Woody plant invasion at a semi-arid/arid transition zone: importance of ecosystem type to colonization and patch expansion

Peters, Debra P.C. [1*]; **Yao Jin**[1,2] **& Gosz, James R.**[3]

[1]*Jornada Experimental Range and Jornada Basin LTER, Box 30003, NMSU, Las Cruces, NM 88003-0003, USA;*
[2]*Current address: Adams State College, Alamosa, CO 81102, USA; E-mail jinyao@adamsstate.edu;*
[3]*Department of Biology, University of New Mexico, Albuquerque, NM 87131-0001, USA; E-mail jgosz@unm.edu;*
*Corresponding author; E-mail debpeter@nmsu.edu

Abstract

Question: How do patterns in colonization and patch expansion of an invasive woody plant (*Larrea tridentata*, *Zygophyllaceae*) differ between two grassland ecosystems at a biome transition zone?

Location: Semi-arid/arid transition zone in central New Mexico.

Methods: Frequency of occurrence, height, and surface area of saplings ($n = 134$) and patches of adult plants ($n = 247$) of the invasive shrub, *L. tridentata*, were measured within a mosaic of ecosystems dominated either by the Chihuahuan Desert species, *Bouteloua eriopoda* (*Poaceae*), or the shortgrass steppe species, *B. gracilis*, located within 1 km of the *L. tridentata*-dominated ecosystem. Distances between *L. tridentata* patches and patch area were used to estimate connectivity as a measure of propagule pressure. Sapling age (estimated from height using previously established relationships) and distance to the ***L. tridentata***-dominated ecosystem was used to evaluate patterns in dispersal. Cover by species or functional group inside each *L. tridentata* patch was compared with surrounding vegetation to estimate changes in species composition with patch expansion.

Results: *L. tridentata* saplings ($< 1\%$) and adult patches (15%) occurred less frequently in *B. gracilis*-dominated ecosystems than expected based on areal extent of this ecosystem type. Propagule pressure did not differ with distance from the core ecosystem dominated by *L. tridentata*. Evidence for both local and long-distance dispersal events was found. Similar relationships between number of plants and patch area in both grassland types indicate similar patterns in patch expansion. Cover of perennial forbs was higher and cover of dominant grasses was lower in *L. tridentata* patches compared with the surrounding vegetation for both ecosystem types.

Conclusions: Spatial variation in *L. tridentata* saplings and patches at this biome transition zone is related to the different susceptibilities to invasion by two grassland ecosystems. The persistence of grasslands at this site despite region-wide expansion by *L. tridentata* may be related to the spatial distribution of *B. gracilis*-dominated ecosystems that resist or deter invasion by this woody plant.

Keywords: Biome transition; Chihuahuan Desert; Ecotone; Invasive species; Patch dynamics; Patch structure; Shortgrass steppe.

Introduction

Invasion by aggressively spreading indigenous and non-indigenous plant species into resident ecosystems occurs globally with important consequences for ecosystem properties and processes (Drake et al. 1989; Reynolds & Stafford Smith 2002). Successful colonization and expansion of a plant species depend on its life history characteristics, including propagule pressure, relative to characteristics of the resident ecosystem, such as species traits, environmental conditions, natural enemies, and biological inertia (e.g. Rejmánek & Richardson 1996; Von Holle et al. 2003; Von Holle & Simberloff 2005). For many species, invasion is variable in time and space as a result of these fine-scale interactions between invading plants and resident ecosystems (Godfree et al. 2004). Most fine-scale studies have focused on indigenous species expansions into a single resident ecosystem and the resulting shift in species dominance and ecotone or boundary location (e.g. Allen & Breshears 1998; Mast & Wolf 2004). Comparisons of invasion into multiple resident ecosystems are often conducted at stand, community, or biome scales without a consideration of plant- and patch-scale interactions (e.g. Davis et al. 1998; Lonsdale 1999). Our goal was to understand how fine-scale invasion success of one species differs between two resident ecosystems at the same site by considering patterns in both plant colonization and patch expansion.

