Western North American Naturalist

Volume 78 | Number 2 Article 1

6-26-2018

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Western North American Naturalist 78(2), © 2018, pp. 119–125

Dune habitat trends of an endangered species, *Penstemon haydenii* Wats. (blowout penstemon), in Carbon County, Wyoming

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Abstract.—*Penstemon haydenii* Wats. (blowout penstemon, blowout beardtongue) is an early-succession plant species that is adapted to the dynamic habitats found in sand dunes. Following widespread habitat loss, the species was thought to be extinct from 1940 until it was rediscovered in 1968. It was listed as endangered in 1987 under the Endangered Species Act. At the time, it was only known from the Nebraska Sandhills, where its low numbers were ascribed to habitat loss. It was first discovered in Wyoming in 1996, in the Ferris Dunes of Carbon County. To develop a proxy for historic Wyoming habitat trends and a context for current conditions, we reconstructed the history of dunes where *P. haydenii* is presently located. Twelve georeferenced aerial photograph sets and digital imagery from 1946 to 2015 were analyzed to trace currently occupied dune areas back over the 70-year period. All currently occupied dunes were continuously present as areas of active sand over the 70-year timespan. Dune migration averaged 2.9 m/year. Dune extent declined 16.1% (2015 compared to the average). The continuity of active sand dune habitat and asynchronous trends in migration and in aerial extent between dunes and over time indicate a dynamic dune system maintained by wind erosion. These results provide critical context for population and habitat data of *P. haydenii* in Wyoming.

Resumen.—*Penstemon haydenii* Wats. (especie de Penstemon) es una especie pionera en la sucesión ecológica que está adaptada a hábitats dinámicos característicos de un ecositema de dunas. Debido a la pérdida de su habitat, esta especie se consideró extincta en 1940, hasta su redescubrimiento en 1968. En 1987, fue agregada a la lista de especies amenazadas bajo la Ley de Especies en Peligro de Extinción. En ese entonces, solamente se encontraba en las Colinas de Arena de Nebraska, en dónde los pocos individuos de esta especie fueron atribuidos a la pérdida de su habitat. Fue descubierta por primera vez en Wyoming en 1996, en las Dunas Ferris del Condado de Carbón. Para el desarrollo de una estimación de tendencias históricas y condiciones de habitat actuales en Wyoming, reconstruímos la historia de las dunas en que *P. haydenii* se encuentra actualmente. Doce conjuntos de fotografías aéreas geo-referenciadas e imágenes digitales desde 1946–2015 fueron analizadas trazando áreas de duna actualmente ocupadas a lo largo de un período de 70 años. Todas las dunas actualmente ocupadas se encontraron continuamente como áreas de arena activas durante el período de 70 años. La migración de la duna promedió 2.9 m/año. La extension de la duna disminuyó 16.1% (hasta 2015, con respecto al promedio). La continuidad de habitat activo de duna de arena y tendencias asincrónicas en la migración y extención aérea entre dunas a lo largo del tiempo, indica hacia un sistema de dunas dinámico, sostenido por erosión eólica. Estos resultados proporcionan un contexto crítico para poblaciones de esta especie e información acerca de su habitat en Wyoming.

Penstemon haydenii Wats. (blowout penstemon) is an herbaceous perennial that is restricted to early successional habitat of unvegetated or sparsely vegetated sand dunes. It was designated as endangered under the Endangered Species Act in 1987, when it was known only from the Nebraska Sandhills, where it was subject to widespread habitat loss (USFWS 1987). In 1996 it was discovered in Wyoming for the first time by Frank Blomquist, BLM biologist. He photographed it in the Ferris Dunes of south central Wyoming and returned with other botanists to collect it in 1999 (Fertig 2000). In Wyoming, it is restricted to the Ferris Dunes (Fertig 2001, Heidel 2005, 2012, Heidel et al. 2008). There is no connectivity between the Ferris Dunes and the Nebraska Sandhills. The Ferris Dunes are located over 280 km to the west, outside of the Great Plains, and at an elevation 900–1200 m higher than the Nebraska Sandhills.

