COMMUNICATIONS

Ecological Applications, 17(2), 2007, pp. 311–316

SPATIAL AND TEMPORAL PATTERNS OF SEED DISPERSAL: AN IMPORTANT DETERMINANT OF GRASSLAND INVASION

CHRISTOPHER T. DIVITTORIO,[1,3] JEFFREY D. CORBIN,[1,4] AND CARLA M. D'ANTONIO[2]

[1]*Department of Integrative Biology, University of California, Berkeley, California 94720-3140 USA*
[2]*Environmental Studies, University of California, Santa Barbara, California 93106-9610 USA*

Abstract. We measured spatial and temporal patterns of seed dispersal and seedling recruitment for 58 species in a grassland community to test whether seed dispersal could predict patterns of invasion after disturbance. For the 12 most abundant grasses, recruitment of native species was dependent on the propagule supply of both native and exotic species. Variability in seed rain on small spatial (1–10 m) and temporal (within season) scales led to qualitative differences in the outcome of disturbance colonization such that native species dominated disturbances when exotic seed supply was low but failed to establish when exotic seed supply was high. Local dispersal and spatial heterogeneity in species composition promoted coexistence of native and exotic species by creating refuges from high exotic seed supply within native dominated patches. Despite this, copious exotic seed production strongly limited recruitment of native species in exotic dominated patches. Most grasslands in California are presently dominated by exotic species, suggesting that competition at the seedling stage is a major barrier to native species restoration.

Key words: *coexistence; dispersal; disturbance; grassland; invasion; restoration; seed limitation.*

INTRODUCTION

Patterns of dispersal are important determinants of community structure in a variety of ecosystems (Gaines and Roughgarden 1985, Hobbs and Mooney 1985, Clark et al. 1999). Despite this, dispersal is rarely quantified (Levine and Murrell 2003). This lack of information introduces an unknown amount of error into predictions of population and community change (Clark et al. 1999), potentially reducing our ability to predict the response of ecosystems to management or perturbations.

Dispersal influences ecological processes through many different mechanisms. At a population level, dispersal may directly limit abundance if propagules fail to reach otherwise suitable sites. In these populations, experimentally adding propagules should lead to an increase in abundance (Ericksson and Ehrlen 1992, Turnbull et al. 2000). At a community level, restricted dispersal may promote coexistence or alter the outcome of species interactions by limiting the abundance of competitors or mutualists (Tilman 1994, Levine and Murrell 2003). This effect was best demonstrated by Gaines and Roughgarden (1985) who showed that the outcome of competition between intertidal barnacles was contingent on the settlement rate of the stronger competitor. If this type of contingency is widespread, studies of species interactions performed under a single or unspecified dispersal regime may have limited generality.

Dispersal is thought to be particularly important for predicting the spread of invasive species. Several observations support this hypothesis. First, all invasive species are, by definition, initially dispersal limited in their nonnative ranges (Richardson et al. 2000). Second, because susceptibility to invasion varies continuously both within and among communities, biological invasions can be thought of as probabilistic processes (Davis et al. 2000, D'Antonio et al. 2001). This leads to the prediction that increasing propagule supply, or "propagule pressure," should result in increasing likelihood of invasion. These predictions are supported by studies of animal introductions, where increasing the number of introductions or the number of individuals in an introduction event increases establishment (D'Antonio et al. 2001). These predictions are also supported by recent empirical evidence for plants (Von Holle and

Manuscript received 12 April 2006; revised 26 July 2006; accepted 15 August 2006; final version received 12 September 2006. Corresponding Editor: C. L. Boggs.

[3] Present address: 4701 San Leandro Street, Number 54, Oakland, California 94601-5100 USA.
E-mail: cdivittorio@berkeley.edu

[4] Present address: Department of Biology, Union College, Schenectady, New York 12308 USA.

Simberloff 2005, Thomsen et al. 2006), although the generality of these results is not known.

