

Two decades of vegetation change on terraces of a south Texas river

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J. K. BUSH, F. A. RICHTER (Department of Earth and Environmental Sciences, The University of Texas at San Antonio, San Antonio, Texas 78249), AND O. W. VAN AUKEN (Department of Biology, The University of Texas at San Antonio, San Antonio, Texas 78249). Two decades of vegetation change on terraces of a south Texas river. *J. Torrey Bot. Soc.* 133(2): 280–288. 2006.—A chronosequence of stands on floodplain terraces of the San Antonio River in south Texas was sampled in 1983 and resampled in 2003. The youngest resampled stand, an early successional stage originally 19 yrs of age, was an open *Acacia farnesiana* (huisache) woodland. After 20 yrs this stand was a mid-successional *A. farnesiana*—*Celtis laevigata* (Texas sugarberry) woodland, and demonstrated a decrease in *A. farnesiana* density from 427 plants ha⁻¹ to 167 plants ha⁻¹ and an increase of *C. laevigata* density from zero plants ha⁻¹ to 860 plants ha⁻¹. The 25 yr old stands were originally mid-successional *A. farnesiana* woodlands. After 20 yrs, *A. farnesiana* density decreased by 462 plants ha⁻¹ and *C. laevigata* density increased by 1031 plants ha⁻¹. *Acacia farnesiana* basal area decreased by 9.4 m² ha⁻¹, while *C. laevigata* basal area increased by 5.8 m² ha⁻¹. The 27 and 29 yr old stands were originally *A. farnesiana* woodlands, but after 20 yrs were *Celtis* woodlands. The greatest decrease in *A. farnesiana* basal area (12.0 m² ha⁻¹) and the greatest increase in *C. laevigata* basal area (15.9 m² ha⁻¹) occurred in the now 47 yr old stands. The 32 yr old mid-successional stand was originally an *A. farnesiana*—*C. laevigata* woodland, and at 52 yrs was a *C. laevigata* woodland. Both density and basal area of *A. farnesiana* decreased in the successional sequence, while *C. laevigata* density first increased and then decreased, while basal area increased. Significant changes have occurred over the last two decades, however it is predicted that further changes will occur before the communities become mature. A major co-dominant in the mature stands, *Ulmus crassifolia*, was not found in the 52 yr old stand. In addition, several other mature community species including *U. americana*, *Crataegus* sp., and *Ilex decidua* were not found in the 52 yr old stand.

Key words: *Acacia farnesiana*, *Acacia smallii*, *Celtis laevigata*, floodplain terraces, San Antonio River, secondary succession

Because changes in forest succession can take decades, few long-term, direct studies of vegetation change are available (Bell 1997, Hemond et al. 1983). In 1983, we described the forest communities along the San Antonio River in south Texas and developed a generalized model of stand development for these communities. Using 15 spatially separated stands ranging in age from 5 to 150 years, we found that *Acacia farnesiana* (L.) Willd. (huisache) is the early successional woody species that colonizes the old fields within 5 yr of abandonment and becomes the dominant woody plant species within 25 yr (Bush and Van Auken 1987, Van Auken and Bush 1985). By 33 yr, *A. farnesiana* declines and the mid- to late-successional species

Celtis laevigata Willd. (Texas sugarberry) dominates.

In addition to the descriptive work that was used to develop our model of stand development, experimental evidence from several subsequent studies have supported the proposed model. When examining the response of the two dominant species to light intensity, Bush and Van Auken (1986b) showed that *Acacia farnesiana* is a heliophyte, which is common of early successional species and *C. laevigata* is a sciophyte, which is common of later successional species (Grime 1965, Loach 1967, Loach 1970). Further, the response of the two species to soil nitrogen is also very different. In greenhouse studies, it was shown that *A. farnesiana*, a nitrogen-fixing legume, is tolerant of low soil nitrogen and that *C. laevigata* is stimulated by increased levels of soil nitrogen (Van Auken et al. 1985). It was hypothesized that *A. farnesiana* may facilitate (Connell and Slatyer 1977) the colonization of *C. laevigata* by adding nitrogen to the soil early in succession. To further sub-

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Table 1. Original stand age in 1983, number of quadrats sampled, original classification, and a resample age and classification of stands located along the San Antonio River. A total of 15 stands were sampled in 1983 ($n = 4$ for stands >150 yr) and 7 of these were resampled in 2003. The 5, 15, and 19 yr stands were early successional stages where *A. farnesiana* establishment occurs. Stands ranging from 25–33 yr were mid-successional stages, and the stands >150 yr were determined to be late successional communities.

