Composition of a Bottomland Forest on the Colorado River in the Lampasas Cut Plain of Texas

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ABSTRACT

We analyzed a hardwood bottomland forest along the Colorado River in the Lampasas Cut Plain of Texas and described species composition and structure of vegetation. Our analysis was conducted to provide baseline knowledge on the natural vegetation. The bottomland forest was comprised of three vegetational layers: 1) upper canopy of dominant trees including cedar elm (*Ulmus crassifolia*) and green ash (*Fraxinus pennsylvanica*), 2) under canopy of heavily browsed lianas, shrubs, and shorter trees including saw greenbriar (*Smilax bona-nox),* Texas persimmon (*Diospyros texana*), and western soapberry (*Saponaria saponaria*) as well as 3) an herbaceous zone of Canada wild rye (*Elymus canadensis)* and Texas wintergrass (*Nasella leuchotricha*), sedges, as well as both annual and perennial forbs. Cedar elm and green ash were dominant trees but had little regeneration, which may be caused by hydrological differences, grazing by cattle, as well as heavy browsing by white-tailed deer (*Odocoileus virginianus*) and felling and girdling by American beavers (*Castor canadensis*). In addition we compare vegetation with high importance and dominance as well as diversity to other rivers found in the West Cross Timbers of Texas. Published on-line www.phytologia.org *Phytologia 100(2): 128-144 (Jun 22, 2018).* ISSN 030319430.
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Bottomland forests are some of the most widely distributed, biodiverse, and productive of communities throughout southern regions of North America (Braun 1964; Messina and Conner 1998; Baker et al. 2004). Diamond et al. (1987) reported that bottomland forest dominated by sugarberry (*Celtis laevigata* var. *laevigata*), cedar elm (*Ulmus crassifolia*), and pecan (*Carya illinoinensis*) comprised the most widely distributed forest community in Texas. It has been estimated that over one-half of the bottomland forest ecosystem in Texas has been lost (Barry and Kroll 1999) and many, including the Colorado River in this investigation, have had their hydrology changed due to damming (Texas Parks and Wildlife (TPWD) 2012). Because of these losses there is considerable interest in restoration of bottomland forest and preserving remaining tracts of less-altered bottomland forests. However, little is known about community composition of bottomland forests in Texas.

Description of the natural vegetation is an important phase of preservation and restoration of bottomland forests. To date there has been limited description and vegetational analysis of such forest communities (TPWD 2012). The Society of American Foresters (SAF) included qualitative coverage of these forests in its descriptions of forest cover types (Eyre 1980) and the Society for Range Management (Shiflet 1994) excluded most forest range types. Neither group examined understory quantitatively. There are several bottomland forest cover types in the southern region that have relatively open canopies and well-developed lower layers of vegetation including two recognized by the SAF (Eyre 1980): SAF 93, sugarberry-American elm (*Ulmus americana*)-green ash (*Fraxinus pennsylvanica*) and SAF 94, sycamore (*Platanus occidentalis*)-sweetgum (*Liquidambar styraciflua*)-American elm. The latter was previously designated as the sycamore-pecan (*Carya illinoinensis*)-American elm type (Eyre 1954).

Later descriptive studies and subsequent qualitative reports of southern floodplain forests (Diamond et al. 1987; Meadows and Stanture 1997; Twedt and Best 2004; Lockhart and Kellum 2006; Twedt et al. 2010) indicated the widespread sugarberry-elm-pecan forest type to be highly variable in its composition, especially where it is ecotonal to adjacent cover types. The general forest community as found in Texas was described variously as elm/sugarberry parks/woods (McMahan and Frye 1987), sugarberry-elm series (Diamond et al. 1987), sugarberry-elm floodplain forest (Bezanson 2000), and Edwards Plateau floodplain hardwood forest (Elliott 2013). Rosiere et al. (2013) described a form of the sugarberry-cedar elm-pecan forest along the Bosque River in North Central Texas, which aligned with the description of southern floodplain forests described above.

Descriptions of understories of woodlands in eastern and southern forest regions of the United States commonly have been in conjunction with soil surveys under leadership of the Natural Resources Conservation Service (NRCS) as outlined in national range handbooks (Soil Conservation Service 1967, 1976; NRCS 2003) and, more recently, river authorities (Jones-Lewey 2016). In an attempt to generally describe riparian areas across the state, the Nueces River Authority (NRA) produced a field guide, which included some of the common vegetation found in Texas riparian areas (Jones-Lewey 2016). Descriptions of grazeable woodlands are currently written as forest land ecological sites (NRCS 2003). Forest land ecological site descriptions need greater detail regarding forest vegetation, including that of the understory. Likewise, classification of natural communities such as forest alliances and series (Diamond et al. 1987; McMahan and Frye 1987; Bezanson 2000, Hoagland 2000) as well as the field guide by the NRA (Jones-Lewey 2016) have been largely qualitative with limited quantitative information provided.

There have been no published, quantitative descriptions of herbaceous plants occurring along the Texas Colorado River. In an investigation examining mammal habitats, Scales and Wilkins (2003) assessed two riparian transects in Colorado Bend State Park, which occur along the Colorado River in the adjacent Edwards Plateau ecoregion. They identified woody plants in the riparian woodlands as pecan, green ash, black walnut (*Juglans nigra*), plateau live oak (*Quercus fusiformis*), red oak (*Q. rubra*), and American elm but did not quantify the understory.

