Can initial intraspecific spatial aggregation increase multi-year coexistence by creating temporal priority?

Lauren M. Porensky,[1] Kurt J. Vaughn, and Truman P. Young

*Department of Plant Sciences and Graduate Group in Ecology, University of California, One Shields Avenue,
Davis, California 95616 USA*

Abstract. Both intraspecific spatial aggregation and temporal priority effects have the potential to increase long-term species coexistence. Theory and models suggest that intraspecific aggregation can facilitate coexistence via limited dispersal or asymmetric interaction distances. During community assembly, intraspecific aggregation may also delay interactions between more and less competitive species, thus creating opportunities for priority effects to facilitate longer-term coexistence. Few empirical studies have tested predictions about aggregation and coexistence, especially in the context of community assembly or ecological restoration. We investigated (1) impacts of intraspecific aggregation on the assembly of eight-species communities over three years, (2) the scale dependence of these impacts, and (3) implications for California prairie restoration. We planted eight native species in each of 19, 5 m wide, octagonal plots. Species were either interspersed throughout the plot or aggregated into eight, 2.2-m^2, wedge-shaped, monospecific sectors. Over three years, species diversity declined more quickly in interspersed plots than in aggregated plots. Two species had higher cover or increased more in interspersed than aggregated plots and were identified as "aggressives." Four species had higher cover or increased more in aggregated than interspersed plots and were identified as "subordinates." Within aggregated plots, aggressive species expanded beyond the sector in which they were originally seeded. Cover of aggressive species increased faster and reached higher values in sectors that were adjacent to the originally planted sector, compared to nonadjacent sectors. Cover of aggressive species also increased more and faster near plot centers, compared to plot edges. Areas near plot centers were representative of smaller aggregation patches since species were planted closer to heterospecific neighbors. Two subordinate species maintained higher cover near plot edges than near plot centers. Moreover, two subordinate species maintained higher cover when seeded in sectors farther away from aggressive species. These results suggest that initial intraspecific aggregation can facilitate species coexistence for at least three years, and larger aggregation patches may be more effective than smaller ones in the face of dispersing dominants. The creation of temporal priority effects may represent an underappreciated pathway by which intraspecific aggregation can increase coexistence. Restorationists may be able to maintain more diverse communities by planting in a mosaic of monospecific patches.

Key words: California; Central Valley; community assembly; diversity; intraspecific aggregation; native grassland; priority effects; restoration; spatial coexistence; spatial segregation hypothesis.

Introduction

The maintenance of species diversity in the face of competitive exclusion is a major question in ecology (Chesson 2000), as well as in conservation and restoration. Spatial aggregation and temporal priority effects are two mechanisms have been separately posited to counter competitive exclusion and facilitate species coexistence (Weiner and Conte 1981, Hodge et al. 1996, Young et al. 2001). In this study, we combined these concepts by using spatial aggregation to create temporal priority, and asked whether this combination can

facilitate species coexistence and increase diversity in California native prairie (or grassland) restoration.

Recent work indicates that spatial coexistence mechanisms (e.g., patch dynamics or spatial mass effects) can help maintain community diversity over the long term (Chesson 2000, Amarasekare 2003, Leibold et al. 2004). Modeling studies (both theoretical and simulative) suggest that intraspecific aggregation can facilitate species coexistence (e.g., Weiner and Conte 1981, Inouye 1999, Hartley and Shorrocks 2002, Turnbull et al. 2007). Such models generally require limited dispersal or differences between inter- and intraspecific interaction distances. These mechanisms prevent competitive dominants from moving into patches occupied by competitive subordinates, or slow such invasions long enough for other coexistence mechanisms (e.g., immigration or storage in seed banks) to operate (Weiner and Conte

1981, Murrell and Law 2003, Racz and Karsai 2006, but see Vogt et al. 2010).

There have been relatively few empirical studies that experimentally test predictions about intraspecific aggregation and species coexistence (Murrell et al. 2001, Turnbull et al. 2007). Moreover, of the studies demonstrating that intraspecific spatial aggregation can improve the performance of weaker competitors (Stoll and Prati 2001, Rejmanek 2002, Monzeglio and Stoll 2005, Idjadi and Karlson 2007, Mokany et al. 2008, Hart and Marshall 2009, Wassmuth et al. 2009), virtually all were short term (a single growing season), involved relatively few species, and were performed at a single, small, spatial scale. A study by Schmidt (1981) on two clonal perennials (summarized in Rejmanek 2002) is an exception in that it lasted for 30 months. We could find no studies that focused on the community-level consequences of initial intraspecific aggregation. In particular, none compared short-term or long-term diversity in intraspecifically aggregated vs. non-aggregated planting patterns, or examined spatially explicit dispersal patterns within aggregated plots.

This study examined intraspecific aggregation and coexistence in the context of community assembly and restoration. Community assembly dynamics (e.g., which, when, or where species establish) can have long-term consequences for community composition and diversity (Diamond 1975, Drake 1991, Young et al. 2001). Priority effects occur when one species (or ecotype or individual) gains a competitive advantage by arriving at a site before its competitor (Young et al. 2001, Fukami et al. 2005). Conceptually, priority effects are situated at the junction between community assembly and species coexistence. Priority effects can lead to local competitive exclusion and alternate stable states, which can increase regional coexistence (e.g., Hart 1992, Palmer et al. 2002, Chase 2010). Moreover, if they give subordinate competitors an initial advantage, priority effects can facilitate local coexistence between dominant and subordinate competitors (e.g., Hodge et al. 1996, Corbin and D'Antonio 2004).

Most studies of priority effects have focused on when different species arrive at a site (e.g., Alford and Wilbur 1985, Shorrocks and Bingley 1994, Ehmann and MacMahon 1996, Fincke 1999, D'Antonio et al. 2001, Hausmann and Hawkes 2010). In many ecological experiments and restoration efforts focused on plants, temporal priority has been created by altering sowing times. Our experiment explores another way in which temporal priority may be created at a local scale: initial intraspecific spatial aggregation. By delaying local interactions between competitive subordinates and competitive dominants, initial spatial aggregation may reduce levels of interspecific competition experienced by subordinate species during their most vulnerable life stages. Even if dominant species eventually arrive, competitive asymmetry may favor the (now established) subordinate individuals and enable long-term coexistence (Pacala and Weiner 1991, Hodge et al. 1996).

