Western North American Naturalist 80(2), © 2020, pp. 243–252

Rapid invasion by the annual grass *Ventenata dubia* into protected-area, low-elevation sagebrush steppe

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Abstract.—Wiregrass (*Ventenata dubia* [Leers] Coss.), an annual grass from the Mediterranean region of North Africa and Eurasia that has aggressive invasion potential in many North American plant communities, has only recently been reported in low-elevation sagebrush steppe. We first encountered wiregrass in 2014 in the John Day Fossil Beds National Monument, a low-elevation steppe protected area in central Oregon. This discovery was incidental to formal vegetation monitoring that was initiated in the monument in 2009. We first encountered wiregrass in monitoring plots in 2016, and, from plot data, we documented rapid spread during 2017–2019. Wiregrass infestation increased within our 4674-ha monitored area from 21 ha (95% CI, 3 to 106 ha) in 2016 to 138 ha (95% CI, 31 to 265 ha) in 2018, and declined to 63 ha (95% CI, 13 to 119 ha) in 2019, representing a cumulative increase of 300% over the 4-year period. Variation in weather may explain this annual variation in wiregrass. We examined mean monthly water balance deficit during the autumn, winter, and spring preceding each survey year and found evidence of a potential correlation between winter deficit and wiregrass. The lowest winter deficit occurred in 2018 prior to the survey documenting the largest wiregrass increase. Wiregrass exhibited a broad ecological niche within our survey area, occurring across all surveyed elevations and on all but steep southern slopes. Invaded sites were in well-drained clay soils in association with other invasive annual grasses. Our observations contribute to the growing evidence that wiregrass poses a greater threat to low-elevation sagebrush ecosystems than previously recognized. It also illustrates the kinds of external stressors that are impacting sagebrush steppe protected areas and the need for continued early detection and rapid response measures, as well as long-term monitoring of invasions and response effectiveness.

Resumen.—La hierba de alambre (*Ventenata dubia* [Leers] Coss.), un tipo de hierba anual de la región mediterránea del norte de África y Eurasia que tiene una agresión potencial en muchas comunidades de plantas de Norte América recientemente ha sido reportada en estepas cubiertas de artemisa de baja elevación. Encontramos primeramente esta hierba de alambre en 2014 en el Monumento Nacional John Day Fossil Beds, una estepa de baja elevación en un área protegida en el centro del estado de Oregón. Este descubrimiento fue incidental al monitoreo de vegetación formal iniciado en el monumento en 2009. Descubrimos primeramente la hierba de alambre en pequeñas áreas que monitoreamos en 2016 y de esa información, documentamos la diseminación rápida que ocurrió durante 2017–2019. La infestación de esta hierba incrementó dentro de nuestra área observada de 4674 hectáreas donde se encontraron 21 hectáreas (95% de intervalo de confianza, 3–106 hectáreas) en 2016, 138 hectáreas (95% de intervalo de confianza, 31–265 hectáreas) en 2018, el cual disminuyó a 63 hectáreas (95% de intervalo de confianza, 13–119 hectáreas) en 2019, representando un incremento acumulativo de 300% sobre el cuarto periodo anual. Una variación en el clima puede dar explicación esta variación en la hierba de alambre. Examinamos la media del balance del déficit de agua mensual durante el otoño, invierno y la primavera anterior a cada año encuestado y encontramos evidencia de una correlación potencial entre el déficit del invierno y la hierba del alambre. El déficit más bajo del invierno ocurrió en 2018 antes de que se documentara el mayor incremento de la hierba de alambre. Esta hierba demostró un gran nicho ecológico dentro del área de estudio, teniendo lugar en todas las elevaciones examinadas a excepción de las pendientes escabrosas del sur. Los sitios invadidos fueron suelos arcillosos y de buen drenaje asociados con otras hierbas invasivas anuales. Nuestras observaciones contribuyen a la creciente evidencia que la *Ventenata dubia* posee una mayor amenaza para los ecosistemas de baja elevación cubiertos de artemisa del desierto de lo que anteriormente se había descubierto. También ilustra los tipos de detonantes externos que están impactando las áreas protegidas de estepas de artemisa y la necesidad de continuar la temprana detección y la rápida respuesta de medidas, además del monitoreo a largo plazo de las invasiones y la efectividad de respuesta.

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Globally, protected-area networks are confronted by accelerating rates of external threats, including biological invasion, that demand more rapid and active conservation responses than required in the past (Cole et al. 2008, Hobbs et al. 2009, 2010). Protected-area management in sagebrush-steppe ecosystems of western North America exemplifies this highly dynamic and uncertain setting. Throughout the sagebrush steppe, the interactions among historic land-use legacies, drought and climatic changes, altered fire regimes, and biological invasions have resulted in major system state changes. In many places, these interactions have caused steppe plant communities to shift from historic or desirable (reference) states dominated by native perennial forbs, grasses, and shrubs to novel states dominated by Eurasian annual grasses (Chambers et al. 2014).