We conducted the current study to provide descriptions and analyses of bottomland forests of the Texas Colorado River in an ecotonal area between the West Cross Timbers and the Edwards Plateau called the Lampasas Cut Plain (Diggs et al. 1999) and compare it to similar studies conducted in the West Cross Timbers of Texas. Currently there is a need for quantitative data of this forest vegetation, which is lacking for much of Texas (Diamond et al. 1987) and because of ongoing classification and ground-truthing of natural plant communities (Elliott 2013), as well as riparian restoration projects. This investigation provided the first quantitative data for bottomland forests in the Lampasas Cut Plain of Texas.

MATERIALS AND METHODS

The study area was within the Lampasas Cut Plain ecoregion (Diggs et al. 1999) and Cross Timbers and Prairies vegetational area (Correll and Johnston 1979) in Mills County, Texas (Figure 1). The Colorado River in Texas is the longest river confined to the state, which begins in the Caprock Escarpment of the high plains near Lamesa, Texas, and flows to the Gulf of Mexico at Matagorda Bay (Crisp 2012). The specific locality for the investigation was the Timberlake Biological Station near Goldthwaite, Texas downstream from Lake O. H. Ivie, which was constructed 27 years ago at the confluence of the Concho and Colorado rivers (Williams 2016), about 145 km south of Abilene, Texas. This tract had been subjected to grazing by livestock for ≥ 100 years. A resident herd of white-tailed deer (*Odocoileus virginianus*) occurred in the study area. There was evidence of heavy browsing (felling and girdling) by American beavers (*Castor canadensis*). We sampled vegetation from August 30, 2014 to September 26, 2014 using nonpermanent plots, which have been shown to yield few statistically significant differences from permanent plots in riparian vegetation monitoring (Laine et al. 2013).

We used the step-point method (Evans and Love 1957; Bonham 1989) to determine composition of herbaceous and seedling (< 1.0 cm in diameter) species from the bottomland. Plants were sampled randomly with a sharp-pointed pipe and total and relative numbers of hits were recorded. We sampled a total of 3800 points in the bottomland within six rectangular quadrants each of which was 25 by 50 m with the longest dimension parallel to the river bank as described by Ford and Van Auken (1982) and Wood and Wood (1988, 1989). The six areas were sampled on the north side of the Colorado River in two areas that included about 2 km of forested area adjacent to the river. Three samples within the 1.0 km stretch were taken on both sides of an elevated area cut by a rill that entered the river.

For woody vegetation in the bottomland, we used the same six rectangular quadrants, 25 by 50 m to sample all woody species greater than 1.0 cm in diameter. We identified the woody species and measured diameter at breast height (dbh). The dbh was used to calculate basal area. We calculated density (plants/ha), dominance (basal area/ha), and relative-importance values as described by Ford and Van Auken (1982) and Wood and Wood (1988, 1989). Shannon diversity, richness, and evenness were calculated according to formulas in Ludwig and Reynolds (1988).

We also assessed beaver damage at the sites that we sampled. This was accomplished by counting trees that were gnawed, girdled, or downed in the 25 by 50 m bottomland quadrats. The species damaged by beaver were identified and percentages for tree species recorded.

Species of plants were identified and classified using Diggs et al. (1999), which also served as the reference for common and scientific names. We deposited voucher specimens in the herbarium (TAC) at Tarleton State University in Stephenville, Texas. Using classifications for the Great Plains ecoregion, wetland indicator status for plants was obtained from Lichvar et al. (2016).

RESULTS

The bottomland forest was comprised of three vegetational layers: 1) upper canopy of dominant trees including cedar elm and green ash, 2) under canopy of heavily browsed lianas, shrubs, and shorter trees including saw greenbriar (*Smilax bona-nox),* Texas persimmon (*Diospyros texana*), and western soapberry (*Saponaria saponaria*) as well as 3) an herbaceous zone of Canada wild rye, Texas wintergrass (*Nasella leuchotricha*), sedges, as well as both annual and perennial forbs.

There were 13 species of trees sampled in this forest of which all were native. For all woody species >1.0 cm in diameter, cedar elm had the highest relative-importance value (70.7) and greatest dominance as well as the greatest relative cover >1.0 cm of any species of tree (Table 1). In all measured attributes, cedar elm was the most common tree. After cedar elm, the most common trees, >1.0 cm overall, were green ash and western soapberry (Table 1). Most of the tree species had a wetland indicator status of facultative (Table 1).

There was a total of seven species of shrubs and one liana. The most common species of shrub was Texas persimmon (Tables 1 and 2). Prickly-pear cactus (*Opuntia engelmannii* var. *lindheimeri*) was also common on one relatively high bank and occurred in two large clumps. More widely distributed and relatively high in importance was chittamwood (*Sideroxylon languinosum* subsp. *oblongifolium*). Saw greenbriar (*Smilax bona-nox*) was the only liana and accounted for less than 2% of vegetation sampled that was <1.0 cm in diameter. Most of the shrub species had a wetland indicator status of facultative or upland (Table 1). There were no introduced tree or shrub species in the quadrats. However, Chinaberry (*Melia azedarach*) and chastetree (*Vitex agus-castus*) were occasionally observed outside the quadrats.