The work presented here investigated impacts of initial intraspecific aggregation on species coexistence and temporal priority, the scale-dependence of these impacts, and implications for California prairie restoration. Our work moved beyond previous aggregation studies by (1) creating experimental communities that include eight different species, (2) linking aggregation to temporal priority by following experimental communities for three years and documenting dispersal by competitive dominants, (3) using a planting arrangement that allows for examination of scale dependence and species-specific interactions in the face of this dispersal, (4) reporting on community-wide consequences (species diversity), and (5) working at a scale more relevant to ecological restoration. We hypothesized that spatial aggregation would increase multi-year diversity by delaying interspecific interactions between aggressive species and subordinate species, and that this result would be more pronounced at broader ($>10 m^2$) spatial scales than at finer ($<1 m^2$) spatial scales. Our goal is not only to improve understanding of intraspecific aggregation as a coexistence mechanism, but also to make results more applicable for practitioners trying to create and maintain diverse communities (see also Wassmuth et al. 2009).

In particular, a better understanding of how spatial aggregation impacts priority effects could have important implications for ecological restoration. In restoration projects, it is often difficult to establish subordinate species in the face of competition from aggressive dominants (Kiehl et al. 2006, Aronson and Galatowitsch 2008, Wassmuth et al. 2009). In California prairie restoration projects, some seeded species are so successful that other seeded species are completely eliminated within one or two years (e.g., Lulow 2004). One possible solution is to plant these subordinate species earlier than the dominants (i.e., provide temporal priority; Lulow 2004). However, this strategy requires practitioners to correctly identify which species will be aggressives and subordinates at a given site, and to plant desired species (and control weeds) over longer time frames. Spatial aggregation may allow restoration practitioners to reduce the time and money associated with incomplete site knowledge and successive plantings by instead using a patchy "monoculture mosaic" approach. Identifying the spatial scale at which spatial aggregation becomes important will also help practitioners to design appropriate planting strategies.

METHODS

Study site

The experiment is located in the Plant Sciences Agricultural Research Fields on the University of California, Davis campus (38.54° N, 121.78° W). Soil at the study site is classified as Yolo Silt Loam and was maintained fallow for more than three years by biannual

tilling prior to the start of this experiment. The site is located in the Central Valley of California, USA and experiences an interior Mediterranean climate with a high inter- and intra-annual variability in both the amount and timing of precipitation. Over the past 55 years, annual average precipitation at a station <5 km from the study site has been 442 mm (range: 152–914 mm), with more than 95% of the total annual precipitation falling between October and April. Summer (dry season) maximum temperatures average 32°C, and winter (wet season) minimum temperatures average 5°C.

Experimental design

Within the site, we established 19 octagonal plots in a grid. Each plot had a diameter of 5 m, and plots were separated from one another by 2 m. Site preparation involved light tillage followed by herbicide application after the first fall rains in 2007. Plots were planted on 6–8 February 2008, irrigated once at the end of March 2008, and periodically weeded until July 2009.

We chose eight native California prairie species to represent multiple functional guilds, life forms, and life history strategies (Appendix A). Species included four grasses (*Elymus glaucus*, *Elymus triticoides*, *Melica californica*, and *Stipa pulchra*), two non-leguminous forbs (*Calandrinia ciliata* and *Grindelia camporum*), and two leguminous forbs (*Trifolium bifidum* and *Trifolium willdenovii*). Only one of the eight species (*E. triticoides*) tends to reproduce vegetatively. We used expert knowledge to determine seeding rates (Appendix A) that approximate those currently used in local restoration plantings (seed suppliers and practitioners, *personal communication*). During the first growing season, we discovered that our *E. glaucus* seed was contaminated with *E. triticoides* and *Elymus trachycaulus*. Therefore, we averaged cover of all *Elymus* species at the plot level for statistical analyses (but *E. triticoides* and *E. glaucus* were included separately for species richness calculations).

Six "interspersed" plots were broadcast seeded with the eight-species mixture. In the 13 remaining plots, each of the eight species was broadcast seeded into a wedge-shaped 2.2-m^2 sector of each octagonal plot to create an "aggregated" arrangement (Fig. 1a). All plots received the same total amount (by mass) of seed per species. Within the aggregated treatment, we chose 13 species arrangements that allowed us to examine the impacts of different neighbor pairings on coexistence. All possible individual species pairings were replicated at least three times across the 13 arrangements. In the field, aggregation treatments (13 aggregated plots and six interspersed plots) were assigned randomly to the 19 plots, and the 13 species arrangements were randomly assigned to the 13 aggregated plots.

In 2008, 2009, and 2010 (a total of three growing seasons), we determined the reproductive abundance of each species by monitoring at the peak of flowering,
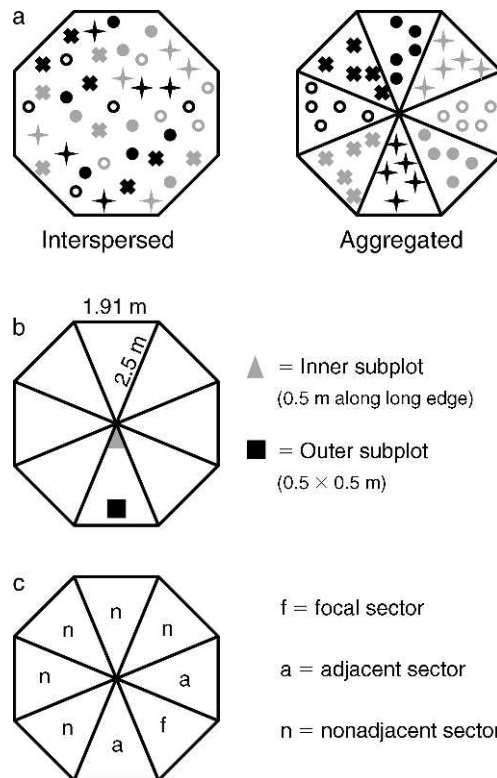

FIG. 1. Experimental design. (a) Planting designs for interspersed and aggregated plots. Each symbol–shading combination represents seed of one species. (b) Location of inner and outer subplots within a sector. Inner subplots are closer to heterospecifics (and therefore representative of smaller aggregation patches) than outer subplots. (c) Sectors were identified as focal (f), adjacent (a), or nonadjacent (n) for analysis of spatial patterns within aggregated plots.

which varied by species and across years (April–July). For each species in each sector of both interspersed and aggregated plots, we visually estimated aerial percent cover.