Several authorities have suggested that sagebrush steppe is one of the most threatened ecosystem types in the United States, despite it being geographically widespread (Noss et al. 1995, Chambers and Wisdom 2009, Davies et al. 2011). The steppe protected-area network does little to offset this situation, representing only a fraction (~1%) of the biome (Caicco et al. 1995, Stoms et al. 1998) and exhibiting vulnerability to the same suite of external "outside-in" cumulative impacts as unprotected steppe does. For example, Bangert and Huntly (2010) reported that many of the historically ungrazed islands of vegetation surrounded by barren lava (kipukas) within Craters of the Moon National Monument and Preserve in southern Idaho were dominated by the exotic annual cheatgrass (*Bromus tectorum* L.). Nearby, Powell et al. (2013) described fire-driven state transition to exotic annual grassland in the City of Rocks National Reserve, which is also in southern Idaho. In Oregon, Rodhouse et al. (2014) revealed that as much as 75% of the ~5800-ha John Day Fossil Beds National Monument was heavily invaded by annual grasses and assigned low priority for strategic conservation measures. In all 3 of these examples, the portions of low-elevation steppe characterized by the native overstory shrub Wyoming big sagebrush (*Artemisia tridentata* Nutt. *wyomingensis* Beetle & Young) were most heavily impacted, reflecting the scientific consensus that xeric, low-productivity steppe exhibits low resilience to fire and is highly vulnerable to annual grass invasion (Chambers et al. 2014). This observed trend in steppe protected areas is of added conservation concern and motivates accelerated use of surveillance and monitoring to identify emerging patterns of biological invasion and other threats that guide strategic evidence-based prioritization of protected-area steppe landscapes for proactive conservation and restoration.

Here, we report on the discovery of an incipient infestation and rapid spread of the winter annual grass *Ventenata dubia* (Leers) Coss., also called North Africa grass or wiregrass, at John Day Fossil Beds National Monument in central Oregon. Wiregrass, named after French botanist Pierre Etienne Ventenat (Hitchcock and Cronquist 1973:674), is a recent invader with origins in the Mediterranean region of southern Europe and northern Africa (Barkworth et al. 2007). Wiregrass was first documented in the Spokane area of Washington in 1952 (Barkworth et al. 2007). Wiregrass is a well-established nuisance in the mesic agricultural hayfields, grasslands, and rangelands of the inland Northwest but has not been thought to present a threat to xeric low-elevation steppe (Pavek et al. 2011, Wallace et al. 2015). Jones et al. (2018) provided the first published report of widespread wiregrass infestations in xeric sagebrush steppe; prior reports had been limited to more mesic and higher-elevation portions of the region. The ecology of wiregrass is not well understood, especially within the context of niche differences exhibited between its native and invaded ranges, but it continues to surprise western American land managers by its apparent niche breadth. The infestation reported here was detected during field surveillance efforts associated with an ongoing long-term steppe monitoring program conducted in the monument and in other National Park Service sites in the region (Yeo et al. 2009).

Recent studies into the life history traits of wiregrass have taken place in the grassland ecosystems (e.g., Palouse Prairie) of the PNW. One such study (Wallace et al. 2015) found that the species had a greater seedling survival rate when under complete (100%) litter cover, revealing a positive feedback loop with thatch-maintained microsite moisture. A greenhouse experiment by Bansal et al. (2014) added to this understanding by demonstrating that total cumulative soil moisture was apparently

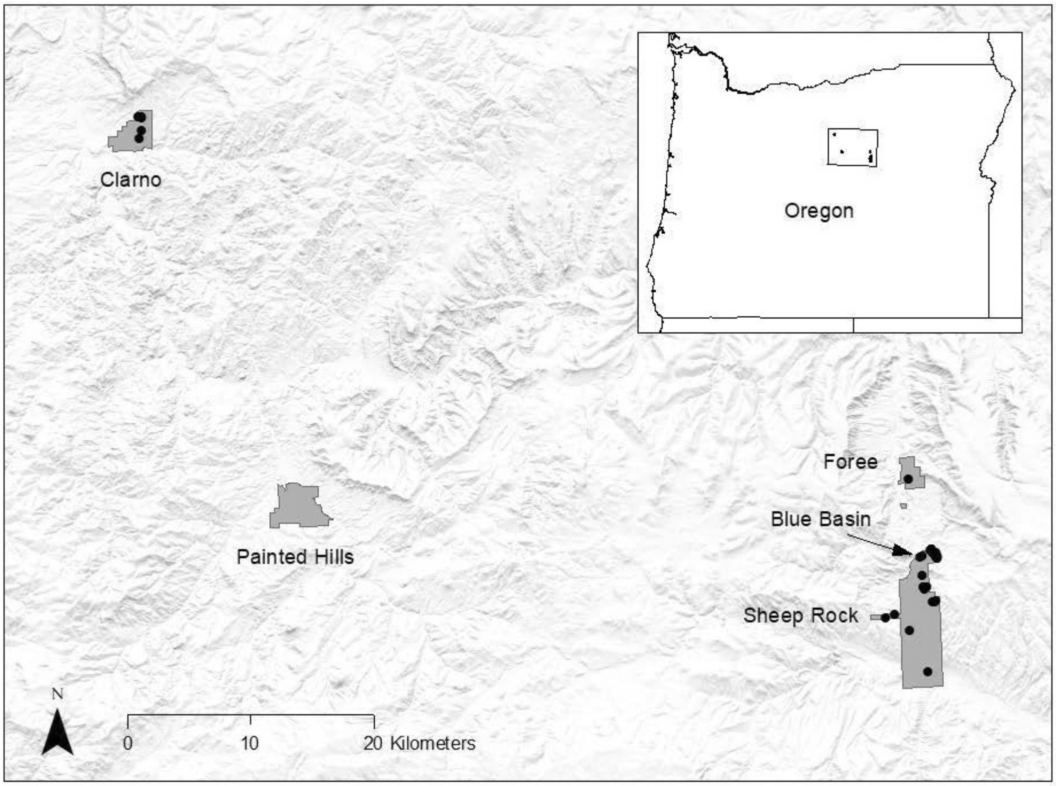

Fig. 1. The John Day Fossil Beds National Monument, showing 4 disjunct units: Clarno, Painted Hills, Foree, and Sheep Rock. The northern portion of Sheep Rock is referred to as Blue Basin and has a separate sampling frame (see Fig. 2) for purposes of postfire monitoring. Black dots symbolize the plot locations where wiregrass was recorded.

more important to wiregrass germination than timing and intensity of precipitation events. However, the recent discoveries reported by Jones et al. (2018) in more southerly and xeric steppe suggest that previous assumptions about the species' ecology and restriction to mesic locales may need revision.