There is a body of literature on the historic distribution and abundance of *P. haydenii* and loss of its active sand dune habitats in the

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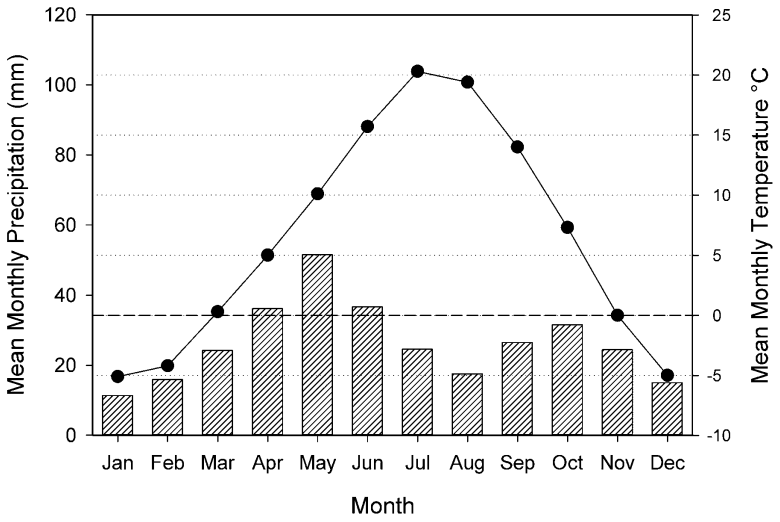

Fig. 1. Climogram showing monthly mean precipitation and mean temperature averages for the period 1980–2010 at Dune 15 (PRISM Climate Group 2016). This figure is reprinted from Tilini et al. (2017) as allowed under the CC0 1.0 Universal Public Domain Dedication.

Nebraska Sandhills (Pool 1914, Stubbendieck et al. 1982, 1989, 1997). The successional processes involved in habitat extent, as stated in the original listing decision, were related to some combination of fire, ungulate grazing, wind, drought, and, later, human interventions. Information on the species' distribution, habitat, and habitat trends was absent in the Ferris Dunes until 2000, when the first surveys ensued, followed by monitoring in 2002 and by this habitat study a decade later. In brief, *P. haydenii* is now known from 22 active sand dune locations in the Ferris Dunes (Fertig 2001, Heidel 2005, 2012, 2016), 16 of which are the large dunes addressed in this study.

Adaptations of *P. haydenii* to sand dune habitat include adventitious roots that maintain the species in shifting sand (Stubbendieck et al. 1989) and a positive growth response to sand abrasion (Stubbendieck et al. 2010). The possibility that the species has a seedbank was proposed in Nebraska (Kottas 2008) and was supported by more recent seed ecology work in Wyoming (Tilini 2013, Tilini et al. 2016, 2017).

METHODS

Study Area

The Ferris Dunes cover about 500 km² (Gaylord 1984) at the eastern end of the Ferris Mountain Range as it converges with the Seminoe Mountains in central Wyoming (42.19°, −107.16°). The dune field has an abundant supply of loose sand in a dry, windy climate (Kolm 1982, Gaylord 1984) with a range of conditions from stabilized to active dunes.

Soils of the Ferris Dunes are Typic Torripsamments (Munn and Arneson 1998). The dune sands are considered soil habitat even though pedogenic horizons are essentially absent in the active dunes. Plant growth on these dunes provides evidence that these unconsolidated substrates that might otherwise be considered parent materials are functioning as soils (Buol et al. 2003).

The Ferris Dunes are typical parabolic dunes with bowl-like blowouts, U-shaped rims above the blowouts, and slopes to the side and downwind from the blowouts. They also include dunes confluent with steep slopes at foothill positions that are semiparallel to the wind directions and appear as more or less linear steep sand slopes interrupted by blowouts. Together these zones of loose sand constitute a continuous dune area.

Mean annual precipitation in the Ferris Dunes is 28.8 cm (1946–2015; PRISM Climate Group 2016), with the peak monthly precipitation mean of 5 cm occurring in May, closely followed by the April and June monthly means (Fig. 1, 1980–2010; PRISM Climate

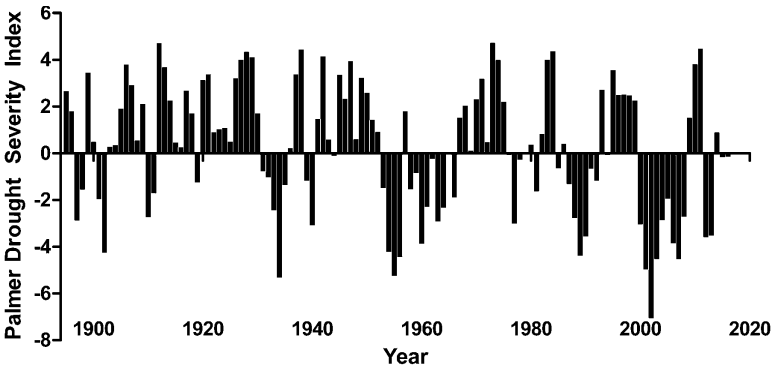

Fig. 2. Annual trends in the Palmer Drought Severity Index for the Upper Platte Watershed (1895–2016).