Within aggregated plots, we also counted the number of individuals (genets) and estimated percent cover of each species in two subplots within each sector: the innermost 0.5 m of the sector (inner subplot) and a 0.5 × 0.5 m quadrat placed 30 cm inside the outer edge of the sector (outer subplot, Fig. 1b). Individuals in "inner" subplots were seeded less than 0.2 m from heterospecific neighbors, while individuals in "outer" subplots were seeded 0.4–0.8 m from heterospecific neighbors. The inner and outer subplots were therefore representative of smaller and larger aggregation patches, and could be used to evaluate the scale dependence of spatial aggregation effects.

Statistical analyses

For each year in each plot, we calculated diversity from cover data using the Shannon-Wiener Index, which incorporates species richness as well as species evenness. We used repeated-measures ANOVAs to analyze
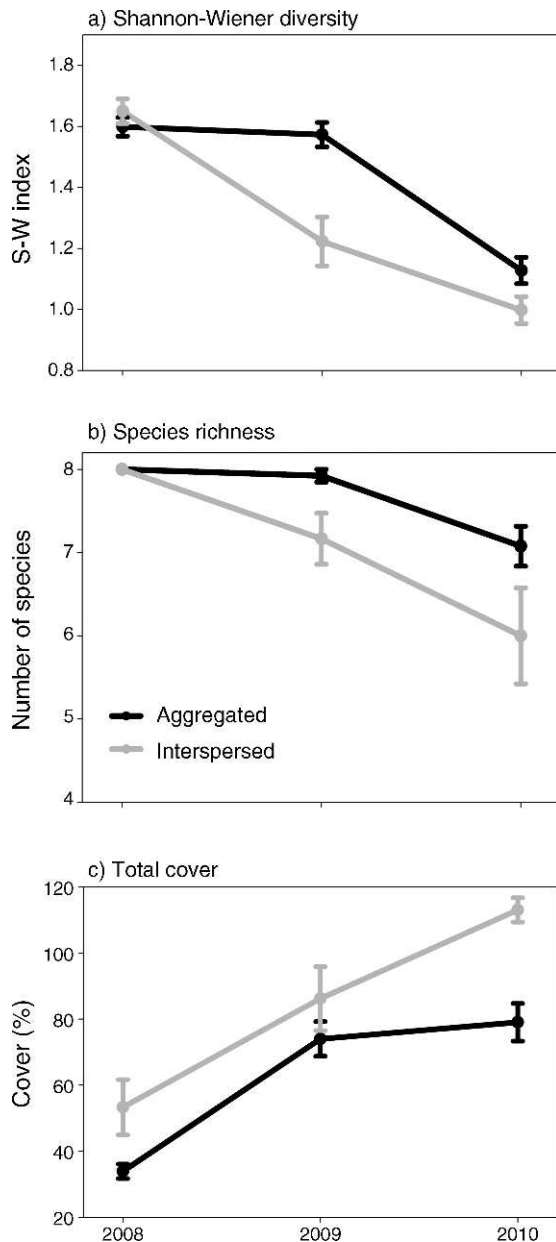
FIG. 2. (a) Shannon-Wiener (S-W) diversity index, (b) species richness, and (c) total cover (mean ± SE) in interspersed and aggregated plots over three years. Total cover values can exceed 100% because they represent the sum of cover values estimated separately for each species.

diversity (exponentially transformed Shannon-Wiener index; see Jost 2006), total cover, and cover by species as respective dependent variables with aggregation treatment as the independent variable. We performed these and subsequent analyses in SAS 9.2 (SAS Institute, Cary, North Carolina, USA) and used transformations or variance weighting when necessary in order to meet the assumptions of the models.

We used results from the plot-level cover analyses to define species as either aggressive (cover was higher or increased more in interspersed than aggregated plots), neutral (cover was not associated with aggregation treatment), or subordinate (cover was higher or increased more in aggregated than interspersed plots). We then investigated spatial dynamics of aggressive and subordinate species within the aggregated plots. For each aggressive species, in each plot, we assigned each sector one of three distance categories: the sector into which that species was originally planted (focal sector), sectors adjacent to the focal sector, or sectors nonadjacent to the focal sector (Fig. 1c). For each plot, we calculated average cover and density for inner and outer subplots across sectors within each distance category. We analyzed data from adjacent and nonadjacent sectors for 2009 and 2010 to determine whether cover or density was related to patch scale (inner or outer subplot; Fig. 1b) or distance from the species' focal sector (adjacent or nonadjacent; Fig. 1c). We only analyzed data from 2009 and 2010 because, during the first growing season (2008), each species had virtually no cover or density in sectors where it was not seeded (Fig. 4).

For each pair of subordinate and aggressive species we assigned each plot to one of two categories: subordinate adjacent to aggressive or subordinate nonadjacent to aggressive (Fig. 1c). For each plot, we calculated cover of subordinate species for inner and outer subplots (averaged across sectors).

For all spatial analyses, we used split-split plot ANOVA models with distance category as a main-plot effect, location within sector (inner or outer) as a subplot effect, and year as a sub-subplot effect. To account for temporal nonindependence we used conservative degrees of freedom to calculate P values for year and all interactions with year.

RESULTS

Diversity and total cover: interspersed vs. aggregated plots

Spatial aggregation increased plot-wide species diversity and decreased total cover. Diversity declined more quickly in interspersed plots than in aggregated plots (Fig. 2a; aggregation treatment $F_{1,17} = 6.54$, $P = 0.02$; time $F_{2,34} = 99.07$, $P < 0.0001$; time × treatment $F_{2,34} = 14.65$, $P < 0.0001$). Species richness showed the same pattern (Fig. 2b), although we were unable to statistically analyze this response variable because data did not meet MANOVA assumptions. Total cover was higher and increased faster in interspersed plots (Fig. 2c; aggregation treatment $F_{1,17} = 14.64$, $P = 0.001$; time $F_{2,34} = 117.17$, $P < 0.0001$; time × treatment $F_{2,34} = 3.31$, $P = 0.05$).