The John Day Fossil Beds National Monument, hereafter referred to as "the monument," is located in central Oregon, USA (Fig. 1), in the transition between the Blue Mountains and the Columbia (Umatilla) Plateau physiographic provinces. The climate is semiarid, with a 30-year mean annual precipitation of 27 cm (WRCC 2016). The monument comprises geographically separate units that total ~5800 ha: Clarno, Painted Hills, Foree, and Sheep Rock (note that due to recent wildfire activity, we also identify Blue Basin in the northern portion of Sheep Rock as a separate subunit for purposes of monitoring and planning; Figs. 1, 2). Livestock (sheep) grazing was discontinued in the Sheep Rock and Painted Hills Units upon their acquisition by the National Park Service in the late 1970s. Grazing continued until 2001 in portions of Clarno. Monument topography is heavily eroded, rugged, deeply dissected terrain with upland soils mapped primarily as droughty, volcanic, ash-derived, well-drained clay-textured soils and with aridic soil moisture and mesic temperature regimes (Erixson et al. 2011). The native upland plant communities are xeric Wyoming and basin big sagebrush steppe ecosystem types, dominated by Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis* [Beetle & Young]) and basin big sagebrush (*Artemisia tridentata* spp. *tridentata* [Nutt.]), large-stature perennial bunchgrasses, most conspicuously bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh.] A. Love), and deep-rooted perennial forbs including species of *Lupinus* and *Astragalus*. Western juniper (*Juniperus occidentalis* Hook.) occurs as widely

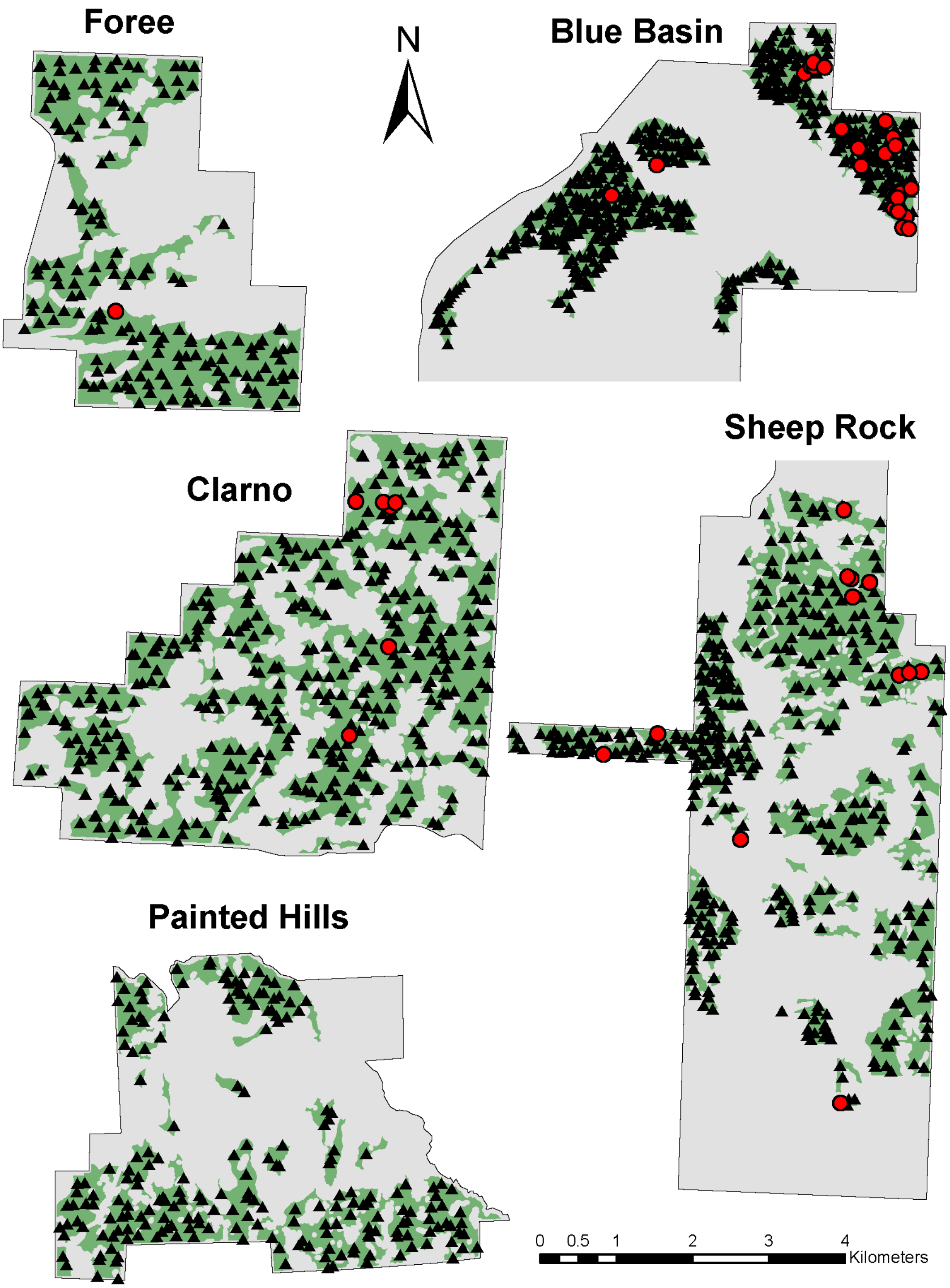

Fig. 2. Sampling frames (in green) developed for vegetation monitoring in management units of the John Day Fossil Beds National Monument. Black triangles symbolize plot locations. The Clarno and Blue Basin (the northern portion of Sheep Rock) frames were surveyed in 2016 with 371 plots; all frames were surveyed in 2017 with 1181 plots. Blue Basin was surveyed in 2018 and 2019 with 151 plots in each year. Red circles represent plots where wiregrass (*Ventenata dubia*) was recorded.