Of the herbaceous species, 23 were native and five were introduced (Table 2). Native perennial grasses comprised much of the herbaceous vegetation in the floodplain and were dominated by Canada wildrye and Texas wintergrass. Four forbs, pigeonberry (*Rivinia humilus*), betony noseburn (*Tragia betoncifolia*), cowpen daisy (*Verbesina encelioides*), and introduced horehound (*Marrubium vulgare*) were relatively common and generally more abundant than other forbs (Table 2). Most herbaceous species had a wetland indicator status of upland or facultative upland (Table 2). Spiny-aster (*Chloracantha spinosa*) was the only facultative wetland species (Table 2). There was little regeneration of woody vegetation as evidenced by only 3.4% of total trees and shrubs being < 1.0 cm in diameter (Table 2). Honey mesquite, Texas persimmon, and western soapberry had the greatest percentages of small saplings (Table 2).

Beaver damage was greatest on the cedar elms, with 67% of damage occurring on cedar elm trees (Table 3). Richness, Evenness, and Shannon Diversity in the Texas Colorado River Bottomland, when compared to the Bosque River in the nearby West Cross (Rosiere et al. 2013), was lower than the Bosque River, except in the case of richness of herbaceous and seedling species (Table 4).

DISCUSSION

Quantitative data for woody and herbaceous vegetation in bottomland forest of the Lampasas Cut Plain, including nonnative species, were provided for the first time. Comparison of woody and herbaceous vegetation to other studies near the region, possible successional status within the bottomland forest, herbivory, hydrology, and diversity are discussed.

Little has been published regarding woody vegetation along the Colorado River. Scales and Wilkins (2003) identified the following trees occurring along two transects along the Colorado River in Colorado Bend State Park: pecan, green ash, black walnut, plateau live oak, (red oak), and American elm. At Timberlake Biological Station, we did not sample black walnut or oaks in the bottomland and found much more cedar elm than American elm (Table 1). Patterns of density and importance values for cedar elm along the Texas Colorado River corresponded to those reported for similar forested communities in the region. Composition and structure of the forest along the Texas Colorado River was similar to various woody communities in the Trinity River basin of northern Texas as described by Nixon et al. (1990) and an old-growth bottomland forest along a creek in northeastern Texas (Nixon et al. 1991). In these forests cedar elm and sugarberry were consistently common or dominant trees. Nixon et al. (1991) reported that in a creek-floodplain forest, cedar elm and sugarberry had highest importance values and greatest densities of trees. Duke (2015) pointed out that sugarberry can become invasive when riparian functionality is compromised and may replace key riparian indicator species such as green ash, cottonwood, and black willow. We did not find this to be the case at this site on the Colorado River with cedar elm and green ash being more dominant than sugarberry.

Members of the elm family, like sugarberry, American elm, and cedar elm, occurred in the bottomland (Table 1) and sugarberry is reported to be frequently browsed by ungulates and its fruits are an important food source for many birds (Linex 2014). Linex (2014) and Jones-Lewey (2016) stated that elms are the most widespread and important riparian trees in Texas, which help protect river banks during flooding. Linex (2014) indicated that American elm and cedar elm are frequently browsed by cattle and deer. In our sampling quadrats, sugarberry and elm trees had poor regeneration (Table 2) and if they survived past the seedling stages, small trees were often felled or girdled by beaver (Table 3).

Green ash has relatively extensive coverage across East, Central, and South Texas and is highly tolerant of disturbance growing not only along the streamside but on extremely steep channel slopes (Duke 2015). Jones-Lewey (2016) indicated that green ash is important in protecting banks during floods and one of the most common species of ash in the eastern one-third of Texas. Linex (2014) added that it provided fair browse value for deer and was one of the first trees to grow back in abandoned fields adjacent to or replacing bottomlands. Green ash was the second most important tree species at our study sites but had little regeneration (Tables 1 and 2). Grazing and browsing likely accounted for the lack of green ash regeneration in the Colorado River bottomland. The only common regenerating small trees or shrubs were honey mesquite, Texas persimmon, and western soapberry. Texas persimmon is reported to be only occasionally browsed by cattle and deer, honey mesquite provides fair browse value, and western soapberry is readily browsed by cattle and deer (Linex 2014). Lastly, saw greenbrier, which has a stem diameter <1.0 cm, was relatively common (Table 2) but not as common as that found along the Bosque River (Rosiere et al. 2013), which had not been grazed by cattle in over 50 years. It is reported to be readily browsed by herbivores and its fruits are important to a variety of wildlife (Linex 2014).

TPWD (2012) and Nelle (2015) listed Chinaberry (*Melia azedarach*), Chinese tallow (*Sapium sebiferum*), Japanese honeysuckle (*Lonicera japonica*), and salt cedar (*Tamarix* spp.) as nonnative species that could be problematic in bottomlands associated with the Colorado River in the Lampasas Cut Plain. TPWD also listed tree of heaven (*Ailanthus altissima*) as an invasive tree. Anderson (2006) listed Chinaberry and chastetree as non-native species found in the river corridor near Austin and Bastrop, Texas. Only two species of nonnative woody plants, Chinaberry and chastetree, were observed in the bottomland forest at the study site but these were not sampled in the six quadrats, because they were not common. Chastetree likely escaped from yards near the river. Chinaberry was a rapid-growing species along the San Antonio River (Bush and Van Auken 1984) and a species associated with sugarberry and cedar elm (Van Auken and Bush 1985). Richardson et al. (2007) explained that rivers were very susceptible to invasion by alien plants because hydrologic dynamics and frequent disturbances of streams make them especially effective for dispersal of plant propagules. Bush and Van Auken (1984) commented that Chinaberry along with sugarberry and native colonizing tree species likely became established following flooding. Chinaberry may be considered invasive and spreads rapidly along riparian areas (Jones-Lewey 2016). To date, it is only a minor component of the woody vegetation at this study site.