One invasion thought to be strongly influenced by dispersal and establishment is the dramatic conversion of 7–10 × 10^6 ha of California to domination by exotic grasses over the past 200 years (Huenneke 1989). Although this conversion is thought to have been facilitated by a combination of drought, agriculture, and livestock grazing (Heady 1988), the exotic dominated condition generally persists even after these pressures are eliminated (Bartolome and Gemmill 1981, Stromberg and Griffin 1996). The most commonly invoked mechanism explaining the failure of native species to recover is that competition with nonnative species at the seedling stage strongly limits survival (Bartolome and Gemmill 1981, Dyer and Rice 1997). Support for this mechanism includes Dyer et al. (1996) who reported that survival of seedlings of the native bunchgrass *Nassella pulchra* transplanted into a grassland dominated by nonnative species was 1.1% after one year and 0.1% after three years even though mature individuals were locally abundant.

A second potential mechanism was identified by Hamilton et al. (1999) who found that native species responded positively to addition of both seed and water and concluded that native species were limited by both dispersal and competition. Further evidence for the dispersal limitation hypothesis was presented by Seabloom et al. (2003). They found that a single addition of native seed into plots containing exotic annual grasses resulted in increasing abundance of native species and decreasing abundance of exotic species over four years and concluded that native species were primarily seed limited.

Although both competition and dispersal limitation likely operate simultaneously, their relative importance has profound management implications. If native species are limited primarily by seed availability, restoration may be possible by adding seed of native species without any additional management intervention. However, if native species are limited primarily by competition, restoration is not possible without the much more difficult task of mitigating competition from exotic species. One potential explanation for conflicting empirical evidence is that the relative importance of dispersal vs. competition in limiting native species recovery may be fundamentally contingent on the seed supply of exotic species. This would occur if the impact of competition on native species increases with exotic seedling abundance (Ross and Harper 1972) and exotic species are at times dispersal limited. Despite this, no previous studies in grasslands have examined invasion as a function of both native and exotic seed supply.

To determine the community level effects of different patterns of seed dispersal, we related natural variation in seed rain to patterns of seedling recruitment after disturbance using seed traps and artificial disturbances created along a gradient of native species dominance. This natural experiment was used to test for dispersal limitation by comparing species abundance on disturbances vs. in the seed rain. For native species, a positive correlation between abundance on disturbances and in the seed rain would indicate that native species are dispersal limited. A negative correlation between native seedling abundance on disturbances and seed rain of exotic species would indicate that native species are impacted by interspecific competition. This design allows us to test whether competition, dispersal, or both limits native species recruitment. If native species are limited by competition from exotic species but exotic species are at times dispersal limited, local dispersal may promote coexistence by creating spatial refuges from competition. To increase the generality of our results we used a large number of species and replicated our design across seasons.

METHODS

We performed our study at Tom's Point Preserve, a private grassland preserve located adjacent to Tomales Bay in Marin County, California, USA (38°13′ N, 122°57′ W). The site has not been grazed by livestock for at least 30 years. The climate is mediterranean with cool wet winters, mild dry summers, and summer drought moderated by frequent fog (Corbin et al. 2005). In California, coastal grasslands are distinguished from inland valley grasslands by a more moderate climate regime and greater abundance of perennial species (Heady et al. 1988). Climatic conditions over the course of the study are presented in detail in Corbin and D'Antonio (2004).

In April 2001 we established 56 individual 1-m^2 plots in an ~30 × 50 m rectangular grid, with seven plots on the short side and eight plots on the long side. The study area contained a gradient of native species dominance, with native species cover ranging from 0% to 100%. Data from an immediately adjacent site demonstrated low variability in soil texture, moisture content, and nitrogen availability (J. D. Corbin, *unpublished data*), suggesting that the gradient in native species dominance is most likely caused by historical factors or local dispersal. At each plot we characterized (1) natural seed rain, (2) abundance of all species colonizing experimental disturbances, and (3) cover of all species in the undisturbed local community. Seven plots distributed throughout the site were eventually discarded due to ungulate and anthropogenic disturbance.

