SANDSAGE PRAIRIE: FLORISTICS, STRUCTURE, AND DYNAMICS OF A GREAT PLAINS PLANT COMMUNITY

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ABSTRACT

Sandsage prairie is a shrub-steppe ecological association unique to the Great Plains of North America in which sand sagebrush, *Artemisia filifolia,* is the dominant and diagnostic element. This paper presents the first comprehensive account of the floristics, community structure, and vegetation dynamics of sandsage prairie throughout its distribution. Sandsage prairie occurs in discontinuous tracts throughout western parts of the central and southern Great Plains in association with dune fields and other areas of sand habitat. The most conspicuous element of the vegetation is shrub-steppe dominated by *Artemisia filifolia* with a moderate to dense herbaceous layer dominated by perennial grasses. The relative density of *Artemisia filifolia* canopy cover in the landscape can range from 10% to 50% and is influenced by topographic gradient, climatic variability, fire history, grazing history, and past range management practices. Occurring in mosaic with the shrub-steppe component of sandsage prairie are intergrading but distinct assemblages of herbaceous species tied to varying degrees of disturbance and stabilization within the dune field. A total of 119 plant taxa in 33 families are characteristic of sandsage prairie in the Great Plains, with Poaceae, Asteraceae, Fabaceae, Euphorbiaceae, and Onagraceae the largest families (in descending order). There is a pronounced north-south gradient to the associated flora, with 34 species (29% of the total) being restricted to or most prevalent in either northern or southern stands of sandsage prairie. Sandsage prairie occurs in highly dynamic habitat subject to a host of natural disturbance factors and as a consequence exhibits a high level of heterogeneity in community structure with frequent shifts in species composition and dominance.

RESUMEN

La pradera de artemisia es una asociación ecológica de estepa arbustiva única de las Grandes Llanuras de Norteamérica en la que *Artemisia filifolia* es el elemento dominante y diagnóstico. Este artículo presenta el primer informe complete de la florística, estructura de la comunidad, y dinámica de la vegetación de la pradera de artemisia en toda su distribución. La pradera de Artemisia aparece en extensiones discontinuas en la parte occidental del centro y sur de las Grandes Llanuras en asociación con campos de dunas y otras áreas de hábitat arenoso. El elemento más visible de la vegetación es el matorral dominado por *Artemisia filifolia* con un estrato herbáceo de moderado a denso dominado por gramíneas perennes. La densidad relativa de la cubierta de *Artemisia filifolia* en el paisaje varía del 10% al 50% y está influenciado por el gradiente topográfico, variabilidad climática, fuego histórico, pastoreo anterior, y prácticas anteriores de manejo. Intercalada en el mosaico del componente de matorral de artemisia existen praderas en las que se intergradan distintos conjuntos de especies herbáceas ligadas a grados variables de perturbación y estabilización en el campo de dunas. Un total de 119 taxa vegetales de 33 familias son característicos de la pradera de artemisia en las Grandes Llanuras, con Poaceae, Asteraceae, Fabaceae, Euphorbiaceae, y Onagraceae como las mayores familias (en orden descendente). Hay un gradiente pronunciado norte-sur en la flora asociada, con 34 especies (29% del total) restringidas a más predominantes en las posiciones norte o sur de la pradera de artemisia. Esta pradera está en un hábitat muy dinámico sujeto a tener factores de perturbación natural y como consecuencia exhibe un nivel alto de heterogeneidad en la estructura de la comunidad con cambios frecuentes en la composición de especies y dominancia.

INTRODUCTION

"At evening we encamped within a few miles of the main Republican [River], on a little creek, where the air was fragrant with the perfume of *artemisia filifolia*. … Bare sand hills everywhere surrounded us in the undulating ground along which we were moving; and the plants peculiar to a sand soil made their appearance in abundance."

—*John C. Fremont,* 21 June 1843, encountering sandsage prairie in present-day northeastern Colorado

Extensive dune fields are a significant feature of the Great Plains of North America (Muhs & Holliday 1995). The largest of these is the Nebraska Sandhills which at 49,987 sq km (19,300 sq mi) is the largest dune field in the Western Hemisphere. These areas of sandy habitat support unique biotic assemblages which are classified by NatureServe (2019) into two main ecological systems—Western Great Plains Sand Prairie and Western

J. Bot. Res. Inst. Texas 13(1): 253 – 278. 2019

Great Plains Sandhills Steppe. The latter is distinguished by a strong shrub component and is comprised of *Quercus havardii*-dominated sand shinnery and *Artemisia filifolia*-dominated sandsage prairie.

These three associations—sand prairie, sand shinnery, and sandsage prairie—are the primary expressions of vegetation occupying sand habitat in the western Great Plains (Fig. 1). The flora and ecology of sand prairie is well-documented by a long history of studies in the Nebraska Sandhills (see Bleed & Flowerday (1990) and Johnsgard (1995) for overviews). Likewise, a significant body of literature exists for sand shinnery (see Peterson & Boyd (1998) and Dhillion & Mills (1999) for overviews).

In contrast, knowledge of the biology and ecology of sandsage prairie is deficient and fragmented. While useful information can be found in state-level botanical, ecological, range management, and wildlife management literature, no comprehensive description of this unique Great Plains plant community exists. Such knowledge is critically needed given the imperiled status of sandsage prairie throughout its range (*Artemisia filifolia / Andropogon hallii* Shrubland is ranked G3, globally vulnerable to extinction, by NatureServe) and in most of the eight states in which it occurs. This paper presents the first account of the floristics, structure, and dynamics of sandsage prairie throughout its distribution.

Historical Background

The first recorded scientific encounters with sandsage prairie came in 1820 as botanist and physician Edwin James traveled with Major Stephen Long's Expedition westward across present-day Nebraska to the Rocky Mountains in Colorado, then south into New Mexico and back east through the Texas Panhandle and across Oklahoma (Goodman & Lawson 1995; Evans 1997). James collected the type specimen of *Artemisia filifolia* Torr. somewhere along the Platte or South Platte River, the label on the holotype at NY stating "Arid plains of the Platte." Kaul et al. (2011) place the type locality along the South Platte River near present-day Roscoe in Keith County, Nebraska, which the expedition traversed between June 23 and 25. In his account of the expedition for these days, James (1823) noted "extensive districts covered entirely with loose and fine sand" and the abundance of "several types of wormwood, (Artemisia)." The expedition again encountered sandsage prairie in August as they followed the Canadian River eastward from its junction with Ute Creek in northeastern New Mexico across the Texas Panhandle (Goodman & Lawson 1995). As described by James, "the surface of the country is mostly of a loose sand, bearing tufts of wormwood [*Artemisia*]."

James' encounters with sandsage prairie on the Platte River and Canadian River represent the northern and southern edges of its distribution in the Great Plains. Early reports of this plant community from the interior portions of its range include that of John C. Fremont (1845), who in 1843 traversed sandy habitat on the upper reaches of the Republican River watershed in northeastern Colorado "where the air was fragrant with the perfume of *artemisia filifolia*," and Friedrich Adolph Wislizenus (1848) who in 1846 encountered sandhills along the Cimarron River in southwestern Kansas where "different species of artemisia…cover the whole plain."

The earliest published accounts of the floristic composition of habitat supporting sandsage prairie came at the end of the nineteenth century. Carleton (1892) described plants characteristic of "sandy regions" of the Oklahoma Panhandle and adjacent parts of Kansas and Texas based on his travels through the region in 1891. Hitchcock (1896) enumerated plants collected by C.H. Thompson in southwestern Kansas in 1893 and listed species collected in the sandhills along the Arkansas and Cimarron rivers. Hitchcock (1898) subsequently published a paper on the "Ecological Plant Geography of Kansas" in which he described "Sand-hill Vegetation." The first recognition of a plant community in which *Artemisia filifolia* is the diagnostic element came in 1900 when Pound and Clements described an *Artemisia filifolia* Formation in *Phytogeography of Nebraska*.

The most detailed descriptive studies of the flora and ecology of sandsage prairie have been made in eastern Colorado. In an investigation of natural vegetation as an indicator of the capabilities of land for crop production in the Great Plains, Shantz (1911) studied sandsage prairie in the Wray Dune Field in the northeastern part of the state. Shantz's study sites were revisited in the 1980s by McGinnies et al. (1991). Weaver (1919) included an analysis of 14 sandsage prairie species in his massive publication (171 pages) on the ecological relations of roots, his findings based on field work in the Black Squirrel Dune Field in east-central Colorado.

