succession Study (BSS) – a long-term, fine-scale study of post-agriculture succession in central New Jersey which provides an unique opportunity for studying temporal variations and contingencies within vegetation (Pickett et al. 2001). Because BSS began with an existing seed bank and an adjacent old-growth forest as a source of propagules, it is reasonable to expect that most species will appear early in succession, before closure of the plant canopy. In fact, BSS was originally designed to test Egler's initial floristic composition hypothesis (Egler 1954; Pickett et al. 2001). Quantitative tests of Egler's hypothesis using the BSS data (Myster & Pickett 1988) have focused on early stages of succession. Therefore, little is known about the pattern of colonization and establishment in later successional stages. Vegetation cover developed quickly and became closed early under the mesic conditions of the BSS, however the degree of canopy closure fluctuated between years as was indicated by multiple peaks of total cover (Pickett 1982). Due to the temporal variability of vegetation canopy we expect some fluctuation of colonization success as well, i.e. we hypothesize that colonization windows may not be restricted to early successional stages. This study examines the following questions: 1. Do plant colonization opportunities change over successional time? i.e. what is the magnitude of fluctuation of colonization rate over succession? 2. How is the temporal variation of total cover, colonization and extinction related among old fields of different initial conditions? Are these patterns synchronized by rainfall variability? 3. Are transitions in species dominance mediated by the fluctuation of rainfall and its influences on colonization dynamics?

Study site

The site of the Buell-Small Successional Study (BSS), one of the longest continuous studies of old field succession, comprises ten old fields around the Hutcheson Memorial Forest, an old-growth forest located 11 km from New Brunswick, NJ, USA (40°30' N, 74°24' W). The climate is subcontinental temperate with 1120 mm precipitation distributed evenly throughout the year. Mean annual temperature is 11.7 °C, mean January temperature is 0 °C, mean July temperature is 24 °C. Soil is silt loam, shallow, poorly horizonated, endodynamomorphic soil. The sizes of fields range from 0.5 ha to 1 ha. Within each of the ten fields, 48 permanent plots are arranged in a regular pattern that varies somewhat with the shape of the field. Fields were abandoned as pairs in alternate years from 1958 to 1966. The fields differed in season of abandonment (autumn or spring), final crop (hay field or row crops) and soil treatment (plowed or intact vegetation). Vegetation was sampled yearly in late July or early August from 1958 to 1979, and in alternate years since 1980. At each sampling, the percent cover of all species present in the permanently marked 0.5 m × 2.0 m plots was recorded. For the present study we choose six old fields that have a similar landscape context – all are adjacent to the old growth forest (Fig. 1). Their other characteristics, including last crop, mode and season of abandonment, and the times of abandonment were different (Table 1). Vegetation data were analysed for the period between 1967 and 1979, when all fields were sampled annually. Data from the New Brunswick weather station < www.ncdn.noaa.gov > indicated that rainfall in the area varies considerably between years (Fig. 2). From this data, we defined drought as a month with precipitation less than 60% of the long-term average for that month.

Due to the mesic climate, vegetation cover increased rapidly after abandonment of the agricultural fields. Total cover exceeded 100% very early in the succession and increases further, eventually stabilizing around 150% (Meiners et al. 2002). Field scale species richness showed a slight increasing trend over time while the local richness remained the same, fluctuating around 12-13 species per plot. The closed multilayered canopy involves a highly competitive environment (Bartha et al. 2000). Increasing species richness at the field scale concurrent with constancy of species richness at the plot scale suggest a dynamic environment with high species turnover and spatial differentiation. For details about other post-agricultural vegetation trends see Pickett (1982) and Pickett et al. (2001).

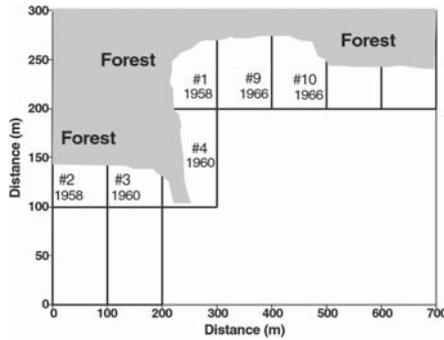


Fig. 1. Schematic map of the study site with the array of abandoned fields. Numbers #1, #2, ..., #10 refer to the particular old fields. The years of abandonments are also indicated.