Previous investigations, as well as qualitative descriptions of bottomland forests (Bush and Van Auken 1984; Diamond et al. 1987; McMahan and Frye 1987; Bezanson 2000), generally placed less emphasis on shrubs and provided little data and analysis of herbaceous layers of bottomland-hardwood forests. By contrast, this investigation included the understory of the forest. Density and dispersion of trees combined with the absence of lianas and relatively low number of seedlings and saplings of trees formed a canopy sparse enough for development of an herbaceous understory dominated by native perennial grasses along the Colorado River. Herbaceous layers of the forest along Colorado River were similar to those reported for bottomland forests of the West Cross Timbers in Texas (Rosiere et al. 2013). Nixon et al. (1991) reported about the same number of shrubs for a creek-bottom forest, but most of these shrubs, other than woody vines, were absent from the forest adjacent to the Colorado River.

Canada wildrye and Texas wintergrass were herbaceous co-dominants in the bottomland forest but in a quadrat sampled in an area that had not been grazed and was adjacent to the quadrats in this study (Nelson unpublished data), broadleaf woodoats were more common. Broadleaf woodoats are reported to stabilize soils on steep banks (Jones-Lewey 2016), and to be grazed as well as browsed (Linex 2014). Loss of broadleaf woodoats (*Chasmanthium* latifolium)by being grazed and browsed out of the bottomland contributes to erosion of river banks. Canada wildrye and broadleaf wood oats were dominants in a West Cross Timbers bottomland (Rosiere et al. 2013) and broadleaf woodoats is common on the floodplains along rivers in the Texas Hill Country (Gustafson 2015). They are viewed as dominants in late-seral to climax vegetation along streams and floodplains throughout much of Oklahoma (Tyrl et al. 2008) and Texas (Gould 1975). Canada wildrye is reported as excellent forage for livestock and is browsed by deer when young but can become susceptible to overgrazing (Linex 2014; Jones-Lewey 2016). Texas wintergrass was an upland plant that occurred mostly in elevated areas of the study sites. It provides fair to good grazing for cattle and fair browse for deer (Linex 2014). There were relatively few species of sedge (*Carex*) and umbrella sedge (*Cyperus*) sampled (6% of total), which are often wetland species, and may indicate negative changes in hydrology when reduced or absent (Jones-Lewey 2016).

TPWD (2012) listed King Ranch bluestem (*Bothriochloa ischaemum* var. *songarica*) and Bermuda grass (*Cynodon dactylon*), as nonnative species that could be problematic in bottomlands associated with the Colorado River in the Lampasas Cut Plain. There were four introduced grasses with Bermuda grass being the most common on the Colorado River (Table 2). Bermuda grass, which comprised 5% of the total herbaceous coverage provided some stability for river banks but often out-competed native plants, which frequently provided greater bank stability (Jones-Lewey 2016). Bermuda provided good forage for livestock but not deer and is known to survive saturation by flooding for up to three weeks (Linex 2014). We did not sample King Ranch bluestem in our bottomland quadrats but observed it in the uplands adjacent to the bottomland.

Pigeonberry, betony noseburn, and cowpen daisy were relatively common native forbs that were facultative or upland classified plants and often in environments that were recently disturbed. Pigeonberry is reported to occur in stream bottomland woods (Diggs et al. 1999) in shaded areas (Gustafson 2015), which was where it occurred on the Colorado River. Linex (2014) states that it is occasionally grazed by cattle and browsed by deer and is likely spread into bottomlands by birds (Linex 2014). Betony noseburn is common on sandy soils (Diggs et al. 1999), which were common along the Colorado River. Cowpen daisy is known from sandy soil in many disturbed habitats (Diggs et al. 1999; Gustafson, 2015), which was where it was more abundant on the Colorado River. Pigeonberry is known from stream bottomland woods (Diggs et al. 1999) and prefers shaded areas (Gustafson, 2015), like the bottomland woods on the Colorado River. A fourth forb, spiny-aster (*Chloracantha spinosa*) was the only facultative wetland species. Its rhizomes help stabilize river banks and young plants are eaten by deer and cattle (Linex 2014).

Frostweed was not common along the Colorado River (Table 2). Frostweed is viewed as a species typical of middle stages of succession (Tyrl et al. 2008), but a study (Thompson and McKinney 2006) of various successional stages in a river bottomland forest in Tennessee with similar composition and structure to the one reported herein, reports frostweed to be associated with higher seral states. In the Colorado River bottomland, frostweed was often associated with perennial grasses in more open spots within the herbaceous layer. Its lack of abundance in this investigation might be due to the Colorado River herbaceous layer being at an earlier stage of succession or to differences in herbivory (Linex 2014).

The only introduced forb on the Colorado River was horehound, which often grows near cow lots or under shade where cattle and other livestock such as sheep and goats congregate and the soil has high nutrient levels (Diggs et al. 1999). In the Colorado River bottomland sampled, disturbed areas caused by cattle were mainly where horehound was sampled.

In terms of bottomland forest succession along the Colorado River, we concluded that the cedar elm-green ash community was representative of the potential natural vegetation (Zerbe 1998) or climax floodplain forest (Braun 1964) for this ecological site. Composition and structure was consistent with traditional descriptions ranging from that of forest cover types (Eyre 1980) to classification for conservation of plant communities (Diamond et al. 1987; Hoagland 2000). This was in contrast to Holcomb (2001) that suggested cedar-elm-green ash as the mid-successional stage.

