

## WOODY PLANT ESTABLISHMENT AND SPATIAL HETEROGENEITY IN GRASSLANDS

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**Abstract.** Root exclusion experiments demonstrated the importance of belowground competition between grasses and *Prosopis glandulosa* (honey mesquite) during the critical seeding establishment phase of the woody plant life cycle. Belowground available volume accounted for 67% and 79% of the variance in first- and second-year *Prosopis* seedling growth and survival, respectively. Available volume in the vertical dimension was more important than that in the horizontal dimension. Trials spanned years with contrasting annual precipitation, suggesting that root competition occurs in years of near-average as well as below-average annual rainfall. Spatial heterogeneity in canopy gaps and belowground biomass was also quantified in a *Schizachyrium*–*Paspalum* grassland matrix and evaluated with respect to *Prosopis* seedling establishment. Of the 100 grid points encountered in four grass stands, 62% were unoccupied; and 50% of these exceeded 80 cm<sup>2</sup> (~10 cm diameter). Gaps ≥ 10 cm in diameter were sufficient for successful *Prosopis* germination and survival after one (40%) and two (15%) growing seasons. Herbaceous root biomass was statistically comparable among stands, but point-specific biomass varied three orders of magnitude (<50 g/m<sup>2</sup> to >3000 g/m<sup>2</sup>). In addition, root biomass was temporally variable, ranging from a mean (±1 SE; g/m<sup>2</sup>) of 768 (86) in a year of below-average annual rainfall (1996; 721 mm) to 1108 (104) in a year of roughly average annual rainfall (1995; 1032 mm). It is often assumed that grasslands dominated by productive, late seral species will be resistant to woody plant encroachment; and that grazing, by reducing the ability of grasses to competitively exclude woody seedlings, makes grasslands susceptible to tree/shrub invasion. However, given the substantial annual variation in belowground biomass observed in this study, it seems reasonable that ungrazed grasslands may be more susceptible to woody plant encroachment in some years and more resistant in others. Furthermore, given the substantial spatial variation in aboveground gap area and belowground biomass, there may be numerous low-competition microsites for woody plant seedlings within ungrazed grasslands. A high degree of temporal and spatial variability in gap area and belowground biomass may therefore help explain successful establishment of woody seedlings in ungrazed or lightly grazed, late seral grasslands in the absence of fire. We found no correlation between aboveground structure and belowground biomass at scales of 1–10 m<sup>2</sup>. Thus, readily quantifiable attributes such as grass basal area or gap area could not be used to infer site susceptibility to woody plant seedling establishment.

**Key words:** competition; grassland; mesquite; *Paspalum*; *Prosopis glandulosa*; savanna; *Schizachyrium*; woody plant encroachment.

### INTRODUCTION

Woody plant proliferation in grasslands and savannas over the past century has been widely documented and its causes debated (Archer 1994, 2002, Archer et al. 1995, Van Auken 2000). This phenomenon has long been a concern of land managers because it adversely affects herbaceous productivity and livestock handling, thus threatening the sustainability of pastoral, subsistence, and commercial livestock grazing (Fisher 1950,

1977, Rappole et al. 1986). More recently, shifts from grass to woody plant domination are drawing interest because attending biophysical (Asner et al. 1998, Hoffman and Jackson 2000) and biogeochemical (Schlesinger et al. 1990, Scholes and Hall 1996, Archer et al. 2001) changes may have global consequences for land surface–atmosphere interactions and the carbon cycle (Houghton et al. 1999, Schimel et al. 2000, Pacala et al. 2001). An important first step in understanding shifts from grass to woody plant domination is understanding how woody plant seedlings establish in grass-dominated patches.

A variety of factors, including climate, soils, and disturbance, interact to determine the relative abundance of trees, shrubs, and grasses in dryland ecosystems (Walker 1987, Scholes and Archer 1997). The co-occurrence of these contrasting life-forms has long been of interest to ecologists. Observations of differ-

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ences in root architecture and distribution prompted Schimper (1903) to suggest that "moisture in the subsoil has little influence on the covering of grass; only moisture in the superficial soils is important to it . . ." and that woody plants are favored by moist subsoil "regardless of whether rain falls frequently or rarely . . ." Recent reviews substantiate the general differences in root depth distribution between grass and woody plant life-forms (Jackson et al. 1996) and supports Walter's (1971) two-layer soil moisture hypothesis which proposed that resource partitioning in tree/shrub-grass systems occurs because grasses preferentially utilize resources in the upper portion of the soil profile, whereas woody plants obtain resources from greater depths. Although there are exceptions (e.g., Le Roux et al. 1995), research in tropical (Knoop and Walker 1985) and subtropical (Brown and Archer 1990, Midwood et al. 1998) savannas, temperate grasslands (Bragg et al. 1993), and shrub-steppe (Sala et al. 1989, Dodd et al. 1998) has supported this hypothesis. However, while the two-layer soil moisture hypothesis may explain interactions among established plants with well-developed root systems, it cannot explain how woody plants avoid, reduce, or tolerate competition with grasses during the critical seedling establishment phase, when their roots are largely confined to the portion of the soil profile dominated by grasses.

In order for woody plants to persist and increase in density within a matrix of grasses, periodic seedling establishment is typically required. Most biomass in grasslands is belowground (Dahlman and Kucera 1965, Sims and Singh 1978, Richards 1986, Jackson et al. 1996). Accordingly, several studies suggest belowground rather than aboveground competition has the greatest influence on woody plant seedling establishment in grass-dominated patches (Adams et al. 1992, McPherson 1993, Wilson 1993a, b, 1998). Observations that simulated roots (plastic wires) can reduce plant establishment suggests competition may occur for space (McConnaughay and Bazzaz 1992) as well as for water and nutrients. Because root biomass in grasslands may be heterogeneously distributed (Brown and Archer 1989, Milchunas and Lauenroth 1989), woody plants may preferentially establish in microsites where grass root biomass is low or where above- and belowground gaps in the grass layer (i.e., Coffin and Lauenroth 1990, Van Auken and Bush 1990, Aguilera and Lauenroth 1995, Owens et al. 1995) are formed by climate- or disturbance-induced mortality or reductions in plant basal area. This possibility has seldom been evaluated (McPherson 1997). Alternatively, establishment may occur during seasons (Brown and Carter 1998) or years when resource availability is high and competition is minimal (Harrington 1991, Brown et al. 1998, Brown and Archer 1999).

