Using a Grass of the Anthropocene as a Functional Guide to Restore Sagebrush-Steppe

Authors: Hamerlynck, Erik P., and Boyd, Chad S.

Source: Rangelands, 43(3) : 117-120

Published By: Society for Range Management

URL: https://doi.org/10.1016/j.rala.2021.03.005

Using a grass of the Anthropocene as a functional guide to restore sagebrush-steppe

By Erik P. Hamerlynck and Chad S. Boyd

On the Ground

- Native perennial grass restoration in the Great Basin is limited by low seedling establishment.
- Native seedling establishment is decreased by increased competition from exotic annual grasses and altered fire regimes and have not had sufficient time to adapt.
- Non-native bunchgrasses like crested wheatgrass have adapted to human management of grazing systems and possess physiological traits that increase seedling establishment in dynamic rangelands.
- We review ecophysiological traits underlying crested wheatgrass success in the Great Basin and suggest these could guide native bunchgrass plant material selection and development.

Keywords: climate change, crested wheatgrass, ecophysiology, demography, restoration.

Rangelands 43(3):117–120

doi 10.1016/j.rala.2021.03.005

Recently, Svejcar et al.[1] identified technical challenges to restoring native species in sagebrush steppe and suggested developing strategic frameworks combining seed coating/packaging technology with specific planting methods, seeding rates, and timing of planting to overcome seasonal stresses and phenological/demographic bottlenecks to improve establishment of native plant populations. However, Svejcar et al.[1] did not directly address developing similar frameworks to guide improvement and selection of plant materials. They did summarize findings showing how crested wheatgrass (*Agropyron cristatum*), a Eurasian exotic widely planted across US sagebrush steppe, historically gained popularity and posited some of the mechanisms by which it does so, but did not examine where or why these features originated. Our purpose is to show that even a cursory examination of the systems crested wheatgrass occurs in provides considerable insight into what is needed to select and develop native plant materials with comparable versatility in the Great Basin sagebrush steppe.

Across rangeland systems of the Central Plains, Intermountain West, and Pacific Coast regions, Native North Americans were skilled land managers, and practiced landscape-scale practices like burning to encourage forage production, with distinct effects on North American plant community structure and dynamics.[2-4] But, especially in comparison to Central Plains grasslands, there is evidence that Great Basin sagebrush steppe was not as intensively managed, principally because it did not regularly support large populations of grazing herbivores.[5] This stands in marked contrast with Eurasian steppe systems where crested wheatgrass evolved. Although modern humans have been in North America and Eurasia for millennia, Eurasian grassland and steppes have a longer history of larger, more intensive and diverse pastoral grazing systems across a broad swath of rangeland plant communities that developed in dramatically different soils and climate regimes.[6-13] Starting in at least 8,500 to 8,000 BCE, grazing lands across Eurasia came under increasingly intensive human management under a wide range of socio/politico/economic systems, most of which were structured to support traditional year-long grazing regimes in grassland and rangeland that first reduced in area after expansion of other agrarian land-use practices, and then in secondary rangelands developing after abandonment of these converted agrarian areas.[13-18]

Thus, in addition to adapting to a huge range of natural biotic and abiotic variation, crested wheatgrass successfully adapted to complex, extensive, and shifting mosaics of anthropogenic land use management practices that varied in intensity, duration, and extent. There is evidence the Eurasian crested wheatgrass complex, consisting of crested wheatgrass (which combines fairway crested wheatgrass

[*Agropyron cristatum*] with standard or desert crested wheatgrass [*A. desertorum*] as crested wheatgrass) and Siberian wheatgrass (*A. fragile*) represent a single gene pool, comprised of diploid, tetraploid, and hexaploid forms of a common genome, with a high degree of hybrid fertility between ploidy levels.[19,20] As crested wheatgrass is largely reproductively self-incompatible and relies extensively on outcrossing,[19] locally developed adaptive traits could have readily spread across Eurasia, with ploidy levels modulating trait expression and effectiveness.