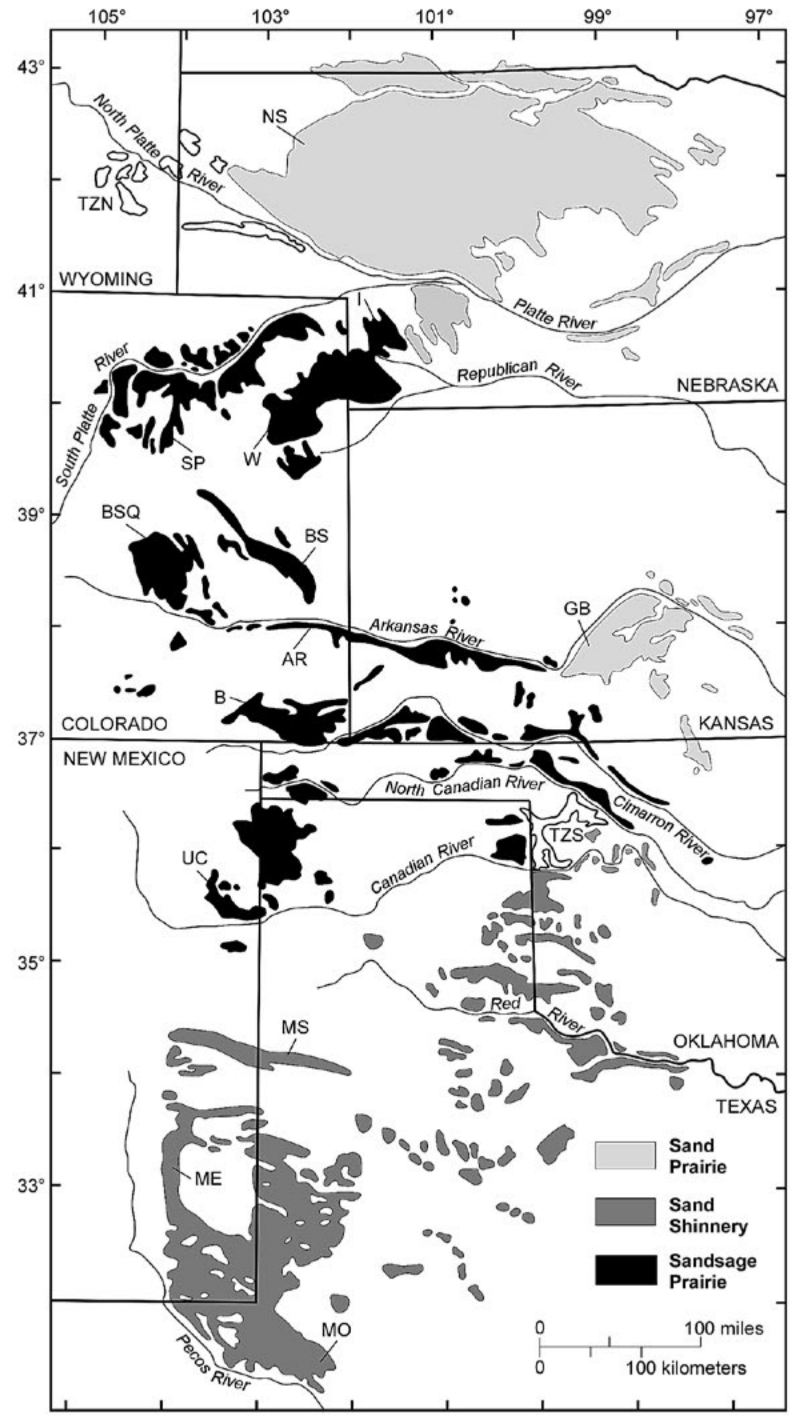

Fig. 1. Map showing the distribution of sandsage prairie in the Great Plains, USA. Dune fields: **AR,** Arkansas River; **B,** Baca; **BS,** Big Sandy; **BSQ,** Black Squirrel Creek; **GB,** Great Bend; **I,** Imperial; **ME,** Mescalero; **MO,** Monahans; **MS,** Muleshoe; **NS,** Nebraska Sandhills; **SP,** South Platte; **UC,** Ute Creek; W, Wray. **TZN** = Transition Zone North. **TZS** = Transition Zone South. Dune field locations and names compiled from Muhs & Holliday (1995, 2001) and Schmeisser et al. (2010).

Ramaley's (1939) foundational study of sandsage prairie vegetation was based on work carried out in the South Platte Dune Field in northeastern Colorado. Daley's (1972) important master's thesis, "The Native Sand Sage Prairie of Eastern Colorado," was based on research in the South Platte, Wray, Big Sandy, and Baca dune fields. Kelso et al. (2007) studied patterns of rarity, disjunction, and succession in the dune communities in the Black Squirrel Dune Field. See Figure 1 for the locations of these dune fields.

Considerable literature exists on the impacts of grazing intensity, prescribed fire, and other rangeland management practices on sandsage prairie, with the aim of sustaining beef cattle production while maintaining or improving plant and soil resources. A number of such studies have been carried out in northwestern Oklahoma at the Hal and Fern Cooper Wildlife Management Area and the Southern Plains Range Research Station (Oklahoma State University) and in northeastern Colorado at the Eastern Colorado Research Center (Colorado State University). While focused on rangeland management, these studies yield helpful insights into the structure and dynamics of sandsage prairie. Similarly, studies aimed at understanding the ecology and conservation needs of the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*), an at-risk species, have contributed to better understanding of and appreciation for sandsage prairie.

To date, no comprehensive description of the floristic composition and structure of sandsage prairie throughout its range has been published, although considerable information exists in state-level botanical, ecological, range management, and wildlife management literature (Table 1).

Ecological Classification and Nomenclature

The shrub *Artemisia filifolia* is the dominant and diagnostic element in the flora of sandsage prairie. While sandsage prairie is an ecological association of the Great Plains, the range of *Artemisia filifolia* extends considerably beyond—southward into northern Mexico (Chihuahuan Desert) and westward across New Mexico into Arizona, southern Utah, and southeastern Nevada (Colorado Plateau and Great Basin). As in the Great Plains, *Artemisia filifolia* is often a dominant shrub of sandy habitat in these regions and is the principle indicator species of a number of plant communities, but the associated shrubs and herbaceous species in these communities have strong desert affinities (Brown 1994; MacMahon 2000) and lack the co-dominant graminoid component that characterizes sandsage prairie.

A variety of technical and nontechnical names have been used to designate *Artemisia filifolia* associations in the Great Plains. The fundamental issue regarding ecological classification is whether these associations should be recognized as shrubland or grassland. NatureServe (2019) treats the *Artemisia filifolia* / graminoid associations in the Great Plains as shrubland, as do vegetation classification systems for Colorado (CNHP 2005), Kansas (Lauver et al. 1999), Oklahoma (Hoagland 2000), and Texas (Elliott et al. 2009–2014). However, this vegetation is more accurately termed shrub-steppe, as are the various types of *Artemisia*-dominated associations in western North America where the herbaceous layer has a moderate to dense canopy dominated by perennial graminoids (West & Young 2000). The technical name *Artemisia filifolia* steppe is here recommended.

Of the various nontechnical names used for *Artemisia filifolia* associations in the Great Plains (Table 2), "sandsage prairie" is used here since it is widely published in botanical, ecological, range management, and wildlife management literature and is the most often used colloquial name for this plant community.

METHODS

The study was based on direct reconnaissance of sandsage prairie occurrences by the author coupled with review of published literature. Field observations were made over several years throughout the range of sandsage prairie in the Great Plains including major dune fields and areas of sand habitat in Colorado, Kansas, Nebraska, New Mexico, Oklahoma, Texas, and Wyoming. Sandsage prairie occurrences were located with guidance from state-level vegetation maps, herbarium specimen data of diagnostic species, county soil maps, and published literature.

Table 1. State-level literature providing ecological and floristic information on sandsage prairie.

Colorado:	Shantz 1911; Weaver 1919; Ramaley 1939; Costello 1944; Rogers 1953; Daley 1972; Sims et al. 1976; Davis & Bonham 1979; Shaw et al. 1989; McGinnies et al. 1991; Clark 1996; Rondeau 2003; Hazlett 2004; Kelso et al. 2007; Neid et al. 2007; Kuhn et al. 2011; Rondeau et al. 2011; Rondeau 2013; Rondeau et al. 2018
Kansas:	Hitchcock 1896, 1898; Cornelius & Atkins 1946; Simonett 1960; Richards 1968; Kuchler 1974; Rush et al. 1982; Sexson 1983; Hulett et al. 1988; Lauver et al. 1999; VanNimwegen et al. 2008; Kuhn et al. 2011
Nebraska:	Pound & Clements 1900; Farrar 1993a, 1993b; Kaul & Rolfsmeier 1993; Rolfsmeier & Steinauer 2010; Locklear 2017b
New Mexico:	Heerwagen 1956; Dick-Peddie 1993; Griffith et al. 2006; Hazlett et al. 2009
Oklahoma:	Bruner 1931; Blair & Hubbell 1938; Duck & Fletcher 1944; Sherwood & Risser 1980; Collins et al. 1987; Sims et al. 1987; Hoagland 2000; Vermeier et al. 2001; Cordova et al. 2005; Barber 2008; Hoagland 2008; Hazlett et al. 2009; Doxon 2011; Winter et al. 2011a, 2011b; Buthod & Hoagland 2015
South Dakota:	Von Loh et al. 1999
Texas:	Allred 1956; Jackson 1965; Rowell 1967; Griffith et al. 2004; Nesom & O'Kennon 2008; Hazlett et al. 2009; Elliott et al. 2009-2014
Wyoming:	Maxwell & Brown 1968

Table 2. Colloquial names for *Artemisia filifolia* associations in the Great Plains.

Sand-Sage Community	Ramaley 1939
Sandsage-Grassland	Duck & Fletcher 1944
Sandsage-Bluestem Prairie	Kuchler 1964
Sandsage Prairie	Kuchler 1974
Xeric Sandhills Prairie	Launchbaugh & Owensby 1978
Sandsage Mixed-Grass Prairie	Kaul & Rolfsmeier 1993
Sand Sagebrush-Mixed Prairie	Berg 1994
Sand Sagebrush Prairie	Gillen & Sims 2006
Sand Sagebrush Shrubland	Winter et al. 2011

ECOLOGY

Distribution

Sandsage prairie occurs in discontinuous tracts throughout western parts of the central and southern Great Plains, the total range extending approximately 600 km (375 mi) from north to south (Fig. 1). Kuchler (1985) mapped major occurrences of sandsage prairie in southwestern Nebraska, eastern Colorado, southwestern Kansas, and western Oklahoma. Significant tracts also occur in northeastern New Mexico and the upper part of the Texas Panhandle. Detailed state-level mapping of sandsage prairie is available for Colorado (Rondeau et al. 2011), Kansas (Kuchler 1974), Nebraska (Kaul & Rolfsmeier 1993), Oklahoma (Hoagland 2008), and Texas (Elliott et al. 2009–2014).

The most extensive tracts of sandsage prairie are associated with major dune fields and sand areas of the Great Plains (Fig. 1), the largest being the South Platte Dune Field of northeastern Colorado (7500 sq km; 2896 sq mi), the Wray Dune Field of northeastern Colorado and southwestern Nebraska (6680 sq km; 2579 sq mi), and the Black Squirrel Dune Field of east-central Colorado (3570 sq km; 1378 sq mi) (area estimates per Madole 1995). Sandsage prairie is the dominant vegetation of these dune fields.