Landscapes composed of a mosaic of different resident ecosystems, such as those found at biome transition zones, provide an opportunity to examine the importance of plant- and patch-scale processes to invasion success (Peters et al. 2006). For example, in the Chihuahuan Desert of North America, woody plant expansion has often involved spread of native species, such as *Larrea tridentata* (Creosote bush), into perennial grasslands dominated by species such as *Bouteloua eriopoda* (Black grama). At the regional scale, areas dominated by *L. tridentata* have increased ca. 50-fold

since the 1850s (McCraw 1985; Gibbens et al. 2005); however, little is known about fine-scale processes controlling invasion dynamics of this species. In central New Mexico, U.S.A. where the northern extreme of the Chihuahuan Desert forms a transition zone with the shortgrass steppe biome, *L. tridentata* abundance is spatially variable across the landscape, from isolated plants and patches of variable sizes growing in grassland ecosystems to large areas dominated by this woody species. We hypothesized that spatial variation in the occurrence of saplings and patches of *L. tridentata* is related to differential invasion success in ecosystems dominated by grass species from different biomes.

Invasion success depends on both the colonization of plants and the expansion of patches through time. Successful colonization depends on propagule pressure, dispersal of propagules, and suitable microsite conditions for germination and establishment (Von Holle & Simberloff 2005). Although *L. tridentata* frequently produces viable seeds in the northern Chihuahuan Desert, similar to congeneric plants in the Sonoran Desert (Abe 1982), little is known about its dispersal vectors. The large, heavy seeds do not have a particular adaptation for dispersal, and are likely dispersed across a range of distances by small animals, birds, and water rather than by wind (Boyd & Brum 1983). Little is known about specific micro-environmental conditions required for germination and establishment by *L. tridentata*, although high soil water content can inhibit germination (McGee & Marshall 1993). Invasion success also depends on patch expansion resulting from an increase in number of adult plants within a patch (Mack et al. 2000). Patch expansion of *L. tridentata* is limited to the recruitment of new individuals by seed; clonal growth by this species has not been documented in the northern Chihuahuan Desert.

Landscapes at this transition zone consist of a mosaic of ecosystems dominated either by *B. eriopoda* or its congeneric, *Bouteloua gracilis* (Blue grama), a dominant species in the shortgrass steppe. These species share some characteristics, such as a low growth form and drought tolerance, however, they also differ in characteristics that may affect invasion success by *L. tridentata*. In particular, we expected that saplings and patches of *L. tridentata* would occur less frequently in *B. gracilis*-dominated ecosystems than in *B. eriopoda*-dominated ecosystems because of site-level differences in soil properties and plant-level differences in morphology. Seedlings of *L. tridentata* are particularly sensitive to high water availability and the growth of fungus (McGee & Marshall 1993). *B. gracilis*-dominated ecosystems at this site occur on fine-textured soils with low evaporation rates and in low-lying areas that can accumulate water, thus high soil water contents near the soil surface may inhibit germination of *L. tridentata* seeds compared with *B. eriopoda*-dominated ecosystems that occur on well-drained sandy loam uplands (Kröel Dulay et al. 2004). In addition, the well-developed crown structure and high density of surface roots of *B. gracilis* plants may limit space available for seedling establishment by *L. tridentata* compared with the open canopy structure and loose collection of stolons associated with *B. eriopoda* plants (Coffin & Lauenroth 1991; Peters 2000).

We also expected these differences in microsite conditions would result in differences in species composition of *L. tridentata* patches located within the two ecosystem types. Although there is overlap in the species found in both *B. eriopoda*- and *B. gracilis*-dominated ecosystems at this site, some species are only found in one or the other ecosystem type (Kröel Dulay et al. 2004). Thus, the species available to colonize each patch may vary with ecosystem type.