Group 2016). Moisture conditions conducive to dune erosion cycles in the Ferris Dunes are indicated by the cyclic pattern of drought conditions over consecutive years (NOAA 2017; Fig. 2). PRISM data (1947–2015) indicate that only 3 months in the past 49 years had monthly precipitation <0.1 cm, and 2 of those 3 were during the study period (0.069 in June 2013, 0.088 in June 2012). At the other end of the spectrum, only 4 months in the past 49 years have had monthly precipitation >10 cm, and one was during the study period (12.58 cm in May 2015).

Eolian activity of the Ferris Dunes in the Holocene has been reconstructed by Gaylord (1984). He also provided a basis for characterizing current activity in measuring wind and sand grain size and found that the largest grain size (0.5+ mm) required wind speed >4.7 m/s for sustained movement (Gaylord 1983). Wind above this threshold commonly occurs in December through April, with higher wind speeds in the eastern part of the Ferris Dunes, lower wind speeds near the Ferris-Seminoe Mountain barrier, and increased atmospheric instability and wind turbulence with terrain irregularity (Dawson and Marwitz 1982, Marrs and Gaylord 1982, Gaylord 1983, 1984, Gaylord and Dawson 1987).

The Ferris Dunes are colonized by 3 rhizomatous grasses—*Redfieldia flexuosa* (Thurb.) Vasey (blowout grass), *Elymus lanceolatus* (Scribn. & Sm.) Gould (thickspike wheatgrass), and *Achnatherum hymenoides* (R. & S.) Barkw. (Indian ricegrass)—and by the dicot, *Psoralidium lanceolatum* (Pursh) Rydb. (lemon scurfpea) (Fertig 2001, Heidel 2012), which has a deep and extensive root system (Weaver and Fitzpatrick 1934, McGregor 1986). *Penstemon haydenii* is restricted to bare sand or sparsely vegetated early-succession dune habitat in association with these species.

Dune Landscape Trends

Dune landscape trends were analyzed at 16 large dune areas occupied by *P. haydenii.* Existing aerial imagery showing partial or complete coverage of habitat occupied by *P. haydenii* was acquired for 12 years between 1946 and 2015 (Table 1). The aerial imagery was either digitally collected (2006 and later), or scanned from film or prints at 1200 dpi.

Erdas Imagine 11.0.2 (Intergraph Corp., Englewood, CO) was used to georeference images from 1977 and before. Leica Photogrammetry Suite 11.0.2 (Intergraph Corp.) was used to orthorectify the 1982 imagery using the USGS 10-m digital elevation model. Images from 1994 to 2015 were delivered already orthorectified (USGS 2014, APFO 2015). Active sand areas were digitized manually within ArcMap 10.0 (ESRI, Redlands, CA) to demarcate all sparsely vegetated habitat of active sand dune.

Active boundaries of 16 dunes were manually digitized using ArcMap 10.0 at scales of 1:2000 to 1:10,000 for each year of available imagery, for a total of 176 polygons. A point was digitized at the tip of the downwind leading edge of active sand for each dune. The distance between these tips and temporally successive leading edges was measured. Annual movement rates were thus calculated to compare dune migration rates with overall dune area trends. To determine prevailing 70-year trends, the area of active dune polygons were graphed and the mean, standard deviation, and coefficients of variation for total dune area were calculated for each dune.

Table 1. Image sets used in analysis of total active dune area and downwind active dune area delineation. Image sources included the U.S. Geological Survey (USGS 2014), the U.S. Bureau of Land Management (BLM), and the U.S. Department of Agriculture–Aerial Photography Field Office (APFO 2015).