Germinable seed rain was measured using seed traps. We constructed traps out of circular 20.3 cm diameter × 2.5 cm deep clear plastic trays with holes in the bottom for water drainage. The trays were filled two-thirds full with locally collected soil that was autoclaved for 90 minutes to kill dormant propagules. One set of traps was deployed from April to July 2001 (early season) and the other from July to September (late season). Thus, early season seed traps received early season seed rain only, and late season seed traps received late season seed rain

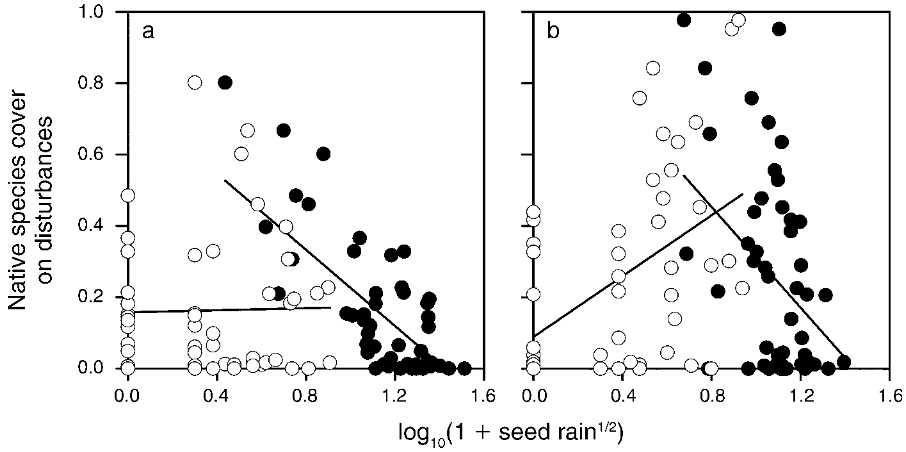

FIG. 1. Seed rain per trap of native (open circles) and nonnative (solid circles) species in (a) early and (b) late season vs. proportional cover on experimental disturbances. Exotic seed rain was negatively related to native cover in both early season ($r^2 = 0.471$, $N = 49$ plots, $P < 0.001$) and late season ($r^2 = 0.166$, $N = 49$ plots, $P = 0.004$). Seed rain of native species showed no relationship with native cover in early season ($r^2 = 0.001$, $N = 49$) but was positively correlated in late season ($r^2 = 0.220$, $N = 49$, $P = 0.001$).

only. Traps were brought intact to the Oxford Tract greenhouse facility in Berkeley, California and watered 2–4 times per week starting in October and ending in March after all germination had stopped. All samples were then stored in the greenhouse without water for six more months to simulate summer drought. After this time, watering was resumed for two weeks and stopped after no further germination was observed. All seedlings were identified and removed as they germinated.

Seedling establishment was characterized by sampling small-scale experimental disturbances created once in April 2001 (early season) and again in July (late season) adjacent to seed traps from the corresponding spatial location and time period. Thus, early season disturbances intercepted early + late season seed rain whereas late season disturbances intercepted late season seed rain only. Disturbances were created to mimic excavation mounds created by fossorial mammals such as western pocket gopher (*Thomomys bottae* Mewa). These animals are ubiquitous features of temperate grasslands, can turn over >30% of the surface area annually, and are hypothesized to be important promoters of exotic species invasions (Hobbs and Mooney 1985, Peart 1989*b*, D'Antonio 1993, Schiffman 1994, Stromberg and Griffin 1996). Soil for the disturbances was collected locally, autoclaved for 90 minutes, and formed into mounds ~20 cm in diameter by 5 cm tall. Vegetation was partially cleared from beneath the mounds to more accurately simulate disturbance caused by tunnel excavation (Hobbs and Mooney 1985). Colonization on disturbances was sampled in early May 2002 in order to observe the outcome of seedling competition after one growing season. We used a circular 20 cm diameter sampling frame to visually estimate absolute canopy cover for all species using the median of each of the following cover classes: 0%, <1%, 1–5%, 5–10%, 10–15%, . . . , 95–100%. To account for disintegration of the mound edge we left a 0.5-cm buffer between the frame and the sampled area.