The objective of this study was to (a) quantify spatial heterogeneity and relationships between grass basal area and belowground biomass in a late seral *Schiza-*

*chyrum-Paspalum* grassland; and (b) experimentally evaluate the space requirements for establishment of *Prosopis glandulosa*, an invasive woody plant in southwestern USA rangelands. It was hypothesized that (1) survival and growth of *P. glandulosa* would increase with increasing belowground "available volume" and (2) for a given "available volume," growth and survival would be greatest when the resource volume was vertically arrayed and least when horizontally arrayed.

## METHODS

### Study site

Field experiments were conducted at the Texas A&M Native Plant and Animal Conservancy in east-central Texas, near College Station (30°35' N, 96°21' W) on post oak (*Quercus stellata*) savanna sites codominated by the perennial bunchgrasses *Schizachyrium scoparium* (little bluestem) and *Paspalum plicatulum* (brownseed paspalum) (plant nomenclature follows Correll and Johnston [1979]). Mean annual rainfall (990 mm) in this area is bimodally distributed, with peaks in April and September. Annual precipitation during the study was 1032 mm (1995) and 721 mm (1996). Mean monthly temperatures range from 11°C in January to 29°C in July. The frost free period averages 270 days and extends from March through November. Soils are classified as a Lufkin series, fine, smectitic, thermic Oxyaquic, Vertic, Paleustalfs (Mowery et al. 1958) with an A horizon extending to a depth of 30 cm and underlain by a B<sub>tg</sub> horizon. The sites had been protected from domestic livestock and fire since 1957. See Brown and Archer (1989) for more detailed descriptions of vegetation and soils.

### Quantification of above- and belowground heterogeneity

A 4 × 6 m grid of 1 × 1 m cells was established in tree-free areas in each of four stands codominated by *S. scoparium* and *P. plicatulum*. In July 1996, the area around each grid-line intersection free of perennial grasses was determined (subsequently referred to as the gap area), along with the basal area of and distance to the nearest bunch/clump of grass. Soil cores (3-cm diameter, 50-cm depth) were collected at each grid point in July 1995 and July 1996 (1996 coring locations were randomly offset by ~6 cm from the 1995 coring locations). Previous work on this site indicated that coring to 50 cm would capture >90% of the root biomass in the upper 75 cm of the soil profile (Brown and Archer 1989). Soil cores were subdivided into 10-cm segments. Roots were extracted by hydropneumatic elutriation (Smucker et al. 1982), dried at 40°C, weighed, and ashed to quantify ash-free root biomass (Bohm 1979). The cumulative distribution functions (CDFs) of aboveground gap area, belowground biomass, and plant basal area on the four sites were compared (pairwise) using Kolmogorov-Smirnov good-

ness-of-fit test, which produces the ks statistic (Sokal and Rohlf 1981). Due to nonnormal distributions that could not be transformed, analysis of variance for site differences was not performed for aboveground gap area or plant basal area. Belowground biomass was pooled across all sites, subdivided into three size classes (<600, 600–1200, and >1200 g/m<sup>2</sup>) and further subdivided according to soil depth. An analysis of variance and least-squares means multiple comparison test was performed using size class, soil depth, and their interaction as principal factors (SAS 1982, Littell et al. 1992).

#### *Woody plant seedling establishment*

Six depth and diameter combinations of belowground root-free volumes (subsequently referred to as “available volume”) were created by inserting PVC tubes of various lengths (3, 10, and 40 cm) and diameters (10 or 20 cm) into the ground in December 1994 when grasses were dormant. The six length × diameter combinations generated root-free volumes ranging from 236 to 12 566 cm<sup>3</sup>. One pair of tubes had the same available volume (3141 cm<sup>3</sup>) presented in different diameter × length combinations (10 × 40 vs. 20 × 10 cm). Two sets of controls consisted of patches without root-exclusion tubes.

Five tubes per diameter/length combination were installed at random in each of the four stands inventoried for grass basal area, gap area, and belowground biomass (for a total of 30 tubes per site). Upon insertion, the tops of the tubes were flush with ground level. Installation of excluders created local disturbances to the grass canopy and litter layer. To standardize for this, we removed all litter in the immediate vicinity of all of the excluders. Four seeds of *P. glandulosa* were placed on the mineral soil surface of the root-free soil volumes in March 1995; seedlings were subsequently thinned to one per tube two weeks after germination. There were a total of 20 plants per treatment after thinning. Control treatments (no root exclusion or zero depth and diameter) consisted of randomly placing seeds on mineral soil in zones between bunch grasses and ≥1 m away from any excluder tube. To account for the removal of litter from the vicinity of excluders, we also removed litter from a similarly sized zone around control seed placements. To test the effect of litter removal, we also planted a second set of control seeds in patches where litter was left intact. These will subsequently be referred to as “Control –” and “Control +,” respectively.

Seedlings were monitored for survival, height, and number of true leaves for two years. Survival (arcsin transformed; Sokal and Rohlf 1981), number of leaves, and seedling height at the end of each year were analyzed using multivariate repeated-measures analysis of variance (SAS 1982) with principal factors of tube diameter, tube depth, and their interaction. Only live seedlings were used in computing means of morpho-

metric parameters. A least-squares means multiple comparison test was used for each parameter (survival, number of leaves, and seedling height) with principal factors of tube diameter, tube depth, and their interaction (SAS 1982). An additional least-squares means multiple-comparison test of growth parameters and survival was performed using belowground available volume as the principal factor. Furthermore, separate curve-fitting regression analyses were performed comparing belowground available volume effects on seedling survival, height, and number of leaves (SPSS 1999).

The root exclusion experiment assumed that decomposition of severed grass roots and container-restriction effects would have negligible effects on *Prosopis* seedling growth. This assumption was evaluated in a controlled-environment experiment. Soils obtained from the study site were sieved through a 2-mm screen and the extracted roots were saved. These root-free soils were then amended with one of two levels of grass root biomass: none and 1.2× that of mean (0–50 cm) field root biomass (quantified as described in *Methods: Quantification of above- and belowground heterogeneity*). There were six replicates for each treatment. Amended and root-free soils were put into 40 cm long PVC tubes (10 or 20 cm diameter). The tubes were maintained at field capacity in a controlled-environment chamber (35°:25°C day : night and 14:10 hr light : dark) to allow decomposition of roots. After three weeks, four scarified *P. glandulosa* seeds were planted in each tube and subsequently thinned to one plant shortly after germination (Cohort 1). Seedling survival, stem height, basal diameter, and above- and belowground biomass were quantified after 30 d (by which time *P. glandulosa* roots had reached the bottom of most tubes). After harvesting these seedlings, the experiment was repeated for an additional 30 d (Cohort 2) using the same soils to determine if there might be further nutrient inputs from an extended period of root decomposition. At the end of the second trial, soils in each tube were thoroughly mixed and a subsample from each tube was analyzed for carbon and nitrogen concentration (Carlo Erba NA-1500 elemental analyzer; CE Elantech, Lakewood, New Jersey, USA). Seedling growth was analyzed using an analysis of variance with root amendment (+, –), tube diameter (10 and 20 cm), and their interaction as factors.