Holcomb (2001) used the qualitative and generic pattern that Hodges (1997) proposed for bottomland forests of the Atlantic and Gulf Coastal Plains and it was not clear how relevant the general coastal model of Hodges (1997) would be for the inland Lampasas Cut Plain ecoregion. The forest investigated by Barry and Kroll (1999) and Holcomb (2001) was along the Elm Fork of the Trinity River in the more mesic East Cross Timbers, whereas the forest along the Colorado River occurred in the more arid Lampasas Cut Plain (Diggs et al. 1999).

Quantitative studies of bottomland hardwood forests have been less common than qualitative analyses. Furthermore, quantitative investigations generally were limited to woody species as, for example, those of similar bottomland forests along the San Antonio River (Bush and Van Auken 1984; Van Auken and Bush 1985), Trinity River (Nixon et al. 1990), and Spring Creek in the Blackland Prairie (Nixon et al. 1991). Barry and Kroll (1999) concluded that a sugarberry-cedar elm-green ash bottomland forest was the climax community for a similar bottomland habitat. Nixon et al. (1991) reported that green ash was a dominant tree along with species of elm, pecan, sugarberry, and species of oak. Similarly, green ash was the second most important species in the forest of our study.

Pecan was an uncommon species in our investigation and was not reported as being highly important by Barry and Kroll (1999) or Rosiere et al. (2013). Holcomb (2001) conducted studies following those of Barry and Kroll (1999) on the same tract and concluded that pecan was a dominant of the seral stage that preceded the sugarberry-elm-green ash community. This was consistent with the sugarberry-cedar-elm-pecan community that Rosiere et al. (2013) described, in which pecan was, perhaps, a subclimax species that persisted into the climax forest.

Van Auken and Bush (1985) studied secondary succession of a climax forest on terraces of the San Antonio River and explained that sugarberry and cedar elm became dominant in advanced stages of development of forests, whereas pecan established earlier in the successional sequence and persisted into the climax forest. The few pecans we encountered on the Colorado River were small and not larger, older trees such as were sampled along the Bosque River (Rosiere et al. 2013). Limited recruitment of pecan as one of the dominant species was consistent with Rice (1965). It appeared that sugarberry and cedar elm were the climax dominants, while pecan was a member of the climax as a persistent subclimax species (Rosiere et al., 2013). Burns and Honkala (1990) categorized pecan as subclimax. Perhaps pecans have only recently become established along this portion of the Colorado River and/or old trees have died. Pecan provides poor to fair browse value for deer (Linex 2014), but it was low in numbers of < 1.0 cm samples taken along the Colorado River. However, because browse value of pecan is poor to fair at best (Linex 2014), it seems unlikely that low pecan regeneration was due to herbivory.

Braun (1964) and Kellison et al. (1998) concluded that sugarberry is nearly ubiquitous in bottomland forests throughout the south-central region, whereas cedar elm is more restricted, being confined primarily to western parts of this region. The large amount of cedar elms along the westward Colorado River supported this hypothesis. According to Wagner (2003), there were three types of dominant overstory plant communities in the limestone-dominated Central Texas/Edwards Plateau region: bald cypress (*Taxodium distichum*) and sycamore (*Platanus occidentalis*); pecan and sugarberry; and sugarberry and elm. Based on these two observations, the bottomland forest on this portion of the

Colorado River is more like forests in the Cross Timbers ecoregion of Texas and was less like Edward's Plateau sites near Bastrop and Austin, Texas (Anderson 2006).

We also concluded that herbivory is likely affecting regeneration of woody species and perennial herbs in the Colorado River bottomland. Beaver are not common in the Hill Country (Gustafson 2015) but appear to be common and detrimental at this study site on the Colorado River in the Lampasas Cut Plain. They can occur in burrows in river banks (Wilson and Ruff 1999; Schmidly 2004) rather than in lodges generally located away from banks, which was the case at the Colorado River study site. Because of their extensive modification of freshwater environments, beaver may be considered keystone animals as ecosystem engineers in many areas (Jones et al. 1994; Wilson and Ruff 1999; Karklins 2017); however, when they become too abundant and act as a dominant in the ecosystem, they have caused negative changes in the bottomland ecosystem (Townsend and Butler 1996; Gibson and Olden 2014; Karklins 2017). We observed only small amounts of cottonwood or willow in our quadrats indicative of a possible preference of these species by beaver. Beaver eat bark and leaves of many shrub and tree species but cottonwood and willow are preferred (Wilson and Ruff 1999). Small et al. (2016) reported that in northern New Mexico, the most important plant variable for the presence of beavers was willows (*Salix* spp.) and that grazing by cattle, as currently practiced on Forest Service grazing allotments, disrupted the beaver-willow mutualism, rendering streams unsuitable for beaver. The scarcity of willows and cottonwoods in the bottomland may be due to heavy grazing by cattle, browsing by white-tailed deer, and large numbers of American beaver, or lack of bottomland flooding. However, willows and cottonwoods did occur more often in the near-riparian zone, 2.5 m from the water's edge (Nelson unpublished data), which is steep and therefore not as accessible for herbivores. Black willow and cottonwood provide good browse and is often heavily used by cattle and deer (Linex 2014). Additional investigations into the role of beaver in these bottomlands is needed.