scattered savannah in some uplands, with denser-canopied woodlands occurring in only a few discrete areas. The monument has repeatedly experienced prescribed and wild fires that have removed most of the native shrub cover (e.g., Rodhouse et al. 2014, Reed-Dustin et al. 2016, Mata-González et al. 2018). Wildfires were reported in Clarno in the mid-1980s and mid-1990s, and we observed one in August 2011 that effectively burned the entire unit. Two wildfires (simultaneously as a complex) burned Blue Basin in 2015. Also, a series of resource management–prescribed fires were applied in the Foree, Sheep Rock, and Painted Hills Units during the late 1990s and early 2000s, ostensibly to benefit native vegetation. Despite protection from livestock grazing and other land-use pressures (i.e., as a protected area), the monument has been heavily invaded by the nonnative annual grasses cheatgrass and medusahead (*Taeniatherum caput-medusae* L.), apparently exacerbated by these fires (Rodhouse et al. 2014, Reed-Dustin et al. 2016).

Monitoring of the monument upland plant communities began in 2008, following methods outlined by Yeo et al. (2009). Monitoring surveys followed a spatially balanced randomized design (Stevens and Olsen 2004) within mapped sampling frames arranged within monument units (Fig. 2). Frame boundaries were developed around soil survey polygons and their associated ecological site descriptions (Yeo et al. 2009). Areas removed from the monitoring sampling frames and, hence, the statistical scopes of inference included steep slopes >30° and barren, fossil-bearing eroded ash beds. The total area included within sampling frames was 4674 ha, ~80% of the monument's uplands.

Within frames, surveys consisted of the randomized placement of 1-m^2 quadrats, wherein live foliar cover of a suite of principal native and nonnative plant species was estimated visually (ocular estimation) and binned in Daubenmire (1959) cover categories (0%, 1%–5%, 5%–25%, 25%–50%, 50%–75%, 75%–95%, and 95%–100%). Sample sizes within frames were large (>100 plots per frame per year). Quadrat locations were temporary (not marked and therefore surveyed only once), and new random samples were drawn for each annual survey. Surveys were conducted annually or, in some frames, every 2–3 years during 2008–2018 as program capacity permitted. However, special effort was made to conduct annual monitoring in some monument units in response to wildfires (Clarno in 2011 and Blue Basin in 2015). Fig. 1 illustrates the samples accumulated during 2016–2019. A total of 1854 randomly located plots were surveyed over the 4 years. In 2016, only 371 plots were surveyed within Clarno and Blue Basin (Fig. 2). In 2017, all frames were included (monument-wide survey) and the sample size was 1181. In 2018 and 2019, only the Blue Basin was surveyed, with 151 plots surveyed in each year.

Our randomized design and large sample sizes (151 in the years of least effort) supported robust inferences about wiregrass across the landscape. We used a design-unbiased analytical approach rather than a model-based approach, and thus no assumptions about the underlying distribution of the data were required. We used survey design weights (inverse inclusion probabilities, $\pi_{i,t} = n_{i,t}/N_i$, where $n_{i,t}$ is the sample size for frame i in year t and N_i is the area [m^2] of frame i) to account for annual variation in frames surveyed and sample sizes, and we used weighted Horvitz–Thompson population estimators (Thompson 2002, Stevens and Olsen 2004, Yeo et al. 2009) to summarize wiregrass infestation within frames (as in a stratified random sample).

We evaluated wiregrass occurrences within the context of environmental gradients, including elevation and topographic position measured as

$$\sin(\text{radians}[\text{slope}]) \times \cos(\text{radians}[\text{aspect}]),$$

which provides a single metric of insolation or "northness" ranging from −1 for steep south slopes, to 0 for flat ground, to 1 for steep north slopes. We used 10-m digital elevation models from the U.S. Geological Survey (https://catalog.data.gov/dataset/usgs-national-elevation-dataset-ned) to generate elevation, slope, and aspect. We summarized patterns of wiregrass cover along environmental gradients, with a focus on elevation, slope, aspect, and weather. We used mean monthly water balance deficit (potential evapotranspiration minus actual evapotranspiration; Stephenson 1990) during the autumn (September–November), winter (December–February), and spring (March–May) preceding each season's vegetation survey as a

TABLE 1. Estimates of area (ha) infested by wiregrass (*Ventenata dubia*), by year and cover class, within sampling frames (see Fig. 2).

