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Chapter 9

Succession and Restoration in Michigan Old Field Communities

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At the time of European settlement (1820s), the plant communities of southern Michigan, in the upper-Midwest of the United States, were a mixture of forest and grasslands, the distribution of which was determined by a combination of soil, topographic, and climatic drivers (Albert et al. 1988). A history of repeated glaciations and the moderating effects of being surrounded by three of the Great Lakes of North America resulted in a complex of community types that was more varied than in other states at similar latitude in North America. For example, Comer and others (1995) analyzed notes and maps made by the General Land Office Survey (GLOS) during the mid-1800s and determined that there were ten different natural communities in the area of the W.K. Kellogg Biological Station in southwest Michigan.

Grasslands and oak savannas were extensive in southern Michigan at the time of European settlement and covered approximately 194,000 hectares of the state (Chapman 1984). The prairie systems of southwest Michigan were part of the "prairie-peninsula" (Transeau 1935) that likely developed 4,000–8,000 years ago during an extended drier climatic period, which probably also promoted frequent wildfires (MDMVA 2001; Clark et al. 2002). Although records are scant, it is likely that even at the time of European settlement the extent of grassland communities in southern Michigan was influenced by native Americans (Mascouten and Potawatomi tribes), who commonly set fires to maintain open areas for hunting (Legge et al. 1995). Large-scale conversion of the vegetation came with the settlement of this area in the 1830s by European-Americans, primarily from New England (Gray 1999).

European settlement resulted in the conversion of forest and grassland openings to small farms and villages, and farming (along with forestry) was

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the major economic activity of the area until the mid-1950s. Agricultural statistics for the area report that wheat, followed by corn and oats, were the most common row crops from 1850 to 1953. Since 1954, corn has become the dominant crop grown in this area, with soybeans the second most common crop (Tomecek and Robertson 1996). Few herbicides or pesticides were used in conventional agricultural practices in this area until after World War II. The increase in the availability and use of inorganic fertilizers and pesticides began in the 1950s, interestingly accompanying the transition to corn and soybeans as dominant row crops in the region. These human activities, together with fire suppression and the introduction of nonnative species (e.g., multiflora rose, *Rosa multiflora*, Thunb. ex Murr., and garlic mustard, *Alliaria petiolata* (Bieb.) Cavara and Grande) resulted in increasing fragmentation and degradation of the remaining small areas of pristine habitat in the region. Rising land costs, changes in agricultural markets, and the loss of economic opportunities in rural Michigan over the past thirty years have caused a demographic shift from rural areas to midsized cities (Hathaway 1960; Frey 2005). Suburban sprawl has caused further loss of agricultural land in southern Michigan, creating a new set of challenges for efforts to restore and retain native communities in this area (Knight 1999). There is increasing concern about (and both legal and public support for) the restoration of natural areas in Michigan. However, there are only limited numbers of studies that can be used to guide restoration efforts in this region.

Successional Studies at the W. K. Kellogg Biological Station

The W. K. Kellogg Biological Station (KBS) has a rich history of research related to understanding the mechanisms of succession following the abandonment of agricultural lands. KBS is located in southwest Michigan (42° 24′ N, 85° 24′ W; elevation 288 m) and includes over 1,500 ha of land that reflect the matrix of crop fields, old fields, second-growth forests, wetlands, and small lake systems typical of this region (Burbank and Gross 1992; Tomecek and Robertson 1996). The climate is strongly influenced by the Great Lakes, with an average annual rainfall of 890 mm (about half falling as snow) and a mean annual temperature of 9.7 °C. The principal soils at KBS are Typic Hapludalfs (Austin 1979), and most of the region consists of fertile outwash plain deposits and sandy loam soils from the Wisconsin glaciation events 12,000 years ago (Foster 1992). The station has supported ecological research and teaching since the 1950s, with a growth in these activities in the mid-1960s corresponding with the hiring of a full-time resident director and research faculty.