Improperly managed white-tailed deer can cause significant damage to riparian vegetation by their consumption of forbs and shrubs as browse (Nelle 2015). White-tailed deer were observed in the Colorado River bottomland frequently. Nelson Dickinson and Van Auken (2016) reported that large vertebrate herbivores, mainly white-tailed deer, significantly affected the survival and density of juvenile bigtooth maple (*Acer grandidentatum*) at Lost Maples State Park in Texas. Cogger et al. (2014) tabulated that at bottomland forest restoration sites along the Upper Mississippi River and its tributaries, white-tailed deer browsed 46% of tree seedlings and preferred American elm over green ash.

Livestock grazing has affected almost all riparian areas in the state and is considered one of the most significant disturbances affecting them (Nelle 2015). Removal of cattle from riparian areas in the Northwestern Great Basin resulted in dramatically increased coverage in riparian vegetation (Batchelor et al. 2015). Also, cattle are reported to play a role in mesquite seed dispersal (Ansley et al. 2017), and may have contributed to its higher regeneration in the quadrats at our study site. Nelle (2005a; 2005b) concluded that heavy grazing, watering, and loafing by cattle damages riparian vegetation, generally leading to destabilized river banks. One instance of beneficial impacts reported for cattle grazing was that ephemeral wetland diversity increased with cattle grazing, which removed exotic grasses from the wetlands (Marty, 2005). In the stretch of the Colorado River bottomland sampled, there were few to no ephemeral wetlands and our data suggested that herbivory by cattle, deer, and beaver activity may have impeded regeneration of trees and shrubs (Table 2).

Another possibility for reduced regeneration of woody species and herbaceous perennials is low flow hydrology. Low flow hydrology during droughts and flood flow events have been documented in changing riparian vegetation (Hardy and Davis 2015). Most bottomlands have been disrupted by dams, which separate and isolate remnant floodplains changing riparian biodiversity (Johnson 2002). This part of the Colorado River was most changed by the construction of a dam near the confluence of the Colorado and Concho rivers, which became Lake O. H. Ivie (Crisp 2012; Williams 2016). The primary disturbance and stresses influencing bottomlands in semi-arid regions have been associated with river flow where flooding resets the successional cycle (Shafroth et al. 2002; Hardy and Davis 2015) and provides inundation critical for wetland adapted plants (Dawson et al. 2017). In a study that examined hydrology, green ash and Texas persimmon were found to have the highest percent survival in drier stretches of the river (Kolka et al. 1998). At our site, shrubs like honey mesquite, Texas persimmon, and western soapberry are regenerating more often than other woody species (Table 2). Dawson et al. (2017) found native soil propagule banks to be intact along rivers, which after appropriate inundation can produce diverse mixtures of potential natural climax species and Alldredge and Moore (2014) found that changes in flood magnitude limited occurrence of wetland species. Wetlands are defined by having species with greater than 50% obligate or facultative wetland categories (Alldredge and Moore 2014) and government agencies have expanded their wetland definition to include bottomland hardwood forests (Kellison and Young 1997). The Colorado River bottomland forest was not dominated by wetland species. Alldredge and Moore (2014) reported this to be true of the Sabine River in East Texas as well. Riparian areas should contain a mix of obligate wetland, facultative wetland, and facultative species depending on water availability and it is important that riparian areas have species from the facultative group to provide stability due to hydrological change (Asher et al. 2015). This stretch of the Colorado River was mostly facultative upland and upland species with the only facultative wetland species present in the Colorado River bottomland being black willow and spiny aster.

Jones-Lewey (2016) listed indicators of riparian health, which include an active floodplain, energy dissipation during floods, new plant colonization, stabilizing vegetation, age diversity, species diversity, plant vigor, water storage, and establishment of equilibrium between erosion and deposition. At our study site, the Colorado River rarely reaches the bottomland due to upstream damming. When it does flood, there is such an increased flow that energy is often not dissipated by vegetation, which results in disequilibrium in erosion and deposition (Nelson personal observation). Therefore, we found areas with poor plant colonization in the near-riparian (Nelson unpublished data) but also due to high-levels of herbivory. There is stabilizing vegetation in the bottomland forest but it is disproportionately upland plants with wetland plants being rare. Jones-Lewey (2016), pointed out that the lack of wetland plants likely indicates poor water storage capacity for the bottomland. Based on the evaluation system of Jones-Lewy (2016), this portion of the Texas Colorado River was in an at-risk condition and will require management to restore it to a highly functional condition.

Diversity at this site on the Colorado River is different from other studies. The nearest location to the Colorado River that has examined diversity is the Bosque River in Erath County, which is about 120 km northeast of the Timberlake Ranch study site. It had higher diversity in every category except richness of herbaceous species and seedlings when compared to the Colorado River. There were few seedlings in the Colorado River bottomland, so much of the richness was due to herbaceous species, which may have been higher due to disturbance by herbivores and altered flood regimes. These relatively high levels of herbivory were lacking in the Bosque River bottomland (Rosiere et al. 2013). Nixon et al. (1990) reported mean Shannon-Weiner diversity for trees (>1 cm diameter) from four sites in the upper basin of the Trinity River, which was dominated by cedar elm, sugarberry, and green ash, as 2.5. This was higher diversity than that of the Bosque (2.2) and the Colorado (1.5) rivers. Nixon et al. (1990) examined woody plant communities within the Trinity River basin and reported that the less moist, western communities had lower mean diversity. Our data from the Colorado River supported this trend. It is also possible that the degradation of the Colorado River in terms of reduced hydrology and high herbivory contributed to its low diversity values in trees (> 1.0 cm in diameter) but lower levels of precipitation in the west might have a greater effect as hypothesized by Nixon (1990).