Methods

Within each field, total cover was calculated as mean value per quadrat in a particular year. Species richness was considered at two different scales: plot scale: mean value per quadrat, and field scale: total number of species in all quadrats within a field. The cumulative number of species was defined at field scale as the number of species in year (*t*) plus all newly arrived species in the next year (*t* + 1). Local colonization was calculated as the number of species appearing in a plot in year (*t*) that were not present in the previous (*t* - 1) year. Percent rate of local colonization was expressed as the number of new species appearing in a plot in year (*t*) divided by the number of species present in year *t*. Percent rate of local extinction was expressed as the number of species disappearing from that plot between year (*t* - 1) and year (*t*) divided by the number of species present in year (*t* - 1) (cf. Gibson & Brown 1991). For each field, the mean percent colonization rate and mean percent extinction rate were calculated. All analyses were restricted to the vascular flora.

For measuring synchrony of temporal fluctuations of given characteristics between fields we used a simple index proposed by Buonaccorsi et al. (2001).

A_{ij} = (number of times series *i* and *j* move in the same direction)/(*T* - 1), i.e. it measures how the two series change together over *T* time points. A_{ij} ranges between 0 and 1, where 1 means maximum synchrony.

Table 1. Characteristics of the old fields. Year = year of abandonment; Mode, season = mode and season of abandonment.

Old field	Year	Final crop	Mode, season	% edge in forest
#1 C3	1958	Soybean & sorghum	Unplowed, autumn	44.6
#2 D1	1958	Soybean & sorghum	Unplowed, autumn	36.1
#3 D2	1960	Soybean & sorghum	Unplowed, spring	37.8
#4 D3	1960	Soybean & sorghum	Plowed, spring	27.0
#9 C4	1966	Soybean	Plowed, autumn	28.7
#10 C5	1966	Soybean	Unplowed, autumn	31.1

Results

Plant colonization windows over time

There is an open colonization window at the beginning of succession, with many species appearing yearly in the early stage (Fig. 3a). After about 5 yr, this window began to close, with fewer new species coming every year. The number of colonization events fluctuated between 0 and 10 at the field scale, suggesting short periods of window closing and opening. These data are for a species' first occurrence in a sampling unit, i.e. it does not account for recolonization events. Species accumulation curves are very similar among fields, with fast increases over the first 5 yr and slower increases thereafter (Fig. 3b). Despite the relative closing of early successional window for colonization, the second half of flora (ca. 80 species, most of them perennials) has been collected during the later successional stages.

Considering the local colonization events, the number of new species per year ranged between 0 and 18 at the plot scale. In the period between 1967 and 1979 when all fields were sampled annually, the mean local colonization varied between 24.0% and 54.9% (Fig. 4a), while the mean local extinction ranged between 20.3% and 52.7% (Fig. 4b). The total cover of vegetation was always above 100 percent during this period (Fig 4c). However, the degree of closure varied between 100 and 210 %.

Synchrony of community characteristics

When rates of colonization and extinction are treated as a function of calendar date rather than successional age, we found remarkable synchrony among fields in the temporal courses of mean local colonizations and

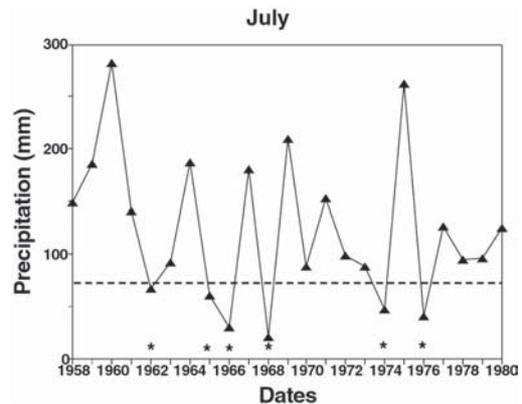


Fig. 2. Time series 1958-1980 of total rainfall in July, the month with the largest long-term average precipitation. The mean July rainfall over this period was 123 mm. Horizontal dashed line indicates the 60% of mean precipitation. Years with less than 60% of mean rainfall were defined as drought years.