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An important but unfortunately little-known experiment that demonstrated the importance of land use history was initiated at KBS in the early 1960s (Davis and Cantlon 1969; Foster 1992). John Cantlon, then professor of botany at Michigan State University, initiated a replicated field experiment at KBS (figure 9.1, SF1) to examine the effect of past land use on successional trajectories. This study quantified the long-term effects of a previous experiment designed to evaluate alternative control methods (herbicide, fire) for *Agropyron repens* (*Elymus repens*, quack grass). There were also long-term effects of a walnut tree crop (where *Rhus typhina*, smooth sumac, were planted as nurse plants) on the successional pathways and community composition of this site (Werner 1972; Foster 1992). Analyses of the vegetation dynamics over the six years following abandonment (Holt 1972; Werner 1972), and twenty-five years after abandonment (Foster 1992), revealed the important role of past land use. In contrast to the standard view of successional pat-

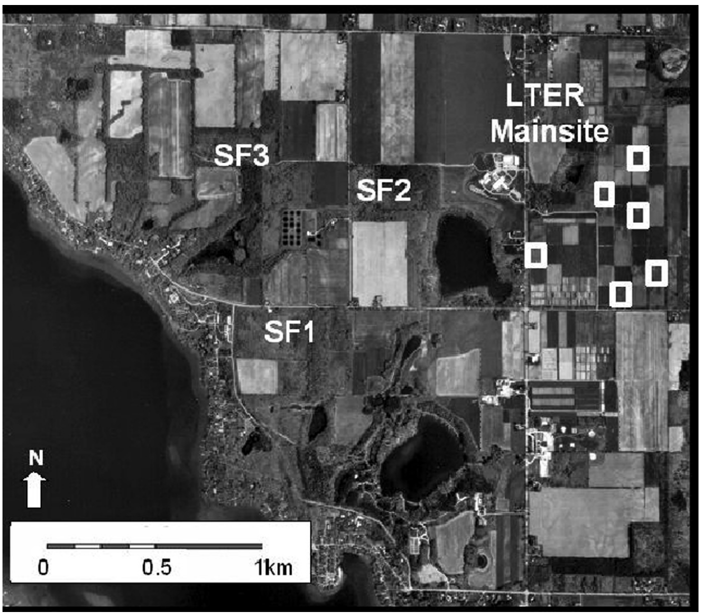

FIGURE 9.1. Aerial photograph of the main site of the W.K. Kellogg Biological Station (KBS) (source: Abrams Aerial Survey, 7 May 1993), with labels indicating locations of successional fields (SF1, SF2, SF3) used for observational studies of old field succession and the KBS Long Term Experimental Research project (LTER) experimental main site, where the replicate experimental successional fields are located (outlined in white). For further details see http://lter.kbs.msu.edu/experimental Design.html.

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terns that predicts consistent transitions from old field, to shrubland, to climax deciduous forest (see Drury and Nesbit 1973 for a critical review of this paradigm for North America), Cantlon's work showed that the trajectory of succession was highly influenced by the land use prior to abandonment and initial patterns of colonization. Sites that had been planted to *Rhus typhina* had higher densities of tree seedlings than other areas (Werner and Harbeck 1982; Foster and Gross 1999). In contrast, areas that had been initially dominated by either *A. repens* or *Poa* species (*P. compressa* or *P. pratensis*), most likely as a consequence of preabandonment herbicide trials done on the site, followed very different successional trajectories.

Subsequent short-term experimental studies in old fields in and around the KBS area have shown the important role that colonization dynamics and seed limitation, particularly traits related to seed dispersal, seed size, and seedling traits (Gross and Werner 1982; Emery 2005; Houseman and Gross 2006), competition from established vegetation (Foster and Gross 1997; Foster and Gross 1998; Foster 1999), and small-scale disturbance (Gross 1984; Goldberg and Gross 1988) can play in determining the arrival time and persistence of species in successional fields in this area. However, deriving generalizations about successional dynamics from these studies is difficult because they were all conducted at different times in old fields of various ages and land use histories. Several authors have commented on the limitation of chronosequences for interpreting successional dynamics because of the likely important (and typically unknown) effects that differences in land use history and spatial location can have on these processes (e.g., Pickett et al. 2001).