| Stand # | Original classification | Original stand age | # of quadrats | Resample stand age | Current study classification |
|---------|-------------------------------|--------------------|---------------|--------------------|-------------------------------|
| | Grassland | 5 | 36 | | — ¹ |
| | Open <i>Acacia</i> woodland | 15 | 80 | | — ¹ |
| 1 | Open <i>Acacia</i> woodland | 19 | 60 | 39 | <i>Acacia-Celtis</i> woodland |
| 2 | <i>Acacia</i> woodland | 25 | 48 | 45 | <i>Acacia-Celtis</i> woodland |
| 2 | <i>Acacia</i> woodland | 25 | 40 | 45 | <i>Acacia-Celtis</i> woodland |
| 3 | <i>Acacia</i> woodland | 27 | 48 | 47 | <i>Celtis</i> woodland |
| 3 | <i>Acacia</i> woodland | 27 | 50 | 47 | <i>Celtis</i> woodland |
| 4 | <i>Acacia</i> woodland | 29 | 60 | 49 | <i>Celtis</i> woodland |
| | <i>Acacia</i> woodland | 29 | 40 | | — ¹ |
| 5 | <i>Acacia-Celtis</i> woodland | 32 | 40 | 52 | <i>Celtis</i> woodland |
| | <i>Acacia-Celtis</i> woodland | 33 | 20 | | — ¹ |
| | <i>Celtis-Ulmus</i> forest | >150 | 336 | | — ² |

¹ Stand disturbed.

² Not resampled.

stantiate the potential facilitation of *C. laevigata* by *A. farnesiana* it would have to be shown that soil nitrogen was limiting in the earlier stands where *C. laevigata* was present and growth was reduced compared to *A. farnesiana*. Measurements of soil nitrogen indicated that the earlier sites were low in soil nitrogen, and soil nitrogen increased with succession (Bush and Van Auken 1986a). In addition, levels of soil nitrogen below the canopy in mid-successional stands were twice as high as in adjacent open areas.

Finally, transplant experiments in the field confirmed greenhouse experiments (Lohstroh and Van Auken 1987, Van Auken and Lohstroh 1990). Maximum growth of *A. farnesiana* occurred in the open (full sunlight) compared to beneath the mature *A. farnesiana* canopy (shade) and other factors tested (root competition, nutrient additions, and herbivory) had no significant effect on growth (Lohstroh and Van Auken 1987). Maximum growth of *C. laevigata*, on the other hand, was found under mature *A. farnesiana* canopies, and least in the adjacent open areas (Van Auken and Lohstroh 1990).

The resource ratio hypothesis suggests that succession results from a temporal gradient of limiting resources and species' physiological response to these changing resources (Luzuriaga et al. 2002, Rastetter et al. 2001, Tilman 1985). Both light (limiting to *A. farnesiana*) and nitrogen (limiting of *C. laevigata*) changed dramatically as these stands develop over time (Bush and Van Auken 1986b, Lohstroh and Van Auken 1987). The changes in light and soil nitrogen associated with this chronsequence, in conjunc-

tion with the physiological responses of *A. farnesiana* (a nitrogen-fixing heliophyte), suggests that this species would dominate early in succession when nitrogen was limiting and light was high. Later in the succession as canopy closure limited light levels and soil nitrogen increased due to decomposition, *A. farnesiana* no longer had an advantage, and gives way to *C. laevigata*, a sciophyte intolerant to low levels of soil nitrogen.

In order to test whether these plant communities do follow this general pattern of development, we revisited several of the sites sampled in 1983. Our objective was to describe the changes which have occurred in these communities over the last 20 years.

Materials and Methods. In 1983, Van Auken and Bush (1985) sampled and phytosociologically compared fifteen distinct plant communities located on the San Antonio River floodplain terraces in Bexar and Wilson Co., Texas. In the current study, seven of the original younger (non-mature) stands in Bexar Co. (29° 32' N, 98° 28' W) were resampled (Table 1). The climate is subtropical-subhumid, with mild winters and hot summers (Thorntwaite 1948). Temperatures in January range from an average low of 4° C to an average high of 17° C and in July from 23° to 36° C. The average annual rainfall is 79 cm (Arbingast et al. 1976, Carr 1967). All stands (ranging from 1–5 ha), except the mature ones (> 150 yr), had been cleared for agriculture and then abandoned, based on examination of aerial photographs and interviews with

local residents. Selected stands depicted various stages of a postulated chronological sequence from open field to mature forest (Table 1). All stands were located on an alluvial clay-loam Mollisol of the Frio Series classified as a fine, mixed, thermic, cumulic haplustoll (Taylor et al. 1966).

Approximately one-tenth of each stand was sampled and data for equal-aged stands (25, 27, and 29), and stands 32 and 33 yrs were pooled to show mean densities and mean basal areas changes in time. Stands which were originally 19, 25, 27, 29, and 32 yrs were resampled and at the time of the second sampling were 39, 45, 47, 49, and 52 yrs post-abandonment (Table 1).