Year	Source	Project	Date	Coverage	Image scale
1946	USGS	GS-CM	1–9 Aug	Partial	1:27,000
1949	USGS	GS-JG	4 Oct–2 Nov	Complete	1:33,000
1954	USGS	VV ASM 15 AMS	23 Aug	Complete	1:60,000
1975	BLM	RWIR	28 Jun	Complete	1:32,000
1977	USGS	GS-VEHJ	16 Oct	Complete	1:80,000
1982	BLM	WY82AC	7 Jul–26 Aug	Complete	1:24,000
1994	USGS	NAPP[a]	22 Jul	Complete	1:40,000
2001	USDA	NAPP[a]	16 Jul	Complete	1:40,000
2006	USDA	NAIP[b]	13 Jul	Complete	1-m GSD
2009	USDA	NAIP[b]	22 Jul	Complete	1-m GSD
2012	USDA	NAIP[b]	11 Jul	Complete	1-m GSD
2015	USDA	NAIP[b]	18 Jun	Complete	0.5-m GSD

[a]National Aerial Photography Program
[b]National Agricultural Imagery Program

Table 2. Leading-edge dune movement since 1946, mean total active dune area, and 2015 values for 16 dunes in the Ferris Dune field. Dunes 1, 8, and 15 are highlighted as examples in Fig. 3.

	Dune movement		Total active dune area				
Dune	Net leading-edge movement (m)	Mean net movement (m/year)	Mean total active dune area (ha)	SD	CV	2015 Total active dune area (ha)	Difference between 2015 and mean total active dune area (ha)
1	506	7.3	25.5	3.2	0.13	26.1	0.7
2	−5	−0.1	12.1	8.7	0.72	6.2	−6.5
3	131.5	1.9	4.5	0.5	0.11	4.5	0
4	388	5.6	21.0	4.9	0.23	15.5	−5.5
5	143.9	2.1	23.5	4.3	0.18	21.7	−1.8
6	−2.6	0	27.3	5.2	0.19	22.8	−4.5
7	711.2	10.3	91.6	18.3	0.20	83.5	−8.1
8	651	9.4	15.9	3.4	0.21	13.1	−2.8
9	86	1.2	21.1	10.6	0.50	12.4	−8.7
10	1181	17.1	124.0	24.4	0.20	110.8	−13.2
11	−34.7	−0.5	16.6	12.7	0.76	4.6	−12.0
12	263	3.8	42.5	5.9	0.14	34.5	−7.9
13	−593	−8.6	21.4	8.9	0.42	9.8	−11.6
14	52	0.8	11.0	1.7	0.15	8.9	−2.2
15	−311	−4.5	79.5	19.1	0.24	76.2	−3.3
16	48	0.7	5.8	1.5	0.25	5.4	−0.4
Total			543.4			456.0	
Mean	201.0	2.9	34.0	8.3	0.3	28.5	−5.5

Results

Average dune area (extent of active sand) for the 16 large active dunes currently supporting *P. haydenii* was 34.0 ha (4.5–124.0 ha) from 1946 to 2015, and mean migration rate was 2.9 m per year (Table 2). No new dunes appeared during the 70-year period and none disappeared. All dunes changed in size and almost all changed in location. Only 1 dune was larger in 2015 than its 70-year average. The total area of active dunes in 2015 was 16.1% lower than the 70-year mean, a net reduction of active dune habitat.

Three of the dunes that present contrasts in dune trends, as mapped in Fig. 3, are highlighted in Table 2. Dune 1 is the only dune that has expanded in areal extent over the 70-year period. It shows an unimpeded migration with consistent outlines and stable migration rates over time. Dune 8 has had a recent spurt of expansion, mainly since 2001. Dune 15 is stationery or retreating and the only one that has not migrated, but it is an exceptionally steep dune with gravity-aided instability. It is also the longest dune occupied by *P. haydenii* and may act as its own source

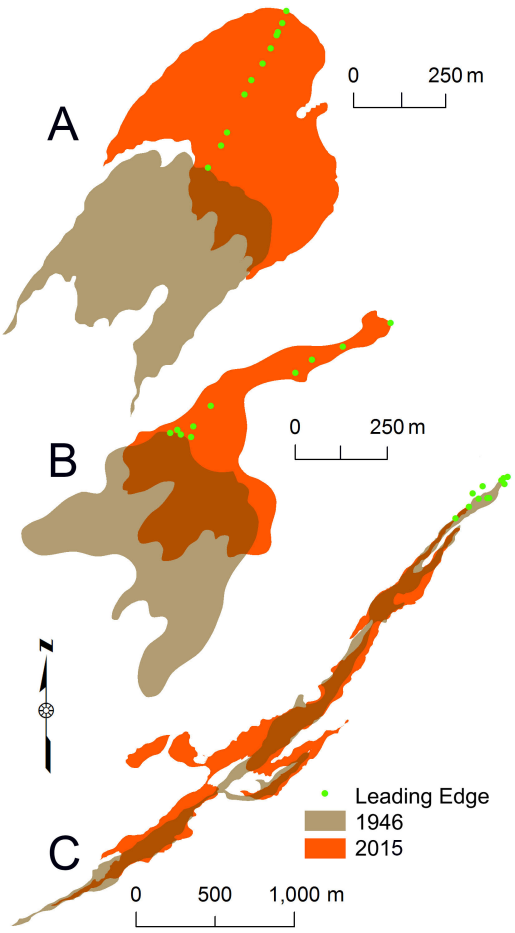

Fig. 3. Digitized extent of 3 active sand dune areas in Carbon County, Wyoming, in 1946 and 2015: **A,** Dune 1; **B,** Dune 8; **C,** Dune 15.