Unfortunately there are few studies in North America in which a replicated set of experimental plots has been established to follow long-term successional dynamics. The Buell-Small Succession study established in 1958 by Murray Buell, Helen Buell, and John Small at the Hutcheson Memorial Forest associated with Rutgers University in New Jersey (USA) is a remarkable exception (see chapter 8).

The formation of the Long Term Ecological Research Project (LTER) at KBS let us address concerns about the general lack of replicated studies on old field succession by developing long-term monitoring of successional dynamics of old field communities. This has allowed us to test hypotheses regarding how ecological processes vary in old fields and to explore hypotheses about how plant communities develop in this region. In the following sections, we describe both experimental and observational studies from the KBS LTER and discuss how the results from each can contribute to a greater understanding of successional processes, which in turn can inform restoration of native grasslands and forests in this area.

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Old field Succession Studies at the KBS LTER Site

The KBS Long Term Ecological Research site (figure 9.1) was established in 1988 with a grant from the U.S. National Science Foundation. The project focuses on understanding ecological processes within row crop agriculture and comparing these agricultural systems to unmanaged old fields and forests (e.g., Robertson et al. 1997). The KBS LTER main site was established in a 42 ha field that had been cultivated in row crop agriculture for more than 100 years (mostly continuous corn) (Robertson et al. 1997). The entire site was planted to corn in 1987, followed by a winter rye (*Lolium*) cover crop, and then planted to soybeans in 1988. In spring 1989, treatment plots were established after plowing the entire site. Four treatments on the main site are different management systems for annual row crop agriculture (conventional to organic), and two are perennial crops (alfalfa and poplars) managed for biomass production. One treatment was established to examine early-successional, old field plant dynamics by abandoning plots after spring tillage in 1989 (six replicate, 1 ha plots; see Huberty et al. 1998 for details). To slow woody plant invasion and to keep the old field plots in a herb-dominated successional state, prescribed burns were initiated in 1997, and these plots are now burned in the spring two out of every three years.

Observational Studies of Successional Dynamics in Old Fields at KBS

In 1993, monitoring plots were established in three old fields at KBS that are representative of midsuccessional systems of the area to provide an additional reference base for comparative studies. These sites are sampled at a spatial and temporal scale identical to that of the experimental plots, facilitating comparisons between the younger, experimental plots and older communities. Both the observational and experimental old field systems of the KBS LTER reveal important insights about successional dynamics that can inform efforts to restore native grasslands in the region.

The three reference old fields of the KBS LTER site (figure 9.1) represent a range of prior land uses and times since abandonment, and are typical of the area, providing a general reference for long-term successional dynamics of old fields in the region (figure 9.2a). In each field, a 1 ha, permanent, sampling plot has been established. Plant community composition is determined annually from five 1 m^2 subplots within each large plot. Changes in plant species composition are based on summed species abundances across the five subplots, allowing for more accurate estimates of woody species abundances, as well as grass and forb species composition. A number of soil and ecosystem

(a)

(b)

Figure 9.2. (a)Typical Michigan old field plant community; (b) prescribed burn at the KBS LTER main site experimental successional fields, April 2004.

processes are monitored annually in these fields at the same spatial scale and temporal frequency as in the experimental site.

Successional Field 1 (figure 9.1, SF1) is located in Cantlon Field, a 3 ha field abandoned from agriculture in 1964. As described above, this field has a history of ecological studies dating from the 1960s (Davis and Cantlon 1969; Foster 1992). Cantlon Field was actively cultivated from the 1850s until 1964 in a wheat-alfalfa-corn rotation, except for a walnut tree crop and the

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herbicide application experiment described earlier. After abandonment, *Agropyron repens* and *Rhus typhina* quickly established as dominants, and by 1992 the field was dominated by these species and several exotic cool-season grasses, specifically *Bromus inermis* and *Phleum pratensis* (Burbank and Gross 1992; Foster 1992).