				95% Confidence interval	
Year	Cover class	*n* (plots)	Area (ha)	Lower bound	Upper bound
2016	0%	365	1870.25	1851.24	1889.26
	1%–5%	5	19.93	1.02	38.83
	5%–25%	1	1.58	0.00	4.26
	25%–50%	0	0.00	0.00	0.00
	50%–75%	0	0.00	0.00	0.00
	75%–95%	0	0.00	0.00	0.00
	>95%	0	0.00	0.00	0.00
2017	0%	1160	1852.51	1837.99	1867.03
	1%–5%	15	28.03	15.02	41.05
	5%–25%	3	7.33	0.00	14.98
	25%–50%	2	3.49	0.00	8.94
	50%–75%	1	0.39	0.00	1.04
	75%–95%	0	0.00	0.00	0.00
	>95%	0	0.00	0.00	0.00
2018	0%	140	1753.94	1692.64	1815.25
	1%–5%	7	87.70	31.80	143.60
	5%–25%	2	25.06	0.00	54.64
	25%–50%	0	0.00	0.00	0.00
	50%–75%	1	12.53	0.00	33.95
	75%–95%	1	12.53	0.00	32.83
	>95%	0	0.00	0.00	0.00
2019	0%	146	1829.11	1787.54	1870.69
	1%–5%	4	50.11	13.94	86.28
	5%–25%	0	0.00	0.00	0.00
	25%–50%	1	12.53	0.00	33.02
	50%–75%	0	0.00	0.00	0.00
	75%–95%	0	0.00	0.00	0.00
	>95%	0	0.00	0.00	0.00

summary metric of weather. Water balance deficit data were provided by the National Park Service (Tercek et al. 2020) as gridded raster data at 1-km resolution. Methods used to generate the water balance deficit data were developed by Thornthwaite and Mather (1955) and Lutz et al. (2010) and are increasingly applied to aid understanding of vegetation dynamics in arid ecosystems (e.g., Stephenson 1990, Dilts et al. 2015). Water balance deficit is a parsimonious way to synthesize the cumulative impacts of temperature, precipitation, and soil water–holding capacity in terms relevant to plant growth.

We used the *spsurvey* package (Kincaid and Olsen 2017) in the R statistical environment (R Core Team 2019) to draw annual random samples using the generalized random tessellation stratified (GRTS) spatially balanced design, and we used the *cat.analysis* function in *spsurvey* to estimate population means, totals, and variances for categorical data (i.e., estimated proportions within each cover class category). We used the "local" GRTS variance estimator (vartype = "local" in *spsurvey*), which provides a more efficient estimate for spatially balanced designs than the standard simple random sample variance estimator (Stevens and Olsen 2004). We restrict our estimation and scope of inference to these frames and the monitored portion of the monument, as well as suggest that our findings are therefore conservative; wiregrass likely occurs outside of monitored areas.

We first identified wiregrass within the monument during summer 2014, incidental to formal monitoring, while we were walking among plots for another complementary study (Reed-Dustin et al. 2016, Mata-González et al. 2018). Prior to this time (beginning in 2008), the species was not included in principal species lists (see Yeo et al. 2009), although it was identified as a potential invader as early as 2012 and added to monument watch lists in 2014 (Hoh et al. 2015). In general, prior to discovery, the species was thought to be unlikely in such low-elevation, arid sites. Therefore, it is highly likely that the species was present in low abundance prior to 2014. The species was not encountered in plots in 2015 but was

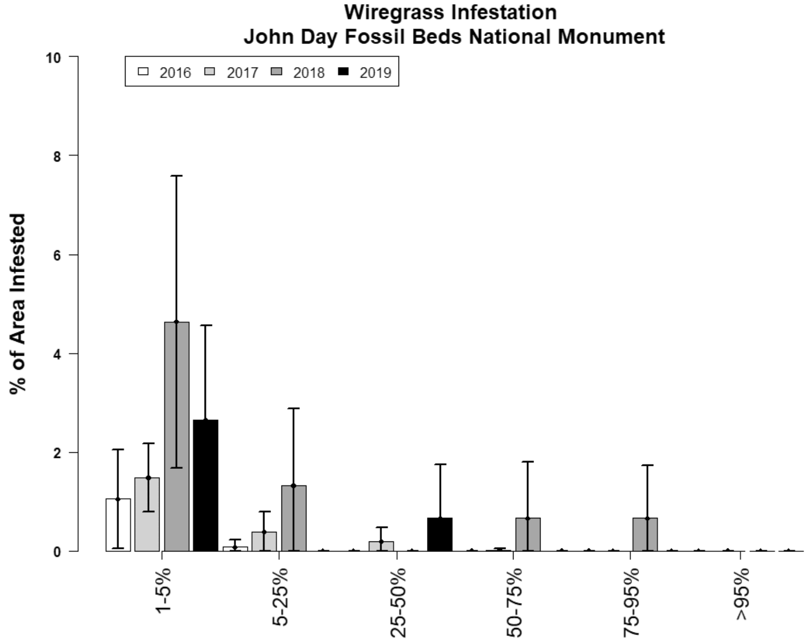

Fig. 3. Proportion of monitored area (sampling frames) infested by wiregrass (*Ventenata dubia*), estimated for each cover class category. Error bars represent 95% confidence intervals. These proportions were converted to hectares of infestation using design-unbiased estimation, supported by large and spatially balanced random samples within a priori sampling frames.

recorded during 2016 in 2 plots in the Clarno Unit and in 4 plots in the Sheep Rock Unit (Table 1, Fig. 2). The following year, in 2017, wiregrass was found in 17 plots within the Sheep Rock Unit (including one in Foree) and in 4 plots within the Clarno Unit (Table 1, Fig. 2). In 2018, there were 11 plot encounters in the Sheep Rock Unit (Blue Basin portion; Table 1, Fig. 2). In 2019, there were 5 plot encounters in the Sheep Rock Unit (Blue Basin portion; Table 1, Fig. 2). No surveys were conducted in Clarno, Foree, or Painted Hills during 2018–2019. The species has not yet been documented in Painted Hills (Fig. 2), although we suspect that it occurs there.