In the absence of long-term observations, spatial patterns of saplings and patches can be used as indicators of colonization and patch expansion dynamics (e.g. Mast & Wolf 2004). We used spatial patterns of *L. tridentata* saplings and patches located across a mosaic of ecosystems dominated by either *B. eriopoda* or *B. gracilis* to address three objectives related to our hypothesis: to compare (1) the presence of *L. tridentata* saplings and patches and (2) the size distribution of saplings or plants, and functional group composition of patches, in ecosystems dominated by either *B. eriopoda* or *B. gracilis*; and (3) to provide insights as to the importance of colonization and patch expansion processes to the observed patterns in saplings and patches.

Methods

Study area

This study was conducted at the Sevilleta National Wildlife Refuge (SEV) Long Term Ecological Research site in central New Mexico, USA (34.4° N, 106.7° W, 1600 m a.s.l.). Long-term (80 a) mean annual precipitation is 232 mm (SD =79 mm) (Hochstrasser et al. 2002). Long-term mean monthly temperature over the same time period ranges from 2.6 °C (January) to 24.6 °C (July). Soils range from sandy loam to loamy sand with a calcium carbonate layer at varying depths (15 to > 50 cm) and stages of development. Grazing by cattle has been excluded from the site since 1973, although native herbivores occur at low densities (pronghorn antelope, rabbits) or infrequently at high densities (e.g. grasshoppers). Landscapes on the McKenzie Flats where this study was conducted consist of a mosaic of areas primarily dominated by one of the two *Bouteloua* species and ecotones between these areas. This study focused on *L. tridentata* saplings and patches of adult plants occurring

within ecosystems dominated either by *B. eriopoda* or *B. gracilis*, and located within 1 km of the ecosystem dominated by *L. tridentata*.

Sapling patterns

The presence and size distributions of saplings of *L. tridentata* in each ecosystem type were determined for two locations (ca. 1 km² total area) selected in December (2002) to represent the *L. tridentata*-to-grassland transition across the McKenzie Flats. Each location contained *L. tridentata*-dominated ecosystems at the south that merged northward into a mosaic of *B. eriopoda*- and *B. gracilis*-dominated ecosystems containing isolated plants and patches of *L. tridentata*. The height and two crown diameters (longest and its perpendicular) were measured for all *L. tridentata* saplings (≤ 0.5 m height) in each location. Surface area of the canopy of each sapling was calculated from the two diameters by assuming an ellipsoid shape. Each sapling was geo-referenced using a hand-held global positioning system (GPS). Vegetation in the ca. 50 m² area surrounding each sapling was visually estimated as either dominated by *B. eriopoda*, *B. gracilis* or other species.

Aerial photos from 1998 ground-truthed by field surveys were used to estimate the amount of area in each location dominated by either *B. eriopoda* or *B. gracilis*. Ecosystems dominated by each grass species are easily differentiated by colour and structure on the photos. These estimates of area were used to determine the expected number of *L. tridentata* saplings in each ecosystem type based on area of dominance. χ^2-analysis was then used to compare the observed and expected number of saplings in each ecosystem type.

Patch patterns

Presence and size distributions of *L. tridentata* patches consisting of adult plants > 1 m in height within each ecosystem type were determined in five characteristic locations (ca. 5000 m² each) selected for sampling in March (2001) that included multiple areas dominated by either *B. gracilis* or *B. eriopoda* as well as containing a range of sizes of isolated patches of *L. tridentata*. All established *L. tridentata* patches within each location were counted and selected for sampling. The perimeter of each patch was measured and the geo-referenced location was obtained using a hand-held GPS unit. Similar to the sapling data, aerial photos were used to calculate the expected number of patches in each community type (proportional to area), and χ^2-analysis was used to compare the observed and expected values. Size frequency distributions of patches (i.e. surface area) in each community type were compared using Kolmogorov-

Smirnov two-sample tests.