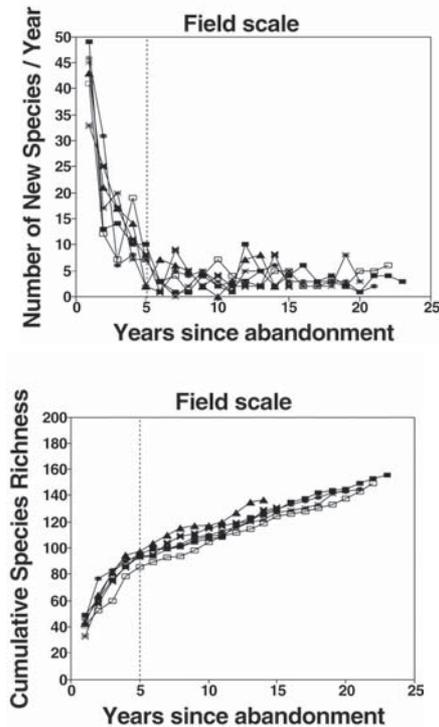


Fig. 3. The number of new species and species accumulation curves over successional time at the scale of abandoned fields.

extinctions (including recolonization events, Table 2). Similarly, when total cover is considered as function of calendar date, there is a similar synchrony among old fields despite their different initial conditions, developmental stages and species compositions. The index of synchrony between pairs of old fields calculated for the characteristics depicted in Fig. 4a-c has values mostly above 0.75 indicating high degree of synchrony (Table 2). One of the youngest fields, Field #9 has smaller values with all other fields, i.e. it is less synchronized. There were considerable temporal collapses of vegetation cover in drought years (Fig. 4c).

Community fluctuation and the replacement of dominant species

Newly colonizing species or those which are undergoing localized extinction are typically of low abundance. Therefore, we expect that species with low cover values are the major contributors to extinction and colonization rates. However, our analyses showed that the abundances of dominant species were also affected by drought events and consequently were correlated with community observed fluctuations. We found that transitions between major successional stages were connected with drought events in Field #1 (Fig 5a, b). It is clear that