These raw counts of plot encounters cannot be used to infer trends (e.g., an increase and then a decrease in the Sheep Rock Unit) because of annual variation in the frames surveyed. However, when frame areas are accounted for in design-unbiased estimations of population means and totals via weighting and under assumptions of frame-wide representativeness of samples, it is evident that the proportions of monument sampling frames that were invaded increased by 300% during the 4 years of formal monitoring of the invasion. Estimated size of infestation within our 4674-ha monitored area increased from 21 ha (95% CI, 1–43 ha) in 2016 to a peak of 138 ha (95% CI, 31–265 ha) in 2018, tapering to 63 ha (95% CI, 14–19 ha) in 2019 (Fig. 3, Table 1). Additionally, we estimate an increasing trend in the higher cover classes, evidence of densification of wiregrass within invaded patches (Fig. 3).

We found evidence of a potential relationship between winter water balance deficit and wiregrass cover (Fig. 4). Mean monthly deficit from 2011 to 2019 varied seasonally from year to year and was most variable in winter. We observed the wettest (lowest deficit) winter in 2018, prior to the largest spike in wiregrass (Table 1, Figs. 2, 4). Counterintuitively, the driest winter was in 2016, when wiregrass was first observed in our survey plots, although establishment within the park had already occurred (i.e., at least by 2014). Notably, winter 2014 was also a relatively wet (low-deficit) winter (Fig. 4). Plots where wiregrass was recorded occurred across a wide range of environmental conditions. For example, the

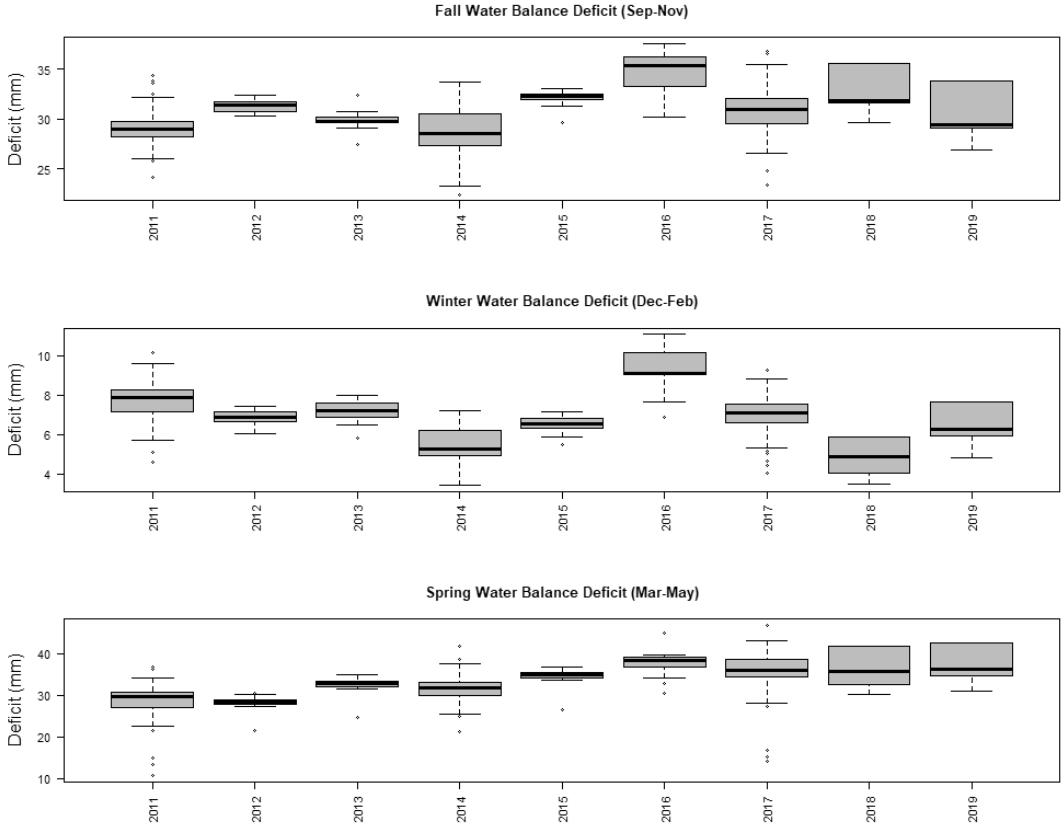

Fig. 4. Mean annual water balance deficit (potential evapotranspiration minus actual evapotranspiration) during fall (September–November), winter (December–February), and spring (March–May) for the John Day Fossil Beds National Monument, 2011–2019. The 4 years of monitoring surveys examined for wiregrass (*Ventenata dubia*) spread were 2016 to 2019, and they varied widely in winter deficit, though they varied less during fall and spring. The winters of 2014 and 2018 were notably wet (low deficit) and correspond, respectively, to when wiregrass was first observed in the monument and when wiregrass peaked in observed foliar cover and extent across the monument.

elevational gradient of wiregrass plots (555–1007 m) was similar to the entire surveyed elevational gradient (421–1255 m). Similarly, the gradient of topographic position of wiregrass plots was comparable to the entire surveyed gradient, although flat and northerly aspect steep slopes were more common. Plots with wiregrass occurred on deep, well-drained clay and clay-loam soils, although these soil conditions are prevalent across the monument and this pattern is not necessarily indicative of wiregrass habitat association per se. Likewise, all but one plot also had cheatgrass present, which was expected given the ubiquitous distribution of cheatgrass within the monument. Twenty wiregrass plots (46%) also had medusahead present.

State-transition conceptual models used to articulate hypotheses about ecological change in sagebrush steppe ecosystems typically map cheatgrass dominance as a quasi-terminal state maintained by positive feedback from accelerated fire regimes (e.g., NRCS 2005, Bagchi et al. 2013) and possibly reversed through restoration, but the models also anticipate subsequent shifts to other novel states (e.g., Stringham et al. 2003:108). It is increasingly apparent that multiple kinds of ecological surprises and state transitions are possible in sagebrush steppe: cheatgrass die-off is one example (Boyte et al. 2015), while transition from cheatgrass dominance to other nonnative species represents another. Our monitoring results add evidence that wiregrass is actively spreading into sagebrush steppe and describe a potential alternative state transition pathway beyond cheatgrass.