Canopy cover by species (*B. gracilis*, *B. eriopoda*) or functional group (other grasses, forbs and shrubs other than *L. tridentata*) and litter inside and outside each patch were estimated visually in 1-m² quadrats. Because sampling was conducted in early spring prior to germination of annuals, cover was only estimated for perennials. Total cover was taken as the sum of all groups except *L. tridentata* and litter. Number of quadrats sampled within each patch depended on patch size: only one quadrat was possible for patches consisting of one *L. tridentata* plant. As patch size increased, additional quadrats were sampled as patch area allowed up to a maximum of four. In addition, four randomly positioned quadrats located at 2 m distance from each patch edge were sampled for all patches to represent the ecosystem type surrounding each patch. Ecosystem type (*B. gracilis*- or *B. eriopoda*-dominated) was determined by the species with the larger average cover in these four quadrats.

Analyses were conducted using two-way ANOVA to compare: (1) cover between species or functional groups within each of four locations (*L. tridentata* patches either in *B. eriopoda* or *B. gracilis*-dominated ecosystems, resident ecosystems dominated either by *B. eriopoda* or *B. gracilis*), and (2) cover for each species or functional group between *L. tridentata* patches and the corresponding ecosystem type, either *B. eriopoda* or *B. gracilis*. Means were compared using the Least Significant Difference method with $p < 0.05$.

Colonization and expansion processes

We used the relationship between saplings or patches and distance to the *L. tridentata*-dominated ecosystem to provide insights to colonization and patch expansion processes, and in particular dispersal and propagule pressure. Sapling age is often used to approximate the timing of dispersal events. Thus, the relationship between sapling age and distance from the *L. tridentata*-dominated ecosystem was used to examine patterns in propagule dispersal. Sapling age was estimated using a previously established relationship between *L. tridentata* sapling height and age: age (a) = height (m) × 31.0; R^2 = 0.83; $p < 0.001$ (D. Moore, J.M. Francis & J.R. Gosz unpubl. data).

Connectivity among patches based on nearest neighbour distances was used to estimate propagule pressure. A structural metric was used to calculate the connectivity between each patch i and all other patches that combines the area of each *patch$_j$* and *distance$_{ij}$* between *patch$_i$* and each *patch$_j$* (Moilanen & Nieminen 2002; Calabrese & Fagan 2004):

$$\text{connectivity}_i = \sum \left(\text{patch area}_j / \text{distance}_{ij} \right) \qquad (1)$$

where $i \neq j$,

Distance from each geo-referenced sapling or patch to the *L. tridentata*-dominated ecosystem was measured using geographic information system software (ARC/INFO). Regression analyses were then used to relate either sapling age or connectivity with distance. Since connectivity combines the effects of patch area and distances among patches, we also examined the separate relationships between patch area (a measure of propagule availability) or distance to the nearest neighbouring patch (a measure of local propagule dispersal) with distance from the *L. tridentata*-dominated ecosystem.

Results

Colonization of saplings

Although *B. gracilis* dominated 22% of the area, of the 134 *L. tridentata* saplings located, only one was found in this ecosystem type (1%). Most saplings found in *B. eriopoda*-dominated ecosystems (54%) were small (≤ 0.1 m^2), but a wide range of sapling canopy areas, 0.1 to 2.5 m^2 was observed (Fig. 1a).

Patch survival and expansion

Of the 247 *L. tridentata* patches of adult plants sampled, 85% ($n = 210$) were in *B. eriopoda*-dominated ecosystems and only 15% ($n = 37$) were in *B. gracilis*-dominated ecosystems. The number of patches in *B. gracilis* ecosystems was significantly fewer than expected ($p < 0.0001$) based on areal extent of this ecosystem. The number of patches of each size class relative to the total number of patches was similar for all patch sizes located in *B. gracilis*- and *B. eriopoda*-dominated ecosystems, except for the smallest (≤ 4 m^2) and largest sizes (≥ 300 m^2) where significantly more patches ($p < 0.05$) were found in *B. eriopoda*-dominated ecosystems (Fig. 1b). For both ecosystem types, patch size ranged from 0.07 to 598 m^2 with most patches (65%) smaller than 10 m^2; only 5% of the patches were larger than 100 m^2. Patch area was linearly related ($R^2 = 0.79; p < 0.0001$) to the number of *L. tridentata* plants per patch with no significant difference in this relationship between patches in the two ecosystem types (not shown).