We sampled the species composition of the local, undisturbed community in early June 2001 while annuals were still identifiable. Three 20-cm^2 quadrats were located randomly within each 1-m^2 plot, and absolute canopy cover was visually estimated using the cover classes mentioned previously. Twelve dominant grass species were identified (seven exotic, five native; >80% total relative canopy cover). These comprised native perennials *Festuca rubra* L., *Deschampsia caespitosa* (L.) Beauv. ssp. *holciformis* (C. Presl) W. E. Lawr., *Elymus glaucus* Buckley, *Danthonia californica* Bolander, and *Calamagrostis nutkaensis* (C. Presl) Steudel; exotic annuals *Avena barbata* (Link), *Bromus diandrus* Roth, *Bromus hordeaceous* L., *Vulpia myuros* (L.) C. Gmelin, and *Aira caryophyllea* L.; and exotic perennials *Holcus lanatus* L. and *Lolium perenne* L. Nomenclature follows Hickman (1993). Due to difficulty in identifying some seedlings, *Festuca* and *Deschampsia* were combined for the analysis. Linear least squares regressions were performed to compare the abundance of native species in the local community, on experimental disturbances, and in the seed rain (SYSTAT 11, SYSTAT Software, Richmond, California, USA). One-way ANOVA with Tukey post hoc tests was used to detect differences in seed rain of native and exotic species in early and late season. A paired *t* test was used to test for differences in native cover on early vs. late season disturbances. Seed rain counts were untransformed for *t* tests and ANOVA and log$_{10}$(1 + $x^{1/2}$)-transformed for regressions.

RESULTS

A total of 58 species were encountered in the study. For the 12 most abundant grasses, a total of 22 605 seedlings were counted and identified from seed traps.

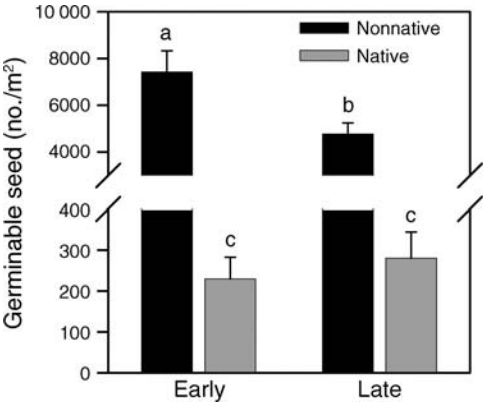

FIG. 2. Seed rain of native and nonnative species in early and late season. One-way ANOVA detected significant differences among native and exotic seed rain in early and late season ($F = 47.592$, df = 3, 192, $P < 0.001$). Seed rain of nonnative species decreased from early to late season ($P < 0.001$) whereas seed rain of native species did not change. Seed rain of nonnative species was more than one order of magnitude greater than native species seed rain in both early season ($P < 0.001$) and late season ($P < 0.001$). Note the break in scale of the *y*-axis.

Native cover on disturbances was negatively related to the seed rain of exotic species in both seasons (Fig. 1). In contrast, native cover on disturbances was not consistently related to the seed rain of native species, exhibiting no relationship in early season (Fig. 1a) and a positive relationship in late season (Fig. 1b).

Delaying disturbance until late in the season resulted in an increase in native cover ($t = 4.543$, df = 48, $P < 0.001$). However, this did not correspond to a significant increase in native seed supply (Fig. 2). Instead, this increase in native cover corresponded to a substantial late season reduction in exotic seed supply (Fig. 2). During this time, the composition of native species in the seed rain did not change significantly, while exotic species exhibited a shift from annual species in early season to perennial species in late season (C. DiVittorio, *unpublished data*).