## RESULTS

### *Above- and belowground spatial heterogeneity*

Mean (±1 SE) belowground biomass (g/m<sup>2</sup>) to a 50 cm depth was statistically comparable among the four sites in both 1995 (1108 ± 104,  $P = 0.84$ ,  $F = 0.29$ ) and 1996 (768 ± 86,  $P = 0.86$ ,  $F = 0.25$ ). Mean belowground biomass in 1995 was significantly greater than in 1996 ( $P = 0.01$ ,  $F = 7.60$ ). Paired comparisons of 1995 belowground biomass distributions revealed

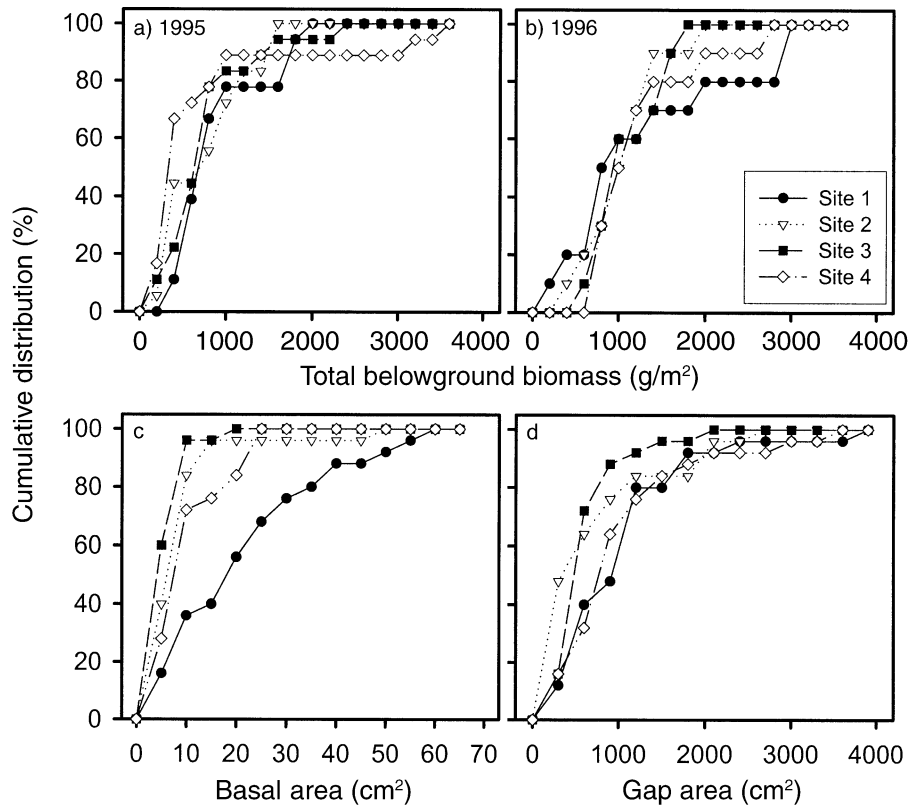


FIG. 1. Cumulative distribution functions (%) for mean belowground biomass in four *Schizachyrium-Paspalum* stands in a post oak savanna, central Texas (USA), in (a) 1995 and (b) 1996, and for (c) basal area and (d) aboveground gap area of each bunch/clump encountered in 1996.

no significant differences between sites ( $P > 0.05$ , Fig. 1a). However, in 1996, the low root biomass year, cumulative distribution functions (CDFs) differed between Sites 1 and 4 ( $P = 0.002$ ,  $ks = 0.61$ ) and between Sites 3 and 4 ( $P = 0.02$ ,  $ks = 0.50$ , Fig. 1b). About 40% of the 96 points sampled in 1996 had  $<500$   $g/m^2$  of root biomass;  $\sim 20\%$  had a root biomass of  $>1000$   $g/m^2$  (Fig. 1b). There was considerable horizontal (Fig. 2) and vertical (Fig. 3) variability in the distribution of belowground biomass. Belowground biomass at point locations was 118–2929  $g/m^2$  in 1995 and 20–3434  $g/m^2$  in 1996. Mean belowground biomass declined exponentially with depth in high ( $y = 1438e^{-0.15x}$ ,  $r^2 = 0.97$ ,  $P < 0.01$ ), medium ( $y = 530e^{-0.11x}$ ,  $r^2 = 0.93$ ,  $P < 0.01$ ), and low ( $y = 222e^{-0.06x}$ ,  $r^2 = 0.83$ ,  $P < 0.05$ ) total root biomass patches (Fig. 3). Differences in high, medium, and low total root biomass patches were confined to the upper 40 cm; at 40–50 cm, root biomass was comparable ( $P > 0.05$ , least-squares means multiple comparisons test) among all patches.

Grass plant or clump basal area and aboveground gap area was also variable. Site 1 had the highest mean basal area per plant ( $20.5 \pm 3.2$   $cm^2$ ) and Site 3 had the lowest ( $4.4 \pm 0.8$   $cm^2$ , Fig. 2, Table 1). Paired comparisons of basal area CDFs showed differences between Sites 1 and 2 ( $P = 0.002$ ,  $ks = 0.60$ ) and Sites

1 and 4 ( $P = 0.04$ ,  $ks = 0.40$ ). Sites 2 and 3 were dominated by small plants (basal areas  $<20$   $cm^2$ ), whereas Site 1 had greater proportion of larger plants (see Fig. 1c). The percentage of sample points not occupied by grass plants ranged from 52% (Sites 3 and 4) to 84% (Site 1). Mean ( $\pm 1$  SE) gap area across all sites was  $772 \pm 132$   $cm^2$  and ranged from 533 to 966  $cm^2$  (Fig. 2, Table 1). Paired CDF comparisons indicated significant differences between Sites 1 and 2 ( $P = 0.01$ ,  $ks = 0.27$ ) and Sites 1 and 3 ( $P = 0.03$ ,  $ks = 0.24$ ); all other paired site comparisons were nonsignificant ( $P > 0.05$ , Fig. 1d). About 50% of gaps exceeded 1000  $cm^2$ . There was no relationship between aboveground gap area and total belowground biomass ( $P > 0.05$ ,  $r^2 = 0.02$ , Fig. 4a) nor between grass plant basal area and the associated gap area ( $P > 0.05$ ,  $r^2 = 0.002$ , Fig. 4b).