Cover in *B. eriopoda*- and *B. gracilis*-dominated ecosystems surrounding *L. tridentata* patches was low for all species and functional groups other than the dominant grasses, either *B. eriopoda* (Fig. 2a) or *B. gracilis* (Fig. 2b). Cover of perennial forbs and shrubs other than *L. tridentata* had the lowest cover values for both ecosystem types. Cover of vegetation inside *L. tridentata* patches located within *B. eriopoda*-dominated
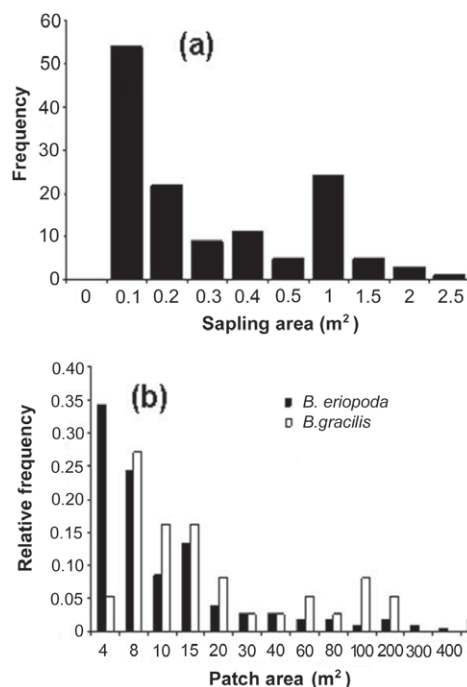

Fig. 1. a. Frequency distribution of the area of *Larrea tridentata* saplings found within *B. eriopoda*-dominated ecosystems. One sapling found in a *B. gracilis*-dominated ecosystem is not shown. **b.** Frequency distribution of the area of *L. tridentata* patches found within either *B. gracilis*- or *B. eriopoda*-dominated ecosystems.

ecosystems were also dominated by this grass species with lower cover of other groups (Fig. 2c). By contrast, patches located in *B. gracilis*-dominated ecosystems had similar cover of all species or functional groups except shrubs other than *L. tridentata* (Fig. 2d). Patches of *L. tridentata* had significantly higher cover of perennial forbs and lower cover of the dominant grasses for both ecosystem types.

Dispersal and propagule pressure

There was no relationship between sapling age and distance of a sapling from the *L. tridentata*-dominated area (not shown). The oldest saplings (> 15 a) were found both at the shortest (< 100 m) and longest distances (> 700 m) from the area dominated by *L. tridentata*. A wide range of sapling age was found for several distances. For example, saplings ranged in age from 4 to 18 years old between 600 and 700 m.

Connectivity was significantly related to distance from the *L. tridentata*-dominated ecosystem for patches in both grassland types combined (Fig. 3a). In general, patches located closer to the *L. tridentata*-dominated area had lower connectivity than patches located at
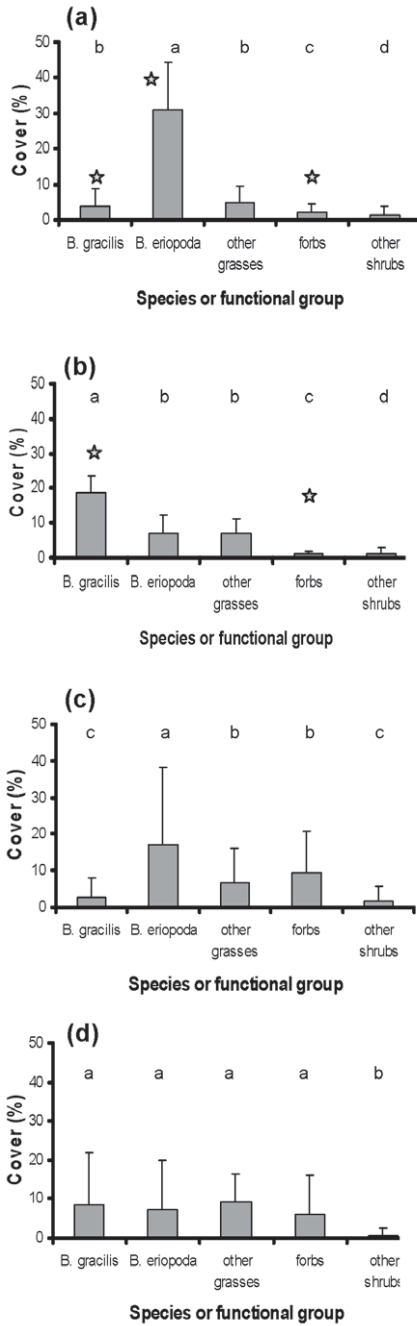
Fig. 2. Cover by species or functional group for four locations: **(a)** Ecosystems dominated by either *B. eriopoda* or **(b)** *B. gracilis*, and for **(c)** *L. tridentata* patches located within ecosystems dominated by either *B. eriopoda* or **(d)** *B. gracilis*. Different letters indicate significant differences in cover among species and functional groups within each location; * indicates significant differences in cover for each species or functional type between locations (i.e. *L. tridentata* patches and the surrounding resident ecosystem).