As in the initial sampling, stands were sampled using belt transects parallel to the river, with 5×5 m quadrats (Grieg-Smith 1964). The number of quadrats sampled in each site was determined by the size of the stand and density stabilization curves, and are presented in Table 1. All live and dead woody plants in the quadrats were identified and measured. All woody plants greater than 1.0 cm in diameter at breast height (1.4 m) were classified as trees. Total density (plants ha^{-1}), total basal area ($\text{m}^2 \text{ha}^{-1}$), and individual species density and basal area were calculated for each stand. Means and standard errors of the total density, total basal area, *A. farnesiana* density and basal area, and *C. laevigata* density and basal area were calculated over the quadrats for all the resampled stands. Some of the younger stands were not resampled due to recent or continued disturbances since the original sampling.

Nomenclature followed Correll and Johnston (1979). Total density, total basal area, and the density and basal area of the earlier successional woody species, *Acacia farnesiana* (L.) Willd., (*A. farnesiana* = *A. smallii*; Clarke et al. 1989), and the late successional woody species *Celtis laevigata* Willd. are graphed as a function of stand age. Data from the original study is presented, in addition to the resampled data for the non-mature stands. In addition, changes in total density, total basal area, and density and basal area of *A. farnesiana* and *C. laevigata* between the original and resampled stands are presented. The changes in both live and dead stems are also shown.

As with the previous study, detrended correspondence analysis (DECORANA) was used to determine, identify, and distinguish the stands and trends based on species composition (Hill 1979). Original and resampled data of each

stand (rather than the means of similar age stands), as well as mean data from the mature stands was used in the analysis. The influence of rare species was reduced by using a 'down-weight rare species option' from the Community Analysis Package (Pisces 2002). Spearman's Rank Correlation was used to determine significant correlations ($P \leq 0.05$) between the age of the stands and DCA axes for both density and basal area.

Results. In the original study, total woody plant density increased from zero in the five yr old community to approximately 1500–2100 plants ha^{-1} in the 15–33 yr old stands (Fig. 1A). By 2003, total density increased to about 3000 plants ha^{-1} . More dramatic shifts were observed with total basal area. Total basal area was less than $5 \text{ m}^2 \text{ha}^{-1}$ up to 19 yrs, and then increased and remained at about $20 \text{ m}^2 \text{ha}^{-1}$ in all of the mid-successional stands, including those resampled (Fig. 1B). In the mature stand the mean (± 1 standard error) total density and total basal area was 1350 ± 181 plants ha^{-1} and $24.4 \pm 1.7 \text{ m}^2 \text{ha}^{-1}$, respectively.

Acacia farnesiana density increased from 0 plants ha^{-1} in the original five yr old stand to approximately 500 plants ha^{-1} in stands 15–29 yrs old (Fig. 1C). However, as these stands develop over time, *A. farnesiana* density was < 100 plants ha^{-1} in the stands > 39 yrs old and was not even observed in the 52 yr old and mature stands. Basal area of *A. farnesiana* reached a maximum of $13 \text{ m}^2 \text{ha}^{-1}$ in the 25 yr old stands and decreased in older stands (Fig. 1D). Conversely, *C. laevigata* was not found in stands less than 19 yrs old (Fig. 1E). The maximum density of *C. laevigata* was 1567 plants ha^{-1} in the 32 yr old stands, and then decreased from this maximum to approximately 400 plants ha^{-1} in the mature community. *Celtis laevigata* basal area followed a similar trend, increasing from zero to approximately $15.8 \pm 2.2 \text{ m}^2 \text{ha}^{-1}$ in the 52 yr old stand (Fig. 1F). These values were similar to *C. laevigata* basal area in the mature stands (approximately $14 \text{ m}^2 \text{ha}^{-1}$).

From 1983–2003, total live density for the 19 yr old stand decreased only slightly (120 plants ha^{-1}), however density of the dead woody plants decreased by 567 plants ha^{-1} (Fig. 2A). This large loss of woody plants resulted from the disappearance of standing dead *Baccharis neglecta* Britt. (Roosevelt weed) from this stand. In stands originally 25 and 29 yrs old, total live density increased as much as 1000 plants ha^{-1}