and sink for *P. haydenii* seed. These 3 dunes together constitute half of the dune areas recorded in monitoring studies on public land that have ever supported over 300 plants of *P. haydenii* (Heidel 2007, 2012, 2018). Changes in migration rate and aerial extent are asynchronous between dunes, and there is not a single dune trend apparent at the scale of this study.

DISCUSSION

Sand dunes are irreplaceable self-organizing landforms that support specially adapted species (Ryberg et al. 2015) such as *P. haydenii.* The persistence of active dunes in Wyoming over a 70-year period indicates that *P. haydenii* habitat may have been continuous in the Ferris Dunes during that time. This suggests systemic differences between the species' habitats in Wyoming and Nebraska. In the latter, active sand movement and the distribution of *P. haydenii* are concentrated in the blowout bowl. When vegetation becomes established in the Nebraska Sandhills blowout bowls, the active sand habitat disappears. Sand dune blowouts in the Nebraska Sandhills often disappear over years or decades (Fritz et al. 1992).

There are also contrasts between Nebraska and Wyoming in extent of the dune systems and extent of occupied habitat for *P. haydenii*. The Nebraska Sandhills cover over 50,000 km^2, the largest area of sand dunes in the Western Hemisphere (Swinehart 1998, Schmeisser et al. 2010), which is about 2 orders of magnitude more extensive than the Ferris Dunes. However, active sand areas occupied by *P. haydenii* in the Nebraska Sandhills are mostly confined to the blowout depressions in the dune, which are typically 0.1–0.3 ha in size (Fritz et al. 1992). This is about 2 orders of magnitude smaller than the average dune area occupied by the species in the Ferris Dunes (Table 2).

In Wyoming, Tilini (2013) and Tilini et al. (2017) measured sand depth changes along a subjectively placed 400-m transect running through part of the *P. haydenii* population in Dune 15. They documented eolian-generated sand surface changes of +20 cm deposition to −40 cm erosion over a 12-month period. We have not addressed changes at this scale, vertically or laterally, or the local formation and breakup of blowout rim features and other fine-scale dune zonation. Local features and changes to them may have as great or greater bearing on habitat organization and suitability than areal extent and migration rates. If occupied habitat suitability changes at this scale, then local changes may exert as much or more influence on population numbers as landscape-scale changes. We hypothesize that the large-scale habitat changes reflected in dune extent and migration are linked to local changes and to stabilization and destabilization phases. The flux inherent in the system may influence and mask *P. haydenii* population trends. Determining mechanisms of habitat persistence was identified as a key information need in a 5-year review (USFWS 2012).

The persistence of dunes demonstrated by this study supports the case for a landscape-

scale management framework to buffer active dune areas upwind and downwind of populations. A framework such as this would serve to maintain dune succession processes and minimize system extremes in stabilization or destabilization. In Wyoming, *P. haydenii* habitat lies within an Area of Critical Environmental Concern designated by the BLM to manage and protect the species on BLM-administered lands, with upwind and downwind boundaries demarcated to buffer active sand dunes.

Acknowledgments

This study was supported by the U.S. Department of the Interior Bureau of Land Management and the University of Wyoming, Wyoming Natural Diversity Database through Challenge Cost-share Agreement L12AC20036. Nebraska researchers laid the foundation for this study. Special thanks go to James Stubbendieck, Kay Kottas, and Ron Weedon for their insights into *Penstemon haydenii* habitat and status in Nebraska. Kassie Tilini and Susan Meyer kindly provided *P. haydenii* seed ecology results in a thesis and in publications. We are grateful to Terry Booth, William Lauenroth, Stephen E. Williams, and 2 anonymous reviewers who provided reviews of earlier manuscript drafts. Finally we thank Jimena Golcher-Benavides, who provided translation.

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Received 30 May 2017
Revised 1 March 2018
Accepted 14 March 2018
Published online 26 June 2018