Successional Field 2 (SF2) is located in Louden Field, a 7 ha field abandoned from agriculture in 1948. There is little specific information on land use history of the field before 1911, though it was most likely in row crop cultivation. The field was fallow from 1911–15, and was a sheep pasture from 1915–42. A rotation of corn-oats-wheat was planted in the field from 1942–48, but no fertilizers or herbicides were applied during this time (Stergios 1970). In 1970, vegetation surveys showed that the field was dominated by a combination of *Poa compressa* and *Agropyron repens*, two exotic cool-season grasses (Stergios 1970). By the 1980s, the field was mostly composed of mixed grasses and *Solidago* spp. (Goldberg and Gross 1988). Woody species began to establish in the field in the 1970s (Werner and Harbeck 1982), and tree establishment and growth has continued to the point that the area is codominated by herbaceous plants, oaks (*Quercus* spp.), and black cherry trees (*Prunus serotina*) (Burbank and Gross 1992).

Successional Field 3 (SF3) is located in Turner Field, a 5 ha field last cultivated in a row crop rotation in 1963 (Gross and Werner 1982). Soils in the field are sandy and well drained. In 1992, when the LTER monitoring study was established, the field was dominated by several forb species, including *Hieracium* spp., *Aster pilosus, Solidago* spp., and *Centaurea maculosa*, and a mixture of cool-season grasses. *Prunus serotina*, a native weedy and woody colonizer, was also beginning to establish at this time (Burbank and Gross 1992).

Changes in the composition of the vegetation in each of these three fields have been regularly monitored annually since 1993 (except in 1998–99) as part of the KBS LTER sampling. The three fields differ markedly in aboveground production, species richness, composition, and the abundance of native and nonnative species (figure 9.3). SF3 has almost twice the nonnative species richness as the other two fields, while SF1 has very low native species richness compared with the other two sites. The ratio of native-to-nonnative species has consistently been higher in SF2 than the other two fields, potentially reflecting that it was abandoned from pasture rather than from row crops. Over a ten-year period of LTER monitoring, there were only small changes in species richness and composition in these fields; nonnative species richness declined slightly in SF3, while total species richness, especially of native species, increased in SF2 (figure 9.3).

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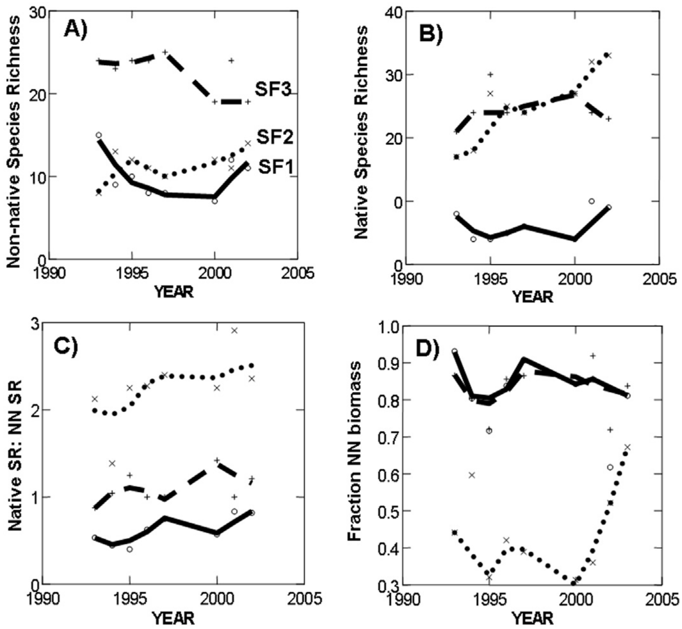

Figure 9.3. Patterns of (a) nonnative and (b) native species richness through time in successional old fields; (c) ratio of native to nonnative (NN) species in each field; (d) fraction of total aboveground biomass contributed by nonnative species. For all panels, SF1 is the solid line, SF2 is dotted, and SF3 is dashed. Fit lines are based on Locally Weighted Scatterplot Smoothing (LOWESS) to indicate general trends in the data.