Cover by species: interspersed vs. aggregated plots

Two species demonstrated aggressive behavior (i.e., cover was higher or increased more in interspersed than aggregated plots). Total *Grindelia camporum* cover was
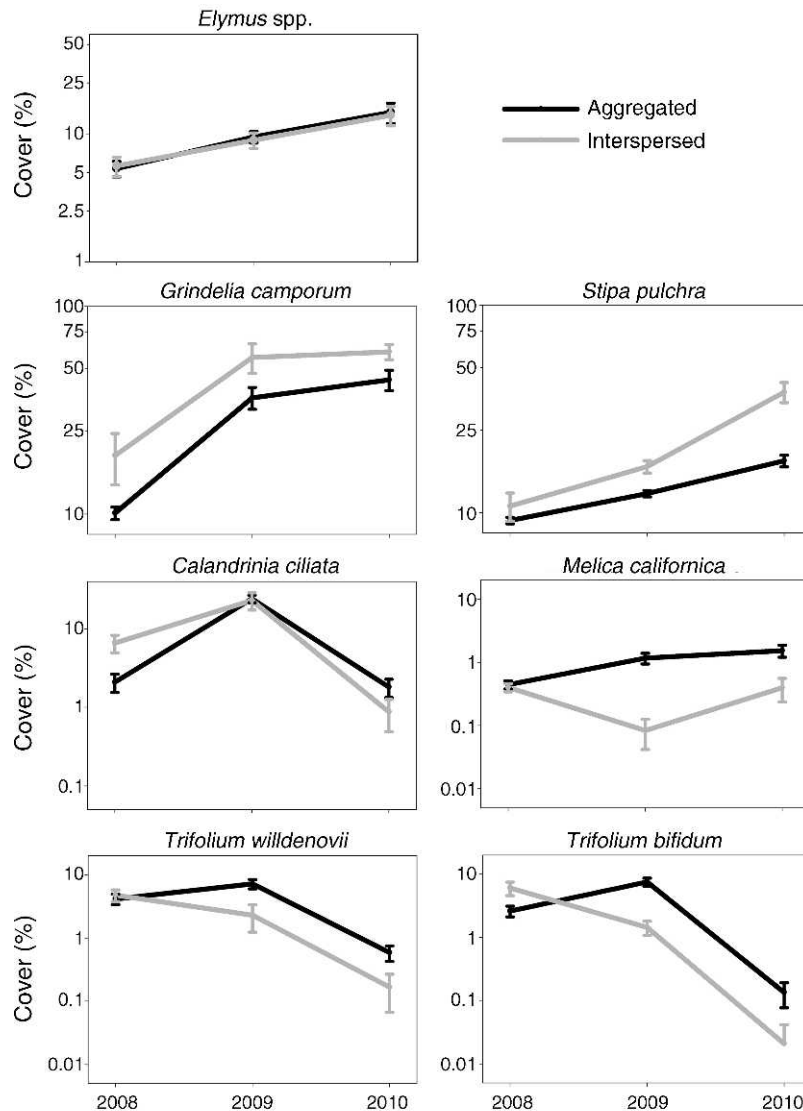
FIG. 3.   Cover (mean ± SE, presented on a logarithmic scale) of each planted species in interspersed and aggregated plots over three years.

50% higher on average in interspersed plots (Fig. 3; aggregation treatment $F_{1,17} = 6.33$, $P = 0.02$; Appendix B). For *S. pulchra*, total cover increased faster and was 67% higher on average in interspersed plots (Fig. 3; aggregation treatment $F_{1,17} = 32.15$, $P < 0.0001$; time × treatment $F_{2,34} = 12.84$, $P < 0.0001$; Appendix B).

The combined response of *Elymus* species was neutral with respect to spatial aggregation. Cover of these species increased over time regardless of spatial planting pattern (Fig. 3; Appendix B).

Four species showed subordinate behavior (i.e., cover was higher or increased more in aggregated than interspersed plots). *Melica californica* cover only increased in aggregated plots (Fig. 3; aggregation treatment $F_{1,17} = 13.70$, $P = 0.002$; time × treatment $F_{2,34} = 7.30$, $P = 0.002$;