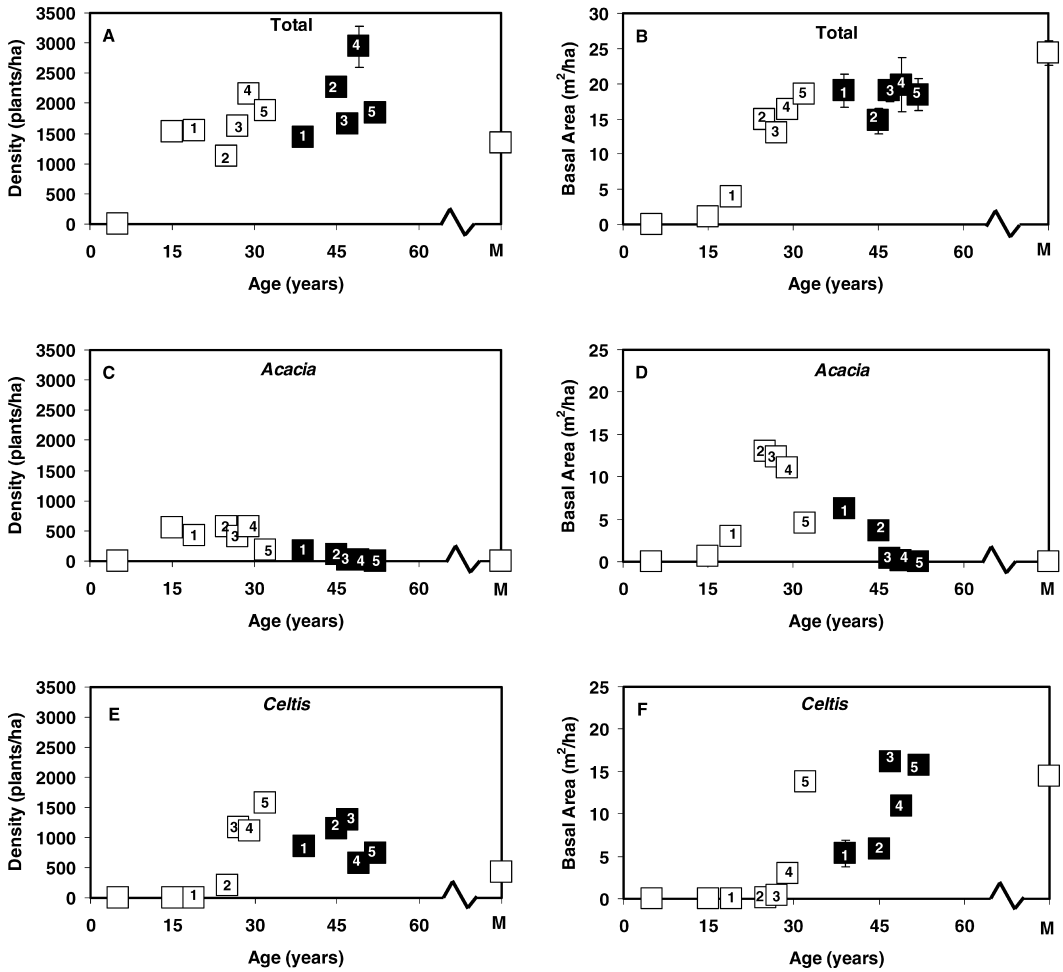


FIG. 1. Changes in A) total density, B) total basal area, C) *Acacia farnesiana* density, D) *Acacia farnesiana* basal area, E) *Celtis laevigata* density, and F) *Celtis laevigata* basal area as a function of stand age in yrs. □ indicate data from stands sampled in 1983 and ■ indicate data from stands sampled in 2003. Boxes with the same number indicate stands that were sampled in 1983 and resampled in 2003. Error bars are standard error of the means. If error bars are not shown, they were smaller than the height of the box in the figure. M = mature community.

over the 20 yrs, with only slight changes in dead density. Total live density of the 27 yr old stand increased by only 27 plants ha⁻¹. In the 32 yr old stand, there was only a slight decrease in total live density, but total dead density decreased by 865 plants ha⁻¹ due to the falling of the standing dead *A. farnesiana*. Total live basal area of the 19 yr old stand increased approximately 15 m² ha⁻¹ over the 20 yrs, with total dead basal area increasing 5 m² ha⁻¹ (Fig. 2B). Both live and dead basal area in the 25 yr old stand changed very little, however in the 27 and 29 yr old stand there was an increase in both live and dead basal area. Live basal area remained the same over the 20 yrs for the 32 yr

old stand, but dead basal area decreased by approximately 10 m² ha⁻¹ apparently because of the fall of dead *A. farnesiana*.

Density of live *A. farnesiana* over the 20 yr period between sampling decreased in all of the stands resampled, with the greatest reduction of 552 plants ha⁻¹ in the 29 yr old stand (Fig. 2C). The density of dead plants increased in the 19, 25, and 27 yr old stands, with the greatest increase in the 19 yr old stand. In the 29 and 32 yr old stands, the density of dead plants decreased, with the greatest reduction of 833 plants ha⁻¹ in the 32 yr old stand, which was due to tree fall. Live basal area of *A. farnesiana* increased only in the 19 yr old stand (Fig. 2D).