In the southern part of its geographical range in western Oklahoma and the adjacent upper Texas Panhandle, stands of sandsage prairie occur in mosaic with sand shinnery. Within this transition zone, some areas of the landscape are dominated by sand shinnery with smaller inclusions of *Artemisia filifolia* while in other areas sandsage prairie dominates. In areas of co-occurrence, sand shinnery mostly occupies higher topographic positions such as hillcrests. In western Oklahoma, elements of Cross Timbers oak woodland vegetation also occur in some of these mosaic communities (Cordova et al. 2005). This area is indicated as Transition Zone South (TZS) in Figure 1.

A second area of transition occurs at the northern limits of the range of sandsage prairie, indicated as Transition Zone North (TZN) in Figure 1. Tracts of sandsage prairie do not occur within the Nebraska

Sandhills of north-central Nebraska and adjacent South Dakota, but stands of *Artemisia filifolia* do occur in belts along the edges of the western half of this massive dune field. Kaul & Rolfsmeier (1993) mapped this vegetation as "Sand Hills borders mixed-grass prairie" to distinguish it from the "Sandsage mixed-grass prairie" of the dune fields of southwestern Nebraska, noting the former combined elements of sand prairie, sandsage prairie, and western Great Plains mixed grass prairie. In eastern Wyoming, stands of *Artemisia filifolia* sometimes occur in mosaic with shrub-steppe dominated by *Artemisia cana*, which becomes the prevailing vegetation of well-drained coarse-textured soils in the northern Great Plains (Miller et al. 2011). The physiognomy of *Artemisia cana* steppe is very similar to that of sandsage prairie with *Bouteloua gracilis* and *Calamovilfa longifolia* the co-dominant grasses (Thilenius et al 1995).

Berg (1994) estimated that "sand sagebrush-mixed prairie" covered approximately 12 million acres (5 million hectares) in the Great Plains. This is nearly equivalent to the estimated 12.75 million acres of sand prairie rangeland in the Nebraska Sandhills. Colorado appears to have the most sandsage prairie of any state, estimated at nearly 2 million acres (809,000 hectares) with more than 80% of this on private lands (Rondeau et al. 2011).

Physiography

The geographical distribution of sandsage prairie is mostly limited to the High Plains, Colorado Piedmont, and Plains Border sections of the Great Plains Physiographic Province (Fenneman 1931). The High Plains section extends from western Nebraska and southeastern Wyoming into eastern New Mexico and the Texas Panhandle. The surface geology of the High Plains section is influenced by Neogene Period non-marine deposits of the Ogallala Group (Miocene to earliest Pliocene). The Colorado Piedmont and Plains Border sections lie to the west and east (respectively) of the High Plains. The major streams of these regions have excavated into and largely removed the Ogallala deposits of the High Plains, exposing older geological formations beneath. Elevations within the overall distribution of sandsage prairie range from 447 m (1476 ft) on the east (Cimarron River in Woods County, Oklahoma) to 1690 m (5545 ft.) on the west (Chico Basin in El Paso County, Colorado), but elevations of most occurrences in the heart of the overall distribution range from 915 to 1220 m (3000–4000 ft).

As noted above, the largest tracts of sandsage prairie are associated with major dune fields and sand areas of the Great Plains (Fig. 1). An extensive literature exists concerning the origin, geomorphology, stratigraphy, and dynamics of Great Plains dune fields (Simonett 1960; Madole 1995; Muhs & Holliday 1995; Muhs et al. 1996; Cordova et al. 2005; Madole et al. 2005; Schmeisser et al. 2010). The topography of these dune fields is often complex and varies from level plains to low rolling hills with relatively flat crests to choppy sandhills with steep sides. Local relief can range from a few meters to as much as 60 m (200 ft) and slope from 0 to 60 percent.

In addition to major dune fields, stands of sandsage prairie are associated with relatively flat sandy terraces and benches immediately adjacent to and above riparian channels of streams and creeks. In the White River Badlands of South Dakota, stands of *Artemisia filifolia* are associated with unique eolian cliff-top sand deposits along escarpment crests (Rawling et al 2003). Relatively small bands of *Artemisia filifolia* can also be associated with pockets of coarse-textured soils weathered from outcroppings of sandstone bedrock.

Climate

The climate of the region in which sandsage prairie occurs is essentially the same as that of shortgrass steppe region as described by Pielke & Doesken (2008) and can be summarized as semi-arid with a strong seasonal cycle, large and rapid temperature changes, frequent and persisting dry weather, winds that are moderate to strong year round, and occasional very vigorous storms. Precipitation is the single most important climatic variable controlling plant community ecology in the western Great Plains.

The average annual total precipitation within the overall distribution of sandsage prairie ranges from 635 mm (25 in) on the east (Waynoka in Woods County, Oklahoma) to 305 mm (12 in) on the west (Chico Basin in El Paso County, Colorado), with occurrences in the heart of the overall distribution receiving on average from 381 to 457 mm (15–18 in) of total annual precipitation. Within these averages, seasonal precipitation amounts can and do vary greatly from year to year. At an agricultural research station near Akron in northeastern Colorado, average annual precipitation was 419 mm (16.5 in) for the period 1908 to 1985, but ranged from a low of 254 mm (10 in) in 1939 to a high of 686 mm (27 in) in 1946 (McGinnies et al. 1991). Growing season (April-September) precipitation contributes 70% to 82% of the annual moisture across the region (Pielke & Doesken 2008).

Periodic drought is a recurrent local and regional event throughout the distribution of sandsage prairie. The extended drought of the 1930s hit hardest in the "Dust Bowl" region of the Great Plains, with the most extreme drought occurring in southeastern Colorado the adjacent parts of Kansas, New Mexico, and Oklahoma, and the upper Texas Panhandle (Worster 1979) where significant tracts of sandsage prairie occur. Rondeau et al. (2018) studied the effects of repeated severe drought on grassland communities including sandsage prairie in east-central Colorado, where total annual precipitation in 2002 (< 100 mm; 4in) and 2012 (127 mm; 5 in) was even lower than the driest years of the 1930s. They concluded that *Artemisia filifolia* may be at the limits of its drought tolerance range in southeastern Colorado, where average annual total precipitation is 305 mm (12 in).

Soils

Soils supporting sandsage prairie are mostly formed in sandy eolian parent material and are very deep, excessively drained to well drained, and rapidly to moderately permeable. Soil texture classes range from sand to fine sand to loamy fine sand to fine sandy loam. Sandsage prairie occurs in association with a number of different soil series throughout its distribution in the Great Plains, but northern stands (Nebraska and northeastern Colorado) are strongly associated with Valent series soils (sands) while the Tivoli series (fine sands) is a predominant soil association of southern stands (Kansas, New Mexico, Oklahoma, and Texas).

In habitat supporting sandsage prairie, rainfall infiltrates rapidly and percolates deeply into the coarse-textured sandy soils with little or no runoff. Evaporation quickly dries out the surface sand but only to a slight depth, leaving a layer of dry sand that reduces further evaporation. Below this surface mulch of 2.5–5 cm (1–2 in), the soil is usually well supplied with moisture (Schantz 1911; Weaver 1919, 1958). As noted by Weaver (1958), "The efficiency of sand in absorbing rainfall without loss by runoff and in almost entirely preventing evaporation is the compensating factor which permits the growth of tall grasses." The generally sparse vegetation of sandsage prairie limits water losses by transpiration, further enhancing the moisture holding capacity of sandy soil. Finally, unlike the fine-textured soils that support shortgrass prairie, soil moisture is not held as tightly in coarse-textured sandy soils. All of these factors enable sandhills habitat to support taller, more mesic-adapted grasses like *Andropogon hallii* and *Calamovilfa longifolia* in an otherwise semi-arid climate.

In his studies of the root systems of plants in sandhills in east-central Colorado, Weaver (1919) observed that 18 of the 19 species examined had their main root development in the first 60–90 cm (2–3 ft) and that the roots of eight species were entirely or nearly confined to the first 60 cm (2 ft), enabling these plants to intercept moisture before it percolates down through the sandy soil. Many of the dominant grasses and forbs of sandsage prairie also occur in the Nebraska Sandhills and diagrams of the root systems of these species show similar morphologies (Tolstead 1942; Weaver 1958; Weaver & Albertson 1956).

Soil texture and topography are closely related in sandhills habitat, resulting in topoedaphic variability and local topoedaphic patterns that influence plant community structure and composition, primarily through effects on spatial and temporal variation in soil moisture (Barnes et al. 1984). Studies in habitat supporting sandsage prairie have clearly demonstrate the relationship between topoedaphic variability and vegetation structure (Shantz 1911; Ramaley 1939; Hullet et al. 1988; McGinnies et al. 1991; Kelso et al. 2007; Winter et al. 2011a).

FLORISTICS OF SANDSAGE PRAIRIE

The Appendix provides an enumeration of plant taxa that are characteristic of sandsage prairie in the Great Plains of North America. The list is based on literature review and the author's field experience. It does not include all plants associated with sandsage prairie throughout its range, but those reported or observed to be dominant, diagnostic, frequent, or occurring regularly in sandsage prairie. It does not include species that occur in wetlands or other hydric habitat within the context of sandsage prairie vegetation. Exotic species that occur in degraded stands of sandsage prairie (e.g., *Bromus tectorum*) are also excluded from the list.

The flora of sandsage prairie consists of 119 taxa in 33 families. The largest families represented are Poaceae (27 species), Asteraceae (19 species), and Fabaceae (10 species). The next largest families (with six species each) are Euphorbiaceae and Onagraceae. Of the 119 plant taxa occurring in sandsage prairie, 34 (29%) are annuals, 10 (8%) biennials (that may also behave as annuals or short-lived perennials depending on environmental conditions), and 75 (63%) perennials (including four shrubs).