Fig. 3. Distance from the ecosystem dominated by *Larrea tridentata* and **(a)** connectivity; **(b)** patch area, and **(c)** distance to the nearest patch for *L. tridentata*. patches located in both ecosystem types.

greater distances; however peak values of connectivity were found between 300 m and 500 m. Patch area and distance to the nearest neighbouring patch were not significantly related to distance from the *L. tridentata*-dominated ecosystem (Fig. 3b, c). Both small and large patches, and short and long distances to the nearest patch were found throughout the sampled areas.

Discussion

Invasibility and ecosystem type

Expansion of invasive species into resident ecosystems involves a sequence of processes, from the dispersal of viable propagules and colonization of saplings to the aggregation of plants into patches, and finally the aggregation of patches into communities and ecosystems that result in shifts in species dominance and changes in ecotone location (Allen & Breshears 1998, Mast & Wolf 2004). In this study, saplings and patches of the aggressively spreading native shrub, *Larrea tridentata*, occurred more frequently in ecosystems dominated by the Chihuahuan Desert species, *B. eriopoda*,
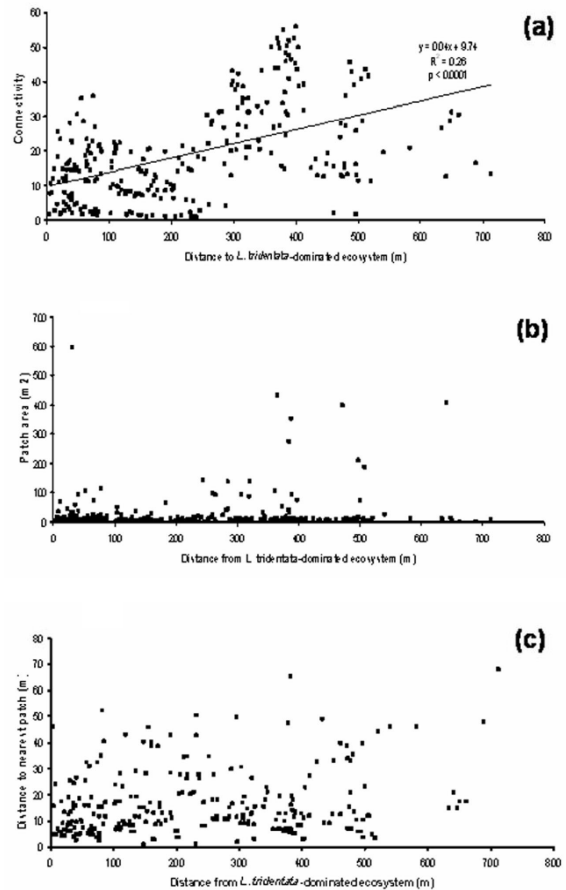
than in ecosystems dominated by the shortgrass steppe species, *B. gracilis*. The smaller percentage of *L. tridentata* saplings (1%) found in *B. gracilis*-dominated ecosystems compared with the percentage of patches (15%) may reflect the smaller area sampled for saplings (1 km^2) compared with patches (25 km^2). In addition, saplings are inherently more difficult to locate than patches. Our results are supported by more extensive sampling at this site showing *L. tridentata* and *B. gracilis* plants rarely occur in the same 100 m^2 quadrat (Peters et al. 2006). Based on our results, invasion across landscapes can be inhibited by susceptible ecosystems located within a mosaic of more invasion-prone ecosystems. We expect that the number and size of more resistant ecosystems as well as their spatial configuration are important characteristics that determine invasion across landscapes. At the biome scale, additional factors can become important. For *L. tridentata*, it is unlikely that this species will continue to expand northward or eastward into the shortgrass steppe biome given its resistance to invasion by *B. gracilis*-dominated ecosystems as well as its temperature requirements for growth (Martinez-Vilalta & Pockman 2002).