Average seed rain of exotic species was greater than that of native species in both seasons by over one order of magnitude (Fig. 2), with total (early + late season) exotic seed rain greater than native seed rain at all but one of 49 plots. Total seed rain of exotic species ranged from 27 to 1103 seeds/trap (mean = 394.6, SE = 35.6) while total native species seed rain ranged from 0 to 72 seeds/trap (mean = 16.5, SE = 2.8). This extrapolates to 834–34 072 seeds/m^2 for exotic species and 0–2224 seeds/m^2 for native species, consistent with published estimates of seed rain in other California grasslands (Peart 1989*a*, Young and Evans 1989, Kotanen 1996). In general, abundance in the local undisturbed community was closely related to abundance in the seed rain and on disturbances, although species-specific differences existed (Fig. 3). Species that fall above the regression line are good dispersers relative to their abundance in the local community. Good dispersers were disproportionately exotic and annual, while poor dispersers were disproportionately native.

DISCUSSION

Although dispersal is widely believed to be an important determinant of community structure, it is rarely measured. This study demonstrates how patterns of dispersal among multiple species can interact to affect the outcome of colonization and invasion. In our study,

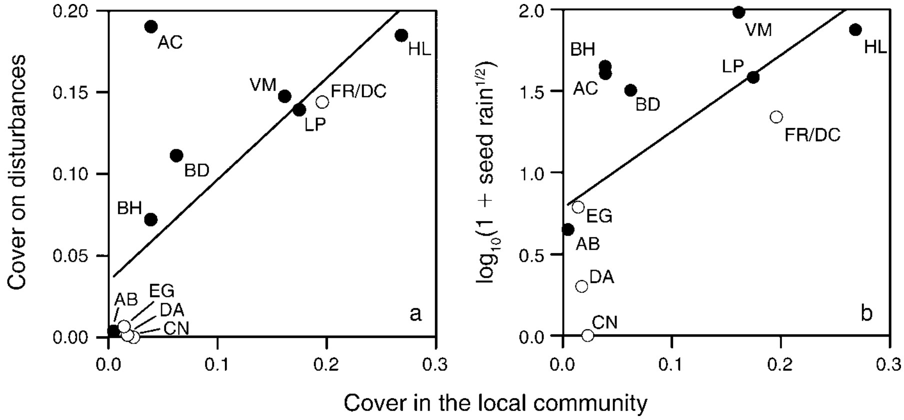

FIG. 3. Proportional cover of individual species in the local undisturbed community vs. (a) relative seedling cover on disturbances and (b) absolute abundance in the seed rain, for native (open circles) and nonnative (solid circles) species. Positive relationships were found for cover in the local community vs. on disturbances ($r^2 = 0.553$, $N = 11$ species, $P = 0.009$) and for local community cover vs. abundance in the seed rain ($r^2 = 0.421$, $N = 11$, $P = 0.031$). Species above the regression line are more greatly represented (a) on disturbances or (b) in the seed rain than would be expected based on their abundance in the local community. Thus, species above and below the line represent good and poor dispersers, respectively. Species codes are: FR/DC, *Festuca rubra/Deschampsia caespitosa*; EG, *Elymus glaucus*; DA, *Danthonia californica*; CN, *Calamagrostis nutkaensis*; HL, *Holcus lanatus*; LP, *Lolium perenne*; VM, *Vulpia myuros*; AC, *Aira caryophyllea*; BD, *Bromus diandrus*; BH, *Bromus hordeaceous*; and AB, *Avena barbata*.

recruitment of native species onto disturbances was dependent on the propagule supply of both native and exotic species. Variability in dispersal on small spatial (1–10 m) and temporal (within season) scales led to qualitative differences in colonization success such that native species dominated disturbances when exotic seed supply was low, but failed to establish when exotic seed supply was high. Although availability of native seed is a precondition for establishment, most grasslands in California are characterized by high exotic seed supply (Young and Evans 1989), suggesting that competition from exotic species is a major obstacle to native species restoration. These results are consistent with the conclusions of Hamilton et al. (1999) who found that although recruitment of the native grass *Nassella pulchra* was ultimately seed limited due to low local abundance, competition with exotic species was a stronger factor limiting the potential for native species recovery.