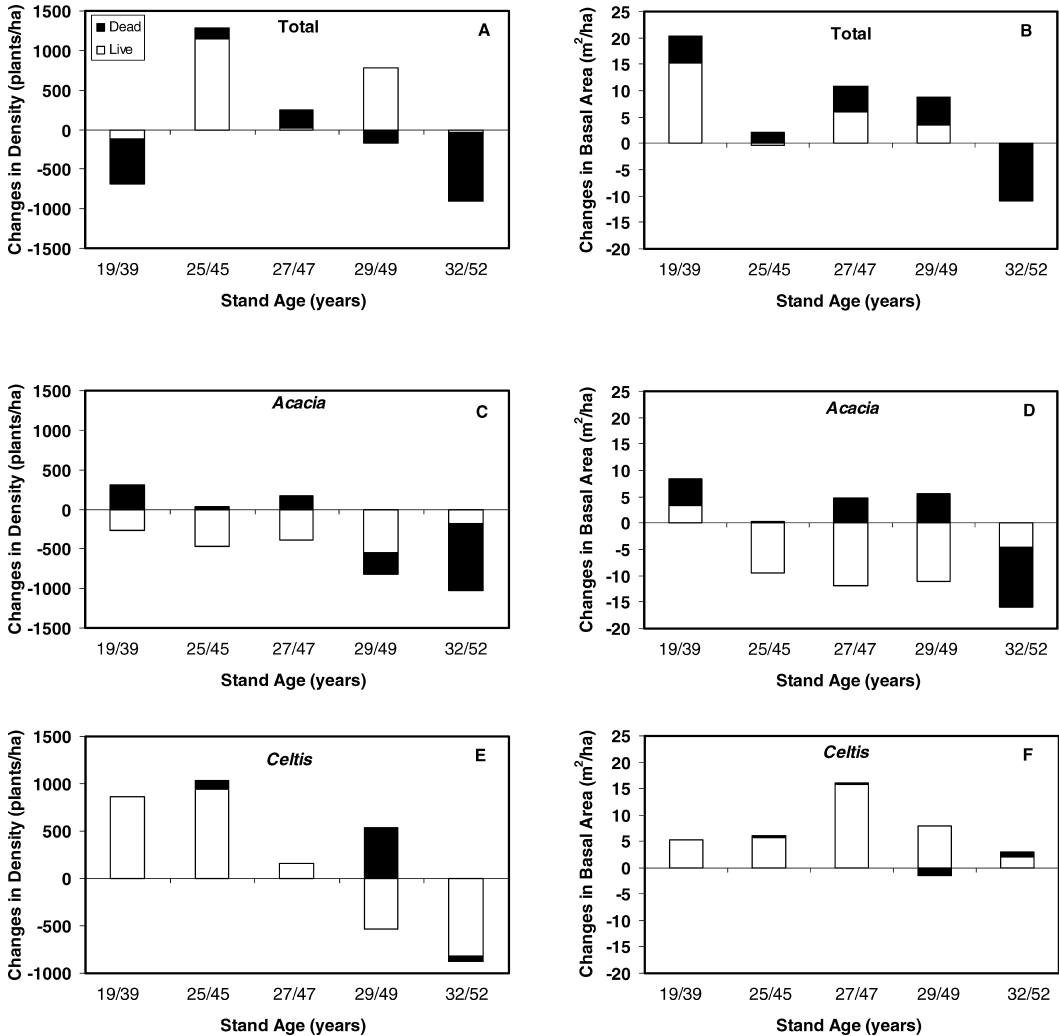


FIG. 2. Changes in live and dead A) total density, B) total basal area, C) *Acacia farnesiana* density, D) *Acacia farnesiana* basal area, E) *Celtis laevigata* density, and F) *Celtis laevigata* basal area from 1983 to 2003 for the stands resampled. The x-axis indicates the age of the stands in 1983 and 2003.

The greatest reductions of live basal area of approximately $10 \text{ m}^2 \text{ ha}^{-1}$ occurred in the 25, 27, and 29 yr old stands. *Acacia farnesiana* dead basal area increased by approximately $5 \text{ m}^2 \text{ ha}^{-1}$ in the 19, 27, and 29 yr old stands, with the 32 yr old stand decreasing by approximately $10 \text{ m}^2 \text{ ha}^{-1}$.

Density of live *C. laevigata* increased by greater than $800 \text{ plants ha}^{-1}$ in the 19 and 25 yr old stands over the past 20 yrs, with only a slight increase in the 27 yr old stand (Fig. 2E). Live density decreased by at least $500 \text{ plants ha}^{-1}$ in the 29 and 32 yr old stands. *Celtis laevigata* dead density increased by $537 \text{ plants ha}^{-1}$ in the 29 yr old stand over the 20 yr period, with only

slight changes in the other stands. Live basal area of *C. laevigata* increased with increasing age up to the 27 yrs stands, with slight increases in the older two stands over the 20 yr period (Fig. 2F). There was very little change in dead *C. laevigata* basal area.