We consider the influence of human activity as a likely key in the development of adaptive plant characteristics that make crested wheatgrass so successful as a sagebrush steppe restoration species. Although North American sagebrush steppe also encompasses a similarly broad range of climate and edaphic diversity as Eurasian steppes, large swaths of North American sagebrush steppe went from seasonal use from nomadic herbivores to intensively, and in many cases continuously, grazed in just a few decades after the introduction of domestic livestock.[1,5] No doubt this had a profound direct effect on native perennial grasses in these impacted areas, as did the subsequent introduction and spread of annual grasses which, with no native counterpart, instituted extremely strong competitive regimes, accelerated fire cycles, and altered soil processes and nutrient cycling.[5,21-23] In less than a generation for some native perennial bunchgrasses,[24,25] a significant proportion of sagebrush steppe abruptly went from the late Pleistocene/early Anthropocene to the middle Anthropocene. Compared with the millennia plant adaptations to these pressures unfolded in Eurasian steppes, it is no wonder developing native plant materials capable of readily establishing into degraded sagebrush steppe is so problematic. We need to look on crested wheatgrass's success as reflecting it as fully a grass of the middle Anthropocene. Recognizing the human element shaped the functional characteristics of this grass—beyond subsequent material selection and modification after its introduction to North America[26,27]—could provide us with a meaningful plant functional framework to assess and select native grass plant material for deployment into human-modified sagebrush steppe rangelands.

Since the advent of European settlement and the spread of invasive annual grasses, native perennial bunchgrasses have shown evidence of rapid evolution of improved competitive ability with invasive annuals, at least at a localized population level.[28-31] In addition, there has been considerable effort to develop and release native plant materials with plant traits to better endure abiotic stress and/or compete against non-native grasses under stressful conditions.[32-35] Still, despite these ongoing natural processes and human efforts, getting native grasses to establish readily from seed remains one, if not the, major barrier to restoring sagebrush steppe ecosystem functionality and resilience.[36] Given the diverse Eurasian pastoral systems crested wheatgrass has adapted to, we posit multiple natural and anthropogenic pressures have resulted in traits and functional attributes that span the demographic cycle from seed germination, seedling emergence and establishment, juvenile and adult vegetative growth, and seed production beyond what has been required of native North American perennial grass species. Given the rapid pace of biotic change in Great Basin plant communities, and the great spatial and temporal range in abiotic environments in which they exist, these adaptations may provide a useful framework for improvement of native plant materials. By establishing the functional mechanisms at each demographic step in crested wheatgrass, we could gain insights into the mechanisms underlying localized variation in the competitive ability in native grasses, as well establishing at what point in their demographic life cycle native grass species fall short.

Here we present results from our recent research that show such an approach can be useful. A key attribute to crested wheatgrass's success is its ability to consistently produce viable seed cohorts, and, although germination rates are similar to native species, crested wheatgrass seedlings are better able to survive through seedling emergence, which poses a strong demographic bottleneck to native grasses.[25,37,38] Four potential mechanisms for how emergence success could be attained are 1) greater investment to reproductive effort, 2) greater energetic seed reserves, 3) seedling tissue quality and relative allocation to aboveground and belowground growth, and 4) higher seedling physiological stress tolerance. We have found crested wheatgrass has seed heads with four-fold higher specific mass (g mass/m^2 surface area) compared with native grasses, and concurrent with seed head photosynthetic capacity and carbon fixation efficiency that was not only greater than in the native grasses studied, but equaled or exceeded its own flag leaves.[39] This higher per unit allocation to reproductive effort and greater capacity for carbon fixation at the site of seed production are consistent with 1) and 2) above and could result in greater investment to both seed quantity and quality, a feature apparently lacking in native grasses.[40] We also found emergent crested wheatgrass and bluebunch wheatgrass (*Psuedororegnaria spicata*) seedlings increased photosynthetic rates in response to defoliation; in the native bluebunch wheatgrass this decreased intrinsic water use efficiency (iWUE = ratio of net photosynthesis to stomatal conductance to water vapor) but increased iWUE in crested wheatgrass,[41] which could facilitate higher carbon fixation under drying soil conditions that typically affect seedling survival.[42] Moreover, defoliation induced a shift to lower root:shoot ratios in crested wheatgrass concurrent with higher aboveground tissue specific mass, and root specific mass was unaffected and considerably lower than in bluebunch wheatgrass, which allocated more biomass to belowground growth.[41] These photosynthetic and tissue allocational responses are consistent with 3) and 4). Moreover, these findings for bluebunch wheatgrass are consistent with a species adapted to *persist* within a variable environment. However, measures of evolutionary success in the Anthropocene may be more about *establishment* and *reproduction* in an environment of increased biotic competition from non-native species and increased abiotic stress from altered fire regimes and greater interannual climate variability.