#### Woody plant seedling establishment and growth

The controlled-environment experiment indicated that tube diameter and root amendments had no significant effect ( $P > 0.05$ ) on *P. glandulosa* seedling biomass, height, or stem basal diameter for either cohort (first or second planting within each tube; data not shown). Concentrations of soil nitrogen and carbon at the end of the 11-wk trial were also statistically



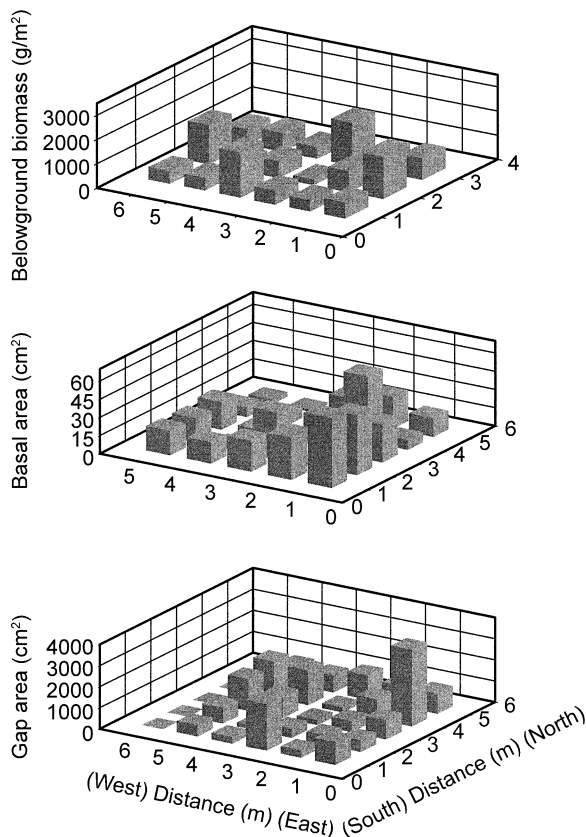


FIG. 2. Variation in mean herbaceous ash-free root biomass ( $\text{g/m}^2$  to 50 cm depth), and perennial grass basal area ( $\text{cm}^2$ ), and aboveground gap area ( $\text{cm}^2$ ), at 1-m intervals within a 6 (N-S)  $\times$  6 (E-W) m grid in July 1996 for a *Schizachyrium-Paspalum* stand (Site 1) in a post oak savanna, central Texas, (USA). See Table 1 for stand means.

comparable ( $P > 0.05$ ) in amended and root-free soils and were not affected by tube diameter (see Jurena 2001).

In field trials, the presence or absence of litter (control + and control -) did not affect *P. glandulosa* seedling survival, height, and number of leaves for either their first or second years of growth (Fig. 5a-f). Survival and growth of *P. glandulosa* seedlings was significantly affected by root-excluder depth, but not by excluder diameter (Fig. 5a-d). First-year survival was enhanced by exclusions to depths  $\geq 10$  cm; second-year survival was enhanced only by exclusion to 40 cm (Fig. 5a, b). Morphometric responses were variable. Height was enhanced by exclusion of roots by 40-cm root excluders during the first and second years of seedling growth (Fig. 5c, d). In the first year of growth, the number of leaves was greater in the 20 cm diameter excluders, but only at the 40 cm depth (Fig. 5e). In the second year of growth, both height and number of leaves were greater with the 40 cm depth root exclusion (Fig. 5d, f). *P. glandulosa* response to herbaceous root exclusion in the vertical dimension was also apparent

when belowground available volume was held constant ( $3143 \text{ cm}^3$ ) but its configuration varied (Fig. 6). Height was greater in the 40 cm depth root excluders (Fig. 6c) during the first year of growth. During the second year of growth, survival, height, and number of leaves were all greater with 40 cm depth root excluders (Fig. 6b, d, and f).

*P. glandulosa* seedling survival was enhanced by increases in total available volume during both growing seasons (Fig. 7). However, the effect of total available volume was nonlinear and was distinctly different for survival vs. growth parameters. First-year seedling survival increased with available volume up to  $1000 \text{ cm}^3$ . Seedlings in their second year showed a similar trend, but with a dampened survival rate. For both seedling age classes, the response to increasing belowground available volume became asymptotic at  $\sim 1000 \text{ cm}^3$ . In contrast, seedling height and leaf production were non-responsive until available volume exceeded  $942 \text{ cm}^3$  (Fig. 8). The greatest seedling height and number of leaves occurred at the largest available volume ( $\sim 12\,566 \text{ cm}^3$ ) and both parameters increased in a nonlinear fashion with increases in available volume (see regression equations in Fig. 8).

## DISCUSSION

### *Above- and belowground heterogeneity*

Maximum rooting depth and the spread of lateral roots of various plant growth forms in semiarid ecosystems may be positively related to aboveground size, but the variability can be great and local rooting patterns may differ substantially (Schenk and Jackson 2002). We observed considerable spatial heterogeneity in root biomass, grass basal area, and gap area within the grassy matrix of this post oak savanna site (Figs. 1 and 2). Belowground biomass in the grassland phase was an order of magnitude greater than that reported for shortgrass steppe (Hook et al. 1994) and comparable to values reported for tallgrass prairie (Benning and Seastedt 1997, McNaughton et al. 1998). Substantial interannual variation in root biomass was evident, as root biomass in July 1996, a low rainfall year, was reduced 23–42% from root biomass in July 1995, a high rainfall year (Fig. 2). Indeed, although mean belowground biomass was statistically comparable among the four stands inventoried, point-specific values spanned two (1995) or three (1996) orders of magnitude. The coefficient of variation of mean root biomass in this tallgrass savanna site (0.38–1.36) was as much as twice that reported for ungrazed shortgrass steppe (0.35–0.44; Milchunas and Lauenroth 1989). This high level of spatial heterogeneity may reflect the fact that, on average, root biomass directly beneath bunchgrasses on this site is about twice that in zones between bunchgrasses (see also Brown and Archer 1989).