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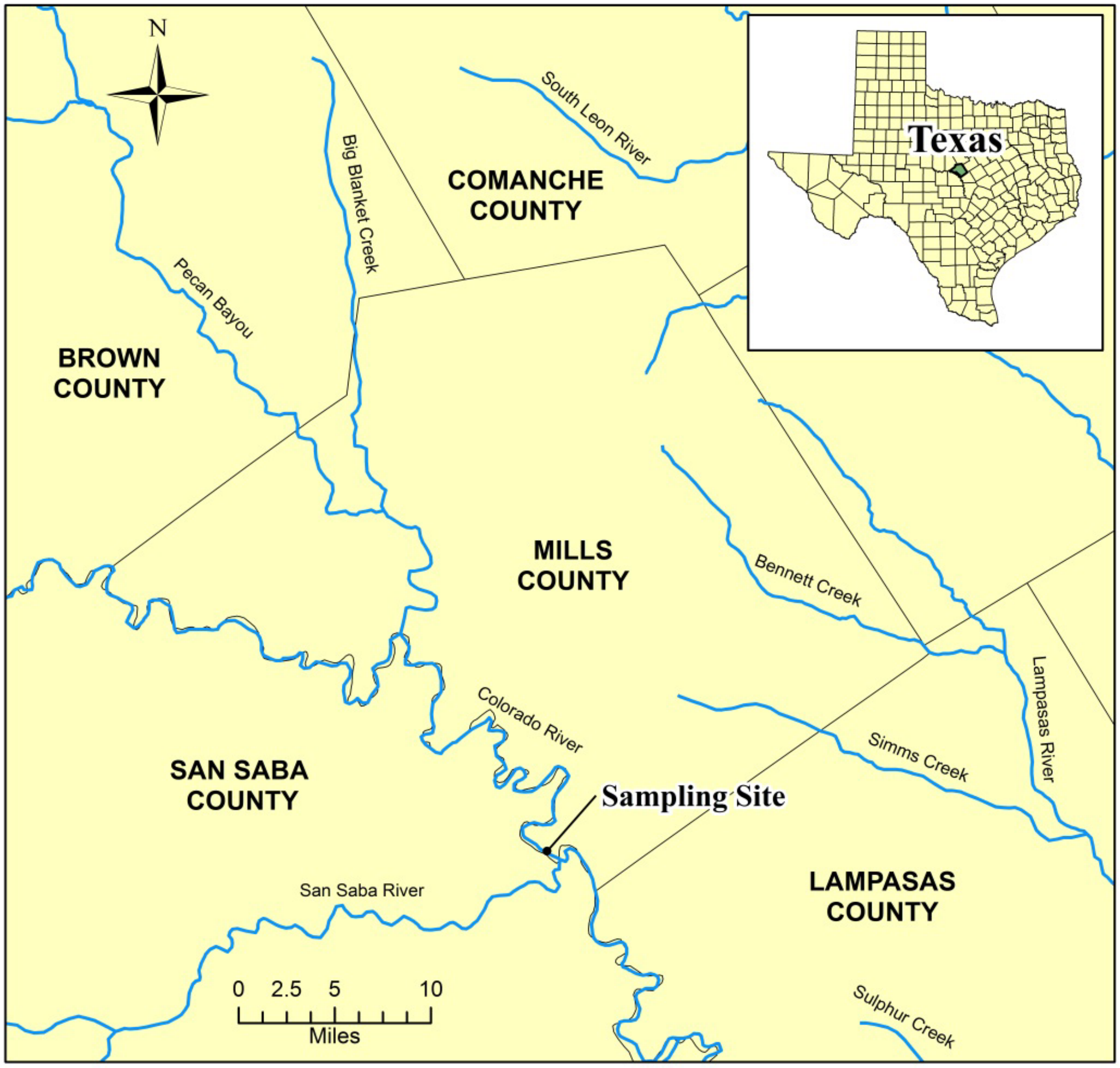

Figure 1. Map showing sampling site along the Colorado River in Mills County, Texas. Inset shows the location of the county in Texas.

Table 1-- Density, dominance, and relative importance values for woody vegetation greater than one centimeter diameter breast height of mixed hardwood bottomland forest of Colorado River, Texas. Wetland classification (Lichvar et al., 2016) is provided after the scientific name.

Common name (Scientific name) Wetland Classification	Density (plants/ha)	Dominance (m^2/ha)	Importance Value (%)
American elm (*Ulmus americana*) Facultative	24.0	37.1	3.9
Black willow (*Salix nigra*) Faculative Wetland	1.3	0.1	0.1
Cedar elm (*Ulmus crassifolia*) Facultative	222.7	1036.8	70.7
Chittamwood (*Sideroxylon languinosum* subsp. *oblongifolium* Facultative upland	4.0	0.1	0.3
Cottonwood (*Populus deltoides*) Facultative	4.0	8.9	1.2
Flame-leaf sumac (*Rhus lanceolata*) Upland	1.3	< 0.1	0.1
Green ash (*Fraxinus pennsylvanica*) Facultative	45.3	204.9	14.1
Honey mesquite (*Prosopis glandulosa*) Facultative upland	1.3	< 0.1	0.1
Pecan (*Carya illinoinensis*) Facultative	2.7	<0.1	0.3
Prickly-pear cactus (*Opuntia engelmannii* var. *lindheimeri*) Upland	2.7	16.8	1.1
Sugarberry (*Celtis laevigata* var. *laevigata*) Facultative	25.3	14.9	2.9
Texas persimmon (*Diospyros texana*) Upland	14.7	0.1	1.2
Western soapberry (*Sapindus saponaria*) Facultative upland	46.7	10.8	4.5
Total	396.0	1,319.7	101.5

Table 2--Species composition as determined by step-point method herbaceous and woody plants (below 1 cm diameter) of mixed hardwood bottomland forest of Colorado River, Texas. An asterisk indicates an introduced species. Vegetation categories and their totals are in italics. Wetland classification ((Lichvar et al., 2016) is provided after the scientific name.