This stability in composition of the plant community in SF1 is apparent in the comparison of functional composition over ten years, with most of the community consisting of perennial grasses and some perennial forbs (figure 9.4a), and a low turnover of species from year to year (figure 9.4b). SF2, and to a greater extent SF3, are much more dynamic, with large increases in woody biomass from 1993–2003 (figure 9.4a), and associated decreases in biomass of the herb community.

Though it is risky to generalize results from only three sites, differences in community vegetation patterns across fields can be attributed to past land use, successional age, soil fertility and geographic location of these sites. For SF1, Foster (1992) found that weed control practices prior to abandonment (herbicides or fire affected early-successional success of three dominant grasses (*Agropyron repens*, *Poa compressa*, *Poa pratensis*), which maintained dominance even through to 2003. In contrast, SF3 has seen large increases in woody species colonization, despite being abandoned at approximately the

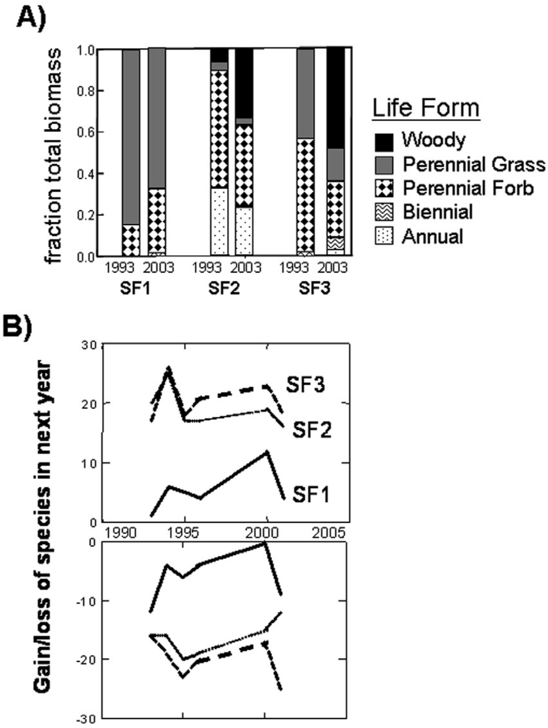

FIGURE 9.4. Change in community composition through time in successional old fields at the KBS. (a) Change in functional group biomass (average aboveground biomass for each field is: SF1: 1993 = 458 g m^{-2}, 2003 = 310 g m^{-2}; SF2: 1993 = 175 g m^{-2}, 2003 = 125 g m^{-2}; SF3: 1993 = 253 g m^{-2}, 2003 = 41 g m^{-2}); (b) species turnover (absolute gain and loss of individual species from year to year) over ten years. SF1 = solid lines, SF2 = dotted lines, SF3 = dashed lines.

same time as SF1. Geographic location may partly explain why SF3 has higher woody biomass than SF1, as SF3 is surrounded by more wooded areas than SF1, which likely allows more opportunities for woody species to invade (Myster and Pickett 1993). SF2 is the oldest field of the three, and has the highest proportion of native species diversity and the lowest nonnative biomass. Interestingly, native diversity is still increasing in this field. Woody species biomass is also increasing, though is lower than SF3. Historically, this field had woodland on only one side (Stergios 1970), which may account for the lower occurrence of woody species in this field.

While differences in the successional trajectories of these three fields can be partially accounted for by prior land use, weed control, and surrounding community types, observational studies cannot identify mechanisms that

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drive differences in successional community composition and trajectory. The replicated, experimental, old field successional plots on the LTER main site help address this shortfall.