Our findings also suggest compensatory photosynthetic responses to herbivory that do not seem to affect herbivory tolerance in adult plants[43,44] may carry over from the seedling stage, when they clearly do. Ultimately, the fact that crested wheatgrass has greater reproductive photosynthetic capacity likely underlies its seedling success, because this could ensure production of seeds with greater energetic reserves to support post-germination seedling growth and would impart a longer emergence and establishment window compared with native grasses. Given the grazing-intensive nature of the diverse pastoral steppe systems crested wheatgrass originated from, developing the ability to withstand loss of parental plant foliage and maintain seed production and supplying seeds with energetic reserves would be particularly advantageous, given that long-term persistence and population dynamics of bunchgrasses are driven primarily by sexual reproduction.[24,25] As factors that define both the ecological and evolutionary success of desired vegetation change, we, as a profession, should re-consider and refine the attributes used to assess fitness of plant materials. We believe this process can benefit significantly from examining key physiological traits at critical demographic stages of successful non-native species, such as crested wheatgrass, that have evolved under stressors comparable to modern-day sagebrush steppe. This is a paradigm shift from apparent indicators of success, such as plant biomass, to more mechanistic and basal indicators of a plant's ability to physiologically cope with specific, and in some cases novel stressors in a world increasingly dominated by the direct and indirect effects of human activity.

Declaration of Competing Interest

None.

Acknowledgments

EOARC is jointly operated by the USDA-ARS and the Oregon State University Agricultural Experiment Station. USDA is an equal opportunity provider and employer. Mention of a proprietary product does not constitute a guarantee or warranty of the product by USDA-ARS, Oregon State University, or the authors and does not imply approval to the exclusion of other products. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

References

1. Svejcar T, Boyd C, Davies K, Hamerlynck E, Svejcar L. Challenges and limitations to native species restoration in the Great Basin, USA. *Plant Ecol*. 2017; 218:81–94. doi:10.1007/s11258-016-0648-z.
2. Anderson MK, Moratto MJ. Native American land-use practices and ecological impacts. In: *Sierra Nevada Ecosystem Project: Final Report to Congress, vol II, Assessments and Scientific Basis for Management Options*. University of California Davis, Centers of Water and Wildland Resources; 1996:187–206.
3. Keeley JE. Native American impacts on fire regimes of the California coastal ranges. *J Biogeogr*. 2002; 29:303–320. doi:10.1046/j.1365-2699.2002.00676.x.
4. Abrams MD, Nowacki GJ. Native American imprint in paleoecology. *Nat Sustain*. 2020; 3:896–897. doi:10.1038/s41893-020-0578-6.
5. Knapp PA. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert: history, persistence, and influences to human activities. *Global Environ Change*. 1996; 6:37–52. doi:10.1016/0959-3780(95)00112-3.
6. van der Maarel E, Titlyanova A. Above-ground and below-ground biomass relations in steppes under different grazing conditions. *Oikos*. 1989; 56:364–370. doi:10.2307/3565622.
7. Asner GP, Elmore AJ, Olander LP, Martin RE, Harris AT. Grazing systems, ecosystem responses, and global change. *Annu Rev Environ Resour*. 2004; 29:261–299.
8. Fernandez-Gimenez ME. Land use and land tenure in Mongolia: a brief history and current issues. In: Bedunah DJ, McArthur ED, Fernadez-Gimienz M, eds. *Rangelands of Central Asia: Proceedings on the Conference on Transformations, Issues, and Future Challenges, Jan 24-30, 2004*. Rocky Mountain Research Station Proceedings RMPS-P-39, Rocky Mountain Research Station; 2006:30–36.
9. Bai Y, Wu J, Pan Q, Huang J, Wang Q, Li F, Buyantuyev A, Han X. Positive linear relationship between productivity and diversity: evidence from the Eurasian Steppe. *J Appl Ecol*. 2007; 44:1023–1034. doi:10.1111/j.1365-2664.2007.01351.x.
10. Lkhagvadorj D, Hauck M, Dulamsuren Ch, Tsogtbaatar J. Pastoral nomadism in the forest-steppe of the Mongolian Altai under a changing economy and warming climate. *J Arid Environ*. 2013; 88:82–89. doi:10.1016/j.jaridenv.2012.07.019.
11. Leonid U, Yuriy R, Vasiliy U, Xiang-yang H, Oxana V, Irina L, Vera U, Wei-bo R, Yong D. Impact of climate and grazing on biomass components of Eastern Russia typical steppe. *J Integr Agric*. 2014; 13:1183–1192. doi:10.1016/S2095-3119(13)60658-9.
12. Erdős L, Ambarli D, Anenkhonov OA, Bátori Z, Cserhalmi D, Kiss M, Kröel-Dulay G, Liu H, Magnes M, Molnár Z, Naqinezhad A, Semenishchenkov YA, Tölgyesi C, Török P. At the edge of two worlds: a review and synthesis on Eurasian forest-steppes. *Appl Veg Sci*. 2018; 21:345–362. doi:10.1111/avsc.12382.
13. Reinecke JSF, Smelansky IE, Trovea EI, Trofimov IY, Trovimova LS. Land use of natural and secondary grasslands in Russia. In: Squires VR, Dengler J, Feng H, Hua L, eds. *Grasslands of the World: Diversity, Management and Conservation*. Taylor and Francis Group: CRC Press; 2018:113–138.
14. Smelansky IE, Tishkov AA. The steppe biome in Russia: ecosystem services, conservation status, and actual challenges. In: Werger MJA, van Staalduinen MA, eds. *Eurasian Steppes. Ecological Problems and Livelihoods in a Changing World*. Plant and Vegetation 6, Springer; 2012:45–101.
15. Girvetz EH, McDonald R, Heiner M, Kiesecker J, Galbadrakh D, Pague C, Durnin M, Oidov E. Eastern Mongolian grassland steppe. In: Hilty JA, Chester CS, Cross MS, eds. *Climate and Conservation: Landscape and Seascape Science, Planning, and Action*. Washington, DC, USA: Island Press; 2012:92–103.
16. Stobbe A, Gumnior M, Ruhl L, Schneider H. Bronze Age human-landscape interactions in the southern Transural steppe, Russia – evidence from high-resolution palaeobotanical studies. *Holocene*. 2016; 26:1692–1710. doi:10.1177/2F0959683616641740.