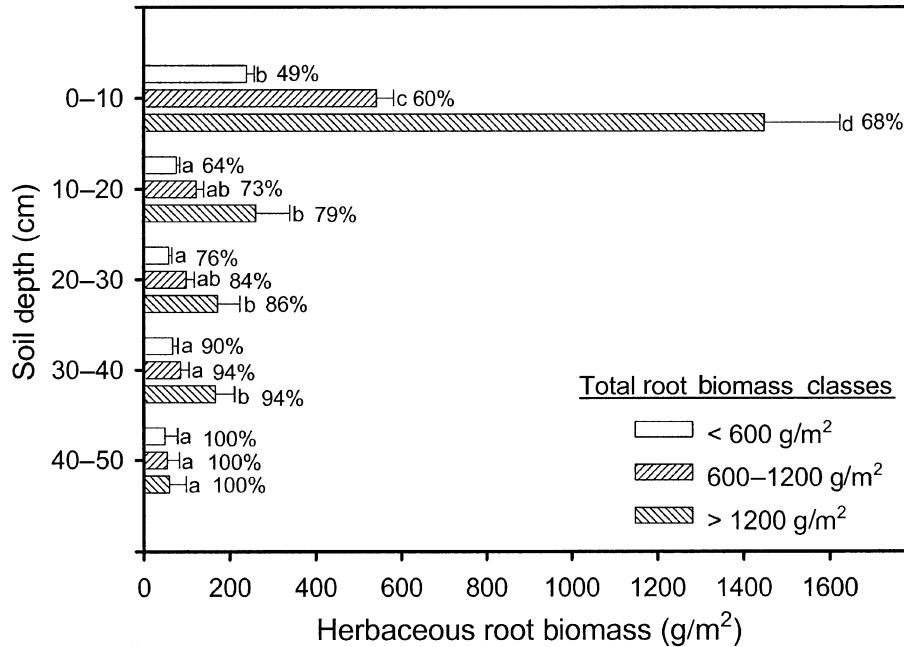


FIG. 3. Mean (+1 SE) ash-free root biomass ( $\text{g/m}^2$  to 50 cm) with soil depth in low (<600  $\text{g/m}^2$ ), medium (600–1200  $\text{g/m}^2$ ), and high (>1200  $\text{g/m}^2$ ) root biomass patches in July 1996. Data are pooled across four *Schizachyrium-Paspalum* stands. Means with the same letter across all depths and patch types were not significantly different ( $P > 0.05$ , least-squares means multiple comparisons test). Percentages to the right of bars are cumulative for total herbaceous root biomass for each biomass class. Curve fit regression equations,  $r^2$  values, and  $P$  values for root biomass across soil depths are:  $y = 1438e^{-0.15x}$ ,  $r^2 = 0.97$ ,  $P < 0.01$  for high root biomass patches;  $y = 530e^{-0.11x}$ ,  $r^2 = 0.93$ ,  $P < 0.01$  for medium root biomass patches; and  $y = 222e^{-0.06x}$ ,  $r^2 = 0.83$ ,  $P < 0.05$  for low root biomass patches.

In many grassland and savanna systems, competition is primarily belowground (Wilson 1998). For purposes of grassland and savanna conservation and sustainable management, it would therefore be useful to be able to map the distribution of belowground biomass using aboveground structural features and hence ascertain community structures that might be most susceptible

to encroachment by undesirable native or alien plants. Management practices might then be modified or devised to promote structures most resistant to encroachment. However, in this tallgrass savanna, like shortgrass steppe (Hook et al. 1994), there was no relationship between aboveground cover patterns and belowground biomass (Fig. 4). This lack of correspondence

TABLE 1. Variation in several measured values in four *Schizachyrium-Paspalum* stands in a post oak savanna, central Texas (USA).

| Value                                  | Year | Site | Mean | 1 SE | CV    | Range    |
|--|------|------|------|------|-------|----------|
| Belowground biomass ( $\text{g/m}^2$ ) | 1995 | 1    | 861  | 118  | 58    | 237–1855 |
|  |      | 2    | 984  | 139  | 45    | 225–1922 |
|  |      | 3    | 1038 | 123  | 38    | 513–1629 |
|  |      | 4    | 1178 | 207  | 56    | 602–2785 |
|  | 1996 | 1    | 1233 | 307  | 79    | 118–2929 |
|  |      | 2    | 757  | 108  | 60    | 197–1559 |
|  |      | 3    | 720  | 118  | 69    | 197–2289 |
|  |      | 4    | 685  | 220  | 136   | 20–3434  |
| Basal area ( $\text{cm}^2$ )           | 1996 | 1    | 20.5 | 3.2  | 77.4  | 0.7–58.0 |
|  |      | 2    | 7.2  | 1.9  | 129.4 | 0.3–49.7 |
|  |      | 3    | 4.1  | 0.8  | 91.2  | 0.1–17.9 |
|  |      | 4    | 8.8  | 1.3  | 73    | 1.3–23.0 |
| Gap area ( $\text{cm}^2$ )             | 1996 | 1    | 966  | 148  | 76    | 202–3632 |
|  |      | 2    | 655  | 140  | 107   | 79–2552  |
|  |      | 3    | 533  | 78   | 74    | 39–1964  |
|  |      | 4    | 936  | 162  | 86    | 39–3526  |

Note: Data for Site 1 are also shown in Fig. 1.

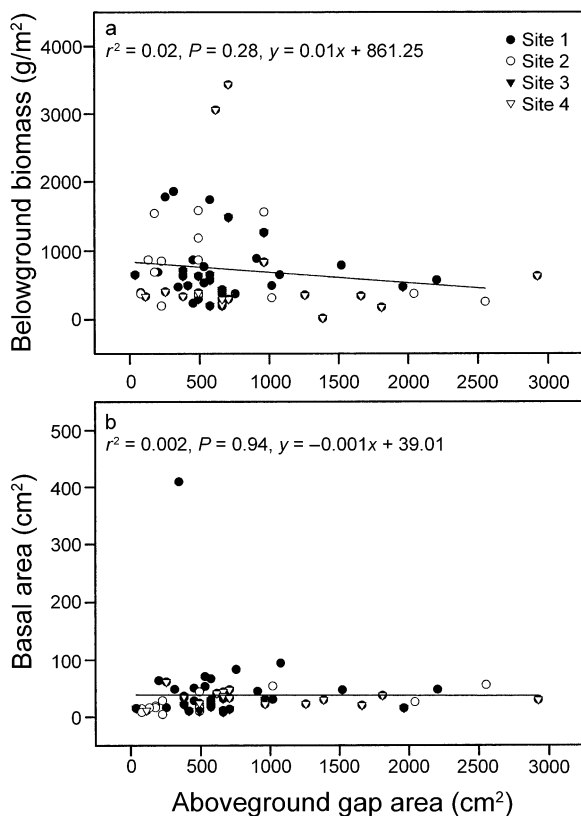


FIG. 4. (a) Belowground biomass ( $\text{g}/\text{m}^2$  to 50 cm for July 1996) and (b) basal area ( $\text{cm}^2$ ) as a function of aboveground gap area ( $\text{cm}^2$ ) in four *Schizachyrium-Paspalum* stands in a post oak savanna, central Texas (USA). Linear fit regression analysis results (equation,  $r^2$ , and  $P$  values) for each year are shown in panels.