Successional Dynamics in Experimental Old Fields

Changes in plant community composition have been documented in the experimental old field plots of the KBS LTER main site (figure 9.1) since 1989. Native and nonnative species richness increased rapidly in the first five years after abandonment but stabilized over the next ten years (figure 9.5). The ratio of native-to-nonnative species has leveled out at around 1:1. Functional composition of the plant communities shows predictable changes from annual-dominated systems to perennial grass- and forb-dominated systems

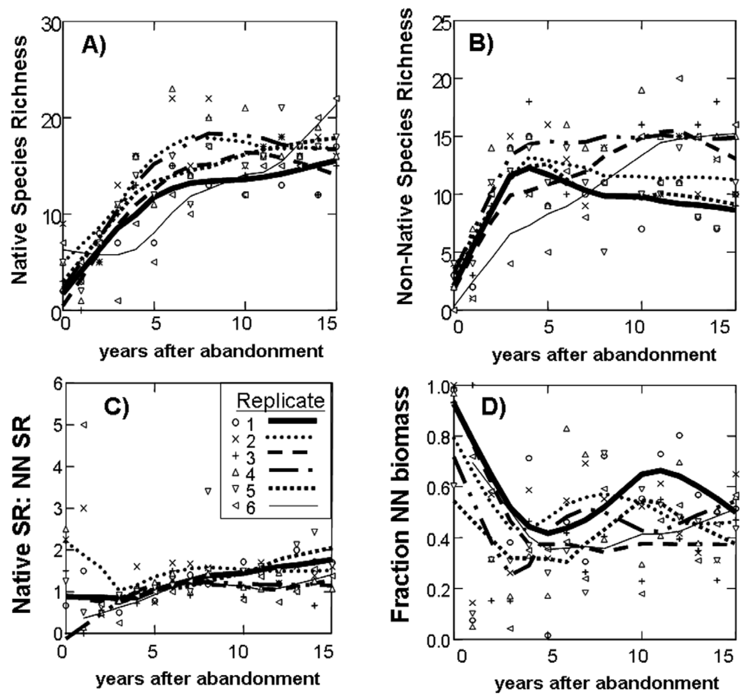

FIGURE 9.5. Patterns of (a) native and (b) nonnative species richness through time in the KBS LTER experimental successional plots; (c) ratio of native to nonnative (NN) species through time; (d) fraction of total biomass contributed by nonnative species. Total aboveground biomass varied between 300–800 g m^{-2} in the most recent five years of sampling. Fit lines are based on Locally Weighted Scatterplot Smoothing (LOWESS) to indicate general trends.

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through time (see Huberty et al. 1998). We used Non-metric Multidimensional Scaling (NMS)(Legendre and Legendre 1998; McCune et al. 2002) to look at changes in species composition in these plots through time. NMS is a multivariate ordination technique that is similar to Principal Components Analysis but uses ranked distances between plots to estimate similarity to avoid assumptions about linearity or unimodality of the community data. Although the six replicate plots started with very different initial community composition, after five or six years they converged to very similar community assemblages (figure 9.6).

Other studies of community assembly and succession have demonstrated that initial community composition can have persistent effects on community diversity and functional structure (Drake 1990; Young et al. 2001). The