None of these species are strictly limited to sandsage prairie but instead also occur in other areas of sand habitat in the Great Plains, primarily sand prairie in the Nebraska Sandhills and sand shinnery in the southern Great Plains. Twenty-nine species associated with sandsage prairie (24% of the flora) are endemic to the Central Grassland of North America (Table 3) and four species are considered globally vulnerable to extinction (NatureServe rank of G3)—*Chenopodium cycloides*, *Dalea cylindriceps*, *Euphorbia carunculata*, and *Euphorbia strictior.*

Two other rare plant species are peripherally associated with sandsage prairie and therefore not included in the Appendix. The recently described *Evolvulus arenarius* (Harms 2014) is known from at least one occurrence in sandsage prairie (Hartley County, Texas) and is likely a species of conservation concern but has not yet been ranked. A species of dodder, *Cuscuta plattensis*, is associated with sandhill habitat in southeastern Wyoming where sandsage prairie is likely the dominant vegetation (Handley & Fertig 2002). Ranked G1 (critically imperiled) by NatureServe, the distribution and ecology of this species need further study.

The total range of sandsage prairie extends approximated 600 km (375 mi) from north to south (Fig. 1). Many graminoids, forbs, and shrubs are associated with sandsage prairie throughout this area. Others are restricted to or more prevalent in northern versus southern stands (Table 4). Eleven species are most strongly associated with northern stands and have floristic affinities with sand prairie vegetation of the Nebraska Sandhills (Pool 1914; Tolstead 1942; Rolfsmeier & Steinauer 2010) and dune vegetation in central Wyoming (Knight 1994; Heidel 2012). Twenty-three species are most strongly associated with southern stands and have floristic affinities with sand shinnery vegetation in Oklahoma, Texas, and New Mexico (Dick-Peddie 1993; Peterson & Boyd 1998; Powell & Worthington 2018). This north-south floristic gradient was first observed by Daley (1972) in his studies of sandsage prairie in eastern Colorado, with a zone of transition occurring in east-central Colorado. Such variation could warrant recognition of a northern and southern expression of sandsage prairie, much as Kuchler (1974) recognized for shortgrass prairie in Kansas.

STRUCTURE OF SANDSAGE PRAIRIE VEGETATION

Describing the structure of sandsage prairie vegetation is challenging. While the most visually conspicuous element in the landscape is shrub-steppe dominated by *Artemisia filifolia* (Fig. 2), any given occurrence of sandsage prairie is a spatially complex, patchy mosaic of intergrading assemblages of species tied to various degrees of disturbance and stabilization within the dune field. In the literature of sandsage prairie ecology, these assemblages have been referred to as associations (Shantz 1911), communities (Ramaley 1939; Hullett et al. 1988), vegetation types (McGinnies et al. 1991), and vegetation zones (Kelso et al. 2007). These assemblages are recognized here as sub-communities.

The Shrub-Steppe Matrix

Shrub-steppe dominated by *Artemisia filifolia* is the primary community of sandsage prairie and provides the matrix by which the sub-communities interface with the vegetation as a whole. It is characteristic of habitat in a late-intermediate stage of stabilization (Fig. 3) and is the equivalent of the "Sand-hills Mixed Association" of Shantz (1911) and the "Sand-Sage Community" of Ramaley (1939). Soils supporting this community have a higher percentage of fine particles than the soils of dune crests, blowouts, and other erosional habitat (Ramaley 1939; Kelso et al. 2007).

Artemisia filifolia is a much-branched shrub that grows 0.5–1 m (1.5–3 ft) tall and 30–60 cm (1–2 ft)

Table 3. Central Grassland endemic plants (per Locklear 2017a) that occur in association with sandsage prairie.

Argemone polyanthemos	*Dieteria canescens* var. *nebraskana*	*Mentzelia nuda*	*Phlox andicola*
Asclepias arenaria	*Dimorphocarpa candicans*	*Mimosa rupertiana*	*Polanisia jamesii*
Astragalus ceramicus var. *filiformis*	*Eriogonum annuum*	*Muhlenbergia pungens*	*Prunus pumila* var. *besseyi*
Chenopodium cycloides	*Euphorbia carunculata*	*Oenothera cinerea* var. *cinerea*	*Redfieldia flexuosa*
Croton texensis var. *texensis*	*Euphorbia strictior*	*Oenothera engelmannii*	*Yucca glauca*
Dalea arenicola	*Hymenopappus flavescens*	*Oenothera rhombipetala*	
Dalea lanata	*Ipomoea leptophylla*	*Oenother serrulata*	
Dalea villosa	*Linum berlanderi*	*Penstemon buckleyi*	

Table 4. Plant species restricted to or most prevalent in northern versus southern stands of sandsage prairie.

Northern	Southern	Southern (cont)	Southern (cont)
Calamovilfa longifolia	*Aphanostephus ramosissimus*	*Lorandersonia baileyi*	*Stillingia sylvatica*
Carex heliophila	*Aristida divaricata*	*Mimosa rupertiana*	
Cirsium canescens	*Calamovilfa gigantea*	*Oenothera cinerea*	
Dieteria canescens	*Dalea lanata*	*Oenothera engelmannii*	
Eriogonum effusum	*Dimorphocarpa candicans*	*Palafoxia rosea*	
Hesperostipa comata	*Euphorbia carunculata*	*Penstemon buckleyi*	
Muhlenbergia pungens	*Euphorbia strictior*	*Phyllanthus warnockii*	
Prunus pumila var. *besseyi*	*Gaillardia pulchella*	*Poa arachnifera*	
Penstemon angustifolius	*Hedyotis humifusa*	*Prunus angustifolia*	
Phlox andicola	*Hymenopappus flavescens*	*Psilostrophe villosa*	
Physaria ludoviciana	*Indigofera miniata*	*Sporobolus giganteus*	

across. The gray-green foliage is aromatic and individual leaves are long and slender (to 40 × 0.5 mm) and divided into threadlike segments. A diagram in Weaver's 1919 paper on the ecological relations of roots (reprinted in *Grasslands of the Great Plains* [Weaver & Albertson 1956]) shows the root system of a ten-year-old *Artemisia filifolia* shrub with a dense, well-branched network of roots in the upper 1 m (3 ft) of soil and a sparingly branched taproot extending 2.4 m (8 ft) below the surface, a morphology that both anchors the plant in the dynamic dune habitat and helps intercept moisture before it percolates down through the sandy soil.

There is no recognized standard for the amount or density of *Artemisia filifolia* canopy cover in the landscape that delineates vegetation as sandsage prairie. Ramaley (1939) observed about 10% canopy coverage by *Artemisia filifolia* in a large tract ("a number of square miles") of what he considered a "typical" sandsage community. In Nebraska, Rolfsmeier and Steinauer (2010) distinguished sandsage prairie as "any community in which sandsage represents a conspicuous part (>5% cover)." Vegetation classification systems for Kansas (Lauver et al. 1999) and Oklahoma (Hoagland 2000) treat sandsage prairie as a type of shrubland where *Artemisia filifolia* forms >25% canopy cover. In a 20 year study of the impacts of grazing intensity and precipitation in western Oklahoma sandsage prairie the average canopy cover of *Artemisia filifolia* was 38% (Gillen & Sims 2004).

In reality, the density of *Artemisia filifolia* in the landscape is influenced by a host of factors. In their study of sandsage prairie in southwestern Kansas, Hulett et al. (1988) found percent canopy cover by *Artemisia filifolia* differed along a topographic gradient, with 10% cover on "level sands," 21% on "dune sands," and 34% on "choppy sands." The relative density of *Artemisia filifolia* is also subject to climatic influences, fire history, and past rangeland management practices. These disturbance factors are discussed under Vegetation Dynamics.

The graminoid component of sandsage prairie typically has a canopy of taller grasses (1–2 m; 3–6 ft) intermixed with mid-height grasses (0.5–1 m; 1.5–3 ft) with an underlayer of short grasses and sedges. Grasses reported as principal components of sandsage prairie throughout the Great Plains are *Andropogon hallii*, *Sporobolus cryptandrus*, *Schizachyrium scoparium*, and *Bouteloua gracilis*, each of which have been recognized as co-dominant with *Artemisia filifiolia* in a particular part of the overall range of sandsage prairie (Table 5).

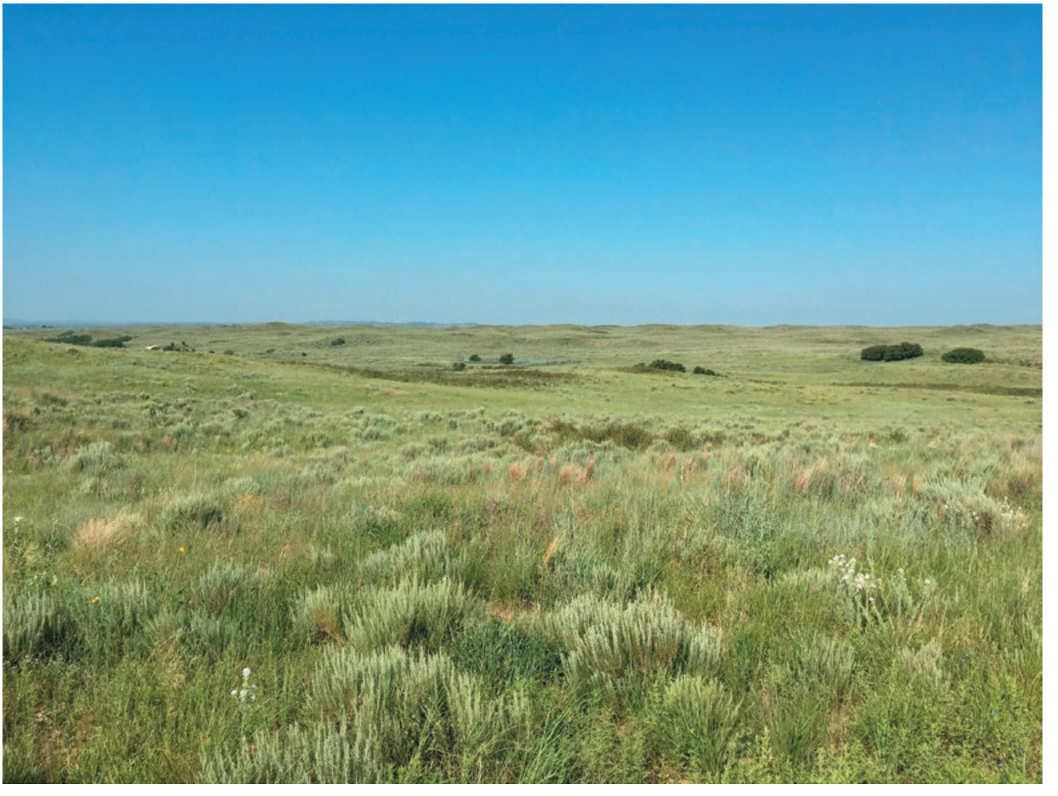

Fig. 2. Sandsage prairie, Hemphill County, Texas. Photo James H. Locklear.