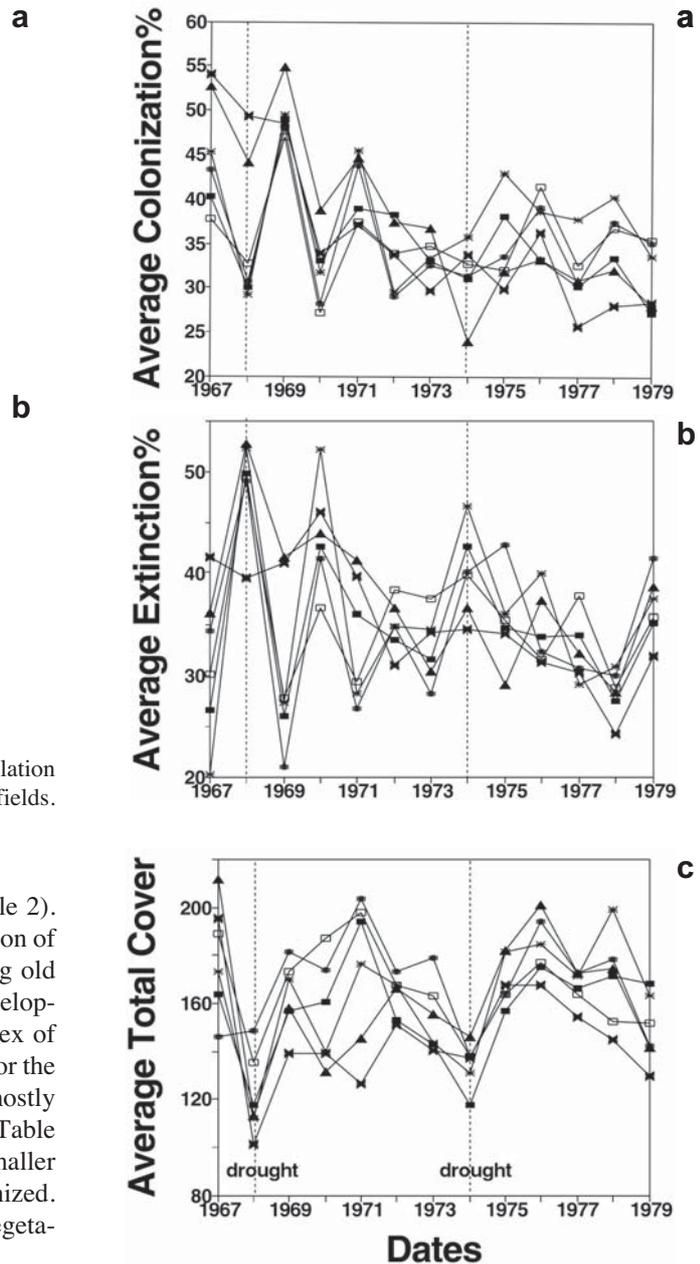


Fig. 4. Time series of mean rate of colonization and extinction, and mean total cover estimated at quadrat scale in the six old fields between 1967 and 1979, the period when all fields were annually sampled. Colonization % is a ratio of the number of species gained per total number of species in the quadrat. Extinction % is a ratio of the number of species lost from the quadrat per number of species in the quadrat in the previous year. Vertical dashed lines indicate the years with drought.

there is a relationship between the transition of species dominance and the drought in 1962. The first stage is represented by annuals and short-lived perennials (e.g. *Ambrosia artemisiifolia*, *Plantago rugelii*, *Daucus carota*),

Table 2. Index of synchrony between old fields.

Pair of fields	Temporal pattern of total cover	Pair of fields	Temporal pattern of colonization	Pair of fields	Temporal pattern of extinction
#1 #2	.917	#1 #2	.750	#1 #2	.833
#1 #3	.750	#1 #3	.750	#1 #3	.917
#1 #4	.917	#1 #4	.833	#1 #4	.833
#1 #9	.750	#1 #9	.750	#1 #9	.583
#1 #10	.833	#1 #10	.833	#1 #10	.833
#2 #3	.667	#2 #3	1.000	#2 #3	.917
#2 #4	.833	#2 #4	.750	#2 #4	.667
#2 #9	.833	#2 #9	.833	#2 #9	.750
#2 #10	.750	#2 #10	.833	#2 #10	.667
#3 #4	.833	#3 #4	.750	#3 #4	.750
#3 #9	.500	#3 #9	.833	#3 #9	.667
#3 #10	.750	#3 #10	.833	#3 #10	.750
#4 #9	.667	#4 #9	.583	#4 #9	.417
#4 #10	.917	#4 #10	.833	#4 #10	.833
#9 #10	.750	#9 #10	.667	#9 #10	.583

while the second stage is dominated by perennial grasses and decumbent herbs (e.g. *Poa compressa*, *P. pratensis*, *Hieracium caespitosum*). Woody vines (e.g. *Toxicodendron radicans*, *Lonicera japonica*) start to increase after the major drought in 1968. The next major vegetation shift happened around the next drought in 1974. Here the stage of perennial grasses and decumbent herbs were replaced by the next vegetation stage characterized by a complex patchwork of erect herbs, woody vines, shrubs and trees (e.g. *Solidago juncea*, *Toxicodendron radicans*,

Lonicera japonica, *Rosa multiflora*, *Cornus florida* and *Acer rubrum*). Similar shifts between the dominance of major functional groups appeared in the other fields as well. However, because of the different initial conditions and the different time of abandonment, the actual stages and their compositions varied. For example, Fields #9 and #10 were 8 years younger than Field #1 and in these fields the exchange between the first and the second stages were coincident with the 1968 drought.