17. Török P, Janišová M, Kuzemko A, Rūsiņa S, Stevanović D. Grasslands, their threats and management in Eastern Europe. In: Squires VR, Dengler J, Feng H, Hua L, eds. *Grasslands of the World: Diversity, Management and Conservation*. Taylor and Francis Group: CRC Press; 2018:64–88.
18. Ventresca Miller AR, Bragina TM, Abil YA, Rulyova MM, Makarewicz CA. Pasture usage by ancient pastoralists in the northern Kazakh steppe informed by carbon and nitrogen isoscapes of contemporary floral biomes. *Archaeol Anthropol Sci*. 2019; 11:2151–2166.
19. Robins JG, Jensen KB. Breeding of the crested wheatgrass complex (*Agropyron* spp.) for North American temperate rangeland agriculture and conservation. *Agronomy*. 2020; 10:1134. doi:10.3390/agronomy10081134.
20. Baral K, Coulman B, Biligetu B, Fu Y-B. Advancing crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] breeding through genotyping-by-sequencing and genomic selection. *PLoS ONE*. 2020; 15. doi:10.1371/journal.pone.0239609.
21. Norton JB, Monaco TA, Norton JM, Johnson DA, Jones TA. Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. *J Arid Environ*. 2004; 57:445–466. doi:10.1016/S0140-1963(03)00104-6.
22. Perkins LB, Nowak RS. Soil conditioning and plant-soil feedbacks affect competitive relationships between native and invasive grasses. *Plant Ecol*. 2012; 213:1337–1344. doi:10.1007/s11258-012-0092-7.
23. Chambers JC, Bradley BA, Brown CS, D'Antonio CD, Germino MJ, Grace JB, Hardegree SP, Miller RF, Pyke DA. Resilience to stress and disturbance and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of North America. *Ecosystems*. 2014; 17:360–375. doi:10.1007/s10021-013-9725-5.
24. Liston A, Wilson BL, Robinson WA, Doescher PS, Harris NR, Svejcar T. The relative importance of sexual reproduction versus clonal spread in an aridland bunchgrass. *Oecologia*. 2003; 137:216–225. doi:10.1007/s00442-003-1332-2.
25. Hamerlynck EP, Davies KW. Changes in abundance of eight sagebrush-steppe bunchgrass species 13 yr. after coplanting. *Rangel Ecol Manage*. 2019; 72:23–27.
26. Rogler GA, Lorenz RJ. Crested wheatgrass – early history in the United States. *J Range Manage*. 1983; 36:91–93. doi:10.2307/3897991.
27. Young JA, Evans RA. History of crested wheatgrass in the Intermountain area. In: Johnson KL, ed. *Crested wheatgrass: its values, problems, and myths.* Symposium proceedings. Logan, Utah, USA: Utah State University; 1986:21–25.
28. Leger EA, Espeland EK. Coevolution between native and invasive plant competitors: implications for invasive plant management. *Evol Appl*. 2010; 3:169–178. doi:10.1111/j.1752-4571.2009.00105.x.
29. Rowe CLJ, Leger EA. Competitive seedlings and inherited traits: a test of rapid evolution of *Elymus multisetus* (big squirreltail) in response to cheatgrass invasion. *Evol Appl*. 2011; 4:485–498. doi:10.1111/j.1752-4571.2010.00162.x.
30. Goergen EM, Leger EA, Espeland EK. Native perennial grasses show evolutionary response to *Bromus tectorum* (cheatgrass) invasion. *PLoS ONE*. 2011; 6:e18145. doi:10.1371/journal.pone.0018145.