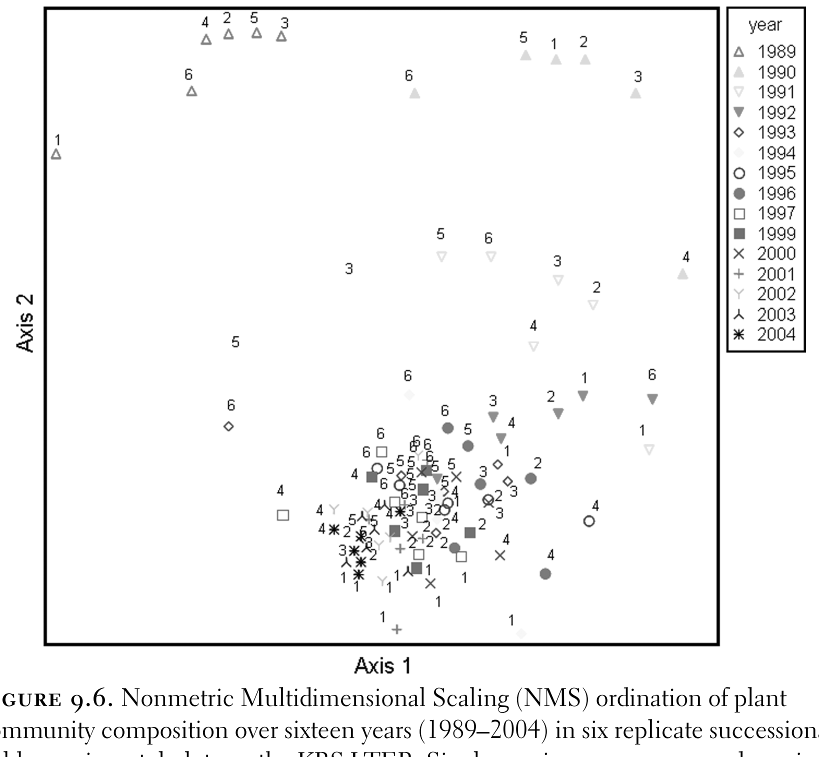

FIGURE 9.6. Nonmetric Multidimensional Scaling (NMS) ordination of plant community composition over sixteen years (1989–2004) in six replicate successional field experimental plots on the KBS LTER. Single species occurrences and species that had less than 1g biomass total over all years and plots were excluded from this analysis. Points are identified by replicate (plot) number (1–6); symbols indicate years. The closer two points are in the ordination, the more similar they are in community composition. The NMS ordination explained 73% of the variation in community composition among plots in two axes.

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similarity in past land use and landscape distribution of these plots, and the use of prescribed burning to control woody plant invasions, may explain the convergence in community structure among replicates despite the initial differences in composition.. Regular disturbances, such as fire, can be an important filter, overriding interactions among species (Hobbs and Huenneke 1992; Booth and Swanton 2002). Indeed, a comparison of community composition in 1996, before burning began, showed strong differences among replicates, especially in woody species invasions (Foster and Gross 1999), which have diminished since regular burning was initiated in 1997.

Old Field Succession and Restoration

While the old field successional studies at the KBS LTER site were not designed to address issues related to grassland restoration these two approaches to studying successional trajectories offer insight into what management efforts could be applied to restore native grassland species and communities on abandoned agricultural land of the midwestern United States. These studies reinforce the importance of understanding the role of land use history, geographic location, disturbance regimes, and seed sources (native and nonnative) in structuring plant communities.

The marked differences in community composition among the three reference old fields suggest that variability in site location and history can lead to very different plant communities. This may be a consequence of differences in initial plant community composition due to cultivation practices or use of herbicides (Foster 1992), compounded by differences in seed sources in the surrounding landscape. Although change in species composition in later-successional old fields is typically slowed once perennials have established (Huston and Smith 1987), our data show that even forty to sixty years after abandonment, species composition in old field communities is very dynamic (figure 9.4). Invasion of woody species may account for this, as the establishment of a canopy by trees and shrubs can alter the abundance of understory herbaceous species (e.g., Werner and Harbeck 1982). Invasion rates of woody species can be influenced by landscape position and the structure of surrounding communities. The higher rate of tree invasion into SF3 likely is due to the proximity of wooded areas that surround this site; however, how this relates to the decline in nonnative (mostly herbaceous) species richness over the past ten years in this field in this site is not apparent (figure 9.3).

Despite large initial differences in plant species community composition, all six experimental old field succession plots converged on similar plant communities within ten years. This convergence may be due to (or facilitated

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by) the introduction of prescribed burning in the early 1990s, as these fields showed strong evidence of diverging prior to the establishment of the burning treatments that was related to differences in the establishment of woody species across replicates (Foster and Gross 1999). Both the season and frequency of burns on the LTER main site may be important explanatory variables for the convergence in community composition and relatively low species richness in the experimental plots. In the upper-midwestern United States, prescribed fires are often implemented in early spring, before the greening of vegetation (Howe 1995). These early-season burns often increase dominance of warm-season grasses, while suppressing nondominant forbs (Copeland et al. 2002). Frequent fires, such as the near-annual burning on the KBS LTER, may reinforce convergence of the plant communities. However, Collins (2000) showed that annual burning of tallgrass prairie systems in the United States caused strong directional change in plant communities compared with sites which were burned on four or twenty year cycles.