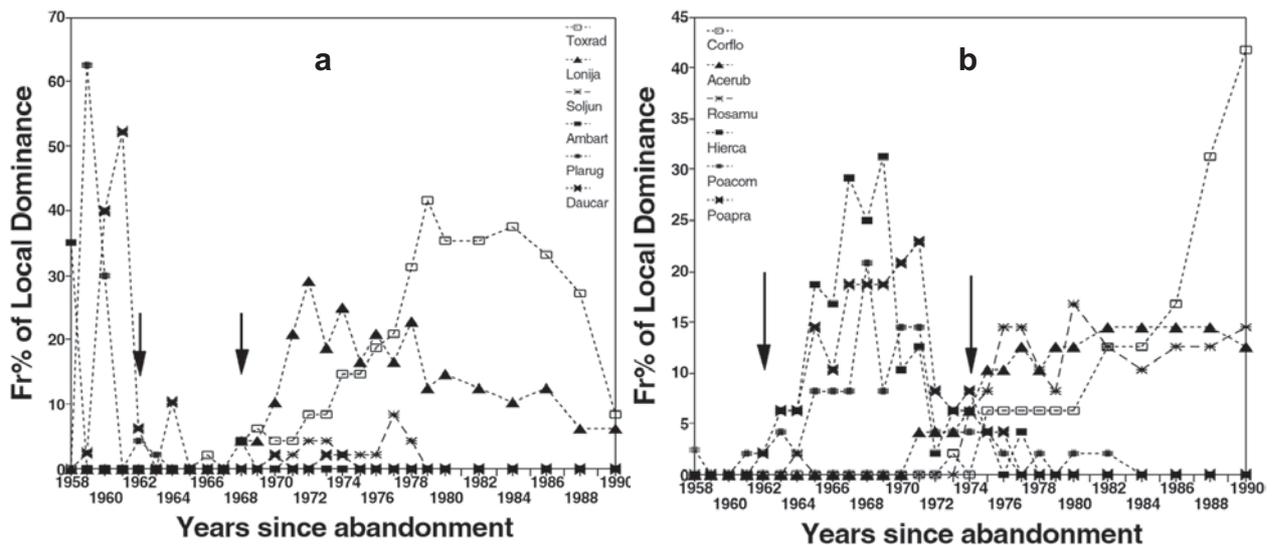


Fig. 5. Temporal pattern of important dominant species in Field#1. The importance of species is shown by the frequency % of quadrats where the particular species are dominant. Vertical arrows indicate years with droughts. **a.** Dominant species of 1st and 3rd successional stages; **b.** Dominant species of 2nd and 3rd successional stages. Abbreviation of species: Toxrad = *Toxicodendron radicans*; Lonija = *Lonicera japonica*; Soljun = *Solidago juncea*; Ambart = *Ambrosia artemisiifolia*; Plarug = *Plantago rugelii*; Daucar = *Daucus carota*; Corflo = *Cornus florida*; Acerub = *Acer rubrum*; Rosamu = *Rosa multiflora*; Hierca = *Hieracium caespitosum*; Poacom = *Poa compressa*; Poapra = *Poa pratensis*.

Discussion

Previous analyses of BSS data found partial support for Egler's initial floristic composition hypothesis. A quantitative test by Myster & Pickett (1988) demonstrated that all annual and biennial species were present in ca. 87% of years during the first 6-yr period. Other studies (Pickett et al. 2001) revealed that woody species can also appear very early in the successional sequence. Although many local colonization events failed, tree species that established early persisted and maintained local dominance in some plots. Recently Wilson (1992) reconsidered Egler's concept and distinguished 'complete' vs. 'pre-emptive' initial floristics. Complete initial floristics assumes that all species are present everywhere in an abandoned field and there are no species arrivals after succession has started. Pre-emptive initial floristics is more realistic, because it assumes spatial variability of initial conditions and emphasizes that species present in a particular locality pre-empt that locale and, consequently, may influence the course of local succession for a long time. Long-term vegetation data of BSS support the validity of pre-emptive initial floristics because of the variability of early successional floristic compositions and multiple successional trajectories found among fields of different initial conditions (Myster & Pickett 1988, 1990). In the present study we extended the analyses to all herbaceous and woody species.

Our results show that 50% of species appeared during the first 5 yr, before perennial species generate a closed canopy. It is clear that there is a plant colonization window in the early successional stage. However, the continuous increase of cumulative species richness indicates that colonization windows are present in the later stages as well.