may reflect that the scale of heterogeneity differs between above- and belowground factors (e.g., Kleb and Wilson 1999).

#### Implications for woody plant establishment

Many controlled-environment experiments and some field experiments suggest that grasslands dominated by productive, late seral species should be resistant to woody plant encroachment, even in the absence of fire, and that grazing promotes woody plant encroachment into grasslands by reducing the ability of grasses to competitively exclude woody seedlings (see Van Auken 2000). However, persistence and abundance of plants in communities may be strongly influenced by variation in the competitive effects exerted by neighbors (Peltzer and Kochy 2001). Thus, spatial and temporal variation in the intensity of competition may generate windows of opportunity for woody-seedling establishment in grasslands. Given the substantial annual variation in belowground biomass observed in the matrix of late seral grasses at this post oak savanna site, it seems reasonable to expect that grass-dominated patches may be more susceptible to woody plant en-

croachment in some years and more resistant to encroachment in other years. Furthermore, given the substantial spatial variation in aboveground gap area and belowground biomass within and between stands, it would appear that in any given year, there may be numerous opportunities for seedlings of woody plants to establish in localized patches where both above- and belowground interference from grasses may be reduced. A high degree of temporal and spatial variability in belowground biomass may therefore help explain the numerous studies documenting successful establishment of woody seedlings in ungrazed or lightly grazed, late seral grasslands in the absence of fire (Brown and Archer 1989, Archer 1995 and references therein, O'Connor 1995).

About 50% of the canopy gaps encountered in the *Schizachyrium-Paspalum* matrix were  $>80 \text{ cm}^2$  ( $\sim 10 \text{ cm}$  in diameter; Fig. 1). Such gaps in the herbaceous layer are quite large from the perspective of an emerging  $\text{C}_3$  shrub seedling. Indeed, establishment of *Prosopis* seedlings after one or two years in 10 cm diameter gaps was  $\sim 60\%$  and  $35\%$ , respectively, when root biomass to 40 cm was low (Fig. 5). The abundance of gaps  $>10 \text{ cm}$  in diameter would thus provide numerous radiation-favorable microsites. One might anticipate that aboveground available area would be most important if it was inversely related to belowground biomass. In such cases, large aboveground gaps could be more suitable for colonization by virtue of their lower root biomass, whereas smaller gaps still suitable from a photosynthetically active radiation-level perspective might be poor colonization sites owing to high root biomass. Such does not appear to be the case at this savanna site, where there was no relationship between aboveground gap area and belowground biomass (Fig. 4a) and where there was an abundance of microsites with relatively low root biomass (Figs. 1 and 2). Thus, a significant proportion of the microsites in the grassy matrix of this savanna site may be suitable for woody plant colonization from both an above- and belowground perspective. This proposition is supported by results from a previous study at this site, which found that experimental reductions in aboveground grass sward height and biomass had little effect on *P. glandulosa* seedling establishment (Brown and Archer 1989, but see Bush and Van Auken 1990).

Although the influence of herbaceous vegetation on woody plant seedling establishment has been the subject of numerous investigations, generalizations as to the relative importance of above- and belowground competition remain elusive (Grace 1995). Increases in aboveground available area positively influence survival of herbaceous plant seedlings (Caruso 1970), their performance (Ross and Harper 1972, Snaydon and Howe 1986), or both (Goldberg and Werner 1983, Mithen et al. 1984, McConnaughay and Bazzaz 1987, McConnaughay and Bazzaz 1990, Aguilera and Lauenroth 1993, 1995, Hook et al. 1994). Competition from