The ability of ecosystems to resist invasion is often related to a combination of biotic and abiotic factors (Von Holle & Simberloff 2005). Examining variation in invasibility between ecosystems located within one site allows some factors to be eliminated, such as climate, which are the same across the landscape. Differences between our ecosystems that likely affect their relative invasibility are rooting densities, plant morphology, soil texture and structure, and water relations (Gadzia 1979; Coffin & Lauenroth 1991; Kröel-Dulay et al. 2004); experiments are needed to determine the key factors affecting *L. tridentata* invasion in these ecosystem types.

Numerous studies have shown effects of invasive species on ecological properties of the resident ecosystem (e.g. Drake et al. 1999; Mack et al. 2000). In our study, perennial forbs was the only functional group with significantly larger cover in patches compared with the surrounding resident ecosystem for both ecosystem types. Similarly, cover of the dominant species, either *B. gracilis* or *B. eriopoda*, was lower in patches than in the surrounding ecosystem. This suggests the successional nature of these patches in that the dominant species are negatively affected and perennial forbs often respond quickly after disturbance (Kerley & Whitford 2000). It is also possible that *L. tridentata* preferentially invades microsites with these abiotic and biotic characteristics.

Recruitment and invasion dynamics

Although *L. tridentata* has expanded throughout much of the Chihuahuan Desert over the past several centuries (McCraw 1985; Gibbens et al. 2005) and many studies have been conducted on individual plant responses (e.g. Reynolds et al. 1999; Miller & Huenneke 2000), little is known about recruitment events as related to invasion dynamics. Our results of estimated sapling ages show that recruitment events may have occurred annually over the past 18 years. These results are in contrast to previous studies that suggest the importance of infrequent, episodic recruitment events for arid and semi-arid shrubs (Barbour et al. 1977; Brown & Carter 1998). There are two explanations for these contrasting results. First, recruitment events that result in infilling between established plants and patches within transition zones (this study) may not be episodic because of high seed availability and locally favorable micro-environmental conditions. The existence of multi-aged saplings at the same distance from the *L. tridentata*-dominated ecosystem supports this explanation. Recruitment events that occur at large distances from the source population may be episodic, and driven by seed availability and extreme climatic events; these long distance dispersal events can be very important to population dynamics (Clark et al. 1999, 2005). In our study, three saplings older than 16 years found at distances greater than 600 m from the *L. tridentata*-dominated ecosystem support the occurrence of infrequent, long distance dispersal events. Most studies have not differentiated between these two types of recruitment events or accounted for the possibility that both types of events may be operating for the same species within a landscape.