Despite the failure of native species to establish when exotic seed supply was high, native species dominated disturbances in late season and in native dominated patches where exotic seed supply was low. This occurred because local dispersal concentrated exotic seed rain inside exotic dominated patches, creating spatial refuges from competition inside native dominated patches. A skewed distribution of exotic seed supply (mean = 12 189 seed/m^2; median = 9761 seed/m^2; mode = 7321 seed/m^2) indicates that most plots received less seed than would be expected based on spatially averaged, or "global" dispersal. These results support the prediction that local dispersal and spatial heterogeneity in species composition promote coexistence by reducing the intensity of interspecific competition (e.g., Tilman 1994, Snyder and Chesson 2003).

Interestingly, native species dominated disturbances when exotic seed supply was low, twice exceeding 95% cover, even though exotic seed supply was greater than native seed supply at all but one of the experimental plots and was never <800 seeds/m^2. This suggests that native species are stronger per capita competitors, but that the intrinsic resistance of native assemblages to invasion is eventually overcome at high (~10 000 seeds/m^2 in this study) exotic seed supply (D'Antonio et al. 2001). We suggest that copious seed production, or "seed swamping," is an important mechanism of invasion in this system for two reasons. First, if competitive strength during seedling establishment is positively density-dependent (e.g., Ross and Harper 1972), copious seed production by exotic species may provide a population level competitive advantage despite per capita competitive inferiority. Second, the probabilistic nature of colonization and invasion (Davis et al. 2000, D'Antonio et al. 2001) suggests that copious seed production may provide an advantage allowing exotic species to colonize a greater proportion of available sites.

Based on these results, we suggest that the seed limitation of native species observed by Seabloom et al. (2003) may be due to underlying seed limitation of exotic species. This hypothesis cannot be tested, however, because the seed supply of exotic species to their experimental plots was not directly quantified. In light of the small scale variability in dispersal found in our study and others (Hobbs and Mooney 1985, Peart 1989*a*), we suggest that direct measurement of exotic seed supply at the plot level would be needed to test this hypothesis. In the restoration experiment described in Seabloom et al. (2003), although exotic species cover prior to native seed addition averaged 40%, most grasslands in California exhibit much greater cover of exotic species, frequently reaching 100% (Dyer et al. 1996).

These results have important implications for attempts to restore grasslands in California and other mediterranean-type ecosystems, as well as for studies of species interactions in general. Although we expect the relative importance of competition and dispersal limitation to vary, assuming that competition from exotic species is not important may lead to flawed restoration strategies. Our results suggest that estimation of exotic seed supply is necessary in order to determine whether adding seed of native species alone will be sufficient to restore native species dominance, or whether control of exotic species is a prerequisite. Competition and seed limitation both likely limit native species recovery in most systems, thus we suggest that restoration plans include both augmentation of native seed production and control of exotic seed production. Although control of exotic species is difficult and expensive, our results suggest that, once established, restored native grasslands should be increasingly stable to invasion as local exotic seed sources are eliminated and biotic resistance to invasion increases (Corbin and D'Antonio 2004). More broadly, our data supports the theoretical prediction that local dispersal promotes species coexistence (Tilman 1994, Snyder and Chesson 2003) and shows that studies of species interactions performed under a single or unspecified dispersal regime may have limited generality.

ACKNOWLEDGMENTS

This research was funded by the California Native Plant Society East Bay Chapter, a John and Mary Gompertz Chair Fellowship, the U.C. Berkeley/Howard Hughes Medical Institute Biology Fellows Program, and Sigma Xi. Audubon Canyon Ranch provided access to the study site. Shele Poetker, Lara Kirkner, Lynette Butsuda, and Kenneth DiVittorio provided field assistance.

LITERATURE CITED

Bartolome, J. W., and B. Gemmill. 1981. The ecological status of *Stipa pulchra* (Poaceae) in California. Madroño 28:172–184.

Clark, J. S., B. Beckage, P. Camill, B. Cleveland, J. HilleRisLambers, J. Lichter, J. McLachlan, J. Mohan, and P. Wyckoff. 1999. Interpreting recruitment limitation in forests. American Journal of Botany 86:1–16.