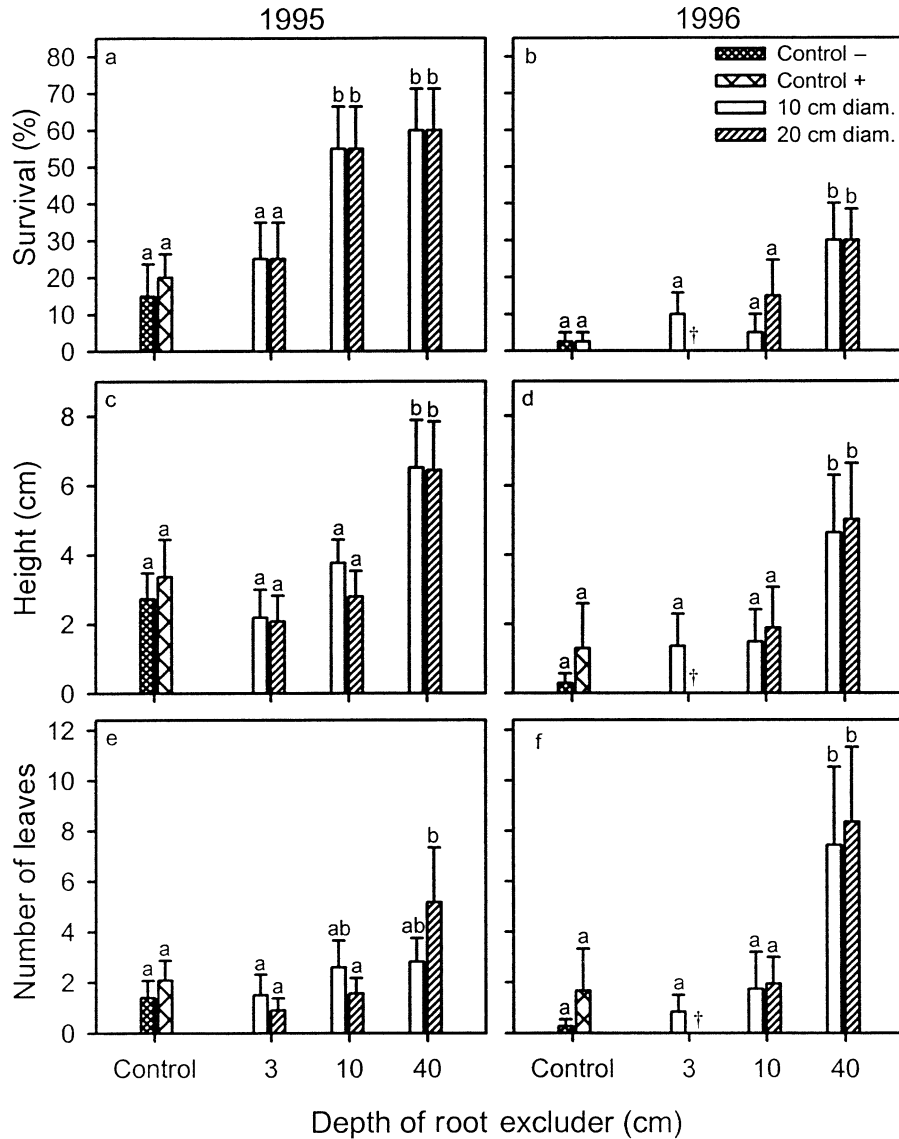


FIG. 5. Mean ( $\pm 1$  SE) survival, height (cm), and number of leaves on *Prosopis glandulosa* seedlings with increasing depth of herbaceous root exclusion (Control [no root exclusion], 3, 10, and 40 cm depths) for plants at the end of their first (a, c, and e) and second (b, d, and f) seasons of growth. "Control -" seedlings were on plots which had been cleared of litter at the beginning of the 1995 growing season. "Control +" seedlings were on plots where litter was left intact. For a given excluder diameter, bars with different letters differed from each other and from the controls ( $P < 0.05$ , least-squares means multiple comparison test).

†No seedlings present, due to mortality.

herbaceous species has also been implicated as a factor regulating woody-seedling establishment based on its effects on short-term growth (Glendening and Paulsen 1955, Van Auken and Bush 1987, 1988, 1989, 1990, Bush and Van Auken 1989, 1990, Diemont and Linthorst-Homan 1989, Polley et al. 1994). In this study, morphometric and survival parameters were monitored with respect to different levels of belowground competitions in conjunction with contrasts in above- and belowground gaps. Our results reinforce the premise that belowground competition is important in grassland

and savanna systems (Adams et al. 1992, McPherson 1993, Wilson 1993a, b, 1998).

Belowground competition among herbaceous plants has been demonstrated in many pot studies (Wilson 1988). However, competition among plants may shift from roots to shoots as productivity increases and species composition changes; and different competitive mechanisms may operate in low- vs. high-diversity vegetation (Peltzer et al. 1998). In field investigations of woody-herbaceous interactions, belowground competition has been shown to influence nutrient uptake



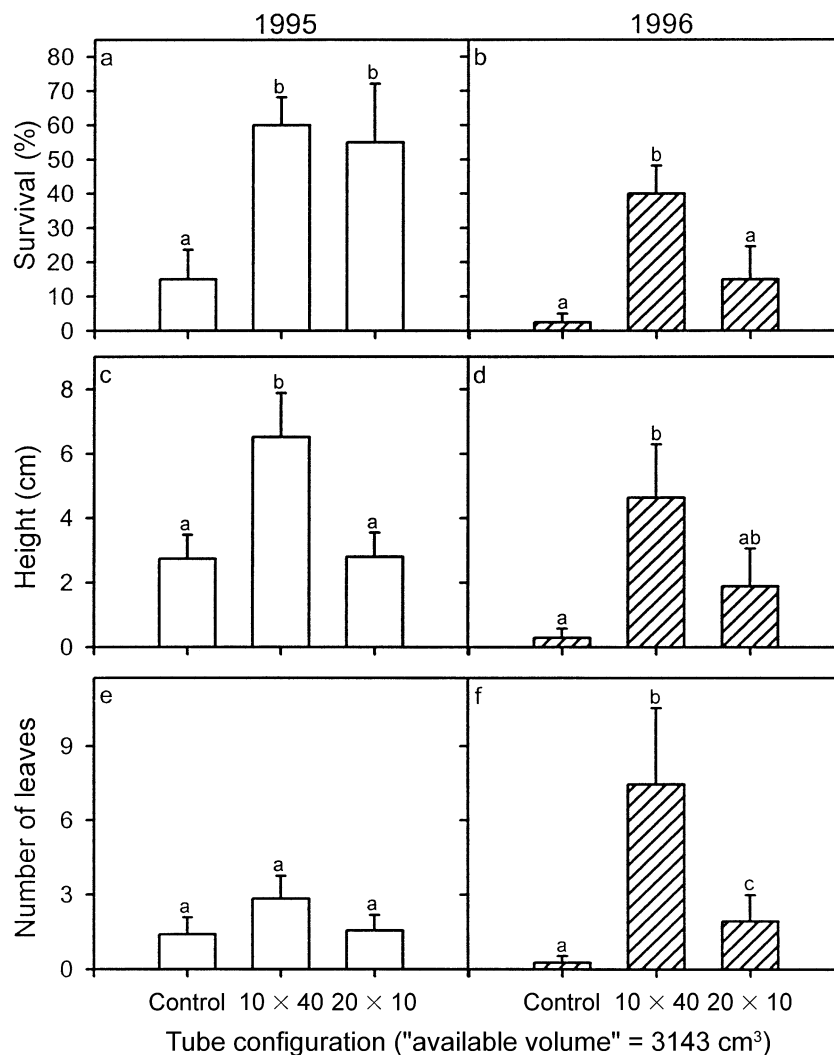


FIG. 6. (a, b) Mean survival (%), (c, d) height (cm), and (e, f) the number of leaves on *Prosopis glandulosa* seedlings growing with herbaceous root exclusion and equal belowground available volume ( $3143 \text{ cm}^3$ ) but in different diameter  $\times$  depth configurations (Control [no exclusion],  $10 \times 40$  cm,  $20 \times 10$  cm). Open and hatched bars represent seedlings at the end of their first and second years, respectively. Within a year, treatments with the same letter were not significantly different ( $P > 0.05$ , least-squares means multiple comparison test). Error bars indicate  $+1$  SE.