Second, recruitment events of *L. tridentata* may be episodic at our site, but they appear to occur every year because of high variation in sapling heights of the same age. High variation in canopy cover with increased height (not shown) suggests microhabitat variation affects sapling growth through time; this microhabitat variation may also be important to the relationship between height and age. In either case, recruitment events have occurred over the past 18 years to result in a population of unevenly-sized *L. tridentata* saplings that are confined to *B. eriopoda*-dominated ecosystems within 1 km from existing *L. tridentata*-dominated ecosystems. Thus, we expect that *L. tridentata* is well-poised to rapidly increase in density through patch expansion and continued infilling when favourable conditions occur because many isolated individuals currently exist within the landscape.
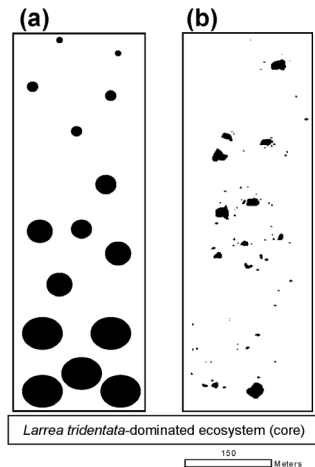
Fig. 4. a. Hypothetical pattern based on 'classic' ecotone theory of decreasing patch size and increasing distance between patches as distance from the ecosystem dominated by *Larrea tridentata* increases (Gosz 1992, 1993). **b.** Patch patterns for one sampling area in this study. *L. tridentata* patches are shown in black.

Insights to invasion processes and dynamics

Dynamics of biome transition zones have been characterized by shifts in species dominance across ecotones as a result of changes in patch structure (Gosz 1993). Thus, the invasion of grasslands by woody plants results from an increase in the number and spatial extent of woody plant patches that shift the location of the ecotone through time and across space (Gosz 1992). At any point in time, the largest and most highly connected patches of woody plants are expected to be located closest to the woody plant-dominated ecosystem or 'core population'. In this 'classic' ecotone model, the woody plant-dominated ecosystem is assumed to be the major source of propagules, seed dispersal by wind is prevalent, and suitable micro-environmental conditions for establishment and growth determine the pattern of expansion across the landscape (Fig. 4a) (Gosz 1993). Our results show a different relationship between patch size and connectivity with distance from the *L. tridentata*-dominated ecosystem in that a wide range of sapling ages, patch sizes, and distances between patches were found with distance. Invasion dynamics and key processes can be inferred from our data. Our results suggest the importance of long distance dispersal events in creating patches across a range of distances from the core ecosystem, similar to animal-dispersed species (Clark et al. 2005). Following dispersal, successful seed germination and seedling establishment would depend on the occurrence of suitable micro-environmental conditions. Expansion of the spatial extent of these patches would occur through local dispersal events that result in

large patches located at variable distances from the core ecosystem; these patches can then act as seed sources for the initiation of new patches at increasingly farther distances or for the infilling of patches at closer distances. Multiple recruitment events followed by patch expansion through time would result in a mosaic of patches of variables sizes and connectivities (Fig. 4b). Our results support a more recent framework that envisions ecotones as consisting of a hierarchy of dynamic patches with different properties, spatial arrangements, and connectivity with other patches that determine invasion dynamics in response to a range of environmental conditions (Peters et al. 2006).

Conclusions

Invasibility is an important characteristic of ecosystems that often determines the ability of an invasive species to expand its spatial distribution. Our results show that invasibility differs for two grassland ecosystems at a biome transition zone with important consequences for broad-scale dynamics across the landscape and shifts in species dominance and ecotone location. Ecosystems dominated by the Chihuahuan Desert species, *B. eriopoda*, had significantly higher frequencies of occurrence of both saplings and patches of *L. tridentata* compared with shortgrass steppe ecosystems dominated by *B. gracilis*. Our results suggest that short- and long-distance dispersal, propagule pressure, and patch expansion processes as well as the presence of micro-environmental conditions for seed germination and seedling establishment are important to variation in *L. tridentata* patch structure. Maintaining *B. gracilis*-dominated ecosystems as part of the landscapes at these transition zones is important in limiting further expansion by *L. tridentata*. The size, density, and spatial arrangement of *B. gracilis*-dominated ecosystems needed to restrict the spatial distribution of *L. tridentata* have yet to be determined.

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