Other widely occurring regular graminoid associates of sandsage prairie include *Aristida purpurea*, *Bouteloua hirsuta*, *Cyperus schweinitzii*, *Elymus elymoides*, *Eragrostis trichodes*, and *Vulpia octoflora*.

A number of other graminoids are of regional importance in sandsage prairie (Table 4). The cool-season *Hesperostipa comata* and *Carex heliophila* are major species in northern stands of sandsage prairie (northeastern Colorado and southwestern Nebraska) but diminish in importance to the south. The warm season grass *Calamovilfa longifolia* is a major species in northern stands but absent from southern stands where it is replaced by *Calamovilfa gigantea*.

Several variants of sandsage prairie have been recognized and distinguished by one or more co-dominant grass species (Table 5). Such descriptions of the diagnostic graminoid component of sandsage prairie should be qualified with the observation that the constituent species and their relative dominance can change locally over time due to year-to-year trends in precipitation and grazing history.

Similar to the graminoid component, many forbs are associated with sandsage prairie throughout the Great Plains while others are more regionally restricted (Table 4). Widespread sandsage prairie forbs include *Abronia fragrans*, *Commelina erecta*, *Croton texensis*, *Dalea villosa*, *Erigeron bellidiastrum*, *Eriogonum annuum*, *Helianthus petiolaris*, *Ipomoea leptophylla*, *Ipomopsis longifolia*, *Mentzelia nuda*, *Oenothera serrulata*, *Palafoxia sphacelata*, *Penstemon ambiguus*, and *Tradescantia occidentalis*. Southern stands of sandsage prairie have a greater diversity of forbs than do northern stands (Table 4).

A few shrubs are consistent components of sandsage prairie. *Yucca glauca* and *Rhus aromatica* var. *trilobata* occur throughout the range of sandsage prairie and in some occurrences are so abundant as to

Fig. 3. Sandsage prairie, Woodward County, Oklahoma. Prominent forbs include *Dimorphocarpa candicans, Helianthus petiolaris, Ipomoea leptophylla,* and *Oenothera rhombipetala.* Photo James H. Locklear.

co-dominate the shrub stratum. *Prunus pumila* var. *besseyi* is more prevalent in northern stands while *Prunus angustifolia* is limited to southern stands.

Open Sand and Blowout Sub-Community

A dune complex supporting sandsage prairie may have areas of highly disturbed habitat with open sand and little or no vegetation. Such habitat typically occurs on the crests and upper windward slopes of taller and steeper dunes. The most eroded sites are called blowouts, where sand is actively moving and there is little or no vegetation present. This habitat supports the Open Sand and Blowout sub-community, which is the equivalent of the "Blow-out Association" of Shantz (1911) and the "Loose Sand and Blow-Out Community" of Ramaley (1939).

Blowouts are irregular or conical craters formed when deep, loose sands are removed by swirling wind action of the prevailing winds, the sand carried from the windward side of the slope and deposited onto the leeward side (Fig. 4). The formation of blowouts has been well documented in the Nebraska Sandhills and the progression of species involved in re-vegetation of blowouts in northern stands of sandsage prairie is very similar to that observed in the Nebraska Sandhills (Rydberg 1895; Pound & Clements 1900; Pool 1914; Tolstead 1942; Stubbendieck et al. 1989). The size of blowouts in dune fields supporting sandsage prairie ranges from less than 15 m (50 ft) to over 600 m (2000 ft) in diameter and from a meter or two to as much as 30 m (100 ft) in depth (McGinnies et al. 1991).

Shantz was the first to describe blowouts in the context of sandsage prairie. Based on his observations in

Table 5. Recognized *Artemisia filifolia* associations in the Great Plains (per NatureServe unless noted).

Artemisia filifolia / Andropogon hallii
Artemisia filifolia / Bouteloua (*curtipendula, gracilis*)
Artemisia filifolia / Calamovilfa longifolia
Artemisia filifolia / Schizachyrium scoparium – Andropogon hallii
Artemisia filifolia / Sporobolus cryptandrus
Artemisia filifolia / Sporobolus cryptandrus – Schizachryium scoparium (Hoagland 2000)
Artemisia filifolia / Rhus trilobata
Artemisia filifolia / Yucca glauca (Shaw et al. 1989)

Fig. 4. Blowout in sandsage prairie, Perkins County, Nebraska. Photo James H. Locklear.

the Wray Dune Field in northeastern Colorado, he identified *Redfieldia flexuosa*, *Psoralidium lanceolatum*, *Muhlenbergia pungens*, and *Dalea villosa* as the most important plants of his "Blow-Out Association." The pioneering role of *Redfieldia flexuosa*, *Psoralidium lanceolatum*, and *Muhlenbergia pungens*, all herbaceous perennials, has been noted in other studies of sandsage prairie in eastern Colorado (Weaver 1919, Ramaley 1939, Kelso et al. 2007), with *Stipa hymnenoides* also being important. A number of small annuals typically proceed or accompany these perennials as early invaders of open sand including *Heliotropium colvolvulaceum*, *Polanisia dodecandra* subsp. *trachysperma*, and *Polanisia jamesii*. Perennial forbs of secondary importance include *Astragalus ceramicus* var. *filifolius* and *Oenothera latifolia*.

Thanks to the ground-breaking work of Shantz, a detailed description of the ecology of blowouts in sandsage prairie is provided in the U. S. Department of Agriculture report, *Changes in Vegetation and Land Use in*

Eastern Colorado: A Photographic Study, 1904–1986 (McGinnies et al. 1991). Shantz took photographs of vegetation in eastern Colorado from 1907–1914, then re-photographed the same sites in the 1940s and 1950s to document the impact of the great drought of the 1930s. He also recorded the species composition of the photographed sites. Shantz's photographs and notes were not published but following his death in 1958 were archived in the University of Arizona Herbarium. W.J. and W.G McGinnies visited Shantz's photo points in 1985 and 1986 and again took photographs of the vegetation and landscape. These series of photographs and associated notes are published in their report and provide strong visual documentation of the process of re-vegetation.

Shantz made photographic studies of several blowouts in the Wray Dune Field near Yuma, Colorado between 1909 and 1914. He identified six stages in the succession of species that re-vegetated blowouts. His stages and the primary associated species associated with each stage were published in McGinnies et al (1991) and are presented in Table 6.

Dune fields with actively moving sand occur in the context of sandsage prairie in western Oklahoma and the upper Texas Panhandle. The most well-known of these is the Little Sahara dunes associated with the Cimarron River in Woods County, Oklahoma. The earliest of the pioneer species of open sand habitat here are annuals including *Heliotropium convolvulaceum*, *Phyllanthus warnockii*, and *Polanisia jamesii* (Sherwood & Risser 1980) (Fig. 5), and the rare species *Euphorbia carunculata* (Waterfall 1948). As in northern stands of sandsage prairie, *Redfieldia flexuosa* and *Psoralidium lanceolatum* are the first perennials to colonize this open habitat.

Stabilizing Dune Sub-Community

Following the initial invasion of a blowout or area of open sand by annuals and pioneering perennials, a secondary suite of species begins to occupy the partially stabilized habitat. In northern and, to a lesser extent, central stands of sandsage prairie, this stage is dominated by *Muhlenbergia pungens*. In southern stands, *Calamovilfa gigantea* is the most prevalent species of partially stabilized habitat.

Although these two grasses have very different growth habits, they play similar roles in stabilizing actively eroding habitat, particularly in choppy dunes and other areas of high relief. *Muhlenbergia pungens* is a tufted, wiry grass that spreads by rhizomes and forms matted clumps 20–50 cm (8–20 in) tall. In older plants, the central part of the mat often dies out leaving an open ring or crescent that catches blowing sand and holds it in place, further stabilizing sandy habitat. *Calamovilfa gigantea* is an ascending species of relatively few stout culms that may reach up to 2.5 m (8 ft) in height and binds sandy soil by a dense network of roots and spreading rhizomes.

Occurrences of this sub-community in northern parts of the range of sandsage prairie are the equivalent of the "Sand-Hills-Mixed Community" of Ramaley (1939) which he described as being dominated by clumps of *Muhlenbergia pungens* and intermediate between blowout and sandsage communities (Fig. 6). Pool (1914) recognized a similar "Muhlenbergia Association" in the Nebraska Sandhills.

This sub-community hosts the highest level of plant species diversity within the overall structure of sandsage prairie vegetation (Schantz 1911; Kelso et al. 2007). A number of forbs are especially characteristic of partially stabilized habitat throughout the range of sandsage prairie, including *Asclepias arenaria* (Fig. 7), *Dalea villosa*, *Erigeron bellidiastrum*, *Helianthus petiolaris*, *Ipomopsis longiflora*, *Mentzelia nuda*, *Palafoxia sphacelata*, *Penstemon ambiguus*, and *Physalis hispida*. A degree of geographic differentiation occurs in this stage of habitat stabilization, with *Phlox andicola* limited to northern stands and *Dalea lanata*, *Indigofera miniata*, and *Stillingia sylvatica* in southern stands.

As vegetation cover increases and the dune habitat becomes more stabilized, this sub-community typically transitions to *Artemisia filifolia* steppe.

Prairie Inclusion Sub-Community

Within dune fields supporting sandsage prairie are areas of relatively low relief or, in more complex terrain, zones of protected habitat such as the lower leeward slopes of dunes and interdunal swales, flats, or "slacks." The soils of such sites are well-drained fine sands and loamy fine sands in contrast to the more coarse-textured

Table 6. Stages in the re-vegetation of blowouts in the Wray Dune Field, Colorado (McGinnes et al 1991).