Common name (Scientific name)	No. hits (%)
Grasses	
*Bermudagrass (*Cynodon dactylon*) Facultative upland	191 (5.0)
Big-top love grass (*Eragrostis hirsuta*) Facultative upland	2 (< 0.1)
Canada wildrye (*Elymus canadensis*) Facultative upland	783 (20.6)
Hall's panic (*Panicum hallii* var. *hallii)* Facultative upland	28 (0.7)
*Japanese brome (*Bromus japonicus*) Upland	1 (< 0.1)
*Klein grass (*Panicum coloratum*) Facultative	1 (< 0.1)
Nimblewill (*Muhlenbergia schreberi*) Facultative upland	4 (0.1)
Purpletop (*Tridens flavus*) Upland	2 (<0.1)
Southwestern bristlegrass (*Setaria scheelei*) Upland	91 (2.4)
*Stink grass (*Eragrostis cilianensis*) Facultative upland	4 (0.1)
Texas wintergrass (*Nasella leuchotricha*) Upland	577 (15.2)
Total Grasses	1684 (44.3)
Grasslike	
Gotthilf Muhlenenberg's caric-sedge (*Carex muhlenbergii* var. *muhlenbergii*) Upland	131 (3.4)
Unknown caric sedge (*Carex* sp.)	94 (2.5)
Unknown flat sedge (*Cyperus* sp.)	5 (0.1)
Total Grasslike	230 (6.1)
Forbs	
Betony noseburn (*Tragia betonicifolia*) Upland	67 (1.8)
Cowpen daisy (*Verbesina encelioides*) Facultative	62 (1.6)
Creeping ladies'-sorrel (*Oxalis corniculata*) Facultative	19 (0.5)
Frostweed (*Verbesina virginica*) Facultative upland	7 (0.2)
*Horehound (*Marrubium vulgare*) Facultative upland	60 (1.6)
Indian mallow (*Abutilon fruticosum*) Upland	5 (0.1)
Pigeonberry (*Rivina humilis*) Facultative	72 (1.9)
Silver-leaf nightshade (*Solanum elaeagnifolium*) Upland	25 (0.7)
Spiny-aster (*Chloracantha spinosa*) Facultative wetland	51 (1.3)
Texas croton (*Croton texensis*) Upland	7 (0.2)
Unknown mint	1 (< 0.1)
Virginia copperleaf (*Acalypha virginica*) Facultative upland	29 (0.8)
Total Forbs	405 (10.7)
Shrubs, lianas, and small trees	
Cedar elm (*Ulmus crassifolia*) Facultative	2 (< 0.1)
Flame-leaf sumac (*Rhus copallinum* var. *latifolia* Upland	1 (< 0.1)
Honey mesquite (*Prosopis glandulosa*) Facultative upland	28 (0.7)
Juniper (*Juniperus* sp.)	1 (< 0.1)
Rusty blackhaw (*Viburnum rufidulum*) Facultative upland	1 (< 0.1)
Saw Greenbriar (*Smilax bona-nox*) Facultative upland	57 (1.5)
Sugarberry (*Celtis laevigata* var. *laevigata*) Facultative	4 (0.1)
Tasajillo (*Opuntia leptocaulis*) Upland	1 (< 0.1)
Texas persimmon (*Diospyros texana*) Upland	15 (0.4)
Texas prickly-pear (*Opuntia engelmannii* var. *lindheimeri* Upland	1 (< 0.1)

Unknown shrub	1 (< 0.1)
Table 2 (cont.) Western soapberry (*Sapindus saponaria*) Facultative	16 (0.4)
Total shrubs and small trees	128 (3.4)
Bare ground	1353 (35.6)
Total Hits	3800 (100.1)

Table 3. Number of samples and percentages of beaver damage in the bottomland (*n*=85) of the Colorado River at Timberlake Ranch.

Beaver damaged woody vegetation	Bottomland (%)
Cedar elm	57 (67.1)
Texas persimmon	13 (15.3)
Sugarberry	12 (14.1)
Cottonwood	2 (2.4)
Green ash	1 (1.2)

Table 4. Richness, Evenness, and Shannon Diversity in the Texas Colorado (TXCO) River Bottomland to that of the Bosque River (Roseiere et al., 2013).

	TXCO River	Bosque River
Woody Richness > 1.0 cm	13	17
Herbaceous & seedling Richness < 1.0 cm	40	30
Woody Evenness > 1.0 cm	0.59	0.77
Herbaceous & seedling Evenness < 1.0 cm	0.66	0.66
Woody Shannon Diversity > 1.0 cm	1.51	2.18
Herbaceous & seedling Shannon Diversity < 1.0 cm	2.42	2.26