Appendix B). Cover of *C. ciliata* peaked in the second growing season and declined in the third season in both aggregation treatments, but the decline was more severe in interspersed than aggregated plots (interspersed plots had half the cover of aggregated plots in 2010; Fig. 3; time × treatment $F_{2,34} = 13.11$, $P < 0.0001$; Appendix B). For the two leguminous forbs (*T. bifidum* and *T. willdenovii*), cover in interspersed plots declined steadily over time, while cover in aggregated plots peaked in the second growing season and declined in the third (Fig. 3; *T. bifidum* time × treatment $F_{2,34} = 10.65$, $P = 0.0005$; *T. willdenovii* time × treatment $F_{2,34} = 5.71$, $P = 0.007$; Appendix B). Even in the third season, cover of the two *Trifolium* species in aggregated plots remained at least three times higher than cover in interspersed plots (Fig. 3).
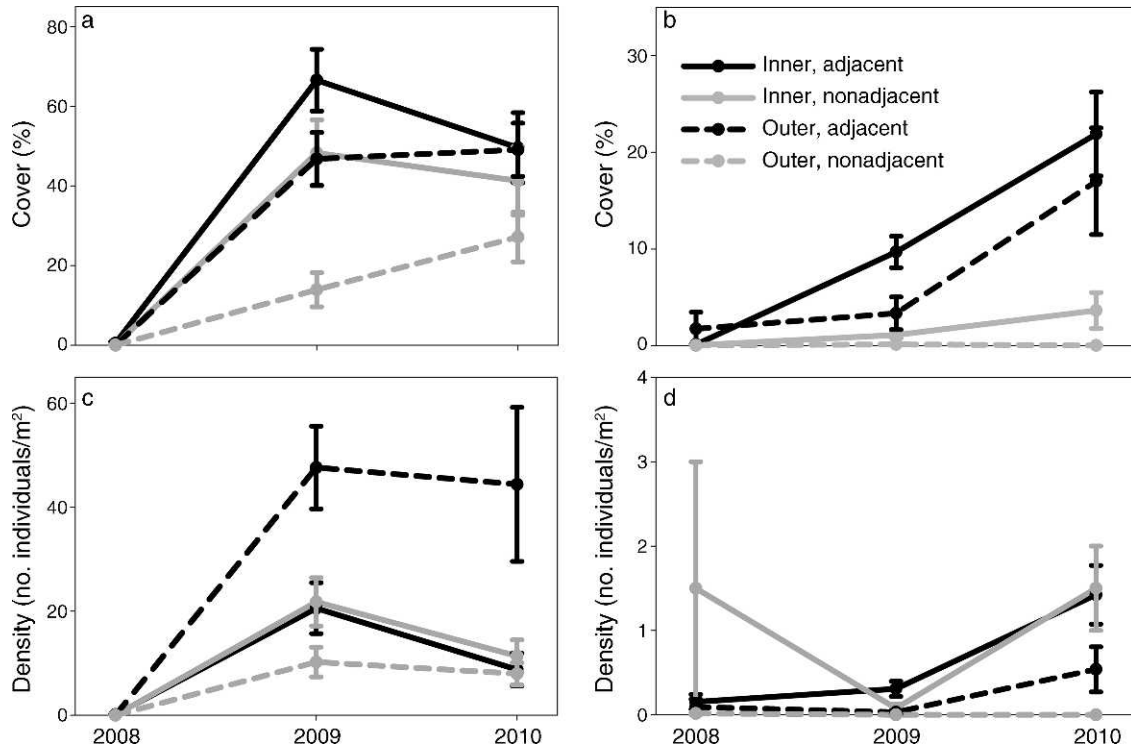
FIG. 4. Spatial patterns of aggressive species in aggregated plots: (a, c) *Grindelia camporum*, (b, d) *Stipa pulchra*. Aggressive species (a, b) cover and (c, d) density (mean ± SE) are shown as a function of time, location within sector (inner vs. outer subplot), and distance from the focal (originally planted) sector.

Aggressive species: spatial patterns in aggregated plots

Within the aggregated plots, cover of aggressive species (*G. camporum* and *S. pulchra*) increased more in areas closer to the originally planted sector (i.e., focal sector, Fig. 1c). Cover was at least 50% higher in inner than outer subplots (*G. camporum* location $F_{1,24} = 12.77$, $P = 0.002$; *S. pulchra* location $F_{1,24} = 42.89$, $P < 0.0001$) and at least 60% higher in sectors adjacent to the focal sector than nonadjacent sectors (*G. camporum* distance $F_{1,24} = 6.21$, $P = 0.02$; *S. pulchra* distance $F_{1,24} = 75.23$, $P < 0.0001$; Fig. 4; Appendix B). Additionally, *G. camporum* cover increased more in inner than outer subplots over time (Fig. 4; location × time $F_{1,48} = 11.51$, $P = 0.001$; Appendix B). For *S. pulchra*, cover increased more over time in adjacent sectors than nonadjacent sectors, and in nonadjacent sectors cover increased more over time in inner than outer subplots (Fig. 4; distance × time $F_{1,48} = 5.69$, $P = 0.02$; distance × location × time $F_{1,48} = 9.87$, $P = 0.003$; Appendix B). For both species, densities showed similar patterns, indicating that changes in cover were due to the dispersal of new individuals, not simply canopy spread (Fig. 4; Appendix B).

Subordinate species: spatial patterns relative to aggressive species

Subordinate species displayed a variety of spatial patterns in aggregated plots. Two subordinate species were affected by distance to heterospecifics (i.e., patch scale, measured via inner vs. outer subplots). Cover of *C. ciliata* declined more rapidly in inner than outer subplots (Fig. 5; location $F_{1,11} = 8.17$, $P = 0.02$; location × time $F_{1,44} = 4.38$, $P = 0.02$), and *M. californica* cover declined in inner subplots but increased in outer subplots (Fig. 5; location $F_{1,11} = 22.25$, $P = 0.0005$; location × time $F_{1,44} = 6.77$, $P = 0.003$; Appendix B).

Two of the subordinate species were also affected by the distance that they were seeded from *G. camporum*. Within outer subplots, *M. californica* cover only increased in sectors nonadjacent to *G. camporum* (Fig. 5; distance $F_{1,11} = 19.21$, $P = 0.001$; distance × location × time $F_{1,44} = 13.68$, $P < 0.0001$; Appendix B). *Trifolium bifidum* cover decreased more rapidly in sectors adjacent to *G. camporum* (Fig. 5; distance $F_{1,11} = 6.02$, $P = 0.03$; Appendix B). *Trifolium willdenovii* cover decreased over time and was not significantly affected by location within sector or distance to *G. camporum* (Fig. 5; Appendix B). No species were significantly affected by distance from *S. pulchra* (Appendix B).