Detrended correspondence analysis ordination for density generally separated the stands by age along the DCA-Axis 1 (Fig. 3A). The stands which were originally sampled in 1983 are found to the right of the DCA-Axis 1, with the youngest of those stands to the far right. The stands which were resampled in 2003 are found to the left on the DCA-Axis 1, with the oldest to the far left. Very little separation occurred for

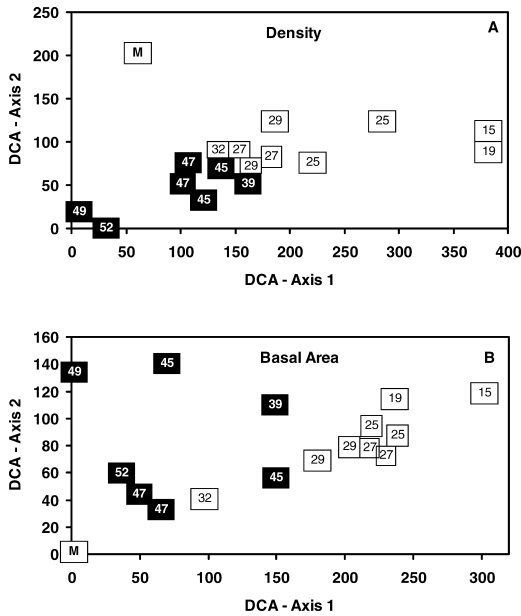


FIG. 3. Community ordination of A) density and B) basal area of stands located along the San Antonio River. Number on the figures are stand age in yrs. □ indicate data from stands sampled in 1983 and ■ indicate data from stands sampled in 2003. M = mature community.

density along the DCA-Axis 2. The two youngest stands which had the lowest species richness and highest densities of *Baccharis neglecta* (Table 2) are those sites found to the right of DCA-Axis 1. Stands which had higher species richness and co-dominance of *A. farnesiana* and *C. laevigata* are found in the middle of the DCA-Axis 1. Finally, the stands dominated by *C. laevigata* are found to the left of the DCA-Axis 1. Detrended correspondence ordination for basal area showed a similar separation along the DCA-Axis 1, with the originally sampled younger stands with high *A. farnesiana* basal area to the right and the older resampled sites dominated by *C. laevigata* to the left (Fig. 3B). There was more separation of the stands along the DCA-Axis 2 using basal area, compared to using density. Stand age and DCA-Axis 1 position were highly correlated for both density and basal area when all stands were used and the mature stand was assigned an age of 150 yrs ($r = -0.95$, $P \leq 0.0001$; $r = -0.97$, $P \leq 0.0001$; respectively). Stand age and DCA-Axis 2 were also significantly correlated for density and basal area, but not as highly correlated as DCA-Axis 1 ($r = -0.52$, $P = 0.0319$; $r = -0.48$, $P = 0.0487$; respectively).

The density of all species found in each stand is presented in Table 2. The species are ranked according to those with the highest densities in the youngest stands. *Baccharis neglecta* had the highest densities in the youngest two stands, and was not found in any of the older stands. *Acacia farnesiana* had the highest density in the younger stands and was not found in the two oldest stands. *Celtis laevigata* was not found in the two youngest stands and had high densities in all stands older than 25 yrs. Two non-native species, *Ligustrum quihoui* (wax-leaf ligustrum) and *Melia azedarach* (chinaberry) had high densities in the older non-mature stands. Two species, *Ulmus crassifolia* (cedar elm, which was only found in the mature stands), and *Acer negundo* (box elder) had high densities in the mature stands. Most of the older, resampled stands had an increase in the number of woody species found.

Discussion. Predictions of a successional sequence on these riparian terraces from spatially isolated stands 20 yrs ago (Van Auken and Bush 1985) have been substantiated in the present study. Relatively rapid changes occurred, however changes were dependent on the age of the stands. The greatest difference in live community density over the 20 yr period occurred in stands that were initially 25–29 yrs of age (mid-successional stands), increasing by as much as 1000 plants ha^{-1} to values as high as 3000 plants ha^{-1} . The least change in live woody plant density occurred in stands which were either 19 yr (early successional) or 32 yr of age (late, mid-successional). These stands also had the greatest change in dead plant density.

There are relatively few studies which show direct long-term changes in plant communities in deciduous forests. Hemond et al. (1983) found tree density declined from 3300 plants ha^{-1} to 2230 plants ha^{-1} in the Connecticut Arboretum Natural Area. Density decreased from 950 to 753 plant ha^{-1} in an Illinois streamside deciduous forest over an 18 yr period (Bell 1997). As indicated in the current study, the changes in density over this 20 yr time period are dependent on the age of the stand. Density increased by approximately 1000 plants ha^{-1} in most of the sites over the 20 yrs. While this increase is different from reported changes in other deciduous forests, other factors may be influencing the rates of change. The actual ages of the stands in Connecticut and Illinois were not presented; however by examining community

Table 2. Density (plants ha⁻¹) for each species encountered in each of the various aged stands. TR = trace (less than 0.5). A—indicate lack of occurrence.

