Near riparian vegetation on the Colorado River at Timberlake Biological Station in the Lampasas Cut Plain of Texas

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ABSTRACT

We analyzed the near-riparian zone along the Colorado River in the Lampasas Cut Plain (LCP) of Texas at Timberlake Biological Station (TBS) and described species composition and structure of vegetation. Our analysis was conducted to provide baseline knowledge on the natural vegetation of this near-riparian zone that has only been examined from North Texas in the Piney Woods ecoregion. The near-riparian zone of TBS was comprised of three vegetational layers: 1) upper canopy of trees including mainly green ash (*Fraxinus pennsylvanica*) and about equal amounts of cedar elm (*Ulmus crassifolia*) and American elm (*U. americana*) 2) under canopy of the liana saw greenbriar (*Smilax bona*-nox) as well as both annual and perennial grasses and forbs. Green ash was the dominant tree and saw greenbriar and Virginia creeper (*Parthenocissus quinquefolia*) were the only two lianas. Dominant grasses and sedges included Canada wildrye (*Elymus canadensis*), switch grass (*Panicum virgatum*) and William Emory's caric sedge (*Carex emoryi*). The dominant forb was Spiny-aster (*Chloracantha spinosa*). In addition, beaver damaged fewer trees in the near-riparian of the Colorado River and diversity was lower compared to a near-riparian zone in the Piney Woods and compared to bottomlands found in the West Cross Timbers ecoregion of Texas. *Published online www.phytologia.org Phytologia 103(3):73-85 (September 27, 2021). ISSN 030319430*.

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Bottomland forests and their associated near-riparian zones 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). 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 near-riparian area adjacent to 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 and preservation of riparian zones. However, little is known about community composition of

the near-riparian zone in Texas, which is defined here as the narrow, dynamic area adjacent to the bottomland and beginning at the water's edge. This region is an extremely important buffer zone for the adjacent bottomland forest and has been shown to differ in species composition from the bottomland in East and North Central Texas (Nixon et al. 1991; 1977; Nixon and Raines 1976).

Description of the natural vegetation is an important phase of preservation and restoration of riparian areas. To date there has been limited description and vegetational analysis of such communities (TPWD 2012) and only four studies for Texas. No investigation in Texas has examined understory quantitatively in near-riparian zones of North Texas. 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 Society of American Foresters (SAF) (Eyre 1980): SAF 93, sugarberry (*Celtis laevigata*)-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). These all examined the broad bottomland forest community but did not examine the dynamic near-riparian community near the water's edge.

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; Nelson et al. 2018) 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).

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.

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. There is only one published, quantitative description of woody and herbaceous plants occurring along the Texas Colorado River (Nelson et al. 2018). 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 shorter trees and shrubs including saw greenbriar (*Smilax bona-nox*), and 3) herbaceous zone of Canada wild rye (*Elymus canadensis*), sedges, as well as both annual and perennial forbs. None of the studies described above examined the near-riparian zone.

Lonard et al. (1997; 1998; 1999; 2000; 2001; 2004), Lonard and Judd (2002), Everitt et al. (1999; 2002), and Zhang et al. (1998) documented riparian vegetation including the near-riparian for the Rio Grande in South Texas, but species composition of the subtropical Rio Grande was too different for comparison to this temperate-region investigation. To our knowledge, the only publications that mentions near-riparian vegetation in temperate North Texas is Nixon et al. (1991) who investigated creekside forest along Spring

Creek, north of Garland, Texas. They found that sugarberry, elms (*Ulmus* spp.), and ashes (*Fraxinus* spp.) were the most important tree species along the creekside. The most prevalent shrubs and small trees were roughleaf dogwood (*Cornus drummondii*), rusty blackhaw (*Viburnum rufidulum*), Carolina buckthorn (*Rhamnus caroliniana*), and eastern red cedar (*Juniperus virginianum*). River grape (*Vitis riparia*), poisonivy (*Toxicodendron radicans*), and Virginia creeper (*Parthenocissus quinquefolia*) were the most common lianas at the site. Shannon-Weiner diversity was 3.40 and richness was 32.