Stage 1	Open sand except for occasional annuals (*Helianthus petiolaris, Polanisia dodecandra* subsp. *trachysperma*)
Stage 2	*Redfieldia flexuosa, Psoralidium lanceolatum*
Stage 3	*Muhlenbergia pungens, Redfieldia flexuosa, Psoralidium lanceolatum, Andropogon hallii*
Stage 4	*Andropogon hallii, Psoralidium lanceolatum, Muhlenbergia pungens, Redfieldia flexuosa*
Stage 5	*Andropogon hallii, Schizachyrium scoparium, Muhlenbergia pungens*
Stage 6	Semi-stable *Schizachyrium scoparium* vegetation type

Fig. 5. Annual forbs *Phyllanthus warnockii* and *Polanisia jamesii* in open sand habitat, Woodward County, Oklahoma. Photo James H. Locklear.

soils of the upper slopes of dunes. This habitat often supports a grass-dominated vegetation in which the shrub component of *Artemisia filifolia* is lacking or significantly reduced. This sub-community is the equivalent of the “Sand Prairie Community” of Ramaley (1939) and typically occurs in relatively small patches or inclusions within the overall context of sandsage prairie.

In northeastern Colorado, this sub-community is dominated by *Andropogon hallii*, *Calamovilfa longifolia*, and *Hesperostipa comata* (Ramaley 1939), a floristic composition similar to that of grassland covering millions of hectares of uplands in the Nebraska Sandhills (Rolfsmeier & Steinauer 2010). Other examples include leeward slopes and interdunal swales in east-central Colorado sandsage prairie with *Andropogon hallii*, *Stipa hymenoides*, *Sporobolus giganteus*, and *Sporobolus cryptandrus* the most important species (Kelso et al. 2007) and “level sands” in southwestern Kansas sandsage prairie dominated by *Bouteloua gracilis*, with *Calamovilfa*

Fig. 6. Stabilizing dune sub-community dominated by *Muhlenbergia pungens,* Dundy County, Nebraska. Photo James H. Locklear.

longifolia and *Sporobolus cryptandrus* also important (Hulett et al. 1988). The forb component is often similar to that of the surrounding shortgrass or mixed grass prairie.

Two grass-dominated associations described by Schantz (1911) as occurring in the context of Colorado sandsage prairie are now greatly diminished in extent and may be of conservation concern. First is a *Schizachyrium scoparium*-dominated "Bunch-Grass Association" that interfaced with his "Sand-Hills Mixed Association" of which *Artemisia filifolia* was an important element. Schantz observed that the former occurred on "stable sands" and the latter on "unstable sands." He described the *Schizachyrium scoparium* type as "the most extensive association on the sand hills of eastern Colorado," but follow up research in Shantz's study region found this vegetation had all but disappeared, presumably due to a shift toward a drier climate in the region, recurrent severe droughts, overgrazing, and conversion to cropland (McGinnies et al. 1991). *Schizachyrium scoparium* still dominates mixed grass prairie on loess soils in northwestern Kansas, southwestern Nebraska, and northeastern Colorado (Hulett et al. 1968; Rolfsmeier & Steinauer 2010), but extensive stands seem to have been eliminated from sandhills habitat in the region.

Shantz also identified a variant of shortgrass prairie dominated by *Aristida purpurea* (his "Wire-Grass Association") that occurred on sandy loam soils in areas of transition between and the *Schizachyrium scoparium*-dominated Bunch-Grass Association of sandhills and the *Bouteloua gracilis – Buchloe dactyloides* shortgrass prairie on clay-loam "hard lands." Follow up research likewise found that very little of this association remained in eastern Colorado "because most of it has been plowed and planted to wheat" (McGinnies et al. 1991). Vegetation resembling this association was recently observed in southwestern Nebraska in the context of sandsage prairie rangeland (Locklear 2017b).

Wetland Sub-Community

Wetlands and even small lakes were once common features of dune fields supporting sandsage prairie. These

Fig. 7. Stabilizing dune sub-community, Cheyenne County, Colorado. Prominent forbs include *Asclepias arenaria* and *Dalea cylindriceps.* Photo James H. Locklear

occurred in interdunal valleys, swales, and depressions where the water table was close to the surface, and along riparian corridors of intermittent streams (Ramaley 1939; Hullett et al. 1988; Farrar 1993a, 1993b; Neid et al. 2007). Such areas have largely disappeared due to depletion of the regional aquifers by irrigation for crop production but historically supported a mosaic of aquatic communities and subirrigated meadow-like vegetation dominated by graminoids like *Elymus smithii* and *Panicum virgatum*.

VEGETATION DYNAMICS

Sandsage prairie occurs in highly dynamic habitat subject to a host of natural disturbance factors, most notably periodic and often severe drought, fire, and herbivory. The independent effects of any one of these factors on community structure can be and often is intensified by interaction with others, such as fire followed by drought. As a consequence, there is a high level of heterogeneity in the structure of sandsage prairie vegetation with frequent shifts in species composition and dominance, not only within the *Artemisia filifolia* steppe component of the vegetation, but also within and between the constituent sub-communities.

In a study of vegetation dynamics of sandsage prairie in western Oklahoma over a 39-year period (1940 to 1978), Collins et al. (1987) observed patterns of increase and decrease at the species level that could be attributed to both fluctuation (a reversible change in dominance within a stable species assemblage) and succession (a more or less directional change in composition and/or dominance). Their results imply that a given stand of sandsage prairie is in dynamic equilibrium with the local environment.

That sandsage prairie is a dynamic plant community is evidenced in the life history traits of the constituent plant species. As noted above, 29% of the plant taxa associated with sandsage prairie are native annuals and another 10% behave as annuals, biennials, or short-lived perennials depending on environmental conditions. This compares to 21% native annuals in the flora of shortgrass prairie in northeastern Colorado (Hazlett 1998). Relatively high percentage of annuals in a flora is characteristic of plant communities subject to periodic natural disturbances such as drought-stressed rock outcrop environments in the southeastern United States (28% annuals per Baskin & Baskin 1985) and gopher-disturbed xeric sandylands on the Texas Gulf Coastal Plain (70% annuals per Schaal & Leverich 1982).

Plants associated with such habitats often exhibit a "fugitive" life history (Platt 1975) adapted to recurring cycles of vegetation disturbance and recovery. In the case of sandsage prairie, annuals like *Heliotropium convolvulaceum* and *Polanisia jamesii* are adapted to quickly exploit disturbed habitats like blowouts and persist in a soil seed bank when competition from other plants increases. Perennial forbs that occur in relatively dynamic habitat within sandsage prairie are often monocarpic like *Cirsium canescens* (Kaul et al. 2011) or polycarpic but short-lived like *Dalea cylindriceps* (Locklear 2013) and *Mentzelia nuda* (Keeler 1987).

Response to Drought

The relative density of *Artemisia filifolia* in a stand of sandsage prairie is subject to climatic influences, and declines in density due to periodic drought have been documented in eastern Colorado (Rondeau et al. 2018) and western Oklahoma (Gillen & Sims 2006). Analysis of data gathered over a 39-year period (1940–1978) in western Oklahoma sandsage prairie showed *Artemisia filifolia* cover fluctuating between 20% and 50% during this time, presumably in response to variation in annual precipitation (Collins et al. 1987).

Artemisia filifolia appears to respond relatively quickly to variability in annual precipitation. Vegetation studies in east-central Colorado found average canopy cover of *Artemisia filifolia* increased over 50% between 1998 and 1999 in response to 14% above average precipitation but decreased over 80% between 2001 and 2002 in response to annual precipitation 68% less than average (Rondeau 2003, 2013).

Review of accounts published by early explorers of the Great Plains led Muhs and Holliday (1995) to conclude that, although at present mostly stabilized by vegetation, at least parts of dune fields in Colorado, Kansas, Nebraska, New Mexico, and Texas were active in the nineteenth century. While modern observations indicate sandsage prairie is fairly resilient to the effects of drought in the Great Plains, there are biological limits to the ability of this vegetation to tolerate prolonged episodes of severe drought (Rondeau et al. 2018).

Response to Fire

Range management studies in western Oklahoma have demonstrated that *Artemisia filifolia* is "highly tolerant to the effects of fire" (Winter et al. 2011b) and "resprouts profusely following fall and spring burns, seemingly without any negative effects on carbohydrate reserves" (Vermeire et al. 2001). This ability to survive and resprout after fire is unique among the shrubby sagebrushes (genus *Artemisia*), with the exception of *Artemisia cana* (White & Currie 1983) which, as noted above, forms a similar shrub-steppe vegetation in sandy habitat in the northern Great Plains.

Information about the historical role of fire in the ecology of sandsage prairie is limited, but wildfire was not uncommon in the southern part of its range. In the 1930s, A.S. Jackson undertook research on wildlife in western Texas at the time of Euro-American settlement in which he conducted interviews of early settlers and reviewed personal diaries, journals, and newspapers of the time. "The picture that emerged," he wrote in 1965, "was one of one of incredibly abundant wildlife in *an environment which seemed to be on fire, somewhere, all of the time* [italics added]."

Several of Jackson's examples come from areas in the upper Texas Panhandle where sandsage prairie is a significant part of the landscape. He cited observations of Haley (1954) in his book on the history of the XIT Ranch, a cattle ranch in the Texas Panhandle that ran for 300 km (200 mi.) along the border with New Mexico and encompassed over 12,000 sq km (3 million acres) of land. Haley describes several great grass fires from the area, which included large tracts of sandsage prairie. A fire in 1885 that broke out around the Arkansas River near the Colorado-Kansas state line, swept south across the Cimarron River into the northwest part of the Texas Panhandle where it consumed "nearly a million acres of grass." Another fire in 1887, "traveled sixteen and one-half miles in about two hours. When it struck the sagegrass in the sand country of the western Panhandle, flames shot high into the air, where the wind caught their tips and hurled them back to the ground to set fire to the grass as much as sixteen feet ahead of the burning portions." By "sagegrass," Haley appears to be referring to *Schizachyrium scoparium*, which he describes elsewhere as being "rusty" in color at maturity.