We documented a 300% increase in wiregrass infestation over 4 years in the John Day Fossil Beds National Monument that could lead to a radical shift in species composition, particularly given the apparent overlap in available niche space within the monument for wiregrass (e.g., deep clay soils are widespread). Our observations add to the recent report by Jones et al. (2018) that wiregrass invasion represents an existential threat to the ecological integrity of the sagebrush steppe, and to steppe protected areas in particular.

We found intriguing evidence that wiregrass spread occurred during relatively wet (low-deficit) winters (relative to the period of observation; Fig. 4). Winter deficit variability was higher than spring variability and similar to, but with greater amplitude than, fall variability. We also found possible evidence that wiregrass may avoid dry south-facing slopes in our monitored area, which, if borne out over time, would support the hypothesis that the species establishes and spreads in wetter sites and in wetter winters within xeric sagebrush steppe. The experimental results reported by Bansal et al. (2014) and Wallace et al. (2015) reinforce this hypothesis, and future ecological studies that explore this concept will be beneficial to land managers trying to anticipate and prioritize surveillance and invasion response. Advances in treatment strategies (e.g., application of Imazipic; Davies and Hamerlynck 2019) are promising, although prevention of establishment and aggressive early-detection and eradication will clearly be more successful than sustained treatment of established infestations (Davies and Hamerlynck 2019). An ongoing challenge for managers trying to capitalize on these insights about wet-year increase and dry-year control and eradication opportunities will be having access to accurate and local-scale weather forecasting that can guide anticipatory planning (Hardegree et al. 2012).

ACKNOWLEDGMENTS

This work was supported by the National Park Service Upper Columbia Basin Network Inventory and Monitoring Program and the John Day Fossil Beds National Monument. Jeff Yeo, Dan Esposito, Matt Hovland, Kraig Esswein, Cooper Malin, and Jim Patrick assisted with fieldwork. Matt Hovland, Kathi Irvine, and Corrinne Oedekerk provided helpful comments during manuscript preparation.

LITERATURE CITED

BAGCHI, S., D.D BRISKE, B.T. BESTELMEYER, AND X.B. WU. 2013. Assessing resilience and state-transition models with historical records of cheatgrass *Bromus tectorum* invasion in North American sagebrush-steppe. Journal of Applied Ecology 50:1131–1141.

BANGERT, R., AND N. HUNTLY. 2010. The distribution of native and exotic plants in a naturally fragmented sagebrush-steppe landscape. Biological Invasions 12: 1627–1640.

BANSAL, S., J.J. JAMES, AND R.L. SHELEY. 2014. The effects of precipitation and soil type on three invasive annual grasses in the western United States. Journal of Arid Environments. 104:38–42.

BARKWORTH, M.E., L.K. ANDERTON, K.M. CAPELS, S. LONG, AND M.B. PIEP. 2007. Manual of grasses for North America north of Mexico. Utah State University Press, Logan, UT. 627 pp.

BOYTE, S.P., B.K. WYLIE, AND D.J. MAJOR. 2015. Mapping and monitoring cheatgrass dieoff in rangelands of the northern Great Basin, USA. Rangeland Ecology and Management 68:18–28.

CAICCO, S.L., J.M. SCOTT, B. BUTTERFIELD, AND B. CSUTI. 1995. A gap analysis of the management status of the vegetation of Idaho (U.S.A.). Conservation Biology 9: 498–511.

CHAMBERS, J.C., B.A. BRADLEY, C.S. BROWN, C. D'ANTONIO, M.J. GERMINO, J.B. GRACE, S.P. HARDEGREE, R.F. MILLER, AND D.A. PYKE. 2014. Resilience to stress and disturbance and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. Ecosystems 17:360–375.

CHAMBERS, J.C., AND M.J. WISDOM. 2009. Priority research and management issues for the imperiled Great Basin of the western United States. Restoration Ecology 17:707–714.

COLE, D.N., L. YUNG, E.S. ZAVALETA, G.H. APLET, F.S. CHAPIN III, D.M. GRABER, E.S. HIGGS, R.J. HOBBS, P.B. LANDRES, C.I. MILLAR, ET AL. 2008. Naturalness and beyond: protected area stewardship in an era of global environmental change. George Wright Forum 25:36–56.

DAUBENMIRE, R.F. 1959. A canopy coverage method. Northwest Science 33:43–64.

DAVIES, K.W., C.S. BOYD, J.L. BECK, J.D. BATES, T.J. SVEJCAR, AND M.A. GREGG. 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biological Conservation 144:2573–2584.

DAVIES, K.W., AND E. HAMERLYNCK. 2019. Ventenata and other coexisting exotic annual grass control and plant community response to increasing Imazapic application rates. Rangeland Ecology and Management 72: 700–705.

DILTS, T.E., P.J. WEISBERG, C.M. DENCKER, AND J.C. CHAMBERS. 2015. Functionally relevant climate variables for arid lands: a climatic water deficit approach for modelling desert shrub distributions. Journal of Biogeography 42:1986–1997.

ERIXSON, J.A., D. COGAN, AND J. VON LOH. 2011. Vegetation inventory project: John Day Fossil Beds National Monument. Natural Resource Technical Report

NPS/UCBN/NRTR—2011/419. National Park Service, Fort Collins, CO. 188 pp.

HARDEGREE, S.P., J.M. SCHNEIDER, AND C.A. MOFFET. 2012. Weather variability and adaptive management for rangeland restoration. Rangelands 34:53–56.