We conducted the current study to provide descriptions and analyses of near-riparian forests of the Colorado River in an ecotonal area between the West Cross Timbers and the Edwards Plateau called the Lampasas Cut Plain (Diggs et al. 1999) at TBS and compare it to similar studies conducted in 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). TBS was a working ranch that raised Braford cattle and Coastal bermudagrass (*Cynodon dactylon*) hay that was donated to Tarleton State University. The Colorado River in Texas, which borders the ranch between Mills and San Saba counties (Figure 1) 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

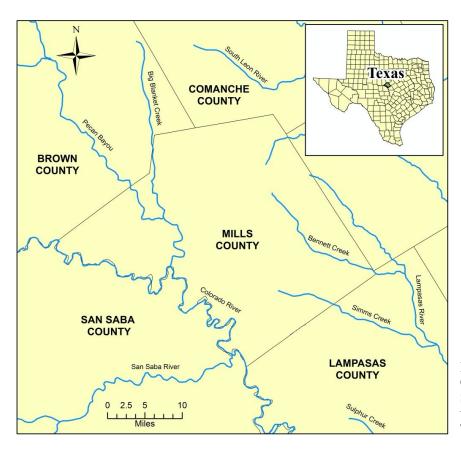


Figure 1. Map showing the Colorado River in Mills and San Saba counties, Texas. Inset shows the location of the counties in Texas.

(Crisp 2012). The specific localities for the investigation was Timberlake Biological Station near Goldthwaite, Texas. The site was 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. We sampled vegetation from March 27, 2015 to July 1, 2015 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 near-riparian within six rectangular quadrants each of which was 2.0 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, 2.0 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 (*Castor canadensis*) 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

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

Table 1. Density, dominance, and relative importance values (IV) for woody vegetation greater than one centimeter diameter breast height of near-riparian zone of Colorado River, Texas at Timberlake Biological Station. 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)	IV (%)
American elm (<i>Ulmus americana</i>) Facultative	110.0	22.3	7.5
Cedar elm (<i>U. crassifolia</i>) Facultative	180.0	12.5	10.5
Green ash (Fraxinus pennsylvanica) Facultative	560.0	832.7	77.5
Sugarberry (Celtis laevigata var. laevigata) Facultative	30.0	6.9	2.0
Virginia creeper (Parthenocissus quinquefolia) Facultative upland	40.0	0.6	2.0
Total	920.0	875.0	99.5

There was a total of two species of lianas and no shrubs or small trees sampled. The species of liana sampled that was >1.0 cm was Virginia creeper (Table 1) and saw greenbriar was the only liana sampled that was <1.0 cm (Table 2). Both of the liana species had a wetland indicator status of facultative upland. There were no introduced woody species in the quadrats. However, Chinaberry (*Melia azedarach*) and chastetree (*Vitex agnus-castus*) were occasionally observed outside the quadrats and chastetree chokes several tributaries that enter the river (Nelson, personal observation).

Table 2. Species composition as determined by step-point method herbaceous and woody plants (below 1 cm diameter) of the near-riparian zone of Colorado River, Texas at Timberlake Biological Station (TBS), 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) Grasses	# Hits (%)
*Bermuda grass (<i>Cynodon dactylon</i>) Facultative upland Broad-leaf woodoats (<i>Chasmanthium latifolium</i>) Facultative upland Canada wildrye (<i>Elymus canadensis</i>) Facultative upland Hall's panic (<i>Panicum hallii</i> var. <i>hallii</i>) Facultative upland *Japanese brome (<i>Bromus japonicus</i>) Upland Switch grass (<i>Panicum virgatum</i>) Facultative Texas wintergrass (<i>Nasella leuchotricha</i>) Upland <i>Total Grasses</i>	5 (1.0) 18 (2.5) 34 (4.7) 7 (1.0) 3 (< 1.0) 21 (2.9) 4 (1.0) 92 (13.1)
Grasslike Gotthilf Muhlenenberg's caric-sedge (Carex muhlenbergii var. muhlenbergii) Upland William Emory's caric sedge (Carex emoryi) Obligate Unknown sedge Total Grasslike	1 (< 1.0) 135 (18.7) 1 (< 1.0) 137 (18.7)
*Catchweed bedstraw (Galium aparine) Facultative upland *Common sow-thistle (Sonchus oleraceus) Upland Creeping ladies' sorrel (Oxalis corniculata) Facultative upland Dock (Rumex sp.) Old-man's-beard (Clematis drummondii) Upland Smartweed (Polygonum sp.) Spiny-aster (Chloracantha spinosa) Facultative wetland Unknown composite Total Forbs	7 (1.0) 4 (1.0) 19 (2.6) 3 (< 1.0) 2 (< 1.0) 2 (< 1.0) 120 (16.7) 3 (< 1.0) 160 (21.3)
Shrubs/lianas Saw Greenbriar (Smilax bona-nox) Facultative upland Total Shrubs	13 (1.8) 13 (1.8)
Trees American elm (Ulmus americana) Facultative Cedar elm (Ulmus crassifolia) Facultative Green ash (Fraxinus pennsylvanica) Facultative Total Trees	8 (1.0) 34 (4.7) 5 (1.0) 47 (6.7)
Bare ground	270 (37.5)
Total Hits	719 (99.1)