(Caldwell et al. 1985) and biomass allocation patterns (Aerts et al. 1991). Few studies have directly addressed belowground effects as they pertain to the establishment of woody plant seedlings in grass-dominated stands. In this field study, *Prosopis* seedlings responded positively to increases in belowground available volume (Figs. 7, 8), consistent with the findings of Bush and Van Auken (1991) and Van Auken and Bush (1997). This response was observed in both years of the experiment, suggesting that root competition between grasses and *Prosopis* seedlings occurs in years of average (1995) and below-average (1996) annual rainfall (Fig. 5). Results further indicated that available volume in the vertical dimension was more important than that in the horizontal dimension (Fig. 6).

This depth effect has been implicated in other experiments with *P. glandulosa* (Brown and Archer 1990, Van Auken and Bush 1997) and other woody species (Bragg et al. 1993, Weltzin and McPherson 1997) and appears to reflect the importance of woody seedlings being able to achieve tap-root extension through and beyond the upper soil horizons which contain the majority of grass root biomass (Fig. 3). Studies with *Prosopis* plants growing in a grassy matrix suggest distinctive resource partitioning of soil moisture among woody and graminoid life-forms, with adult *Prosopis* plants relying primarily on soil moisture at depths  $>1$  m and grasses relying primarily on soil moisture in the upper 0.3 m of the soil profile (Brown and Archer 1990, Boutton et al. 1999). In contrast, water use by *Prosopis*

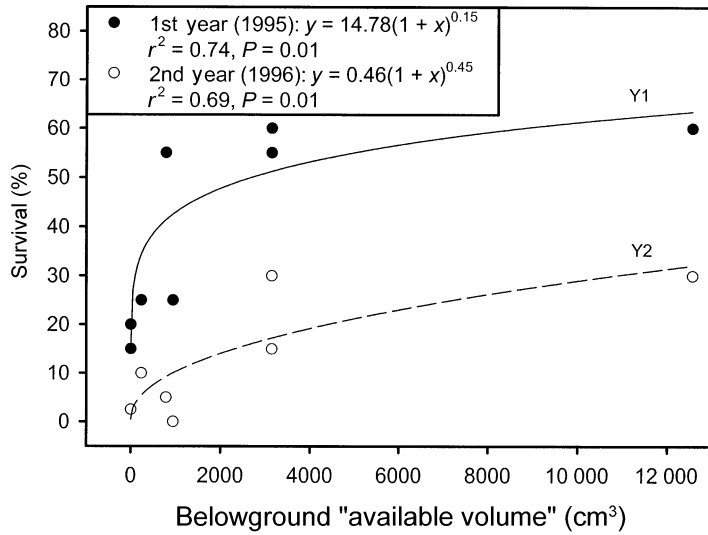


FIG. 7. Survival of *Prosopis glandulosa* seedlings (%) as a function of belowground "available volume." A value of zero designates no herbaceous root exclusion. Solid dots show first-year survival (Y1) and open dots show second-year survival (Y2). Curve fit regression analysis results (equation,  $r^2$ , and  $P$  values) for each year are shown within the panel.

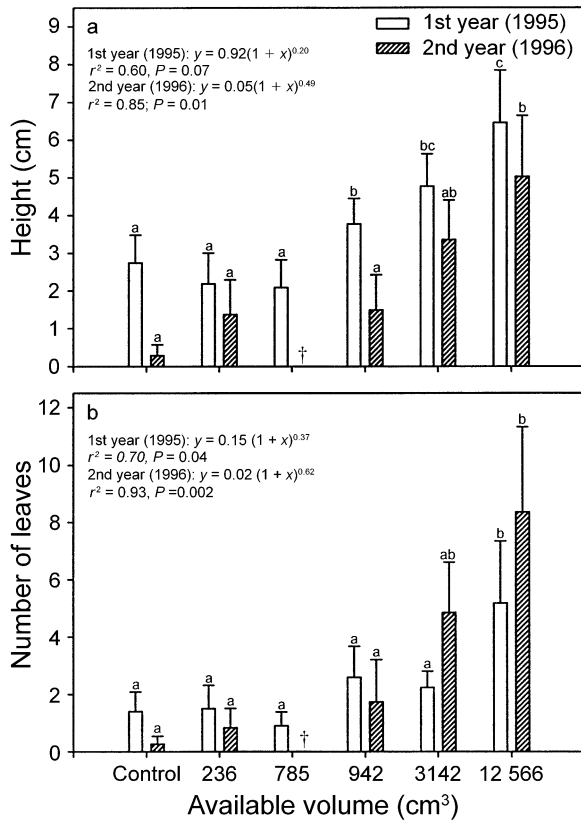


FIG. 8. (a) Mean (+1 SE) height (cm) and (b) the number of leaves on *Prosopis glandulosa* seedlings as a function of belowground "available volume" (Control designates no disturbance and no root excluding device). Open bars and hatched bars denote first and second seasons growth, respectively. Within a year, means with the same letter were not significantly different ( $P > 0.05$ , least-squares means multiple comparison test). Curve fit regression analysis results (equation,  $r^2$ , and  $P$  values) for each year are shown within each panel.

†No seedlings in the 785-cm<sup>2</sup> treatment during the second year of the experiment.

seedlings in their second growing season was primarily a function of soil moisture content between 0.3 and 1.0 m depths (Brown and Archer 1990). Thus, there appears to be a critical one to two year period during which *Prosopis* seedlings might be in acute competition with grasses for soil resources. Reduction of grass root competition to a depth of 40 cm significantly promoted the growth and survival of *Prosopis* seedlings during their first two years of establishment (Fig. 5). Thus, we might expect that woody plant encroachment into grasslands might be a function of the spatial and temporal availability of gaps with low biomass of grass roots. The formation of these gaps, both above- and belowground, may be associated with climatic (rainfall and temperature) variability (Neilson 1986) and local disturbances (Goldberg and Gross 1988). The establishment of woody plants into these gaps could lead to a positive feedback loop causing a conversion from an open grassland to a closed canopy woodland (Archer 1995, Wilson 1998). Unfortunately, as noted earlier, assessments of the distribution and abundance of such gaps cannot be readily inferred from observable above-ground structure. Hence, it will be difficult to readily assess site susceptibility to woody plant encroachment. However, the advent of spatially explicit dynamic simulation models for mixed tree-grass systems (Wiegand et al. 1995, Jeltsch et al. 1997, 1998, Simioni et al. 2000) is a promising framework for assessing spatial and temporal variability in above- and belowground herbaceous biomass and its implications for woody plant seedling recruitment and the long-term structuring of plant communities.

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