| Species | 15 | 19 | 25 | 27 | 29 | 32 | 39* | 45* | 47* | 49* | 52* | M |
|------------------------------------|-----|------|-----|-----|------|------|-----|------|------|------|-----|-----|
| <i>Baccharis neglecta</i> | 913 | 1013 | — | — | — | — | — | — | — | — | — | — |
| <i>Acacia farnesiana</i> | 558 | 427 | 571 | 284 | 572 | 187 | 167 | 114 | 25 | 20 | — | — |
| <i>Parkinsonia aculeata</i> | 39 | — | 57 | 1 | 10 | — | — | 20 | — | — | — | — |
| <i>Prosopis glandulosa</i> | 17 | 113 | 76 | — | 25 | — | 220 | 48 | 13 | — | — | — |
| <i>Celtis laevigata</i> | — | — | 192 | 630 | 1117 | 1567 | 860 | 1209 | 1302 | 580 | 747 | 432 |
| <i>Celtis pallida</i> | — | — | 146 | 56 | 64 | — | 53 | 284 | 46 | — | 13 | — |
| <i>Condalia hookeri</i> | — | — | 54 | — | — | — | 7 | 103 | — | — | — | — |
| <i>Ligustrum quihoui</i> | — | — | 9 | — | 33 | — | — | 308 | 16 | 400 | 40 | — |
| <i>Ehretia anacua</i> | — | — | 4 | — | 35 | 33 | — | 13 | — | 30 | 40 | — |
| <i>Quercus fusiformis</i> | — | — | 4 | — | — | — | — | — | 4 | 80 | 27 | — |
| <i>Aloysia gratissima</i> | — | — | — | 4 | — | — | — | 20 | — | — | — | — |
| <i>Sapindus saponaria</i> | — | — | 4 | — | — | — | — | — | 96 | — | — | 12 |
| <i>Rhus toxicodendron</i> | — | — | — | — | 155 | 13 | — | — | 8 | — | — | 2 |
| <i>Acer negundo</i> | — | — | — | — | 80 | 47 | — | 4 | 21 | 110 | — | 258 |
| <i>Melia azedarach</i> | — | — | — | — | 14 | — | 27 | 20 | 203 | 1270 | 840 | 11 |
| <i>Carya illinoensis</i> | — | — | — | — | 13 | 13 | — | — | 8 | — | — | 8 |
| <i>Bumelia lanuginosa</i> | — | — | — | — | 10 | — | 7 | — | 4 | 150 | — | 73 |
| <i>Cornus drummondii</i> | — | — | — | — | 9 | — | — | — | 13 | — | 13 | 12 |
| <i>Morus microphylla</i> | — | — | — | — | 8 | 13 | — | — | — | — | — | — |
| <i>Fraxinus americana</i> | — | — | — | — | 5 | — | — | — | — | — | — | — |
| <i>Vitis mustangensis</i> | — | — | — | — | 5 | 7 | — | 68 | — | 250 | 67 | 84 |
| <i>Morus rubra</i> | — | — | — | — | 4 | TR | — | — | — | — | — | 4 |
| <i>Diospyros texana</i> | — | — | — | — | — | — | 87 | 17 | 20 | 20 | 53 | 5 |
| <i>Berberis trifoliolata</i> | — | — | — | — | — | — | 7 | — | — | — | — | — |
| <i>Sophora secundiflora</i> | — | — | — | — | — | — | — | 4 | — | — | — | — |
| <i>Parthenocissus quinquefolia</i> | — | — | — | — | — | — | — | — | — | 30 | — | 1 |
| <i>Ulmus crassifolia</i> | — | — | — | — | — | — | — | — | — | — | — | 301 |
| <i>Campsis radicans</i> | — | — | — | — | — | — | — | — | — | — | — | 90 |
| <i>Crataegus</i> sp. | — | — | — | — | — | — | — | — | — | — | — | 31 |
| <i>Ulmus americana</i> | — | — | — | — | — | — | — | — | — | — | — | 24 |
| <i>Ilex decidua</i> | — | — | — | — | — | — | — | — | — | — | — | 2 |

* Stands 39, 45, 47, 49, and 52 were resampled in 2003.

species composition, it appears that they were older than the stands resampled in the present study. The rates of change later in a successional chronosequence may be smaller than earlier in the chronosequence. In addition, the rates of change in density can be influenced by many factors including moisture, elevation, seed dispersal, and proximity to seed sources (Battaglia et al. 2002, Donnegan and Rebertus 1999).