Of the herbaceous species, 75% were native and 25% were introduced (Table 2). Native perennial grasses comprised much of the herbaceous vegetation in the near-riparian zone and were dominated by Canada wildrye, switch grass (*Panicum virgatum*), and broadleaf woodoats (*Chasmanthium latifolium*). Four forbs were introduced but not common with Spiny-aster (*Chloracantha spinosa*), a native forb, was more abundant than other forbs (Table 2). Most herbaceous species had a wetland indicator status of upland or facultative upland (Table 2). Spiny-aster was the only facultative wetland species (Table 2). There was some regeneration of woody vegetation as evidenced by 6.7% of total trees being < 1.0 cm in diameter (Table 2).

Table 3. Number of samples and percentages of beaver damage in the near-riparian zone as compared to the bottomland (Nelson et al. 2018) of the Colorado River at Timberlake Ranch.

Beaver damaged woody vegetation	Bottomland (%)	Near-riparian region (%)
Cedar elm (Ulmus crassifolia)	57 (67.1)	3 (75.0)
Texas persimmon (Diospyros texana)	13 (15.3)	0 (0.0)
Sugarberry (Celtis laevigata)	12 (14.1)	0.0(0.0)
Eastern Cottonwood (Populus deltoides)	2 (2.4)	0.0(0.0)
Green ash (Fraxinus pennsylvanica)	1 (1.2)	1 (25.0)

The little beaver damage surveyed was greatest on cedar elms in the near-riparian area, with 75% of damage occurring on only three trees (Table 3). More damage occurred in the adjacent bottomland forest. Richness, Evenness, and Shannon Diversity in the Texas Colorado River near-riparian zone was much less when compared to the creeks of East Texas and the West Cross Timbers were (Table 4).

Table 4. Richness, Evenness, and Shannon Diversity in the Texas Colorado River near-riparian compared to that of other sites reported in the literature. The abbreviation "NR" indicates the statistic was not reported.

	Near-riparian at Timberlake Biological Station	Adjacent Bottomland (Nelson et al. 2018)	Bosque River Bottomland (Rosiere et al. 2013)	Spring Creek Bottomland (Nixon et al. 1991)	Spring Creek Near-Riparian (Nixon et al. 1991)
Woody Richness > 1.0 cm	5	13	17	32	29
Richness < 1.0 cm	22	40	30	NR	NR
Woody Evenness > 1.0 cm	0.70	0.59	0.77	NR	NR
Evenness < 1.0 cm	0.70	0.66	0.66	NR	NR
Woody > 1.0 cm Shannon Diversity	1.12	1.51	2.18	3.60	3.40
< 1.0 cm Shannon Diversity	2.16	2.42	2.26	NR	NR

DISCUSSION

Quantitative data for woody and herbaceous vegetation in near riparian zones of the Lampasas Cut Plain, including nonnative species, were provided for the first time. The near-riparian forest was comprised of three vegetational layers: 1) upper canopy of dominant trees including mostly green ash, 2) under canopy of lianas, including saw greenbriar and Virginia creeper (*Parthenocissus quinquefolia*) as well as 3) an

herbaceous zone of grasses, sedges, as well as both annual and perennial forbs, which included Canada wildrye, switch grass, and William Emory's caric sedge (*Carex emoryi*). The dominant forb was Spinyaster. The near-riparian community had a depauperate species composition when compared to a Creekside community in the Blackland Prairie ecoregion (Nixon et al. 1991).

Nothing has been published regarding woody vegetation along the near-riparian region of the Colorado River ion Texas. Nixon et al. (1991) found that sugarberry, elms, and ashes were the most important tree species in the near-riparian of Spring Creek to the north and east of TBS. At TBS, green ash dominated the near riparian instead of the more even distribution of several trees reported for Spring Creek. Although green ash dominated, sugarberry, American elm, and cedar elm, occurred in the near-riparian region (Table 1). 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 whitetail deer (*Odocoileus virginicus*). In our sampling quadrats, sugarberry and elm trees had 6.7% regeneration (Table 2), which was greater than in the adjacent bottomland (Nelson et al. 2018).

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 whitetail deer and was one of the first trees to grow back in abandoned fields adjacent to or replacing bottomlands. Green ash was the 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 near-riparian region of the Colorado River.