DISCUSSION

We demonstrated that intraspecific aggregation in 2.2-m² patches can maintain the diversity of experimental eight-species plant communities for at least three years. These results support and extend the findings of previous intraspecific aggregation studies, which were conducted with fewer species at smaller temporal and
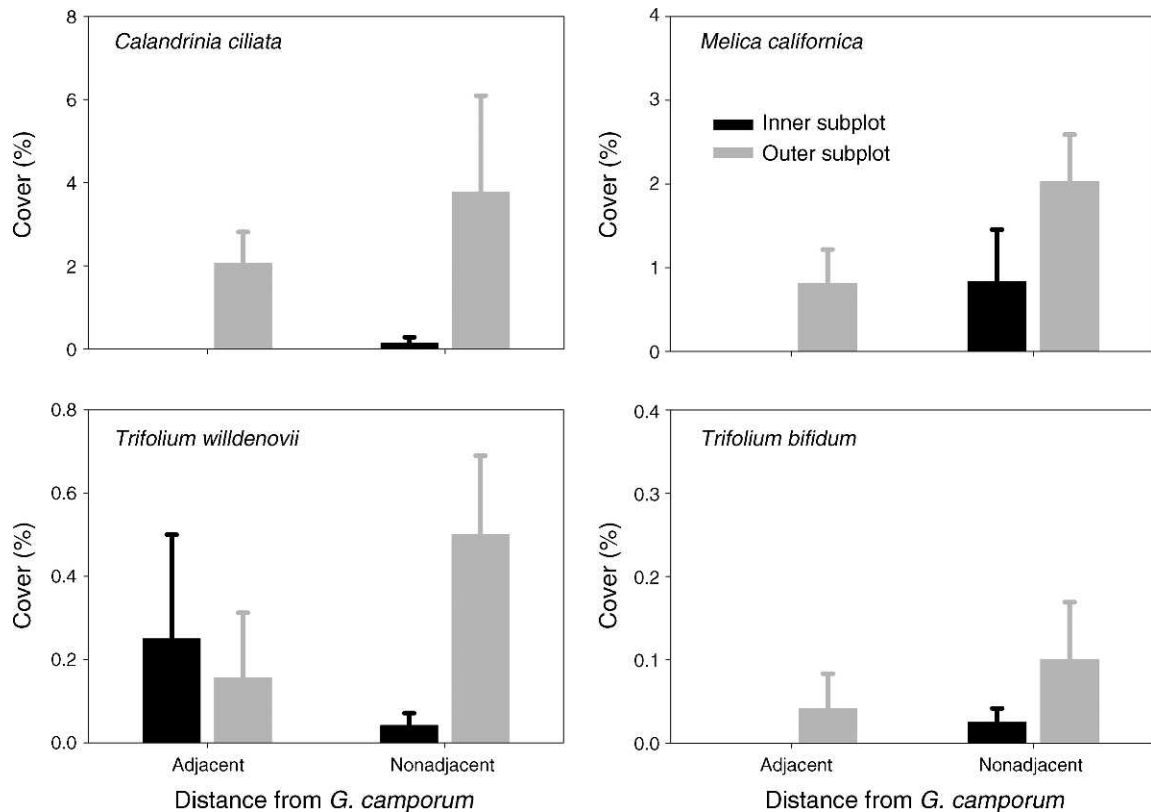
FIG. 5.   Spatial patterns of subordinate species in aggregated plots: cover (mean + SE) of subordinate species in 2010 as a function of location within sector (inner vs. outer subplot) and distance from *G. camporum* (planted in an adjacent sector vs. planted in a nonadjacent sector). By 2010, cover in inner, adjacent subplots had declined to zero for *C. ciliata*, *M. californica*, and *T. bifidum*.

spatial scales (e.g., Stoll and Prati 2001, Monzeglio and Stoll 2005, Mokany et al. 2008, Hart and Marshall 2009, Wassmuth et al. 2009). To our knowledge, this is the first study of intraspecific aggregation that included species diversity as a response variable. In addition, no previous studies appear to have explicitly monitored the dispersal of competitive dominants, or the impacts of this dispersal on subordinate species. Thus, our work provides longer-term evidence that intraspecific aggregation can foster species coexistence and begins to explore the mechanisms driving this result.

Species-specific responses to planting pattern

Responses to planting pattern differed substantially among species. Response patterns did not suggest any consistent signal of pollination or dispersal mode. Within both the aggressive and subordinate species groups, there were wind-pollinated as well as insect-pollinated species and animal- or gravity-dispersed as well as wind-dispersed species. There appeared to be a slight difference in response based on lifespan. Both of the aggressive species were perennial, while three out of four subordinate species were annuals. Of particular interest was the lack of a guild signal; there were both grasses and forbs in both the aggressive and subordinate

classes. These results resemble those of Wassmuth et al. (2009), who examined six species at a smaller spatial scale (0.25-m² patches) and found that after 68 days, two grasses and one forb had higher biomass in intraspecifically aggregated plots.

Over three years, interspersed plots achieved significantly higher total cover than aggregated plots. Several mechanisms could cause this result. Our species-specific cover results suggest that differences in intra- vs. interspecific competition intensity may be responsible: aggressive species were very effective at filling space when they were competing mainly with heterospecifics. By contrast, aggressive species cover remained fairly low in aggregated plots where intraspecific competition intensity was high. The observed difference in total cover between treatments could also be interpreted in terms of more complete utilization of niche space in interspersed communities (e.g., via fine-scale resource partitioning; McKane et al. 2002, Yurkonis et al. 2010), though this second mechanism is intimately connected to the first since differences in competition intensity are probably related to niche overlap. Finally, reduced cover in aggregated plots may reflect Janzen-Connell effects such as the build-up of soil pathogens in dense patches of conspecifics (Petermann et al. 2008). Future research

could explore the relative importance of these different mechanisms.

For all three subordinate forb species, cover values peaked during the 2009 growing season, and peaks were especially pronounced in aggregated plots (Fig. 3). These patterns may reflect an interaction between planting pattern and year effects. Weather patterns during the course of our experiment probably produced distinct "grass years" and "forb years" (sensu Pitt and Heady 1978, Vaughn and Young 2010). The winter of 2008–2009 was drier than average (79% of long-term average precipitation) with a four week mid-winter drought (1.3 mm of precipitation between 26 December 2008 and 21 January 2009; weather data gathered <2 km from the study site). Less rainfall, especially when associated with a mid-winter drought, may favor forbs over grasses (Pitt and Heady 1978). Our results suggest that subordinate forbs were better able to take advantage of favorable weather patterns when seeded in intraspecifically aggregated plots. In contrast, the winter of 2009–2010 was slightly wetter than average (120% of the long-term average) and lacked a substantial mid-winter drought. In 2010, cover of the grasses in our experiment increased, while cover of subordinate forbs declined precipitously (Fig. 3).

Spatial dynamics within aggregated plots: does spatial aggregation create temporal priority?