Studies by Winter et al. (2012) in Oklahoma sandsage prairie demonstrated this vegetation is resilient to the interactive effects of prescribed fire and grazing and that "land managers can readily alter vegetation structure in *A. filifolia* shrublands by restoring the fire-grazing interaction." Their research also suggested that forbs in sandsage prairie compete with grasses for resources and that the interaction of fire and grazing allows forbs a period of release from such competition. The historical frequency of wildfire in sandsage prairie is a matter of speculation, but it may have been 5–10 years (Doxon et al. 2011).

Response to Herbivory

Herbivory is an important factor in the ecology of grassland ecosystems, particularly as it shapes plant community structure and composition (Milchunas et al. 2008). The impacts of herbivory on sandsage prairie are evidenced primarily in the herbaceous component of the vegetation.

The shrub *Artemisia filifolia* is consumed in relatively small quantities by only a few significant herbivores, notably pronghorn antelope (*Anthocarpa americana*) (Koerth et al. 1984), mule deer (*Odocoileus hemionus*) (Sowell et al. 1985), and black-tailed jackrabbits (*Lepus californicus*) (Sparks 1968). Browsing of *Artemisia filifolia* by these mammals would have little to no effect on the structure and composition of sandsage prairie.

The most significant impacts of herbivory in sandsage prairie come through grazing of the graminoid and forb components of the vegetation by large ungulates, currently domestic cattle and presumably bison (*Bison bison*) in the past. No documentation has been found that describes how bison interacted with sandsage prairie prior the elimination of massive herds of this herbivore from the Great Plains by the late 1870s, but observations of bison grazing in the Nebraska Sandhills suggests they would have been attracted to the major grasses of sandsage prairie, notably *Andropogon hallii*, *Calamovilfa longifolia*, and *Hesperostipa comata*, and not deterred by dune topography and sandy soils. Tracts of sandsage prairie would have provided "islands" of these taller grasses in a landscape dominated by shortgrass prairie.

Shantz appears to be the first researcher to comment on the impact of cattle grazing on sandsage prairie, noting in 1911 that cattle had altered stands in eastern Colorado by consuming the major tall grasses *Andropogon hallii* and *Calamovilfa longifolia*, resulting in less competition for *Artemisia filifolia*, which grew into "unusually large plants" under these conditions. While not quantified, his observations are noteworthy since significant stocking of cattle in the region did not begin until the 1880s (Wishart 2013), indicating the reduction/elimination of these grasses occurred in less than 30 years.

Numerous studies have investigated the impacts of cattle grazing intensity or stocking rate on the structure of sandsage prairie, most with a view towards maximizing or at least sustaining forage production for cattle. The operating assumption has been that sandsage prairie can be overgrazed and reduction of competition from the grass and forb component will result in an increase in canopy cover by *Artemisia filifolia*, which will in turn suppress recruitment and growth of herbaceous plants. Long-term studies in western Oklahoma sandsage prairie (20-year time span, Gillen & Sims 2006; 50-year time span, Sims et al. 1995) that show that while differences in grazing intensity can alter the relative abundance of particular grasses and forbs in some years, stocking rate does not significantly affect canopy cover of *Artemisia filifolia* nor produce marked differences in ecosystem function, particularly when compared to weather impacts.

Other impacts are more subtle. A study of the influence of *Artemisia filifolia* on herbage production of *Hesperostipa comata* in eastern Colorado sandsage prairie found that the shrub afforded protection for the grass from grazing, which outweighed the effects on biomass (Davis & Bonham 1979). Another study in Colorado sandsage prairie found increased grazing pressure caused a decline in *Hesperostipa comata* and *Calamovilfa longifolia* and an increase in *Bouteloua gracilis* (Sims et al. 1976).

CONCLUSION

Nebraska writer Jon Farrar (1993b) referred to the sandsage prairie region of the southwestern part of the state as the "Cinderella Sandhills," always in the shadow of the grand Nebraska Sandhills to the north. Certainly, sandsage prairie has been one of the most poorly understood and least appreciated ecological systems in the Great Plains. The research presented in this paper was undertaken to address this knowledge deficit and lay the groundwork for improved management, conservation, and restoration of sandsage prairie. A forthcoming paper (Locklear, in prep.) will present the biodiversity values and ecosystem processes and functions supported by sandsage prairie.

APPENDIX

Annotated list of plant taxa associated with sandsage prairie.

The following compilation enumerates plant taxa that are characteristic of sandsage prairie in the Great Plains, USA. Families are arranged alphabetically within major groups. Taxa are listed alphabetically within their respective families by genus, species, and infraspecific epithet. Synonyms or misapplied names from important early literature are provided in brackets. Life history traits are indicated: Annual (A); Biennial (B); Perennial (P). Taxa with pronounced geographic affinities are noted as Northern (↑) or Southern (↓).

ANGIOSPERMS: MONOCOTS

AGAVACEAE

Yucca glauca Nutt., yucca P

COMMELINACEAE

Commelina erecta L., dayflower P
Tradescantia occidentalis (Britton) Smyth, western spiderwort P

CYPERACEAE

Carex heliophila Mack. [*Carex inops* L.H. Bailey subsp. *heliophila*] (Mack.) Crins], sun sedge P ↑
Cyperus schweinitzii Torr., Schweinitz's flatsedge P

POACEAE

Andropogon hallii Hack, sand bluestem P
Aristida divaricata Humb. & Bonpl. ex Willd., poverty three-awn P ↓
Aristida purpurea Nutt. [*A. longiseta* Steud.], purple three-awn P
Boutelous curtipendula (Michx.) Torr., sideoats grama P
Bouteloua gracilis (Kunth) Lag., blue grama P
Bouteloua hirsuta Lag., hairy grama P
Calamovilfa gigantea Schrib. & Merr., giant sandreed P ↓
Calamovilfa longifolia (Hook.) Scrib., prairie sandreed P ↑
Chloris verticillata Nutt., windmill grass P
Elymus elymoides (Raf.) Swezey [*Sitanion hystrix* (Nutt.) J.G. Smith], squirreltail P
Elymus smithii (Rydb.) Gould [*Agropyron smithii* Rydb.; *Pascopyrum smithii* (Rydb.) Barkworth & D.R. Dewey], western wheatgrass P
Eragrostis secundiflora J. Presl subsp. *oxylepis* (Torr.) S.D. Koch [*E. oxylepis* (Torr.) Torr.], red lovegrass P
Eragrostis trichodes (Nutt.) A.W. Wood, sand lovegrass P
Hesperostipa comata (Trin. & Rupr.) Barkworth [*Stipa comata* Trin. & Rupr.], needle and thread P ↑
Koeleria macrantha (Ledeb.) Schult. [*K. cristata* (L.) Pers.], junegrass P
Redfieldia flexuosa (Thurb.) Vasey [*Muhlenbergia ammophila* P.M. Peterson], blowout grass P
Muhlenbergia pungens Thurb. ex A. Gray, sandhill muhly P ↑
Munroa squarrosa (Nutt.) Torr., false buffalograss A
Panicum virgatum L., switchgrass P
Paspalum setaceum Michx. [*P. setaceum* Michx. var. *stramineum* (Nash) D.J. Banks; *P. stramineum* Nash], sand paspalum P
Poa arachnifera Torr., Texas bluegrass P ↓
Schizachyrium scoparium (Michx.) Nash [*Andropogon scoparius* Michx.], little bluestem P
Sporobolus cryptandrus (Torr.) A. Gray, sand dropseed P
Sporobolus giganteus Nash, giant dropseed P ↓
Stipa hymenoides Roem. & Shult. [*Achnatherum hymenoides* (Roem. & Shult.) Barkworth; *Oryzopsis hymenoides* (Roem. & Shult.) Ricker], Indian ricegrass P
Triplasis purpurea (Walter) Chapman, purple sandgrass A
Vulpia octoflora (Walter) Rydb. [*Festuca octoflora* Walter], sixweeks fescue A

ANGIOSPERMS: DICOTS

AMARANTHACEAE

Amaranthus arenicola I.M. Johnst., sandhill amaranth A
Froelichia floridana (Nutt.) Moq., Plains snake-cotton A

ANACARDIACEAE

Rhus aromatica Aiton var. *trilobata* (Nutt.) A. Gray ex S. Watson [*R. trilobata* Nutt.], skunkbush sumac P

ASCLEPIADACEAE

Asclepias arenaria Torr., sand milkweed P
Asclepias latifolia (Torr.) Raf., broadleaf milkweed P

ASTERACEAE

Ambrosia acanthicarpa Hook., annual bursage A
Ambrosia psilostachya DC., western ragweed P
Aphanostephus ramosissimus DC., plains lazy daisy A ↓
Artemisia filifolia Torr. [*Oligosporus filifolius* (Torr.) Poljakov], sand sagebrush P
Cirsium canescens Nutt. [*C. plattense* (Rydb.) Cockerell], Platte thistle B/P ↑
Dieteria canescens (Pursh) Nutt. [*Machaeranthera canescens* (Pursh) A. Gray; *M. linearis* Greene; *M. ramosa* A. Nelson], hoary tansy-aster A/B ↑
Erigeron bellidiastrum Nutt., sandhills fleabane A
Gaillardia pulchella Foug., blanket flower A ↓
Gutierrezia sarothrae (Pursh) Britton & Rusby, broom snakeweed P
Helianthus petiolaris Nutt., Plains sunflower A
Heterotheca villosa (Pursh) Shinners [*Chrysopsis villosa* Nutt. ex DC.], hairy goldenaster P
Hymenopappus flavescens A. Gray, yellow plainsman B ↓
Lorandersonia baileyi (Wooton & Standl.) Urbatsch, R.P. Roberts, & Neubig [*Chrysothamnus baileyi* Wooton & Standl.; *C. pulchellus* (A. Gray) Green subsp. *bailey* (Wooton & Standl.) H.M. Hall & Clements], Bailey's rabbitbrush P ↓