Changes in basal area were also dependent on the age of the community. The early successional, 19 yr old stand increased from approximately 5 m² ha⁻¹ to 20 m² ha⁻¹ over the 20 yr period, with very little change in the remaining stands. Later mid-successional stands ranging in age from 29 to 52 yrs of age had basal areas of approximately 20 m² ha⁻¹, and the mature stands (> 150 yrs of age) have basal areas of approximately 25 m² ha⁻¹. These values are similar to mature deciduous forests in other parts of the United States with basal areas ranging from approximately 26 m² ha⁻¹ to 38 m² ha⁻¹, depending on the community type and location (Bell 1997,

Fain et al. 1994, Harcombe and Dixon 1984, Held and Winsted 1975, Hemond et al. 1983, Jones et al. 1994).

The age of the stands examined in the present study allowed us to demonstrate the decline of the early successional legume *A. farnesiana* and the increase of the mid- to late successional species *C. laevigata* in these stands. Live density of *A. farnesiana* in all of the stands examined decreased over the 20 yr period, while the youngest three stands showed increases in the dead trees and the two older stands showed decreases in the number of dead trees (Fig. 2). Basal area of *A. farnesiana* increased in the 19 yr old stand, but in the remaining stands live basal area decreased. Similar to the changes in *A. farnesiana* in the current study, growth of *Robinia pseudoacacia* (black locust) in southern Appalachian forests following disturbance decreased after 10–20 yrs (Boring et al. 1981, Boring and Swank 1984). In more xeric plant communities in south Texas, another woody legume, *Prosopis glandulosa* (honey mesquite), appears to be the

early colonizer and facilitator (Archer et al. 1988). Several species of *Acacia* have also been shown to have similar roles including *Acacia schaffneri* (twisted acacia) in the Chihuahuan Desert (Yeaton and Manzanares 1986) and *Acacia nilotica* (prickly acacia) in southern Africa (Smith and Goodman 1987).

In the successional sequence on the terraces of the San Antonio River, it was noted that *C. laevigata* is present in the earliest stages (Van Auken and Bush 1985). We proposed that facilitation was important in the sequence not because germination of *C. laevigata* increased due to the facilitation by *A. farnesiana*, but rather that growth of *C. laevigata* was promoted or facilitated by the nitrogen fixing capabilities of the legume and the input of nitrogen into the soil by *A. farnesiana* (Bush and Van Auken 1986a).

As in the other studies that illustrate successional sequences involving legumes, the current study also shows the dominance of a broadleaf species in later stages, as proposed previously (Van Auken and Bush 1985). Density of *C. laevigata* increased in the 19, 25, and 27 yr old stands and basal area increased in all the stands over the 20 yr period. In southern Appalachian forests where *R. pseudoacacia* is the early successional dominant, the mid- to late successional dominants are broadleaves including *Liriodendron tulipifera* (yellow poplar), *Acer rubrum* (red maple), and *Quercus* spp. (oaks) (Boring et al. 1981). *Celtis pallida* (spiny hackberry) and *Diospyros texana* (Texas persimmon) are two broadleaves that replace *P. glandulosa* in xeric communities of south Texas (Archer et al. 1988). In southern Africa where *A. nilotica* is the early successional dominant, the broadleaf *E. divinorum* is the mid- to late successional dominant (Skowno et al. 1999, Smith and Goodman 1987).

While many changes have occurred over the last 20 yrs in these stands, there were still some substantial differences between the mature stand and the oldest remaining resampled stand (52 yr). Based on density, basal area, and species composition, the 52 yr old stand does not appear to be mature, but rather a late, mid-successional stand. Data suggest that density should decrease by approximately 500 plants ha⁻¹ while basal area should increase by about 5 m² ha⁻¹ as the communities mature. These proposed changes seem to follow the self-thinning rule (Yoda et al. 1963). That is, as populations of high density species mature, population density declines and biomass (measured as basal area) increases. Spe-

cies composition also indicates further changes will occur. While *C. laevigata* had the highest density and basal area in the mature forest, two other species, *Acer negundo* and *Ulmus crassifolia*, could be considered co-dominants (Bush and Van Auken 1984). While *A. negundo* was found in several of the mid-successional stands, the density in the mature site was much higher than any other stand. *Ulmus crassifolia* was only found in the mature site, where it had a very high density. In addition, four other species were only found in the mature stand (Table 2).

This study presents direct long-term observations and measurements of changes in secondary succession over 20 yrs, one of only a few found in the literature. In addition, the successional sequence along the San Antonio River in south Texas is a unique sequence. These results confirm earlier hypothesis based on previous descriptive and experimental studies. Changes over this 20 yr time period were dependent on the age of the stand examined, the parameter being examined, and species being examined. Over the next 20 yr, we would predict that the changes in *A. farnesiana* would be slight in all the stands, since it is already reduced in density and basal area in all stands. *Celtis laevigata* density is likely to decrease, however basal area is likely to remain relatively constant. In addition, several other species which are often considered late successional, such as the *Ulmus* spp., *Acer negundo*, and *Crataegus* sp., may become more prevalent as the stands continue to mature.

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