The rate of colonizations varied considerable between years. Declines of total cover were correlated with peaks of local species extinctions, and were subsequently followed by increased colonization rates, i.e. a colonization window opened after the drought. The synchrony of colonization rates between fields suggests that the opening of colonization windows was due to drought events and not a consequence of intrinsic successional dynamics. The synchrony appeared despite the facts that fields were of different ages and variable composition (Myster & Pickett 1988, 1990). While periods of high extinction rates appear to initiate plant colonization windows, these events may represent transitions away from desired vegetation types (Marrs & Le Duc 2000) and may be in themselves, management concerns. Although drought may induce complex changes, in our case, it had positive overall effect improving the chance of colonization, establishment, and increase of several desired late successional species.

Our results support the general theory of invasibility proposed by Davis et al. (2000). This theory states that fluctuation in resource availability is the key factor controlling invasibility. In periods when resource supply exceed the resource demand of the resident vegetation a window of opportunity is opening for new species to enter the community. Disturbance increase resource availability due to decreasing demand of resident vegetation while eutrophication or weather fluctuation (e.g. wet years) increase gross resource supply. In our case, resource use of resident vegetation might decline due to drought effects as indicated by the correlating events of decreasing total cover and increasing local extinctions in those years. Resource supply (water and nutrients) would increase in the next year with normal or extra precipitation, while resource use by the recovering vegetation would remain low. Remaining available resources could be utilized by the colonizing species. Drought induced resource fluctuation can function during any successional stage, whenever the plant canopy is reduced. This fluctuation may explain the similar, synchronized responses of fields with different age and species composition. Our analysis does not suggest that drought is the exclusive control of colonization dynamics in this system. Other mechanisms such as herbivory, granivory or pest outbreaks may also cause decline in plant cover and therefore open colonization windows. Complex mechanisms with interactions among weather and other community regulators are also possible. However, we expect that effects of animals would be more heterogeneous than rainfall among fields. The remarkable synchronization of temporal patterns across fields is a strong argument for the importance of droughts or other large-scale, system-wide, processes.

Implications for management

Restoration ecology is designed to reverse habitat degradation in a changing world. Restoration practitioners must recognize that target communities are non-equilibrium systems and that restoration must therefore deal with processes rather than states (van Diggelen et al. 2001; Hobbs & Harris 2001). Restoration management based on succession theory endeavours to control successional forces by controlling site availability, propagule availability, and the performance of species (Pickett et al. 1987; Luken 1990; Hobbs & Norton 1996). Due to degradation of natural habitats, propagule limitation has become increasingly important (Zobel et al. 1998; Verhagen et al. 2001; Halassy 2001; Wiegleb & Felinks 2001). When seeds or seedlings have to be introduced artificially, an understanding of the natural controls on establishment success is essential. The success of an introduction depends on the dynamics and states of the resident

vegetation as well as the identity of the colonizer. Descriptive studies and field experiments on the invasibility of vegetation (Crawley 1987; Rejmánek 1989; Peart 1989; Foster 2001) focused on determining invariant trends and simple rules or generalizations with stochasticity and spatial contingencies have rarely been taken into account (but see Meiners et al. 2002). We suggest that the inherent stochasticity of vegetation processes can be used to enhance restoration success.

Our analysis of a long-term permanent plot data set of old field succession revealed high inter-annual variability of vegetation characteristics related to the invasibility of vegetation. In this mesic successional system, a closed canopy of vegetation developed very early following abandonment. Although a closed canopy is expected to prevent colonizations, we recorded considerable colonization during later successional stages.

Half of the species recorded over a 22-yr long succession arrived after the vegetation canopy was already closed. Most of them were native, late successional perennials (including dominant key species). We found ca. 30% inter-annual variation of colonization rate in correlation with the temporal variation of canopy closure, i.e. there was 30% difference in colonization success between 'good' and 'bad' years. Because late successional species often have special habitat requirements (a specialized regeneration niche, *sensu* Grubb 1977), their establishment success is frequently low in early stages of succession when soil and climatic conditions are extreme (Prach 1982). We suggest that the timing of introduction of species into intermediate or late successional systems should be planned with respect to the variability of weather. Based on the theory of Davis et al. (2000), an optimal time for species introduction is a wet year immediately after a drought (or a disturbance). Our analyses in the case of mesic old field succession supported this idea. Furthermore, temporal exchanges of dominant species and the transitions of major successional stages can be connected with extreme weather events. This suggests that restoration activities synchronized with natural weather fluctuations would help to optimize the success of species introductions.

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