31. Baughman OW, Agneray A, Forister ML, Kilkenny FF, Espeland EK, Fiegner R, Horning ME, Johnson RC, Kaye TN, Ott J, St Clair JB, Leger EA. Strong patterns of intraspecific variation and local adaptation in Great Basin plants revealed through 75 years of experiments. *Ecol Evol*. 2019; 9:6259–6275. doi:10.1002/ece3.5200.
32. Staub J, Chatterton J, Bushman S, Johnson D, Jones T, Larson S, Robins J, Monaco T. A history of plant improvement by the USDA-ARS Forage and Range Research Laboratory for rehabilitation of degraded western US rangelands. *Rangelands*. 2016; 38:233–240. doi:10.1016/j.rala.2016.08.004.
33. Mukherjee JR, Jones TA, Adler PB, Monaco TA. Contrasting mechanisms from recovery from defoliation in two Intermountain-native bunchgrasses. *Rangel Ecol Manage*. 2015; 68:485–493. doi:10.1016/j.rama.2015.07.011.
34. Bell BP, Jones TA, Monaco TA. Productivity and morphologic traits of thickspike wheatgrass, Snake River wheatgrass, and their interspecific hybrids. *Rangel Ecol Manage*. 2019; 72:73–81. doi:10.1016/j.rama.2018.09.002.
35. Mukherjee JR, Jones TA, Monaco TA, Adler PB. Relationship between seed mass and young-seedling growth and morphology among nine bluebunch wheatgrass populations. *Rangel Ecol Manage*. 2019; 72:283–291. doi:10.1016/j.rama.2018.11.006.
36. Clements CD, Harmon DN, Blank RL, Weltz M. Improving seeding success on cheatgrass-infested rangelands in Northern Nevada. *Rangelands*. 2017; 39:174–181. doi:10.1016/j.rala.2017.10.003.
37. Wilson SD, Pärtel M. Extirpation or coexistence? Management of a persistent introduced grass in prairie restoration. *Restor Ecol*. 2003; 11:410–416.
38. James JJ, Svejcar TJ, Rinella MJ. Demographic processes limiting seedling recruitment in arid grassland restoration. *J Appl Ecol*. 2011; 48:961–969.
39. Hamerlynck EP, Denton EM, Davies KW, Boyd CS. Photosynthetic regulation in seed heads and flag leaves of sagebrush-steppe bunchgrasses. *Conserv Physiol*. 2019; 7:coz112.
40. Drenovsky RE, Thornhill ML, Knestrick MA, Dlugos DM, Svejcar TJ, James JJ. Seed production and seedling fitness are uncoupled from maternal plant productivity in three aridland bunchgrasses. *Rangel Ecol Manage*. 2016; 69:161–168. doi:10.1016/j.rama.2016.01.003.
41. Hamerlynck EP, Smith BS, Sheley RL, Svejcar TJ. Compensatory photosynthesis, water-use efficiency and biomass allocation of defoliated exotic and native bunchgrass seedlings. *Rangel Ecol Manage*. 2016; 69:206–214. doi:10.1016/j.rama.2015.12.007.
42. Denton EM, Smith BS, Hamerlynck EP, Sheley RL. Seedling defoliation and drought stress: effect of intensity and frequency on performance and survival. *Rangel Ecol Manage*. 2018; 71:25–34. doi:10.1016/j.rama.2017.06.014.
43. Caldwell MM, Richards JH, Johnson DA, Nowak RS, Dzurec RS. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia*. 1981; 50:14–24. doi:10.1007/BF00378790.
44. Nowak RS, Caldwell MM. A test of compensatory photosynthesis in the field: implications for herbivory tolerance. *Oecologia*. 1984; 61:311–318. doi:10.1007/BF00379627.

Authors are: Research Ecologist, USDA-ARS Eastern Oregon Agricultural Research Center, Burns, OR 97720, USA; Research Leader, USDA-ARS Eastern Oregon Agricultural Research Center, Burns, OR 97720, USA