The almost-annual prescribed fires on the KBS LTER may be able to stabilize plant community composition by regulating nonnative species dynamics. Emery and Gross (2005) found that annual burning reduced the population growth rate of an invasive species, though alternate-year burning had no effect. Yet the reintroduction of fire into degraded grasslands or successional fields may not necessarily lead to the reestablishment of native grassland or savannah communities (Anderson et al. 2000; Suding et al. 2004; Suding and Gross 2006). Initial conditions and feedbacks created by the establishment of nonnative species or shifts in abundance of native species can create strong barriers to restoration efforts and send communities along alternate trajectories (Young et al. 2001; Suding et al. 2004).

It is interesting to note that nonnative species abundances in all replicates of the LTER experimental old fields appear to stabilize around 50% cover soon after field abandonment, suggesting that spread in dominance of nonnatives is not necessarily a consequence of initial invasion. One goal of restoration is to increase the native to nonnative species ratio in an area (Suding and Gross 2006), especially in sites where total elimination of nonnative species is impractical (D'Antonio and Meyerson 2002). It is encouraging that nonnative species cover has stabilized, though fire alone seems to be ineffective at further reducing cover of nonnatives in these plots. Some restoration studies have shown that variable fire regimes (e.g., alternating spring and summer burns) can increase native plant diversity (Copeland et al. 2002). Several other restoration studies have shown that fire needs to be coupled with native seed supplementation to effectively reduce abundance of nonnative species (e.g., Maret and Wilson 2005; Suding and Gross 2006)

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Both observational and experimental studies of successional old fields in and around KBS provide evidence that supplementation of native seeds will be an important contributor to the establishment of native species and grassland restoration in this area (Houseman 2004; Suding and Gross 2006). Despite the reintroduction of frequent fire over the past decade, native species richness has stabilized at approximately fifteen to twenty species ha^{-1}. The reference old fields (SF1–3) in the area surrounding the KBS LTER rarely have more than thirty native species per 1 ha plot. Estimates of historic diversity of prairies in the Midwest region range close to 1,000 species (Ladd 1997). The decline and fragmentation of native grassland communities (now estimated at less than 1% of their original area) as a consequence of agriculture and other human activities may make it impossible for “natural processes” to promote the reestablishment of native species on abandoned fields. Competitive pressure from nonnative species that may respond positively to fire (see Suding and Gross 2006) may compound this problem unless native seed sources are supplemented as part of the management.

Conclusion

The patterns of succession observed over the last fifteen years in both the reference and experimental old field communities at the KBS LTER offer insight into how successional processes in the midwestern United States can guide grassland restoration efforts. Land use history, geographic location, disturbance regimes, fertility and seed sources all play important roles in setting the trajectory of successional communities. If native savannah and grassland seed sources had not been lost from the regional species pool due to habitat loss and fragmentation, and if fire had been used as a management tool, the old field sites in the KBS area today might more closely resemble the native prairie-savannah vegetation that historically occurred in this area (Faber-Langendoen et al. 1995; Packard and Mutel 1997; Suding and Gross 2006). Currently, management appears to be effective at creating and maintaining stable, early-successional communities, despite differences in initial community composition. An interactive management approach, combining prescribed fire and native seed addition seems most promising for future restoration efforts.

Some ecologists argue that successful restorations will only be possible once we understand all components of a system (Bradshaw 1987). While our understanding of aboveground patterns and processes of succession is fairly strong, there is some indication that belowground processes may be critical missing links for successful restorations (Camill et al. 2004). Successional old

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fields can have reduced mycorrhizal diversity (Bever et al. 2003), reduced soil organic carbon and nitrogen (Kindscher and Tieszen 1998; Potter et al. 1999), and reduced soil invertebrate abundance (Hanel 2003) compared to intact prairie systems, which may explain the continued low species richness in the KBS successional systems. New and continuing research in these areas at the KBS LTER (e.g., Robertson et al. 2000; Buckley and Schmidt 2001; Grandy 2005) may offer additional insight into successful prairie restorations.

Acknowledgments

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