There were no shrubs or small trees sampled in the near-riparian. Two lianas were sampled in relatively small amounts. Virginia creeper had stem diameters > 1.0 cm and was infrequent (Table 1), but is a common browse species (Linex 2014). Saw greenbrier, which had 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 at the study site but these were not sampled, 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 (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 sampled in the near-riparian. Density and dispersion of trees combined with the small numbers 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 the near-riparian of the Colorado River were similar to those reported for bottomland forests of the West Cross Timbers in Texas (Rosiere et al. 2013; Nelson et al. 2018). Nixon et al. (1991) reported more shrubs for a creek forest in the Blackland Prairie ecoregion, but most of these shrubs, other than lianas, were absent from the forest adjacent to the Colorado River. This could be due to extensive grazing and browsing by herbivores.

Canada wildrye, switchgrass, and broadleaf woodoats were the most common grasses in the understory (Table 2). 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), whereas Canada wildrye was the most common grass in the understory at TBS in the floodplain forest (Nelson et al. 2018). Broadleaf woodoats are reported to stabilize soils on steep banks (Jones-Lewey 2016), and to be grazed as well as browsed (Linex 2014). 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 whitetail deer when young but can become susceptible to overgrazing (Linex 2014; Jones-Lewey 2016). Switchgrass helps to stabilize the dynamic erosional nature of the near-riparian (Linex 2014). The most common sedge was William Emory's caric sedge, which is an obligate wetland species, and may indicate negative changes in hydrology when reduced or absent (Jones-Lewey 2016). Because of reduced hydrology due to upstream damming, its importance in the near-riparian community may become reduced.

TPWD (2012) listed Bermuda grass (*Cynodon dactylon*), as a nonnative species that could be problematic in the Colorado River in the Lampasas Cut Plain. There were two introduced grasses with Bermuda grass being the most common on the Colorado River and Japanese brome being less common (Table 2). However, both were 1.0% or less of the grasses sampled in the near-riparian region. Bermuda grass, which comprised 1% 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 whitetail deer and is known to survive saturation by flooding for up to three weeks (Linex 2014).

Spiny-aster was a facultative wetland species that was the most common forb in the near-riparaian. Its rhizomes help stabilize river banks and young plants are eaten by whitetail deer and cattle (Linex 2014). Creeping ladies' sorrel (*Oxalis corniculata*) was the second most common forb sampled and occurs after disturbance (Diggs et al. 1999), which often occurs in the near-riparian of the Colorado River at TBS.

The only introduced forbs in the near-riparian Colorado River were catchweed bedstraw (*Galium aparine*) and common sow thistle (*Sonchus oleraceus*), which both occur in disturbed areas (Diggs et al. 1999). In the near-riparian of the Colorado River, these two introduced forbs were sampled in disturbed areas caused by cattle.

We concluded that herbivory is likely affecting regeneration of woody species and perennial herbs in the near-riparian of the Colorado River. 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 ecosystem (Townsend and Butler 1996; Gibson and Olden 2014; Karklins 2017). Beaver eat bark and leaves of many shrub and tree species, but Eastern 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 Eastern cottonwoods in the near-riparian of the Colorado River may be due to heavy grazing by cattle, browsing by whitetail deer, and large numbers of American beaver, or lack of bottomland flooding. Willow and Eastern cottonwood provide good browse and is often heavily used by cattle and whitetail deer (Linex 2014). Additional investigations into the role of beaver in the near-riparian of the Colorado River 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 and near-riparian 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, which could be a reason that green ash is more dominant in the near-riparian of the Colorado River.

Feral pigs are considered detrimental to Texas ecosystems (TPWD 2012) and 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). 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 near-riparian of the Colorado River sampled, there were few to no ephemeral wetlands and our data suggested that herbivory by cattle, whitetail 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 river ecosystems 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 Colorado River near-riparian 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). The Colorado River near-riparian was not dominated by wetland species. This stretch of the Colorado River was mostly facultative upland and upland species with the only obligate and facultative wetland species present in the Colorado River being William Emory's caric sedge and Spiny-aster, respectively.

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 and near-riparian areas are dynamic, alternating between flooding and drought cycles. 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 but also due to high-levels of herbivory. There is stabilizing vegetation in the near-riparian region, but it is disproportionately upland plants with wetland plants being less common. 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 TBS study site. It had higher diversity in every category when compared to the near-riparian of the Colorado River. There were few seedlings in the near-riparian of the Colorado River and 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. (1991) reported mean Shannon-Weiner diversity for trees (>1 cm diameter) from Spring Creek as 3.40 and richness was 32. This was higher Shannon-Weiner 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 et al. (1990).

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