Our multi-year data set allowed us the opportunity to examine species movements over time within aggregated plots. We found that aggressive species expanded through time out of their planted sectors, and expansion happened more quickly at smaller spatial scales. Inner subplots, which were ≤20 cm from adjacent sectors, became dominated by aggressive species more quickly than outer subplots, which were 0.4–0.8 m from adjacent sectors. Moreover, aggressive species expanded more quickly into adjacent sectors than nonadjacent sectors. In nonadjacent, outer subplots, subordinate species had a year to establish before the substantial invasion of G. camporum and at least two years to establish before the invasion of S. pulchra. In other words, initial spatial aggregation led to differences in arrival time at the subplot scale.

Our results suggest that the temporal head start obtained via initial spatial aggregation conferred advantages to subordinate species, and advantages were more pronounced in locations where individuals had more time to get established before the arrival of heterospecifics. Two of the four subordinate species (C. ciliata and M. californica) had lower cover in inner than outer subplots, suggesting that they were more suppressed when planted closer to heterospecifics (i.e., in smaller patches). Melica californica and T. bifidum had lower plot-wide cover when they were planted adjacent to the aggressive species G. camporum. Interestingly, no subordinate species were sensitive to distance from S. pulchra. Thus, although both aggressive species expand-

ed into adjacent wedges, only G. camporum's expansion was associated with reductions in cover of subordinate species.

By the third year, G. camporum cover values were fairly similar between the aggregated and interspersed plots, and cover in aggregated plots was similar across all subplots (including nonadjacent, outer subplots, Fig. 4), suggesting that greater species diversity was maintained even after extensive invasion of this species. Nonetheless, it remains to be seen whether species aggregation in these plots merely delays complete dominance by the most aggressive species (albeit for several years), or whether a sufficient delay will allow some species to create patches resistant to this invasion (Rejmanek 2002). In addition to giving subordinates time to establish, delays in the arrival of competitive dominants could also allow other coexistence mechanisms to operate (Hubbell 2001, Levine and Murrell 2003, Racz and Karsai 2006). For example, intraspecific aggregation could weaken aggressive species over time by promoting Janzen-Connell effects (e.g., the build-up of host-specific soil pathogens; Petermann et al. 2008). Delays may also allow subordinate species to establish persistent seed banks that could be revealed by future disturbances, such as fire (e.g., Royo et al. 2010).

Linking initial intraspecific aggregation and temporal priority: spatial priority effects

In some aggregation models, long-term species coexistence is maintained only because dispersal of dominants is so limited that they essentially do not reach other species' patches (e.g., Inouye 1999, Hartley and Shorrocks 2002, Levine and Murrell 2003, Potthoff et al. 2006, Turnbull et al. 2007, Murrell 2010). However, by reducing heterospecific interactions during a plant's most vulnerable life stages, initial intraspecific aggregation may be able to enhance long-term species coexistence despite intrusive dispersal by competitive dominants (Levine and Murrell 2003). We use the term spatial priority to describe temporal priority achieved through initial intraspecific aggregation. Our results suggest that like traditional temporal priority, spatial priority can facilitate long-term coexistence by taking advantage of ontological shifts in competitive ability.

Implications for ecological restoration

The seed mix we used included eight species common in seed mixes for California prairie restoration, and our site preparation and maintenance replicated standard restoration practices. Our results should therefore be relevant for restoration practitioners trying to establish high-diversity communities in this ecosystem. Traditional temporal priority effects have often been used to maintain diversity, but the creation of temporal priority may be hampered by logistics, cost, or lack of site-specific knowledge. For example, the practice of planting forbs one year before grasses probably would not have led to higher diversity at our site, since the most

aggressive species turned out to be a forb (*G. camporum*).

Our results suggest an alternative to providing temporal priority at the scale of entire sites. Planting in monospecific patches within a single season may give subordinate species time (even several years) to establish themselves while aggressive species are spatially held at bay. Of course, planting a monoculture mosaic could present logistical issues, such as a more complex planting effort. Moreover, our results suggest that intraspecific aggregation reduces total cover, at least initially. Reduced cover may be a problem if it leads to increased invasibility in restored areas. We are currently using the experiment presented here to explore impacts of planting pattern on invasibility. However, we suggest that planting in patchy monocultures may be manageable at the scale of most restoration sites (~1–100 ha), in which managers could plant monospecific rows or sets of rows. At these scales, monocultures might make weed control easier by allowing for more specifically tailored control strategies in different parts of the site.

Our findings suggest that initial intraspecific aggregation can facilitate species coexistence for at least three years. Long-term monitoring of this experiment will help clarify whether higher diversity is a transient or persistent phenomenon. Even after three years, it seems clear that initial intraspecific aggregation is an important community assembly process with the potential to foster long-term coexistence and diversity.

Literature Cited

Alford, R. A., and H. M. Wilbur. 1985. Priority effects in experimental pond communities: competition between *Bufo* and *Rana*. Ecology 66:1097–1105.

Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. Ecology Letters 6:1109–1122.

Aronson, M. F. J., and S. Galatowitsch. 2008. Long-term vegetation development of restored prairie pothole wetlands. Wetlands 28:883–895.

Chase, J. M. 2010. Stochastic community assembly causes higher biodiversity in more productive environments. Science 328:1388–1391.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Corbin, J. D., and C. M. D'Antonio. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology 85:1273–1283.

D'Antonio, C. M., R. F. Hughes, and P. M. Vitousek. 2001. Factors influencing dynamics of two invasive C_4 grasses in seasonally dry Hawaiian woodlands. Ecology 82:89–104.

Diamond, J. 1975. Assembly of species communities. Pages 342–444 in M. Cody and J. Diamond, editors. Ecology and evolution of communities. Belknap Press, Cambridge, Massachusetts, USA.

Drake, J. A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. American Naturalist 137:1–26.

Ehmann, W. J., and J. A. MacMahon. 1996. Initial tests for priority effects among spiders that co-occur on sagebrush shrubs. Journal of Arachnology 24:173–185.

Fincke, O. M. 1999. Organization of predator assemblages in Neotropical tree holes: effects of abiotic factors and priority. Ecological Entomology 24:13–23.

Fukami, T., T. M. Bezemer, S. R. Mortimer, and W. H. van der Putten. 2005. Species divergence and trait convergence in experimental plant community assembly. Ecology Letters 8:1283–1290.

Hart, D. D. 1992. Community organization in streams: the importance of species interactions, physical factors, and chance. Oecologia 91:220–228.