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.

Corbin, J. D., M. A. Thomsen, T. E. Dawson, and C. M. D'Antonio. 2005. Summer water use by California coastal prairie grasses: fog, drought, and community composition. Oecologia 145:511–521.

D'Antonio, C. M. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent, *Carpobrotus edulis*. Ecology 74:83–95.

D'Antonio, C. M., J. Levine, and M. Thomsen. 2001. Propagule supply and resistance to invasion: a California botanical perspective. Journal of Mediterranean Ecology 2: 233–245.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528–534.

Dyer, A. R., H. C. Fossum, and J. W. Menke. 1996. Emergence and survival of *Nassella pulchra* in a California grassland. Madroño 43:316–333.

Dyer, A. R., and K. J. Rice. 1997. Intraspecific and diffuse competition: the response of *Nassella pulchra* in a California grassland. Ecological Applications 7:484–492.

Ericksson, O., and J. Ehrlen. 1992. Seed and microsite limitation of recruitment in plant populations. Oecologia 91:360–364.

Gaines, S., and J. Roughgarden. 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proceedings of the National Academy of Sciences (USA) 82:3707–3711.

Hamilton, J. G., C. Holzapfel, and B. E. Mahall. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. Oecologia 121:518–526.

Heady, H. F. 1988. Valley grassland. Pages 491–514 *in* M. Barbour and J. Major, editors. Terrestrial vegetation of California. California Native Plant Society, Sacramento, California, USA.

Heady, H. F., T. C. Foin, M. K. Hektner, D. W. Taylor, M. G. Barbour, and W. J. Barry. 1988. Coastal prairie and northern coastal scrub. Pages 733–760 *in* M. Barbour and J. Major, editors. Terrestrial vegetation of California. California Native Plant Society, Sacramento, California, USA.

Hickman, J. C., editor. 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley, California, USA.

Hobbs, R. J., and H. A. Mooney. 1985. Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. Oecologia 67:342–351.

Huenneke, L. F. 1989. Distribution and regional patterns of Californian grasslands. Pages 1–12 *in* L. F. Huenneke and H. Mooney, editors. Grassland structure and function: California annual grassland. Kluwer Academic, Dordrecht, The Netherlands.

Kotanen, P. M. 1996. Revegetation following soil disturbance in a California meadow: the role of propagule supply. Oecologia 108:652–662.

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

Peart, D. R. 1989*a*. Species interactions in a successional grassland. I. Seed rain and seedling recruitment. Journal of Ecology 77:236–251.

Peart, D. R. 1989*b*. Species interactions in a successional grassland. III. Effects of canopy gaps, gopher mounds and grazing on colonization. Journal of Ecology 77:267–289.

Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6:93–107.

Ross, M. A., and J. L. Harper. 1972. Occupation of biological space during seedling competition. Journal of Ecology 60: 77–88.

Schiffman, P. M. 1994. Promotion of exotic weed establishment by endangered giant kangaroo rats (*Dipodomys ingens*) in a California grassland. Biodiversity and Conservation 3: 524–537.

Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences (USA) 100:13384–13389.

Snyder, R. E., and P. Chesson. 2003. Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. Ecology Letters 6:301–309.

Stromberg, M. R., and J. R. Griffin. 1996. Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. Ecological Applications 6:1189–1211.

Thomsen, M. A., C. M. D'Antonio, K. B. Suttle, and W. P. Sousa. 2006. Ecological resistance, seed density, and their interactions determine patterns of invasion in a California coastal grassland. Ecology Letters 9:160–170.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75:2–16.

Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. Oikos 88:225–238.

Von Holle, B., and D. Simberloff. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology 86:3212–3218.

Young, J. A., and R. A. Evans. 1989. Seed production and germination dynamics in California annual grasslands. Pages 39–45 *in* L. F. Huenneke and H. Mooney, editors. Grassland structure and function: California annual grassland. Kluwer Academic, Dordrecht, The Netherlands.