HITCHCOCK, C.L., AND A. CRONQUIST. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, WA. 730 pp.

HOBBS, R.J., D.N. COLE, L. YUNG, E.S. ZAVALETA, G.H. APLET, F.S. CHAPIN III, P.B. LANDRES, D.J. PARSONS, N.L. STEPHENSON, P.S. WHITE, ET AL. 2010. Guiding concepts for park and wilderness stewardship in an era of global environmental change. Frontiers in Ecology and the Environment 8:483–490.

HOBBS, R.J., E. HIGGS, AND J.A. HARRIS. 2009. Novel ecosystems: implications for conservation and restoration. Trends in Ecology and Evolution 24: 599–605.

HOH, S., T.J. RODHOUSE, D. ESPOSITO, R. SHELEY, AND B. SMITH. 2015. A framework for ecologically based invasive plant management: John Day Fossil Beds National Monument. Natural Resource Report NPS/UCBN/NRR—2015/911. National Park Service, Fort Collins, CO. 64 pp.

JONES L.C., N. NORTON, AND T.S. PRATHER. 2018. Indicators of ventenata (*Ventenata dubia*) invasion in sagebrush steppe rangelands. Invasive Plant Science and Management 11:1–9.

KINCAID, T.M., AND A.R. OLSEN. 2017. spsurvey: spatial survey design and analysis. R package version 3.4.

LUTZ, J.A., J.W. VAN WAGTENDONK, AND J.F. FRANKLIN. 2010. Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. Journal of Biogeography 37:936–950.

MATA-GONZÁLEZ, R., C.M. REED-DUSTIN, AND T.J. RODHOUSE. 2018. Contrasting effects of long-term fire on sagebrush steppe shrubs mediated by topography and plant community. Rangeland Ecology and Management 71:336–344.

[NRCS] NATURAL RESOURCES CONSERVATION SERVICE. 2005. MLRA B10B Central Rocky and Blue Mountains: John Day/Clarno Zone. National Resources Conservation Service, U.S. Department of Agriculture. https://efotg.sc.egov.usda.gov/references/Public/OR/B10B-HCPC05.pdf

NOSS, R.F., E.T. LAROE III, AND J.M. SCOTT. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Biological Report 28. National Biological Service, Washington, DC. 60 pp.

PAVEK, P., J. WALLACE, AND T. PRATHER. 2011. Ventenata biology and distribution in the Pacific Northwest. Page 107 *in* B. McCloskey, Proceedings of the Western Society of Weed Science. Western Society of Weed Science, Spokane, WA.

POWELL, S.L., A.J. HANSEN, T.J. RODHOUSE, L.K. GARRETT, J.L. BETANCOURT, G.H. DICUS, AND M.K. LONNEKER. 2013. Woodland dynamics at the northern range periphery: a challenge for protected area management in a changing world. PLOS ONE 8:e70454.

R CORE TEAM. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org

REED-DUSTIN, C.M., R. MATA-GONAZALEZ, AND T.J. RODHOUSE. 2016. Long-term fire effects on native and invasive grasses in protected area sagebrush steppe. Rangeland Ecology and Management 69:257–264.

RODHOUSE, T.J., K.M. IRVINE, R.L. SHELEY, B.S. SMITH, S. HOH, D.M. ESPOSITO, AND R. MATA-GONZÁLEZ. 2014. Predicting foundation bunchgrass species abundances: model-assisted decision-making in protected-area sagebrush steppe. Ecosphere 5:art108. 16 pp.

STEPHENSON, N.L. 1990. Climatic control of vegetation distribution: the role of the water balance. American Naturalist 135:649–670.

STEVENS, D.L., AND A.R. OLSEN. 2004. Spatially balanced sampling of natural resources. Journal of the American Statistical Association 99:262–278.

STOMS, D.M., F.W. DAVIS, K.L. DRIESE, K.M. CASSIDY, AND M.P. MURRAY. 1998. Gap analysis of the vegetation of the Intermountain semi-desert ecoregion. Great Basin Naturalist 58:199–216.

STRINGHAM, T.K., W.C. KRUEGER, AND P.L. SHAVER. 2003. State and transition modelling: an ecological process approach. Journal of Range Management 56:106–113.

TERCEK, M.T., J. GROSS, D. THOMA, AND K.A. SHERRILL. 2020. Gridded water balance dataset for resource management and ecological studies. Unpublished data *in preparation* for Eos: Science News by AGU. http://www.yellowstone.solutions/thredds/catalog.html

THOMPSON S.K. 2002. Sampling. Second edition. John Wiley & Sons, Hoboken, NJ. 367 pp.

THORNTHWAITE, C.W., AND J.R. MATHER. 1955. The water balance. Publications in Climatology Volume VIII, Number 1. Drexel Institute of Technology, Laboratory of Climatology, Centerton, NJ. 104 pp.

WALLACE, J., P. PAVEK, AND T. PRATHER. 2015. Ecological characteristics of *Ventenata dubia* in the Intermountain Pacific Northwest. Invasive Plant Science and Management 8:57–71.

[WRCC] WESTERN REGIONAL CLIMATE CENTER. 2016. Western Regional Climate Center Station #352173. Western Regional Climate Center, Desert Research Institute, Reno, NV. https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?or2173

YEO, J.J., T.J. RODHOUSE, G.H. DICUS, K.M. IRVINE, AND L.K. GARRETT. 2009. Upper Columbia Basin Network sagebrush steppe vegetation monitoring protocol: narrative version 1.0. Natural Resource Report NPS/UCBN/NRR-2009/142. National Park Service, Fort Collins, CO. 123 pp.

Received 24 September 2019
Revised 15 January 2020
Accepted 28 January 2020
Published online 1 July 2020