Hart, S. P., and D. J. Marshall. 2009. Spatial arrangement affects population dynamics and competition independent of community composition. Ecology 90:1485–1491.

Hartley, S., and B. Shorrocks. 2002. A general framework for the aggregation model of coexistence. Journal of Animal Ecology 71:651–662.

Hausmann, N. T., and C. V. Hawkes. 2010. Order of plant host establishment alters the composition of arbuscular mycorrhizal communities. Ecology 91:2333–2343.

Hodge, S., W. Arthur, and P. Mitchell. 1996. Effects of temporal priority on interspecific interactions and community development. Oikos 76:350–358.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Idjadi, J. A., and R. H. Karlson. 2007. Spatial arrangement of competitors influences coexistence of reef-building corals. Ecology 88:2449–2454.

Inouye, B. D. 1999. Integrating nested spatial scales: implications for the coexistence of competitors on a patchy resource. Journal of Animal Ecology 68:150–162.

Jost, L. 2006. Entropy and diversity. Oikos 113:363–375.

Kiehl, K., A. Thormann, and J. Pfadenhauer. 2006. Evaluation of initial restoration measures during the restoration of calcareous grasslands on former arable fields. Restoration Ecology 14:148–156.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Levine, J. M., and D. J. Murrell. 2003. The community-level consequences of seed dispersal patterns. Annual Review of Ecology, Evolution, and Systematics 34:549–574.

Lulow, M. L. 2004. Restoration in California's Inland Grasslands: the role of priority effects and management strategies in establishing native communities and the ability of native grasses to resist invasion by non-native grasses. Dissertation. University of California, Davis, California, USA.

McKane, R. B., L. C. Johnson, G. R. Shaver, K. J. Nadelhoffer, E. B. Rastetter, B. Fry, A. E. Giblin, K. Kielland, B. L. Kwiatkowski, J. A. Laundre, and G. Murray. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature 415:68–71.

Mokany, K., J. Ash, and S. Roxburgh. 2008. Effects of spatial aggregation on competition, complementarity and resource use. Austral Ecology 8:261–270.

Monzeglio, U., and P. Stoll. 2005. Spatial patterns and species performances in experimental plant communities. Oecologia 145:619–628.

Murrell, D. J. 2010. When does local spatial structure hinder competitive coexistence and reverse competitive hierarchies? Ecology 91:1605–1616.

Murrell, D. J., and R. Law. 2003. Heteromyopia and the spatial coexistence of similar competitors. Ecology Letters 6:48–59.

Murrell, D. J., D. W. Purves, and R. Law. 2001. Uniting pattern and process in plant ecology. Trends in Ecology and Evolution 16:529–530.

Pacala, S. W., and J. Weiner. 1991. Effects of competitive asymmetry on a local density model of plant interference. Journal of Theoretical Biology 149:165–179.

Palmer, T. M., T. P. Young, and M. L. Stanton. 2002. Burning bridges: priority effects and the persistence of a competitively subordinate acacia-ant in Laikipia, Kenya. Oecologia 133:372–379.

Petermann, J. S., A. J. F. Fergus, L. A. Turnbull, and B. Schmid. 2008. Janzen-Connell effects are widespread and strong enough to maintain diversity in grasslands. Ecology 89:2399–2406.

Pitt, M. D., and H. F. Heady. 1978. Responses of annual vegetation to temperature and rainfall patterns in northern California. Ecology 59:336–350.

Potthoff, M., K. Johst, J. Gutt, and C. Wissel. 2006. Clumped dispersal and species coexistence. Ecological Modelling 198:247–254.

Racz, E. V. P., and J. Karsai. 2006. The effect of initial pattern on competitive exclusion. Community Ecology 7:23–33.

Rejmanek, M. 2002. Intraspecific aggregation and species coexistence. Trends in Ecology and Evolution 17:209–210.

Royo, A. A., R. Collins, M. B. Adams, C. Kirschbaum, and W. P. Carson. 2010. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. Ecology 91:93–105.

Schmidt, W. 1981. Über das Konkurrenzverhalten von Solidago canadensis und Urtica dioica. Verhandlungen der Gesellschaft für Ökologie 9:173–188.

Shorrocks, B., and M. Bingley. 1994. Priority effects and species coexistence: experiments with fungal-breeding Drosophila. Journal of Animal Ecology 63:799–806.

Stoll, P., and D. Prati. 2001. Intraspecific aggregation alters competitive interactions in experimental plant communities. Ecology 82:319–327.

Turnbull, L. A., D. A. Coomes, D. W. Purves, and M. Rees. 2007. How spatial structure alters population and community dynamics in a natural plant community. Journal of Ecology 95:79–89.

Vaughn, K. J., and T. P. Young. 2010. Contingent conclusions: year of initiation influences ecological field experiments, but temporal replication is rare. Restoration Ecology 18:59–64.

Vogt, D. R., D. J. Murrell, and P. Stoll. 2010. Testing spatial theories of plant coexistence: no consistent differences in intra- and interspecific interaction distances. American Naturalist 175:73–84.

Wassmuth, B. E., P. Stoll, T. Tscharntke, and C. Thies. 2009. Spatial aggregation facilitates coexistence and diversity of wild plant species in field margins. Perspectives in Plant Ecology, Evolution, and Systematics 11:127–135.

Weiner, J., and P. T. Conte. 1981. Dispersal and neighborhood effects in an annual plant competition model. Ecological Modelling 13:131–147.

Young, T. P., J. Chase, and R. Huddleston. 2001. Community succession and assembly: comparing, contrasting and combining paradigms in the context of ecological restoration. Ecological Restoration 19:5–18.

Yurkonis, K. A., B. J. Wilsey, K. A. Moloney, and A. G. van der Valk. 2010. The impact of seeding method on diversity and plant distribution in two restored grasslands. Restoration Ecology 18:311–321.

SUPPLEMENTAL MATERIAL

Appendix A

Information on species and seeding rates (*Ecological Archives* A022-051-A1).

Appendix B

Statistical tables and a figure showing subordinate patterns in aggregated plots over all three years (*Ecological Archives* A022-051-A2).