Lygodesmia juncea (Pursh) D. Don ex Hook., RUSH SKELETONWEED P
Palafoxia rosea (Bush) Cory, ROSY PALAFOX A ↓
Palafoxia sphacelata (Nutt. ex Torr.) Cory, OTHAKE A
Psilostrophe villosa Rydb., PAPER FLOWER B/P ↓
Senecio riddellii Torr. & A. Gray, RIDDELL'S RAGWORT P
Xanthisma spinulosum (Pursh) D.R. Morgan & R.L. Hartm. [*Haplopappus spinulosus* (Pursh) DC.; *Macheranthera pinnatifida* (Hook.) Shinners], SPINY GOLDENWEED P

BORAGINACEAE
Cryptantha minima Rydb., LITTLE CRYPTANTHA A
Heliotropium convolvulaceum (Nutt.) A. Gray [*Euploca convolvulaceum* Nutt.], BINDWEED HELIOTROPE A
Lithospermum incisum Lehm., FRINGED PUCCOON P
Oreocarya suffruticosa (Torr.) Greene [*Cryptantha jamesii* (Torr.) Payson; *C. cinerea* (Greene) Cronquist var. *jamesii* (Torr.) Cronquist], JAMES' CRYPTANTHA P

BRASSICACEAE
Dimorphocarpa candicans (Raf.) Rollins [*Dithyrea wislizeni* Engelm. var. *palmeri* Payson; *Dimorphocarpa palmeri* (Payson) Rollins], SPECTACLE-POD A/B ↓
Physaria ludoviciana (Nutt.) O'Kane & Al-Shehbaz [*Lesquerella ludoviciana* (Nutt.) S. Watson; *L. argentea* (Pursh) MacMill.], FOOTHILL BLADDERPOD P ↑

CACTACEAE
Opuntia macrorhiza Engelm. [*O. humifusa* (Raf.) Raf., misapplied], Western pricklypear P

CAMPANULACEAE
Triodanis holzingeri McVaugh, HOLZINGER'S VENUS'-LOOKING-GLASS A

CAPPARACEAE
Polanisia dodecandra (L.) DC. subsp. *trachysperma* (Torr. & A. Gray) Iltis [*P. trachysperma* Torr. & A. Gray], RED-WHISKER CLAMMYWEED A
Polanisia jamesii (Torr. & A. Gray) Iltis [*Cristatella jamesii* Torr. & A. Gray], JAMES' CLAMMYWEED A

CHENOPODIACEAE
Chenopodium cycloides A. Nelson, SANDHILL GOOSEFOOT A
Chenopodium pratericola Rydb., DESERT GOOSEFOOT A
Corispermum americanum (Nutt.) Nutt., AMERICAN BUGSEED A
Cycloloma atriplicifolium (Spreng.) J.M. Coult., WINGED PIGWEED A

CONVOLVULACEAE
Evolvulus nuttallianus Schult., SHAGGY DWARF MORNING-GLORY P
Ipomoea leptophylla Torr., BUSH MORNING-GLORY P

EUPHORBIACEAE
Croton texensis Müll. Arg., TEXAS CROTON A
Euphorbia carunculata Waterf. [*Chamaesyce carunculata* (Waterf.) Shinners], SAND-DUNE SANDMAT A ↓
Euphorbia missurica Raf.var. *petaloidea* (Engelm.) Dorn [*Chamaesyce missurica* (Raf.) Shinners; *Euphobia petaloidea* Engelm], PRAIRIE SANDMAT A
Euphorbia serpillifolia Pers. [*Chamaesyce serpillifolia* (Pers.) Small], thyme-leaf spurge A
Euphorbia strictior Holz., PANHANDLE SPURGE P ↓
Stillingia sylvatica L., QUEEN'S DELIGHT P ↓

FABACEAE
Astragalus ceramicus Sheldon var. *filifolius* (A. Gray) F.J. Herm. [*Phaca longifolia* (Pursh) Nutt.], PAINTED MILKVETCH P
Dalea arenicola (Wemple) B.L. Turner [*D. purpurea* Vent.var. *arenicola* (Wemple) Barneby], SANDHILL PURPLE PRAIRIE CLOVER P
Dalea cylindriceps Barneby [*Petalostemon compactus* Swezey], SANDSAGE PRAIRIE CLOVER P
Dalea lanata Spreng., WOOLY DALEA P ↓
Dalea villosa (Nutt.) Spreng. [*Petalostemon villosum* Nutt.], SILKY PRAIRIE CLOVER P
Indigofera miniata Ortega, SCARLET PEA P ↓
Lupinus pusillus Pursh, RUSTY LUPINE A
Mimosa rupertiana B.L. Turner [*Schrankia occidentalis* (Wooton & Standl.) Standl.; *M. quadrivalvis* L. var. *occidentalis* (Wooton & Standl.) Barneby], EASTERN CATCLAW P ↓
Pomaria jamesii (Torr. & A. Gray) Walp. [*Hoffmannseggia jamesii* Torr. & A. Gray; *Caesalpina jamesii* (Torr. & A. Gray) Fisher], JAMES' RUSHPEA P
Psoralidium lanceolatum (Pursh) Rydb. [*Psoralea lanceolata* Pursh; *Ladeania lanceolata* (Pursh) A.N. Egan & Reveal], LEMON SCURFPEA P

LAMIACEAE
Monarda pectinata Nutt., PLAINS BEEBALM A
Monarda punctata L., DOTTED BEEBALM A/B

LINACEAE
Linum berlandieri Hook. [*L. rigidum* Pursh var. *berlandieri* (Hook.) Torr. & A. Gray], BERLANDIER'S FLAX A

LOACEAE
Mentzelia nuda (Pursh) Torr. & A. Gray [*M. stricta* (Osterh.) Stevens], SAND LILY B

MONTIACEAE
Phemeranthus calycinus (Engelm.) Kiger [*Talinum calycinum* Engelm.], GREAT PLAINS FAMEFLOWER P

NYCTAGINACEAE
Abronia fragrans Nutt. ex Hook., SWEET SAND VERBENA P
Mirabilis glabra (S. Watson) Standl. [= *M. carletonii* (Standl.) Standl. (Kelso et al. 2007); = *M. exaltata* (Standl.) Standl. (Rolfsmeier et al. 1999)], SMOOTH FOUR-O'CLOCK P

ONAGRACEAE
Oenothera albicaulis Pursh, WHITE EVENING PRIMROSE A
Oenothera cinerea (Wooton & Standl.) W.L. Wagner & Hoch subsp. *cinerea* [*Gaura villosa* Torr. subsp. villosa], HAIRY GAURA P ↓
Oenothera engelmannii (Small) Munz, ENGELMANN'S EVENING PRIMROSE A ↓
Oenothera latifolia (Rydb.) Munz [*O. pallida* Lindl. subsp. *latifolia* (Rydb.) Munz; *Anogra cinerea* Rydb.], PALE EVENING PRIMROSE P
Oenothera rhombipetala Nutt. ex Torr. & A. Gray, FOUR-POINT EVENING PRIMROSE B
Oenothera serrulata Nutt. [*Calylophus serrulatus* (Nutt.) P.H. Raven], PLAINS YELLOW PRIMROSE P

PAPAVERACEAE
Argemone polyanthemos (Fedde) G.B. Ownbey, PRICKLY POPPY B
Corydalis aurea Willd. subsp. *occidentalis* (Engelm. ex A. Gray) G.B. Ownbey, GOLDEN CORYDALIS A

PHYLLANTHACEAE
Phyllanthus warnockii G.L. Webster [*Reverchonia arenaria* A. Gray], SAND REVERCHONIA A ↓

PLANTAGINACEAE
Penstemon ambiguus Torr., GILIA PENSTEMON P
Penstemon angustifolius Nutt. ex Pursh, NARROW-LEAF PENSTEMON P ↑
Penstemon buckleyi Pennell, BUCKLEY'S PENSTEMON P ↓
Plantago patagonica Jacq. (*P. purshii* Roem. & Schult.], WOOLY PLANTAIN A

POLEMONIACEAE
Ipomopsis longiflora (Torr.) V.E. Grant [*Gilia longiflora* (Torr.) G. Don], LONG-FLOWERED IPOMOPSIS A/B
Phlox andicola E.E. Nelson [*P. douglasii* Hook., misapplied; *P. hoodii* Hook., misapplied), PLAINS PHLOX P ↑

POLYGONACEAE
Eriogonum annuum Nutt., ANNUAL WILD BUCKWHEAT A/B

Eriogonum effusum Nutt. [*E. microthecum* Nutt., misapplied], SPREADING WILD BUCKWHEAT P ↑
Rumex venosus Pursh, WILD BEGONIA P

RANUNCULACEAE
Delphinium carolinianum Walter subsp. *virescens* (Nutt.) R.E. Brooks [*D. virescens* Nutt.], PLAINS LARKSPUR P

ROSACEAE
Prunus angustifolia Marshall, CHICKASAW PLUM P ↓
Prunus pumila L. var. *besseyi* (L.H. Bailey) Waugh [*P. besseyi* L.H. Bailey], SAND CHERRY P ↑

RUBIACEAE
Hedyotis humifusa (A. Gray) A. Gray, MATTED BLUET A ↓

SANTALACEAE
Comandra umbellata Bastard toadflax P

SOLANACEAE
Physalis hispida (Waterf.) Cronquist [*P. pumila* Nutt. subsp. *hispida* (Waterf.) Hinton], SANDHILLS GROUND-CHERRY P

ACKNOWLEDGMENTS

The generosity of the Loveland Garden Club (Garden Club of America) of Omaha, Nebraska is gratefully acknowledged for providing funding in support of range-wide field work for this project. Funding from the Nebraska Game and Parks Commission facilitated sandsage prairie research in Nebraska. Thanks to the Colorado Field Office of The Nature Conservancy for providing access to preserves having sandsage prairie. I thank Dee Ebbeka of the University of Nebraska-Lincoln School of Natural Resources for preparation of the map used as Figure 1. The personal observations and insights of Nathan Andrews, Chris Helzer, Bruce Hoagland, and Gerry Steinauer helped bring clarity. Thanks to Kelly Kindscher, Steven Rolfsmeier, and an anonymous person for helpful review comments.

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